J. Field Ornithol. 79(1):24–31, 2008 DOI: 10.1111/j.1557-9263.2008.00142.x

Nest-site selection by Blue-black Grassquits in a Neotropical savanna: do choices influence nest success?

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Received 6 December 2006; accepted 12 October 2007

ABSTRACT. Nest-site choice affects individual fitness and possibly reflects natural selection of the capacity of individuals to select appropriate microhabitat features. From 2003 to 2005, we examined nest-site characteristics and nesting success of Blue-black Grassquits (*Volatinia jacarina*) in central Brazil. We compared the characteristics of nest sites and nonused sites, as well as the characteristics of successful and unsuccessful nests. Grassquit nest sites were structurally more complex than nonused sites. Shrub height and the interaction between vegetation height and percentage of ground coverage were the most important predictors of nest placement. Grassquits used only four (20%) of the 20 grass species in the study area, with *Paspalum pectinatum* used less than expected based on availability and *Melinis minutiflora* more than expected. The only variable that differed between unsuccessful and successful nests was the distance to nearest conspecific nest; the latter were about twice as far from neighboring nests as unsuccessful nests. The evaluation of microhabitat candidate models indicated that the daily survival probability of nests varied chiefly as a function of the interaction between their external height and inner depth. Greater survival occurred when the external height was minimized in combination with augmentation of internal depth of the nest cup. The link between nest success and the inverse association of external height and internal depth suggests that minimizing the visual cues of nest presence while maintaining a viable incubation chamber can positively affect nest success. Thus, we suggest that nest concealment is the most critical attribute associated with nest site choice for Blue-black Grassquits in the study area. Vegetation cover above the nest seems to be particularly important, perhaps as a strategy to deter visually oriented aerial predators.

SINOPSIS. **Selección del nido de *Volatinia jacarina* en una savana neotropical: la selección del lugar influencia el éxito de anidamiento?**

La selección del lugar de anidar afecta el grado de aptitud del individuo y posiblemente refleja la selección natural sobre la capacidad de los individuos para seleccionar apropiadamente peculiaridades del microhábitat. Del 2003–2005 examinamos las características del lugar de anidamiento y el éxito de anidamiento de individuos de *Volatinia jacarina* en la parte central de Brazil. Comparamos las características de los lugares de anidamiento y los lugares no utilizados, como también las características de nidos exitosos y fracasados. Los lugares utilizados para anidar por el ave resultaron estructuralmente más complejos que los lugares no utilizados. La altura de los arbustos y la interacción con la altura de la vegetación y el porcentaje de cobertura en el suelo fueron los predictores más importantes en la localización del nido. Las aves solo usaron cuatro (20%) de las 20 especies de yerbas presentes en el área de estudio. *Paspalum pectinatum* fue menos utilizada que lo esperado en relación a su disponibilidad, mientras que *Melinis minutiflora* fue utilizada en mayor grado que lo esperado. La única variable que fue diferente entre los nidos no-exitosos y los exitosos fue la distancia entre nidos de la misma especie: los ultimos se encontraron al doble de la distancia que los nidos no-exitosos. La evaluación de diferentes modelos candidatos a evaluar microhábitat indicaron que la probabilidad de supervivencia diaria de nidos, varió como función de la interacción entre la altura externa y la profundidad interna de los nidos. La sobrevivencia fue mayor cuando la altura externa era minimizada en combinación con el aumento de la profundidad interna de la copa del nido. El puente entre el éxito del nido y la asosiación inversa de la altura externa y la profundidad interna sugieren que el minimizar las pista visuales sobre la presencia del nido y a la vez mantener una profundidad interna particular puede afectar positivamente el éxito del mismo. Sugerimos que el esconder el nido es el asunto mas crítico atribuible a la selección del lugar de anidamiento, para el ave, en el lugar estudiado. La vegetación que cubre la superficie del nido parece ser importante, tal vez como una estrategia para pasar inadvertido a depredadores que se orientan visualmente desde el aire.

Key words: Blue-black Grassquit, grassland bird, nest-site selection, nesting success, *Volania jacarina*

Breeding habitats and nest sites used by birds can be described in terms of several variables, such as precipitation, food availability, vegetation cover, and structure, as well as the characteristics of nests and substrates. Microhabitat features of the vegetation used as nest substrates

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are especially important for camouflage and protection from inclement weather, both of which can influence nest success (Paton 1994). Numerous investigators have attempted to determine habitat characteristics associated with nesting success, and Martin (1995) suggested that nest concealment may be the single most important variable. However, specialized predator search strategies may limit the ability of birds to select nest sites that provide significant protection from the suite of potential predators (Liebezeit and George 2002).

To understand the relationship between birds and their habitats, determining the habitat or nest microhabitat features associated with nesting success is important (Kolbe and Janzen 2002). Although this has been the focus of many studies of temperate birds, there are few such data for birds in the tropics where nest predation may be more intense (Martin 1996). Our objective was to determine if a tropical grassland bird subjected to intense nest predation chooses nest microhabitats that minimize nest failure. We studied the nest-site characteristics and reproduction of Blue-black Grassquits (*Volatinia jacarina*), a common Emberizid of grasslands throughout much of the Neotropics. We first examined the use of different plant species as nest substrates relative to their availability, and then asked whether specific nest sites differed from nonused sites available to each pair in a point contiguous to the nest site and within their territory. In addition, we asked whether successful nests differed from unsuccessful nests in terms of associated habitat variables and nest structure. We assumed there were potential nesting microhabitats available that could have been randomly chosen for nest construction and that the frequency of the chosen microhabitat for nest construction may indicate preference (*sensu* Martin 1998, but see Jones 2001).

METHODS

We studied grassquits at two sites about 35 km apart in central Brazil. One area was studied during 2003–2004 and is located on the University of Brasilia campus (15°46′S, 47°52′W). This area consists of a small patch of savanna vegetation containing open grassland and shrubs in an urban environment. The second area, called Fazenda Água Limpa (FAL; 15° 57′, 47° 56′ W), was our study site during 2004–2005. The study area at FAL contains altered savanna vegetation, but in a larger and more natural environment than the study area on campus. The climate in the region is seasonal and characterized by dry winters (May-October) and rainy summers. Annual temperature averages 23°C, and rainfall ranges from 1200 to 1800 mm annually (Coutinho 2000).

We found nests from late January to April by systematically searching through the grass and flushing birds from nests. We marked nests with flagging a few meters away and monitored them every 2–3 d to determine nest fate. We did not handle nestlings and, to minimize disturbance, visits were brief (<30 s). For each visit, we noted nest contents (eggs/chicks) and, just prior to fledging, marked nestlings with permanent aluminum bands (CEMAVE—Centro Nacional de Pesquisa para Conservação das Aves Silvestres). Predation was considered the cause of nest failure when eggs vanished before hatching or nestlings disappeared prior to the estimated fledging date and there were signs of nest disturbance. Nests were considered successful when nestlings disappeared at the estimated time of fledging (± 1 d) and there were no signs of nest disturbance. Observations of feces near nests and the presence of fledglings in nearby vegetation usually provided confirmation that a nest was successful. Deserted nests were those where eggs remained in the nest for over 20 d without hatching.

To minimize disturbance, we collected habitat data at nest locations and on nonused sites after all nests became inactive. Because Blue-black Grassquit territories are small (13–100 m^2; Almeida and Macedo 2001, Carvalho et al. 2006), we collected habitat data in the four cardinal directions at different distances from the nest (1 m to the north, 3 m to the west, 6 m to the south, and 9 m to the east) and at the nest. We chose this range of distances because we did not delineate territories and, because nests could be centrally or peripherally located, we assume these points represented the surrounding habitat available for nesting and had a high probability of falling within a territory. At each point, including the nest, we collected data on 11 habitat variables within a 1-m^2 area, including number of plant species, ground vegetation height, number and height of shrubs, stem diameter of shrubs, number, height, and trunk diameter of trees, percentage of ground vegetation cover, distance to nearest trail or road, and distance to the nearest conspecific nest. For comparison of used and nonused sites, we used only one of the four points (3 m to the west of the nest). For analysis of availability versus use of different plant species as nest substrate, all nests and nonused sites were used. However, it was not possible to analyze nest substrate selection for shrubs because few nests were found in shrubs. Plant species were identified by personnel at the Herbário do Departamento de Botânica (University of Brasilia). For comparison of successful and unsuccessful nests, we also measured seven additional parameters, including nest height, height of nest substrate, diameter of shrub's main stem, depth of nest cup, and the width, length, and external height of the nest cup.

Data analysis. Of 188 nests found, we excluded from analysis nests ($N = 38$) that appeared to have been abandoned before being discovered. Another 68 nests were active (i.e., had adults visiting the nest) for a brief period after being found, but never contained eggs or chicks. These nests, when active for at least three visits, were also included in analyses of nest site placement. Eighty-one nests had eggs and chicks, and were used in all analyses.

We examined the selection of different species of grass as nest substrates using a chi-square goodness-of-fit test. Availability of plant species was calculated using the frequency of each species relative to all species identified in all sampled plots. Data collected at the nest site and at the other four nonused potential sites provided the basis for determining the proportion of the available species in each study area. To test for use and selection of each grass species, we used a statistical technique that calculates simultaneous 95% confidence intervals, based on a modification of the Bonferroni Z-statistic test, for analyzing utilization-availability data (Neu et al. 1974, Byers et al. 1984). If the expected proportion fell outside the confidence limits, the observed value of utilization was considered significantly different from the expected value.

To examine possible differences between nest sites and nonused sites, we used univariate comparisons (Mann-Whitney U-test) to determine important habitat variables for each site separately and for both sites combined. To test for interactions among variables, even those not significantly different in the univariate analyses, we also used nest-site selection models generated through logistic regression with presence (yes or no) of nest at the determined point as the response variable and the study area and habitat variables as predictor variables. Habitat variables included number of plant species, ground vegetation height, number of shrubs and trees, height of shrubs and trees, stem diameter of shrubs, tree diameter at breast height, percentage of ground cover, distance to nearest trail or road, and distance of the nearest neighboring nest. We excluded all variables associated with trees (number of trees, tree height, and tree diameter at breast height) from both univariate and multivariate analyses because few plots contained trees. We did not include year as a variable because study area already designates data sampled in the second study year. We used the Mayfield logistic regression described by Hazler (2004) to evaluate how specific nest and nest-substrate variables affected the probability of nest success with daily survival rate as the response variable. This analysis was preferred relative to the typical logistic regression because nests represent multiple binominal trials, where the event is success (0) or failure (1) and depends on the number of exposure days (i.e., 1 exposure day = 1 trial). For this analysis, we used the predictor habitat variables listed above, as well as those associated with the nest and its substrate. The Mayfield logistic regression assumes that the number of exposure days of nests is known exactly, an assumption that is usually violated. However, the effects of violation are negligible as long as intervals between nest checks are short (Hazler 2004). We conducted nest checks at short intervals of 2–3 d. Another assumption is that nest daily mortality rate is constant over time. In our study population, this assumption was violated because we know (Dias and Macedo, unpubl. data) that nests are more susceptible to predation during the nestling stage. We used the "Last Active-B" approach to determine exposure days because this method had the lowest bias index for nonconstant daily mortality rate when modeled by Manolis et al. (2000), and has been suggested as the most suitable for general use.

We used an information-theoretic approach (Burnham and Anderson 2002) to select the best models to evaluate the impact of different habitat variables on location of nest placement and nest success. Akaike information criterion corrected for small sample sizes (AIC_c), ΔAIC_c (the difference in AIC_c between each candidate model and the model with the lowest AIC_c

Table 1. Grass substrate selection for nest placement in Blue-black Grassquits in central Brazil from 2004 to 2005.

Grass	Total occurrence[a]	Proportion of total occurrence (P_{io})	Number of nests observed	Expected number of nests	Proportion observed in each species (P_i)	Confidence interval in proportion of occurrence
Melinis minutiflora	12	0.02	8	1	0.12	$0.02 \leq P_1 \leq 0.22$
Paspalum pectinatum	159	0.28	8	19	0.12	$0.02 \leq P_2 \leq 0.22$
Urochloa decumbens	200	0.35	25	23.5	0.37	$0.22 \leq P_3 \leq 0.52$
Panicum maximum	200	0.35	26	23.5	0.39	$0.24 \leq P_4 \leq 0.54$
Total	571		67	67		

Confidence intervals, calculated using the Bonferroni Z-statistic, show substrate selection more or less than expected in proportion to substrate availability.

[a] Number of plots where the grass species was present.

value) and Akaike weights (w_i) were used to rank models (Burnham and Anderson 2002). We started with a global model using all variables and selected those models with ΔAIC below 4.00. By comparing the support for each model, we excluded those with little support (ΔAIC> 4.00 and low weights). We used SPSS 13.0 (SPSS Inc. 2004) for all analyses, and report means ± 1 SE.

RESULTS

Of 81 active nests in both study areas, 71% ($N = 58$) were predated, 24% ($N = 19$) fledged at least one chick, and 5.0% ($N = 4$) were deserted or lost due to unidentified causes. Clutch size varied from one to three eggs ($\bar{x} = 2.2 \pm 0.8$, $N = 70$), and 86 young fledged during both seasons combined. Pooling data for both seasons, the Mayfield estimate (Mayfield 1975) of nest success was 0.14 at the University campus and 0.06 for FAL.

Nest substrate. For nests where the substrate was identified, 34% ($N = 35$) were in shrubs and 66% ($N = 66$) in grass. Only 18 of 75 species of shrubs (24%) in our study areas were used by nesting grassquits. Because of the small sample for shrubs, these data were not analyzed. However, nests in grasses were located in only four of 20 grass species in the area, and use of these species (*Paspalum pectinatum*, *Urochloa decumbens*, *Panicum maximum*, and *Melinis minutiflora*) differed from their proportion of occurrence in the area ($\chi^2_3 = 55.7$, $P < 0.001$). *Paspalum pectinatum* was used less than expected based on availability, *U. decumbens* and *P. maximum* were used according to availability, and *Melinis minutiflora*, a rare grass in the area, was used more than expected (Table 1).

Nest sites. Univariate analyses indicated that nest sites at the University Campus area and FAL had a greater diversity of plant species, taller nest substrates, a higher density of taller shrubs with thicker stems, and denser ground vegetation cover than nonused sites (Table 2). After pooling the data from both study sites, results were similar across all variables. For the remaining habitat parameters measured, no significant differences were found. Results from the model building procedures for both study areas indicate that the best model included shrub height and the interaction between ground vegetation height and percentage of cover, suggesting they were the most important predictors of nest-site selection for Blue-black Grassquits (Table 3). The top three models, all included ground vegetation cover, percentage cover of ground vegetation, and shrub height, confirming their importance. Species composition variables, number, and diameter of shrubs, and study area did not have high predictive value for nest-site selection.

Habitat of successful versus failed nests. Analyses using univariate tests show that the only habitat variable that differed between successful and unsuccessful nests in the University Campus area was distance to the nearest conspecific nest. Successful nests were about twice as far ($\bar{x} = 34.8 \pm 6.1$ m, $N = 11$) from neighboring nests as unsuccessful nests ($\bar{x} = 18.1 \pm 2.2$ m, $N = 45$; $U = 110.5$, $P < 0.001$). For the FAL area, we found no habitat differences between successful

Table 2. Comparison of habitat variables at nest sites of Blue-black Grassquits and nonused sites in central Brazil in 2004 and 2005[a].

Variable	University Campus				Fazenda Água Limpa			
	Nest site ($N = 56$)	Nonnest site ($N = 54$)	U[b]	P	Nest site ($N = 32$)	Nonnest site ($N = 32$)	U[b]	P
Number of plant species	3.6 ± 0.2	2.9 ± 0.1	901.0	<0.001	2.1 ± 0.2	1.4 ± 0.1	215.0	<0.001
Ground vegetation height (cm)	108.1 ± 4.6	87.8 ± 1.8	1008.0	<0.001	130.5 ± 5.8	98.5 ± 2.6	193.0	<0.001
Number of shrubs	1.8 ± 0.2	0.9 ± 0.1	885.5	<0.001	1.3 ± 0.2	0.4 ± 0.1	220.0	<0.001
Shrub height (cm)	65.4 ± 4.8	49.7 ± 2.3	359.5	<0.001	75.9 ± 9.1	54.5 ± 5.4	23.0	0.03
Shrub stem diameter (mm)	7.0 ± 0.7	5.6 ± 0.5	473.5	<0.001	7.4 ± 1.1	3.9 ± 0.5	14.0	<0.001
Percentage of cover ground vegetation	0.71 ± 0.03	0.60 ± 0.01	1063.0	<0.001	0.77 ± 0.03	0.63 ± 0.02	392.0	0.1
Distance to nearest trail or road (m)	67.7 ± 11.5	71.6 ± 5.9	1491.0	0.9	25.1 ± 3.9	26.7 ± 2.1	455.0	0.44
Distance neighboring nests (m)	22.3 ± 2.4	22.6 ± 1.2	1500.5	0.94	16.6 ± 1.7	17.0 ± 1.0	474.5	0.61

[a]Values given as means ± 1 SE.
[b]Mann-Whitney tests.

($N = 4$) and unsuccessful ($N = 28$) nests using univariate tests. In this area, we found fewer nests and predation rates were high so the absence of any differences may be due to low statistical power. For both study sites combined, distance to the nearest conspecific nest was greater ($U = 300.0$, $P < 0.001$) for successful ($\bar{x} = 32.5 \pm 5.9$ m, $N = 15$) than unsuccessful ($\bar{x} = 17.7 \pm 1.5$ m, $N = 73$) nests.

Of the numerous habitat candidate models based on the Mayfield logistic regression, we considered only those with the lowest AIC scores (Table 4). These models indicate that the daily survival probability of the Blue-black Grassquit nests varied chiefly as a function of the interaction between external height and inner depth of the nest. The best model is probably the first one because it uses the fewest parameters, and is thus most parsimonious. Daily survival increased with the reduction of the external height and enhancement of inner depth of the nest cup.

DISCUSSION

In our study, 71% of nests were predated, a rate of nest failure comparable to that reported for other Cerrado grassland birds, including 65% for Lesser Elaenias (*Elaenia chiriquensis*; Medeiros 2004), and 68% and 90% for Campo Suiriris (*Suiriri affinis*) and Chapada Flycatchers (*S. islerorum*), respectively (Lopes and Marini 2005). These predation rates are relatively high compared to rates reported for many North American shrubland/grassland birds (36–50%; Martin 1993) and Australian passerines (50–60%; Ford et al. 2001). However, conclusive patterns concerning nest predation rates for tropical birds remain elusive. Some studies suggest very high predation for tropical birds (Mason 1985, Kulesza 1990, Roper 1992), whereas others indicate rates comparable to those of northern temperate species (Marchant 1960, Oniki 1979).

Blue-black Grassquits appeared to favor nest placement on *Melinis minutiflora* (molasses grass). Although only eight nests (12% of nests in grasses) were found on *M. minutiflora*, the use of this species may be biologically relevant because it was used more than expected based on availability (found on only 2% of 571 sampled plots). This is an introduced, invasive species of grass in Brazil that has been highly successful

Table 3. Model selection results for predicting nest-site selection by Blue-black Grassquits in central Brazil in 2004 and 2005.

Model	$-2\log(l)$	K	ΔAIC_c[a]	w_i
Ground vegetation height ∗ percentage cover of ground vegetation + shrub height	163.94	3	0.00	0.68
Ground vegetation height + percentage cover of ground vegetation + shrub height	164.64	4	2.87	0.16
Shrub height + percentage cover of ground vegetation	169.34	3	5.40	0.04
Number of plant species + ground vegetation height + number of shrubs + shrub height + stem diameter of shrubs + percentage cover of ground vegetation	161.88	7	6.90	0.02
Number of plant species + ground vegetation height + number of shrubs + shrub height + stem diameter of shrubs + percentage cover of ground vegetation + study area	161.82	8	9.21	0.01

Models were ranked according to Akaike's information criteria adjusted for small sample size (AIC_c). The values for −2loglikelihood ($-2\log(l)$), number of parameters, including the intercept (K), ΔAIC_c and Akaike weights (w_i) are shown for the model. All models used $N = 174$ sampling points.

[a] The lowest AIC_c value for this analysis was 170.19.

in replacing native savanna grasses (Hoffmann et al. 2004). The four grass species used as nest substrates by grassquits may have structures that provide better nest support or shelter from the weather. In addition, *M. minutiflora* is believed to repel insects and snakes (Watt and Breyer-Brandwijk 1962), and has antitick properties (Thompson et al. 1978, Hernandez et al. 1990, Mwangi et al. 1995), factors that may have also played a role in its use as a nest substrate. Despite apparent preferences for certain plants, we found no evidence that nest substrate influenced nest success.

Our results suggest that greater structural complexity, with greater plant species diversity, taller substrates, more shrubs of greater height and diameter, and more vegetation cover, was an important factor in nest-site selection by Blue-black Grassquits. However, multivariate models indicated that, among these variables, shrub height and the interaction of ground vegetation cover and height were more important in nest-site selection by grassquits. Because nests are usually close to the ground, sites with more vegetation cover and taller shrubs may shield nests from visually oriented aerial predators. A common nest predator for Cerrado passerines is the Curl-crested Jay (*Cyanocorax cristatellus*; M. Marini, pers. comm.), a diurnal species that locates nests visually. Nocturnal terrestrial predators of Cerrado passerine nests include rodents and small marsupials (França 2005) that probably use olfaction to detect nests. Sites with more cover and taller shrubs may also better

Table 4. Model selection results for successful versus depredated nests ($N = 88$) of Blue-black Grassquits in central Brazil in 2004 and 2005.

Model	$-2\log(l)$	K	ΔAIC_c[a]	w_i
External height of nest cup ∗ inner depth of nest cup	104.65	2	0.00	0.29
External height of nest cup ∗ inner depth of nest cup + percentage cover of ground vegetation	102.70	3	0.18	0.26
External height of nest cup ∗ inner depth of nest cup + height of nest shrub	103.00	3	0.47	0.23
External height of nest cup ∗ inner depth of nest cup + ground vegetation height	103.15	3	0.62	0.21

Models were ranked according to Akaike's information criterion adjusted for small sample size (AIC_c). The values for −2loglikelihood ($-2\log(l)$), number of parameters, including the intercept (K), ΔAIC_c and Akaike weights (w_i) are shown for the model.

[a]The lowest AIC_c value for this analysis was 108.77.

protect nesting birds from inclement weather and provide shade.

We found that successful grassquit nests in the University Campus area were twice as far from neighboring nests as unsuccessful ones. For birds with larger territories than Blue-black Grassquits, distance between neighboring nests may not be an important variable. However, internest distance may be important for Blue-black Grassquits because of their small territories and the possible influence of conspecific behavior on the nest success of neighbors. For example, the conspicuous display of male Blue-black Grassquits may attract predators (R. Dias, pers. observ.) and, if so, proximity to other nests and displaying males could increase nest predation rates. Other investigators have also suggested that high nest densities and clumped distributions may increase predation risk for birds nesting in open areas (Krebs 1971, Page et al. 1983, Cresswell 1997).

The characteristics of a nest (Møller 1990) and its placement within a plant (Wilson and Cooper 1998) may be as, or more, important than habitat variables in determining nest success because these characteristics may influence nest concealment. In our study, the best model using microhabitat and nest variables indicated that nest cup architecture had a strong influence on nest success. Daily success rate increased as a function of externally more compact nests combined with deeper inner nest chambers, and a likely explanation for such results is that such nests are less easily detected by predators. More compact nests may be less visible to predators, and deeper nest cups may allow an incubating adult to remain more inconspicuous. Similarly, the probability of nest failure for European Blackbirds (*Turdus merula*) depended on the detectability of nests as well as nest height (Cresswell 1997). Another study, using artificial nests, showed that those with characteristics that may influence nest visibility (higher and with larger external diameter) suffered higher predation rates (Grégoire et al. 2003).

Our results indicate that Blue-black Grassquits choose specific microhabitats as nest sites and that the distance between nests may influence nesting success. Other investigators have also reported microhabitat preferences for nest sites in other species and that nests in preferred sites have a greater success than those at nonpreferred sites (Martin 1998). Our results concerning distances between nests also suggest possible contradictory selective pressures for Blue-black Grassquits. Clustered territories may provide advantages for these grassquits that counterbalance the increased nest predation that may result from such proximity. For example, some individuals may gain a fitness advantage from increased opportunities for extra-pair copulations that occur at high rates in this species (Carvalho et al. 2006). However, this hypothesis remains to be tested.

ACKNOWLEDGMENTS

We thank the staff and students of the Herbário do Departamento de Botânica of Universidade de Brasília for identification of plants. E. Santos, J. Carregaro, R. Maia, and T. Helena provided invaluable help in collecting field data. This study was funded by Fundação Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—CAPES, through a doctoral scholarship to T. Aguilar and by Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq through a fellowship to R. H. Macedo. Logistic and financial assistance were provided by the Fundação de Empreendimentos Científicos e Tecnológicos—FINATEC and Universidade de Brasília. This article was greatly improved by suggestions made by J. Liebezeit and three anonymous referees.

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