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THE DISPLAY OF THE WHITE-WINGED NIGHTJAR

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Abstract.—In 1995, we discovered a population of the poorly known and critically endangered White-winged Nightjar (*Caprimulgus candicans*) in Yata'i (*Butia paraguayensis*) palm cerrado at the Mbaracayú Forest Nature Reserve, Paraguay. We provide the first description of the display of *C. candicans*, as observed in December 1995. The display, which appears to function primarily for mate attraction, took place in small arenas and consisted of a regular flight pattern between perches. Noises that accompany the display appear to be mechanical in origin. The modified shape of the outer remiges of male *C. candicans* suggests a role in the production of this display noise. Male territories were situated exclusively on the upper slopes of ridges in open grassland with a low palm density (termed *campo sucio*). Territories appeared to be relatively clustered, thus suggesting either a lek-mating system or male aggregation due to the use of specialized habitats as encounter sites for mating. Improved knowledge of the species behavior, breeding systems, and habitat use will facilitate its location at other sites and the development of habitat-based conservation management plans.

EL DESPLIEGUE DE *CAPRIMULGUS CANDICANS*

Sinopsis.—En 1995 se descubrió una población de Atajacaminos Ala Blanca (*Caprimulgus candicans*) una especie poco conocida y considerada en peligro crítico, en el cerrado de palmeras Yata'i (*Butia paraguayensis*), de la Reserva Natural del Bosque Mbaracayú, Paraguay. Aquí descubrimos por primera vez el despliegue de *C. candicans*, observado en dicha localidad en diciembre de 1995. El despliegue, que parece funcionar principalmente para atraer a las hembras, se desarrolla en pequeñas arenas y consiste en un patrón regular de vuelo entre perchas. Los sonidos que acompañan el despliegue parecen tener un origen mecánico. La forma modificada de las primarias externas sugiere un rol en la producción de dichos sonidos. Los territorios de los machos fueron encontrados exclusivamente en la parte alta de las laderas de las ondulaciones del terreno, en campo sucio abierto con un densidad muy baja de palmeras. Dichos territorios parece estar relativamente juntos, lo que sugiere un sistema de 'leks' o que los machos se juntan para aparearse al uso de un hábitat especializado. Un mayor conocimiento del comportamiento de la especie, sistema de nidificación y uso de hábitat facilitará la búsqueda de la especie en otras localidades y el desarrollo de planes de conservación basados en el manejo de hábitat.

The White-winged Nightjar (*Caprimulgus candicans*) is one of the rarest

caprimulgids in the Americas (Collar et al. 1992), considered by IUCN criteria to be critically endangered (Collar et al. 1994, IUCN 1996). It is known from two specimens collected in central Brazil in the mid 1820s (Collar et al. 1992), with older evidence from Paraguay (de Azara 1805), and subsequent records from only three widely scattered sites: Emas National Park, Goiás State, Brazil (a series of records in the 1980s, and again in 1995 and 1997; Redford 1985, Collar et al. 1992, Rodrigues et al. 1999, M. Egger, pers. comm.); Beni Biological Station, Yucuma Province, Bolivia (a single male collected in 1987; Davis and Flores 1994); and the Mbaracayú Forest Nature Reserve, Canindeyú Department, Paraguay (a population discovered in September 1995: Lowen et al. 1997).

STUDY SITE

Caprimulgus candicans was studied at Aguara Ñu, an area of cerrado within the Mbaracayú Forest Nature Reserve, Paraguay's most important site for the conservation of threatened bird species (Wege and Long 1995, Lowen et al. 1996b). The reserve protects a variety of habitats including Interior Atlantic Forest, natural grasslands, and cerrado (Madroño N. and Esquivel 1995). Aguara Ñu (centered on 24°10'S, 55°17'W) is a low plateau on the eastern side of the reserve, bordered by two rivers—the Arroyo Guyra Keha and the Río Jejui-mí—and containing 5487 ha of cerrado habitat. It is a natural habitat island isolated from Paraguay's main area of cerrado in Concepción Department, 200 km to the northwest.

The variety of cerrado habitats in Aguara Ñu includes *campo sucio* (grassland with scattered trees and shrubs, in this case *Yata'i* palms (*Butia paraguayensis*)), dense *Yata'i* palm savanna, wet grasslands and marshes, xerophytic woodlands, and gallery forest. Tree species present in the campo sucio include *Tabebuia caraiba* and *Anadenanthera* spp. The southern border of the plateau is formed by a series of low ridgelines separated by shallow valleys whose floors contain saturated grasslands flanking small water courses that join the Arroyo Guyra Keha.

Palm density is highest on the center of the plateau and at the base of each ridge crest. On ridge slopes and the distal part of each crest the campo grassland is more open with fewer palms (campo sucio habitat). Fires frequently occur, especially in the austral spring (notably September) when the grasslands are dry. Most, if not all, are deliberately ignited in surrounding areas of cattle pasture and spread to Aguara Ñu. In October 1994 fire burned most of the area (Madroño and Esquivel 1997), though in 1995 fires were less severe, affecting only one third of the protected area. As a result, much of the grassland was still regenerating from fire damage and plants were estimated to be approximately half their typical stature. Anthills of varying heights are scattered throughout the grasslands.

Fieldwork at this site by BLL from 6–13 Dec. 1995 provides the first information about the species' display and the sounds associated with it. Birds were observed with 10 × 42 Leica binoculars by moonlight and with the aid of a Maglite six cell spotlight and Petzl headtorch. Earlier, JCL

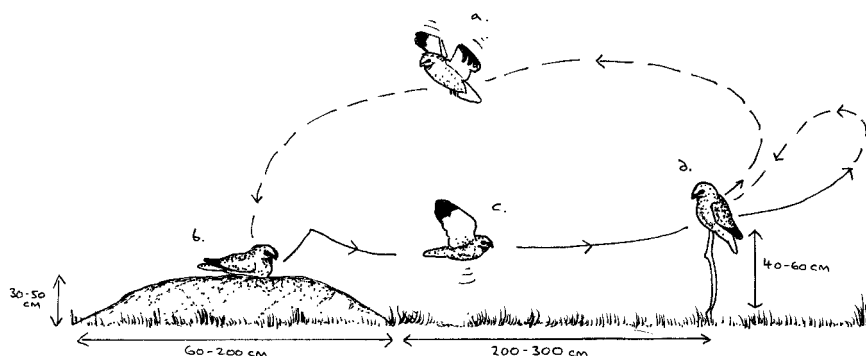


FIGURE 1. Typical display flight of *Caprimulgus candicans* (between perch and anthill), Reserva Natural Bosque Mbaracayú, Paraguay.

had observed display briefly on one occasion on 17 September 1995; this was under similar conditions, and with 7×42 Zeiss binoculars. Display was observed subsequently by RPC and JMB in November–December 1997.

DISPLAY

Our observations revealed the extent of white in the wing to vary among individual male *C. candicans* (López Lanús et al. 1998); females lack any white in the wing or tail (Clay et al. 1998, unpubl. data). For the purposes of this paper, birds showing the maximum extent of white (i.e., predominantly white wings, tail, and underparts) are assumed to be definitive-plumaged males (see photographs in Lowen et al. 1996a).

Only males with fully white wings were observed to display (see López Lanús et al. 1998). Males appeared to be territorial, frequenting display territories with a radius of at least 30 m. Males were present on their territories throughout the night, but only displayed under cloudless conditions with at least some moonlight. On one night of uninterrupted moonlight, displays continued from dusk until dawn. No display was observed on cloudy or moonless nights.

Each display territory studied ($n = 11$) contained between one and three discrete display arenas. Arenas were at least 10 m from palms or trees. It was not possible to determine exact arena sizes, other than distances between salient elements—a principal perch, usually the leafless vertical stem of a small sapling (hereafter referred to as ‘the perch’) situated close to a low, flat anthill (Fig. 1). From this perch, a male nightjar would conduct the majority of its activities. The anthill was generally 200–300 cm from the perch and had a mean diameter of 60 cm (range 40–200 cm). Anthill height varied from 30 to 50 cm and was always below that of the associated perch. Perch height varied from 40 to 60 cm and was higher than the surrounding grass (Fig. 1). Anthill height was always

lower than perch height. Two display arenas lacked a suitable stem; instead, birds used the vertical tower of an anthill as the main perch.

The first stage of the display involved the male flying from the perch to the anthill using an arching, "butterfly-like" flight, with gentle, fluttering wing-beats and the wings held well back (Fig. 1a). The male generally landed on the highest point of the anthill facing in the direction of the perch (Fig. 1b), and gave a short, sharp mechanical "tk" sound immediately before landing (for conjectured origin of this sound, see Discussion). The bird remained only momentarily on the anthill, then flew near vertically about 50 cm up, before following a straight line past the top of the perch (an angle of about 15°; Fig. 1c). The short vertical ascent was accompanied by rapid, shallow wingbeats and a strong, mechanical "grrrrrt" sound (for its conjectured origin, see Discussion). In contrast to the initial weak fluttering flight, the subsequent flight towards and beyond the perch was fast and strong with deep, rapid wingbeats. After flying beyond the perch, the bird then looped back to alight on it (Fig. 1d). The whole display lasted about 4–6 s, the precise trajectory varying according to the relative position of the anthill and perch.

MALE-MALE SPACING AND INTERACTIONS

Male territories were found exclusively on the upper slopes of ridges in areas where the density of Yata'i palms and other trees was notably low compared to surrounding areas (no actual density estimate was made). Territories were found on four ridges, with five territories on one ridge, three on another, and two and one on the remaining two ridges. These latter two ridges were the least studied, and additional territories may have been overlooked. The closest spacing recorded between adjacent display arenas of two different males was 60 m (between anthills). This apparent clustering of male display arenas on the upper slopes of ridges is suggestive of a lek-mating system or male aggregation due to the use of specialized habitats as encounter sites for mating ('landmark' species; see Höglund and Alatalo 1995 for a discussion of these two systems).

On one occasion, the moonlit conditions were good enough to watch two neighboring males displaying 60 m apart simultaneously for 1 h. During this period one male approached the other's territory on three occasions. On each occasion, there ensued a brief chase at a height of 3–4 m. These encounters, although apparently aggressive, never involved physical contact. During the chases, a short, soft whistle "tsher-she-shew" was heard from both birds. When one male was disturbed from its principal arena by the observer, it displayed at a second, and later at a third arena. These three arenas were separated by about 60 m. Males entering the territory of another bird ($n = 3$) were never seen to display at the territory owner's arenas, even when the territory owner had been disturbed either by the other bird or by the observer.

DISCUSSION

Both elements of the sound accompanying the display of male *Caprimulgus candicans* (i.e., the sharp "tk" and the strong "grrrrrt", tape-re-

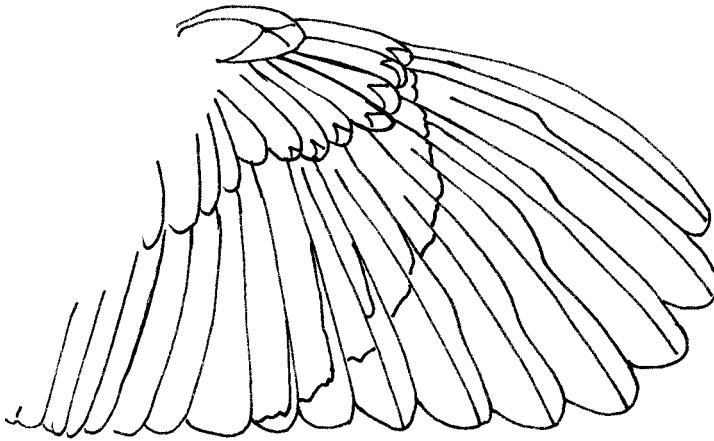


FIGURE 2. Modified wing shape of 'definitive' male *Caprimulgus candicans* caught by hand at Reserva Natural Bosque Mbaracayú, Paraguay.

corded in 1997 by JMB and released as part of Ranft and Cleere 1998) were considered to be mechanical in origin as opposed to than vocal. Although it was not possible to confirm this, the noises sounded 'instrumental' rather than vocal, and at least the "grrrrrt" was always produced in association with a specific rapid wing movement. Noises considered to have been mechanical in origin have been documented for several caprimulgid species, notably the closely related Sickle-winged Nightjar (*Eleothreptus anomalus*; Straneck and Viñas 1994) and White-tailed Nightjar (*C. cayennensis*; Hilty and Brown 1986).

Neither sound produced by *C. candicans* appeared to be due to contact between the wings and the anthill or the wings and vegetation, as has been suggested for sounds produced by male Scissor-tailed Nightjar (*Hydropsalis torquata*; Sick 1993). The sharp "tk" sound is probably made by the bird clapping its wings together below the body immediately prior to landing. We hypothesise that the "grrrrrt" sound is produced by the movement of air through the outer primaries during the rapid wingbeats at the start of the display segment shown in Figure 1c. Occasionally at the start of foraging sallies an attenuated version of the mechanical "grrrrrt" sound was heard. Similar attenuated versions of display-related mechanical noises are produced by many species with such displays during normal activities (e.g., manakins of the genus *Manacus*; Snow 1962).

The wing of male *C. candicans*, although not as highly modified as that of *Eleothreptus anomalus*, is nevertheless modified in shape compared to other New World nightjars of the genus *Caprimulgus*. As can be seen from Figure 2, the wing tip is very rounded, the five outermost primaries being noticeably similar in length, curved and rigid. They are prominently emarginated (all five primaries) and notched (outer three). There is a marked narrowing of each of these primaries near the beginning of each

emargination, with a gradual broadening towards the tip. The curvature and shape of the outer primaries of *C. candicans* is reminiscent of the wing of male *E. anomalus*. The modified shape is also shown to a lesser extent by male Spot-tailed Nightjar (*C. maculicaudus*) and *Hydropsalis torquata*. These outermost primaries also have a very 'rough', almost serrated edge to the inner web, most prominent after the notch. That the wing, and in particular the outermost primaries, are modified in shape suggests they might function in the production of mechanical noises.

The songs of tropical nightjars appear to function primarily in territory defence (Howell and Robbins 1995). This would not appear to be the case with *C. candicans*. No observations were made of birds demarcating territory boundaries (although 'intruding' males were chased), and the mechanical sounds were almost entirely associated with male display at arenas. The main purpose of these sounds, in conjunction with the extensively white plumage, would thus seem to be mate attraction.

Many nightjar species perform flight displays during which prominent white wing and tail patches (Mengel 1972, Cramp 1985) or modified plumes (Olmos and Rodrigues 1990, Mazar Barnett et al. 1998) are exhibited. Both features might be expected to reduce or replace the importance of acoustic signalling. The exaggerated white in the plumage of definitive male *C. candicans* (much reduced or absent in the immature male and female plumages; López Lanús et al. 1998, unpubl. data) can perhaps be considered analogous to highly modified plumes of other species. Moreover, like *C. candicans*, such species (for example, *E. anomalus*: Straneck and Viñas 1994; and Long-trained Nightjar *Macropsalis forcipata*: Olmos and Rodrigues 1990) tend to produce relatively modest vocalizations or mechanical noises.

Displaying male *Caprimulgus candicans* were clearly dependent on a specific habitat type: campo sucio, with scattered anthills and a low palm density. This habitat appeared to be transitional between the dense palm savanna at the base of the ridges and the open, inundated grasslands of the valley sides and bottoms, and is presumably related to edaphic factors (such as soil moisture content). It seems likely that fire also plays an important role in creating the appropriate habitat—most likely in keeping it relatively open and the grass short.

Males displayed with regularity under moonlit conditions during December 1995. This month is notably late for breeding; many species were already breeding in Aguara Ñu by September 1995 (unpubl. data), and the breeding seasons for most species in Paraguay has typically finished by December/January (pers. obs.). Given that a displaying male was also seen and heard on 17 September 1995, it seems likely that *C. candicans* has a relatively protracted breeding season.

The possibility that *C. candicans*, or at least the Aguara Ñu population, has a lek or landmark mating system requires investigation. The confirmation of one of these two possibilities could be of significance to the conservation of the species. Both mating systems imply a reliance on a specialised, potentially very local and, if fire-dependent, ephemeral hab-

itat. Alternatively, display sites may be traditional, with limited possibilities of relocation if they are destroyed. In addition, lek mating systems at least are typified by intense sexual selection and a strong skew in male reproductive success (Höglund and Alatalo 1995). The possibility that just one or two males accrue the majority of copulations could have important consequences for small, isolated populations such as that in Aguara Ñu.

It seems likely that further populations of *C. candicans* await discovery in what cerrado remains within the triangle formed by Emas National Park, Beni Biological Station and the Mbaracayú Forest Nature Reserve. Searches should be focused on areas of relatively open short campo sucio grassland, and would best be conducted during full moon in the austral spring and early summer. Although *C. candicans*, like several other nightjar species possessing exaggerated plumage traits, does not have a loud, distinctive song, the second part of the mechanical display noise can be heard at distances up to 200 m.

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