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FORAGING BEHAVIOR OF KAEMPFER'S WOODPECKER (*CELEUS OBRIENI*), A BAMBOO SPECIALIST

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Abstract. Because of the patchiness of their habitat, its perceived low conservation value, and tendency to burn, bamboo-specialist birds are vulnerable to habitat loss. We documented the habitat use and foraging strategies of *Celeus obrieni*, Kaempfer's Woodpecker, in forested *cerrado* (savanna) with patches of the bamboo *Guadua paniculata* near Pium, Tocantins, Brazil. We surveyed for *C. obrieni*, measured vegetation structure at 30 sites where it was detected and 23 where it was not detected, then compared vegetation characteristics through nonmetric multidimensional scaling and one-way analysis of similarity to determine whether *C. obrieni* was specializing on particular habitat characteristics. We studied the species' foraging and compared the abundance of prey in drilled and nondrilled stems to evaluate its dietary specialization. All sites with *C. obrieni* had large, tall stands of *G. paniculata*, indicating habitat specialization. Drilling most frequently on large, dry stems from 2 to 4 m off the ground, the woodpeckers consumed ants, mainly *Camponotus depressus* and *Azteca fasciata*, which colonize the internodes of bamboo stems. Habitat specialists are more vulnerable to habitat loss or alteration but can serve as indicator species for the reaching of conservation goals. Large stands of forested *cerrado* with patches of bamboo should be conserved for *C. obrieni* to be maintained. The patchiness of bamboo forest may impede dispersal of *C. obrieni*.

Key words: *Celeus obrieni*, *Guadua paniculata*, Tocantins, foraging strategies, vegetation structure.

Comportamiento de Forrajeo de *Celeus obrieni*, un Especialista de Bambú

Resumen. Debido a la distribución en parche de su hábitat, la percepción de su bajo valor de conservación y la tendencia a quemarse, las aves especialistas de bambú son vulnerables a la pérdida de hábitat. Documentamos el uso de hábitat y las estrategias de forrajeo de *Celeus obrieni* en las áreas boscosas de *cerrado* (sabana) con parches del bambú (*Guadua paniculata*) cerca de Pium, Tocantins, Brasil. Muestreamos la presencia de *C. obrieni* y medimos la estructura de la vegetación en 30 sitios donde fue detectado y 23 donde no fue detectado. Luego, comparamos las características de la vegetación a través de análisis de escalamiento multidimensional no métrico y análisis de semejanza de una vía para determinar si *C. obrieni* se especializaba en algunas características particulares del hábitat. Estudiamos el forrajeo de la especie y comparamos la abundancia de presas en tallos perforados y no perforados para evaluar en grado de especialización de la dieta. Todos los sitios con *C. obrieni* presentaron stands grandes y altos de *G. paniculata*, indicando especialización de hábitat. Los carpinteros perforaron con mayor frecuencia tallos grande y secos, entre 2 y 4 m de altura desde el suelo, y consumieron hormigas, principalmente de las especies *Camponotus depressus* y *Azteca fasciata*, las que colonizan los inter nodos de los tallos de bambú. Los especialistas de hábitat son más vulnerables a la pérdida o a la alteración de hábitat pero pueden servir como especies indicadoras para alcanzar objetivos de conservación. Deberían conservarse grandes stands boscosos de *cerrado* con parches de bambú para mantener a *C. obrieni*. La distribución en parche de los bosques de bambú puede impedir la dispersión de *C. obrieni*.

INTRODUCTION

The Brazilian *cerrado* biome is one of the world's most important areas for biodiversity (Mittermeier et al. 2000). It is the second largest biome in Brazil and one of the most endangered by deforestation. Its high biodiversity is explained

by its mosaic of different vegetation types and topographies, encompassing grasslands, *cerrado* (savannas), *cerradão* (forested savannas), riparian, and dry forests (Silva and Bates 2002, Klink and Machado 2005). In addition, dense clumps of bamboo occur along rocky hillsides, in open stretches, and in

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forested areas, often scattered within the riparian vegetation and woody savanna (Soderstrom 1981, Filgueiras 1988, Silva et al. 2004, Pinheiro and Dornas 2008).

The large diversity of arthropods inhabiting the bamboo stands attracts several species of birds, including facultative users of bamboo, near-specialists, and specialists (Rodrigues et al. 1994, Olmos 1996, Kratter 1997, Vasconcelos et al. 2005, Guilherme and Santos 2009, Cestari and Bernardi 2011). Bamboo fruits and dies off cyclically at periods that range usually from 2 to 30 years, depending on the bamboo species, and affect the distribution and abundance of bamboo specialists (Londoño 2001, Jaksic and Lima 2003, Areta et al. 2009, Areta and Cockle 2012). Some of the birds using bamboo are threatened with extinction, owing to habitat fragmentation or loss, which reduce bamboo patches and may make flowering more unpredictably in space and time (Olmos 1996, Vasconcelos et al. 2005, Areta et al. 2009).

In Brazil, several birds specialize in bamboo in the Atlantic rainforest, where bamboo stands cover relatively small areas (Rodrigues et al. 1994, Vasconcelos et al. 2005, Areta 2007, Santana and Anjos 2010), and in the Amazon rainforest, where bamboo stands can cover extensive areas (Parker 1982, Pierpont and Fitzpatrick 1983, Parker and Remsen 1987, Fitzpatrick and Willard 1990, Kratter 1997, Kratter and Parker 1997). However, few bamboo specialists occur in the *cerrado*: the Blackish-blue Seedeater (*Amaurospiza moesta*) (Lopes et al. 2011) and the Kaempfer's Woodpecker (*Celeus obrieni*) (Short 1973). A single species of tyrant, the Pearl-breasted Pygmy-Tyrant (*Hemitriccus margaritaceiventer*), considered a generalist elsewhere, has been observed using enclaves of *cerrado* with epiphytic bamboos in the understory (Aleixo and Poletto 2007).

Short (1973) described *Celeus obrieni* on the basis of a unique specimen collected in 1926 by Emil Kaempfer in the *cerrado* vegetation of the Uruçuí region, in the southern portion of the state of Piauí, Brazil. It was initially considered a subspecies of *C. spectabilis*, which occurs in the Amazon region between Peru and the state of Acre, Brazil (Sick 1997). Because of the absence of subsequent records, Tobias et al. (2006) inferred the "subspecies" was probably extinct. In 2006, 80 years after the first collection of *Celeus obrieni* in the state of Piauí, a female was captured in a bamboo stand mixed with *cerradão* in Goiás, located in the northeastern part of the state of Tocantins, 400 km from the type locality (Prado 2006). Since then, numerous new records of *C. obrieni*, in stands of the bamboo *Guadua paniculata* mixed with forested *cerrado*, have been reported (Santos and Vasconcelos 2007, Hidasí et al. 2008, Pinheiro and Dornas 2008, Dornas et al. 2009, Pacheco and Maciel 2009, Pinheiro et al. 2012). Breeding of *C. obrieni* is also known from stands of *G. paniculata* (Leite et al. 2010).

In the Bolivian *cerrado* and Chiquitano dry forest, stands of *Guadua* can cover more than 1000 ha, produce up to 16 mg ha⁻¹ of fine fuel biomass, and are associated with

high-intensity fires (Veldman 2008). Data on the size and biomass of *Guadua* bamboo stands are unavailable for the Brazilian *cerrado*.

Data on the natural history, foraging, and habitat use of *C. obrieni* are lacking. To fill these information gaps, we studied the species' foraging behavior and the structure of its habitat. First, to determine if this bird is a bamboo specialist, we compared vegetation structure at sites where *C. obrieni* responded to its territorial calls to that at sites where no individuals responded. This knowledge of habitat use should help to define conservation strategies for the species. Second, we focused on the foraging behavior of *C. obrieni*, evaluating prey availability and describing techniques of prey search and capture. Such information should reveal on what resources within its habitat *C. obrieni* is specializing and may aid in understanding why it specializes on large stands of *G. paniculata*.

MATERIAL AND METHODS

STUDY AREA

Our study took place near the city of Pium, located in the central-western portion of the state of Tocantins, Brazil, on the plains of the Araguaia River (Fig. 1). The region is characterized by low topographic relief with elevation varying from 100 to 300 m. The region's climate is hot and humid, with a marked rainy season between November and April. Average temperature ranged from 24 to 26 °C during the wet period and from 28 to 35 °C during the dry period. In Tocantins average precipitation varies from 1800 mm in the northeast to 1000 mm in the south (SEPLAN 2008).

We recorded data in the field from August 2008 to January 2010 in three fragments of *cerradão* at the Javaés farm (with 1400 ha of native vegetation), Ouro Verde farm (1600 ha), and Brasil-Palmeiras farm (440 ha). In the areas studied, the canopy reached up to 17 m and contained trees such as the monkeycomb apeiba (*Apeiba echinata*), South American locust (*Hymenaea courbaril*), tucum (*Bactris glaucescens*), sowarri nut (*Caryocar brasiliense*), and trumpet tree (*Cecropia* sp.), mixed with stands of *G. paniculata*. We also sampled a forested area along the Javaés River, near the Canguçu Private Natural Heritage Reserve (RPPN), where stands of *G. paniculata* do not occur. This last area is 30 km from the farms we studied (Fig. 1), but its vegetation structure is similar, including trees such as *H. courbaril*, *B. glaucescens*, and *Cecropia* sp.

BIRD CENSUS AND VEGETATION STRUCTURE

We selected 53 fixed points, 13 on Javaés Farm, 16 on Ouro Verde, 12 on Brasil-Palmeiras, and 12 along the Javaés River. Within each farm, the average distance between points was 500 m, and 31 of these points had stands of *G. paniculata* in *cerradão* vegetation. Seasonally flooded forest along the Javaés River and *cerradão* without stands of *G. paniculata* constituted the vegetation at the other 22 fixed points. We visited each point three times every month, on consecutive days,

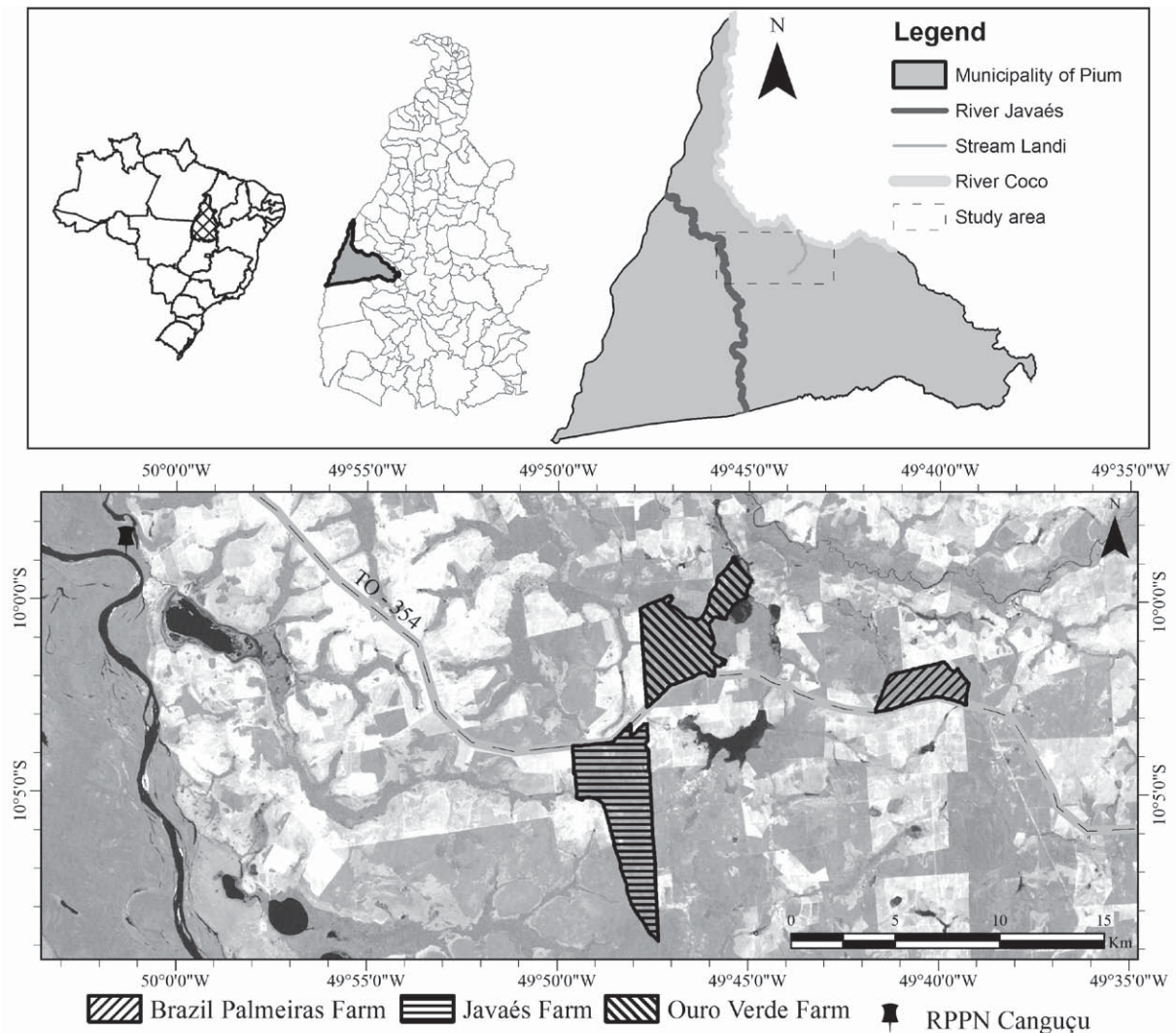


FIGURE 1. Location of the study areas in the municipality of Pium, Tocantins, Brazil. The hatched areas are the Javaés, Ouro Verde and Brasil-Palmeiras farms.

always in the morning when *C. obrieni* seems to be more active. To obtain data on its occurrence and behavior, we broadcast territorial calls and drumming for 5 min at each point. If no response was detected, the observer (GAL) moved to the next point. If the bird was attracted by the broadcast, its behavior was observed from a distance that did not interfere with its activities until it was out of sight. After that, the observer moved to the next point.

At each of the 53 points, we established a 100-m linear transect to measure vegetation structure, for comparisons between sites where *C. obrieni* was detected and not detected. We divided each transect into 10 equidistant segments, in each of which we established a quadrat to measure vegetation structure, totaling 40 sample points for each structure variable per transect. Afterward, we obtained an average of the vegetation measures per quadrat and then per transect, for use in statistical analysis. Measured variables were DBH (diameter

at breast height of trees or bamboo stems), DST (distance [m] from the center of the quadrat to the nearest tree with DBH >10 cm or bamboo clump—maximum distance considered was 5 m), canopy height of trees and/or bamboo clump (m), visually estimated as the number of times a given canopy height was taller than a ~2-m pole), canopy cover by trees and/or bamboo stems, visually estimated by intervals of 20% with a 4-cm-diameter cylinder divided in four sectors; the value for each quadrat was the mean of the four sectors), herbaceous cover near ground level, estimated by intervals of 20% in a radius of 1 m around the nearest tree or bamboo clump edge), and size of the bamboo clump, represented as the number of bamboo stems per clump.

FORAGING STRATEGIES

Following Remsen and Robinson (1990), we used 8×42 binoculars to count and classify the prey search and foraging

techniques of *C. obrieni*. Using their framework, we discriminated among prey searching, attacking, and capturing behaviors. Search comprised movements between foraging sites and included gliding, walking, climbing, running, and short flights within habitat clumps. Attacking included pecking, hammering, and drilling. For prey capture, we indicated whether it occurred inside or on the exterior of a given branch, stem, or trunk.

PREY LOCATION AND ABUNDANCE

The overwhelming majority of foraging we observed was on bamboo stems. Therefore, we compared the location, abundance, and types of prey in stems drilled by *C. obrieni* against stems not drilled stems, randomly collected at all sampling points where an individual was observed. We opened drilled stems and searched them for prey, which we then collected. We considered the stem/internodes as occupied if we found pupae, eggs, or adult insects inside. We recorded the following data for drilled stems: stem length and diameter at breast height; the length, diameter, and height above ground of drilled internodes; the number of holes drilled and their distance to the internode's base; whether the stem was green or dry. When the woodpeckers searched and/or captured prey on other plant species, we collected their leaves and fruits for identification. For undrilled stems, we inspected 15 green and 15 dry (from each point where a woodpecker was observed) for insects present externally or sheltered inside. After cutting a stem down, we measured its length (= height) and diameter with a tape and a caliper before opening it and searching it for prey. If we found prey inside an internode, we measured the internode's diameter, length, and height above ground. All insect samples were stored in tubes containing 90% of alcohol for latter identification.

To complement the data on prey consumed by *C. obrieni*, we examined the stomach contents from three museum specimens also collected in *cerradão* containing stands of *Guadua*. One specimen deposited at the Tocantins Federal University Ornithological Collection (COUFT 0257) was from Goiatins, Tocantins (385 km NW of the study area); the other two deposited at the Museu Paraense Emilio Goeldi were from Matões (A010060 MEG) and Parnarama (A010061 MEG), Maranhão (880 km NW of the study area).

STATISTICAL ANALYSIS

Using Bray–Curtis distances, we checked for possible differences between vegetation structure at sites where *C. obrieni* was and was not detected with nonmetric multidimensional scaling (NMDS) and one-way analysis of similarity (ANOSIM, a nonparametric multivariate method that compares similarities between and within groups). NMDS is one of the most powerful ordination techniques used in community-structure analysis. It does not require a multivariate normal distribution, does not assume linear correlations between variables,

and yields the most accurate representation of underlying data structure (Clarke 1993). Before running NMDS, we standardized the mean of each structural variable measured on each transect by its maximum value. For NMDS we used the autopilot mode in PC-ORD (McCune and Grace 2002). Dimension numbers were defined by the final stress that was compared to randomized runs of the dataset (McCune and Grace 2002).

We used a chi-squared test to compare frequencies of ant colonies in dry and green stems and a Mann–Whitney *U* test to compare the number of holes *C. obrieni* had drilled in these stems. To compare the frequency of holes at different heights inside the internodes, which could be associated with the location of potential prey, we again used chi-squared tests. Since our data on foraging are based on untagged individuals that could have been resampled on the same day or different days, we used the Wilcoxon test to compare ranks of these heights. We used Spearman's rank correlation to test the hypothesis that the number of woodpecker holes increases with internode length, since probability of containing insects should be higher in older (and presumably larger) internodes.

All statistical analyses were based on Zar (2009) and done in Systat 10 (Wilkinson 2000), except for NMDS, for which we used PC-ORD version 4 (McCune and Grace 2002), and ANOSIM, for which we used PAST (Hammer et al. 2001).

RESULTS

Habitat structure at sites where *Celeus obrieni* was detected vs. not detected

We observed *C. obrieni* at 30 of 53 sampling points, and the Mann–Whitney *U* test (Table 1) showed a clear difference in vegetation structure at sites of detection and nondetection, also confirmed by the ANOSIM analysis ($R = 0.674$, $P < 0.0001$) and NMDS ordination. The first two axes of NMDS explained 93.2% of the total variance. The recommended procedure on the NMDS solution was bidimensional: final stress = 11.671, $P < 0.020$, variance associated with axis I = 24.6%, and variance associated with axis II = 68.7% (Fig. 2). Sites with *C. obrieni* were characterized by large bamboo clumps with a predominance of green stems (69%), low canopy cover, and small DST and DBH (due to a mixture of trees and bamboo stems). We did not find *C. obrieni* at any of the 22 *cerradão* sampling points without stands of *Guadua* bamboo, where two other species of woodpeckers, *C. (flavescens) ochraceus* and *Veniliornis passerinus*, were observed occasionally.

FORAGING STRATEGIES

Our characterization of the foraging behavior of *C. obrieni* is based on 81 observations of individuals at 28 sampling points over 41 census days. Because we did not color-band the birds, we do not know the extent to which some these observations represented recurrences of the same individual. Except for two observations of birds in *Cecropia* sp., where their foraging behavior could not be observed, the remaining

TABLE 1. Mann-Whitney *U* test comparing the ranks of variables measured by the point-quadrat method at sites of detection and non-detection of Kaempfer's Woodpecker (*Celeus obrieni*).

Variable	Sites with <i>C. obrieni</i> (median)	Sites without <i>C. obrieni</i> (median)	<i>U</i> -test value
Distance to the nearest tree or bamboo clump (DST)	1.56	2.12	634.5 ^a
Diameter at breast height of trees or bamboo stems (DBH)	6.36	9.47	621.0 ^a
Canopy height (CH)	5.90	6.04	353.0
Canopy cover by trees and/or bamboo stems (CC)	76	90	592.5 ^a
Herbaceous cover near level soil (SC)	6.76	8.1	378.0
Bamboo clump size (BCS)	9.80	0	4.0 ^a

^a*P* < 0.01

79 observations were of individuals foraging on *G. paniculata*. Typical searching movements consisted of individuals that landed at the base of the bamboo stem (between 0.5 and 1.0 m above the ground) and began climbing up and around the stem, inspecting each internode, apparently searching for insect holes or other signs of insects (Fig. 3A). Search time on each stem lasted 30 sec, on average. When stems had no signs of prey, the bird flew to another stem and repeated the same searching procedure (Fig. 3B). Upon finding prey inside an internode, a woodpecker immediately started pecking, making up to four holes. After drilling the internode, it adopted one of two strategies to obtain its prey: the most frequent (82%) consisted of inserting its tongue inside the internode through the perforated hole and removing insects, mainly ants, which it consumed immediately (Fig. 3C). In the other strategy, the bird began drilling the internode and consumed the ants emerging from the interior while they were climbing on the outside of the stem (Fig. 3D).

PRESENCE OF PREY IN UNDRILLED AND DRILLED BAMBOO STEMS

Forty percent (364/900) of the undrilled stems we examined from the sampling points where *C. obrieni* was observed contained one or more colonies of ants and/or Coleoptera larvae, totaling 518 insect samples (since more than one colony and/or larva could be found in the same stem). Ants were the most abundant group of insect, being present in 97% of these 518 samples. The number of ant colonies in the stems varied from one (54%) to six (1%), and stems with at least two ant colonies constituted 78% of the observations. Fifty-nine percent (215/364) of all ant colonies found were located in dry stems ($\chi^2_2 = 28.6$, *P* < 0.01), and their eggs and pupae were

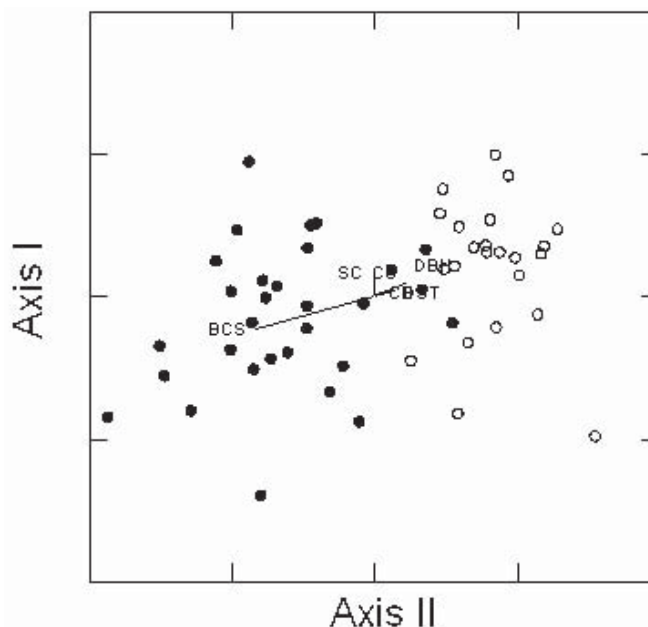


FIGURE 2. Ordination by nonmetric multidimensional scaling, showing that the habitat selected by *Celeus obrieni* is characterized mainly by large and dense stands of *Guadua paniculata* (• = sites of detection of *C. obrieni*; ○ = sites of nondetection). DBH = diameter at breast height of trees or bamboo stems; DST = distance from the center of the quadrat to the nearest tree or bamboo clump; SC = herbaceous cover near ground level; CH = canopy height; CC = canopy or bamboo-stem cover; BCS = bamboo clump size.

frequently found inside and at the base of internodes. Eighty-seven percent of the internodes occupied by ant colonies were found <5 m above ground (median = 2.94 m). We identified 13 species of ants in the undrilled stems, and the three most frequent were *Camponotus atriceps*, *C. depressus*, and *Azteca fasciata*. Together, these three species represented 76% of all samples.

Fifty nine percent of the stems inspected and drilled by *Celeus obrieni* contained ant colonies, and 62% of those stems were dry (Table 2), contrasting with the low frequency of dry stems (31%) in the quadrat samples. The frequencies of the three most common ant species consumed in these stems seem to differ from their frequencies in randomly collected stems, but they were consumed more often in dry or green stems, were they were also more frequently found. *Camponotus depressus*, the largest ant species, was the only ant found on the outside of stems, and it was easily consumed by *Celeus obrieni* in dry stems, where the smallest ant, *A. fasciata*, was not consumed (Table 2).

Celeus obrieni seemed to avoid foraging near the ground, concentrating on internodes between 2 and 4 m above the ground (median = 3.0 m, Fig. 4). Although this median height is similar to heights in which colonies of *A. fasciata* and *Camponotus depressus* were more frequently found, the ranked

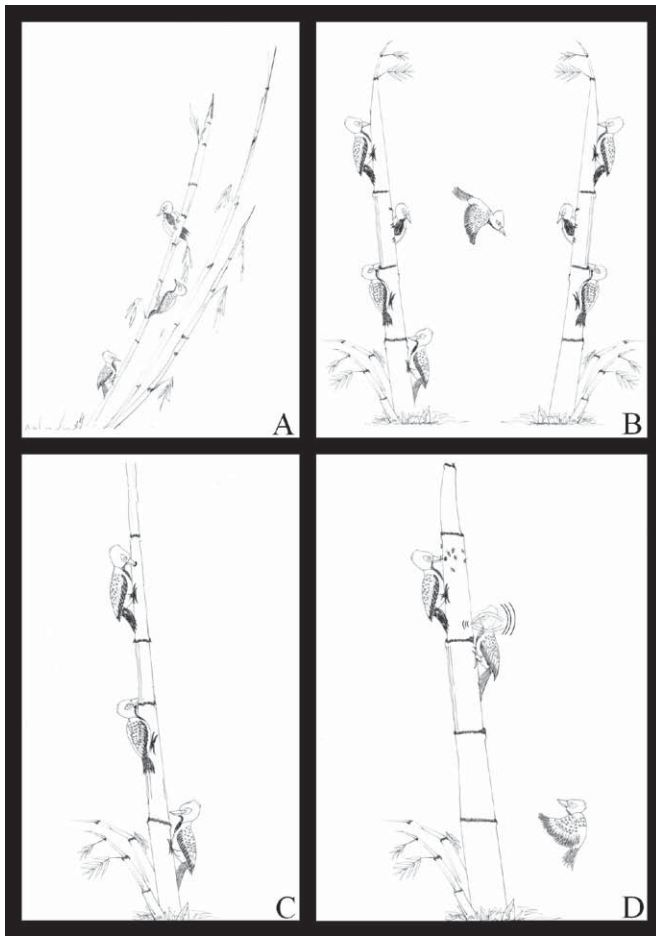


FIGURE 3. (A and B) Foraging behavior of *Celeus obrieni* showing searching behavior: ascent and waiting on a stem and ascent and flight between stems. (C) Attack behavior, showing a bird drilling an internode of bamboo and searching for ants with its tongue. (D) Drumming behavior, when the birds wait for ants to come out from inside the internode. Drawings by Felipe Bittioli R. Gomes.

distribution of heights of all colony and foraging attempts differed significantly (Wilcoxon signed ranks: $Z = 2.549, P < 0.05$).

Sixty-three percent of the internodes inspected and drilled by *Celeus obrieni* were wider and larger than undrilled

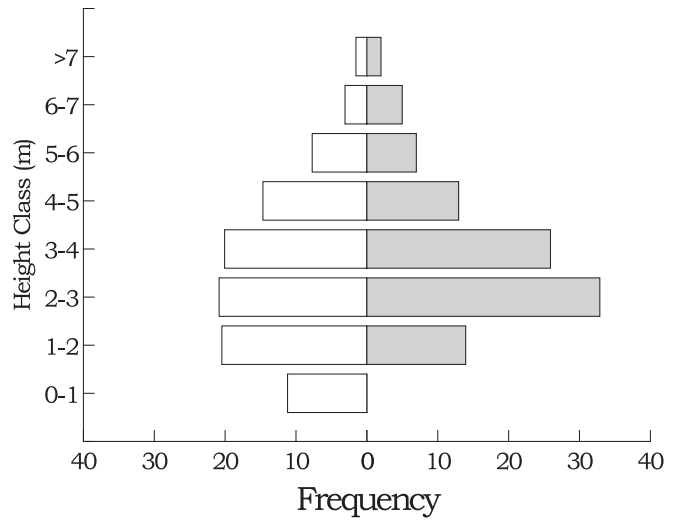


FIGURE 4. Vertical distribution of ant colonies inside internodes of *Guadua paniculata* (white bars), compared to heights of foraging of *Celeus obrieni* (gray bars).

stems. The number of holes the woodpeckers made in the internodes varied from one (55%) to four (8%). The number in dry and green stems did not differ ($U = 4, P > 0.05$), but it rose with internode length ($r_s = 0.305, n = 79, P < 0.01$). Distances between holes and the base of the internodes varied from 1 to 35 cm, but 53% of the holes were between 1 and 5 cm ($\chi^2_6 = 104.5, P < 0.01$).

The stomachs of the three specimens of *C. obrieni* contained ants only. In the male from Goiatins we found 22 pupae and 62 adults, some of which were unbroken and could be identified as *Camponotus depressus*. Stomach contents of the specimens from Matões and Parnarama contained 83 and 154 parts of two unidentified ant species, respectively.

DISCUSSION

HABITAT USE

Guadua bamboos readily invade forest gaps, where they form monospecific stands that can arrest forest succession (Griscom and Ashton 2003). Corroborating the findings of

TABLE 2. Comparisons between frequencies of ant colonies in randomly sampled stems and stems where *Celeus obrieni* foraged.

Ant species	Ant body length (mm)	Median colony height (m)	Median height of woodpecker foraging (m)	Randomly sampled stems (450 green, 450 dry)		Stems on which woodpeckers foraged (32 green, 53 dry)	
				Frequency of ant colonies in green stems (n, %)	Frequency of ant colonies in dry stems (n, %)	Frequency of ant colonies in green stems (n, %)	Frequency of ant colonies in dry stems (n, %)
<i>Azteca fasciata</i>	4	3.5	3.2	75 (17)	10 (2)	14 (44)	0 (0)
<i>Camponotus atriceps</i>	7	2.1	2.4	30 (7)	60 (13)	0 (0)	4 (8)
<i>Camponotus depressus</i>	10	2.4	3.3	7 (2)	76 (17)	1 (3)	26 (49)
All species (including rare species)	—	2.9	3.0	142 (32)	215 (48)	23 (27)	36 (42)

Veldman (2008) in Bolivia, the patches of *G. paniculata* inside *cerradão* that we studied in Brazil were characterized by inverse correlations between canopy openness, DBH of trees, and size of the bamboo clump. The stands of *Guadua* bamboo within the Brazilian *cerrado* are very small in comparison to those in some portions of the Atlantic forest (M. Vasconcelos, pers. comm.) or Amazonia, and at our study sites the population density of *Celeus obrieni* seemed low. Radio-tracking of six individuals (RTP, unpubl. data) revealed their home range covered on average 210 ha (range 30–565 ha) and usually consisted of two or three core areas overlapping with clumps of *G. paniculata*. Low population density, small bamboo patches, and patchiness of this habitat all suggest that movement among and use of multiple stands of bamboo scattered within the *cerradão* may be vital to maintaining populations of *C. obrieni* in this region.

FORAGING STRATEGIES

Celeus obrieni foraged mainly on dry stems (62%). The birds generally made only one hole per internode, capturing ants sheltered inside. Most of the holes were close to the base of the internode, where ant colonies with their eggs and pupae were most often found, a strategy that likely increased the chances of the woodpeckers' obtaining prey. Sometimes, an internode already contained a hole, likely made or enlarged by ants. In these cases, *C. obrieni* drilled in a different location along the internode, causing ants to emerge from both its drill hole and the previous hole, increasing the number of prey emerging on the exterior of the internode, which the bird consumed. The positive correlation between number of holes drilled and size of the internode suggests that holes accumulate over time as a result of multiple foraging attempts, which would be expected if the woodpecker's consumption of ants was not detrimental to an ant colony.

Pecking and then searching for food inside internodes with its tongue was the most frequent foraging technique *C. obrieni* employed (82%). We observed that ants did not readily abandon their colonies, which often contained eggs and pupae, when the internode was drilled, allowing a woodpecker to reach inside and consume ants. Although less frequent, the hammering technique, after drilling, also resulted in prey capture, since we observed ants trying to escape or defend the colony being captured by *C. obrieni* outside the stem.

Various species of woodpeckers capture prey by different techniques (Hogstad 1976, Hooper and Lennartz 1981, Askins 1983, Engstrom and Sanders 1997, Remsen and Robinson 1990, Winkler and Christie 2002), and they often use different techniques according to substrate and prey type (Winkler and Christie 2002), as well as by season and reproductive period (Winkler 1979, Conner 1981, Kattan 1988). The use by *C. obrieni* of a consistent foraging strategy, pecking, suggests a high predictability in prey type, behavior, abundance, and location throughout the year.

FOOD TYPES

Ants are the main prey consumed by *C. obrieni*, with *Camponotus* and *Azteca* the most frequent genera found and consumed. *Celeus obrieni* most often foraged between 2 and 4 m above ground level, matching the range of heights at which these ant species were most frequently found, likely increasing its foraging efficiency. Foraging heights between 3 and 10 m have been observed for the Rufous-headed Woodpecker (*C. spectabilis*) searching for food on the arching horizontal stems of the taller (20 to 25 m) Amazonian bamboo *G. weberbaueri* (Kratter 1997, 1998, Whittaker and Oren 1999, Lloyd 2000, Winkler and Christie 2002, Guilherme and Santos 2009). Preference for ants is typical in woodpeckers. Nearly 60% of all species include ants in their diets, and in some species the proportion consumed varies seasonally between 54 and 97% (Winkler and Christie 2002). Ants of the genera *Camponotus* and *Azteca* are preyed upon by several woodpecker species in the neotropics, and they can be found on various species of trees, including *Cecropia* sp. (Winkler and Christie 2002). Similarly, Torgersen and Bull (1995) found the North American Pileated Woodpecker (*Dryocopus pileatus*) consuming *Camponotus* ants at high rates, corresponding to their frequency in dead trunks. Like some other woodpecker species, *C. obrieni* is an ant specialist, foraging where its prey are most easily found. Because of this species' low abundance, we hypothesize that ant consumption by *C. obrieni* is not detrimental to ant colonies or populations, likely allowing for continuous replenishment of ant stocks after a woodpecker forages (or a colony may even migrate to other internodes), renewing its main prey type.

SPECIALIZATION AND THREATS

Optimal-foraging theory predicts that specialization is possible in a resource-rich environment, where finding valuable prey is feasible in a short time (MacArthur and Pianka 1966, Huey and Pianka 1981). However, specialization is also possible whenever resources are scarce but predictable, requiring efficient exploitation. This applies to the Arizona Woodpecker (*Picoides arizonae*), which changes its foraging habits from the pre-nesting season (specialized feeding behavior) to the nesting season (opportunistic feeding behavior), as its energy requirements rise (Winkler 1979). The foraging behavior of *C. obrieni* suggests that this bird is an optimal forager. A high predictability of ants in stands of *G. paniculata*, and the efficiency of the woodpecker's tactics for search and capture may have allowed its specialization in this habitat and on ants as its main food resource. As *C. obrieni* is highly specialized, it is possible that its population size is strongly correlated with the sizes and ages of *G. paniculata* stands within its home range, which could make this species more vulnerable to habitat fragmentation and environmental hazards. Such vulnerability has also been found in other species of woodpecker associated with specific types of vegetation (Imbeau and Desrochers 2002).

Socolar et al. (2013) tracked the disappearance of several bamboo-specialist birds after large die-offs associated with mass flowerings of clonal patches of *Guadua* in the Peruvian Amazon forest. These massive die-offs represent a challenge for seed-eating bamboo specialists, especially in fragmented habitats, but are probably less challenging to ant-feeding specialists such as *C. obrieni* since ant colonies can persist, at least temporarily, in dry stems. However, habitat fragmentation and fire are common in habitats characteristic of *C. obrieni* (Marcelino et al. 2012). Like other bamboos, *G. paniculata* stands hold large amounts of highly flammable fuel and are susceptible to fire spreading from the surrounding *cerradão*. While bamboo quickly regenerates after fire (Veldman 2008), colonization by ants may be delayed, reducing the carrying capacity of regenerating stands and making dispersion among stands crucial for the persistence of *C. obrieni*.

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