Reproduction of Blue-black Grassquits in central Brazil

Carvalho CBV.[a]***, *Macedo RHF.*[b] *and Graves, JA.*[c]

[a]Conselho Nacional de Desenvolvimento Científico e Tecnológico,
SEPN 509, Bloco A, Sala 304, Edifício Nazir I, CEP 70750-501, Brasilia, DF, Brazil

[b]Departamento de Zoologia, Universidade de Brasília – UnB, CEP 70910-900, Brasília, DF, Brazil

[c]School of Biology, University of St. Andrews, KY16 9TH, Scotland

*e-mail: carlosbenigno@ig.com.br

Received December 6, 2004 – Accepted November 30, 2005 – Distributed May 31, 2007

(With 2 figures)

Abstract

During the reproductive season Blue-black grassquit (*Volatinia jacarina*) males are found in clusters, wherein they exhibit a distinctive display that consists of repeated, vertical leaps while simultaneously producing a brief vocalization. The main objective of this study was to describe details of the species' reproductive behavior in a "Cerrado" area of central Brazil and compare these data with some studies carried out in other areas. The data obtained concerning different aspects of nesting, laying and hatching were generally similar to those obtained in previous studies in other areas. However, we found that the typical clutch size of two eggs per nest is lower, and egg and nestling mortality rates higher in our area than what has been reported elsewhere. Our results suggest that males differ in time expended with different activities according to their reproductive condition and also provide extensive parental care. We found that display execution rates peak in the early morning and in the late afternoon and are higher in the middle of the breeding season. We also found that there is an inverse relation between the height of the display leap and the height of the perch.

Keywords: Volatinia jacarina, display, Cerrado, mating system, nest, Blue-black Grassquit.

Reprodução do tiziu no Brasil central

Resumo

Durante a estação reprodutiva, machos de tiziu (*Volatinia jacarina*) são encontrados agregados e apresentam uma exibição bastante conspícua, que consiste de saltos verticais associados a uma curta vocalização. Através de observações realizadas em uma área de Cerrado na região do Brasil central, este trabalho teve como objetivos detalhar alguns aspectos da biologia reprodutiva de *V. jacarina* e comparar tais dados com os poucos trabalhos existentes sobre a espécie. Os dados obtidos neste estudo com relação aos diferentes aspectos da nidificação, postura e eclosão dos ovos se mostraram semelhantes, em geral, àqueles encontrados em estudos anteriores, diferindo apenas com relação ao número de ovos por ninho (a maioria dos ninhos com apenas dois ovos) e às taxas de predação, que se mostraram mais elevadas. Os dados mostram ainda que machos variam com relação ao gasto de tempo com diferentes atividades de acordo com a condição reprodutiva e que os mesmos investem parentalmente. Foram encontradas ainda, que as taxas de execução de exibição são mais elevadas no início da manhã e no final da tarde, assim como também tem um pico no meio da estação reprodutiva. Encontramos também uma relação inversa entre a altura do salto da exibição e a altura do poleiro.

Palavras-chave: Volatinia jacarina, côrte, Cerrado, sistema de acasalamento, ninho, tiziu.

1. Introduction

The Blue-black Grassquit (*Volatinia jacarina*) is a Neotropical species that ranges from southern Mexico to northern Argentina and Chile (Sick, 1997). A typically granivorous bird, it occurs in open savanna grasslands and more structurally complex areas that have suffered some degree of human disturbance (Antas and Cavalcanti, 1988; Tubelis and Cavalcanti, 2001). Males have a reproductive blue-black plumage with white underwings, while females and juveniles are brownish, with juveniles having some blue-black patches on the head and upperparts (Alderton, 1963; Sick, 1997; Doucet, 2002).

In central Brazil it is possible to find the Blue-black Grassquit most of the year, except from May to August, when individuals practically disappear. From August to October it is common to see individuals foraging in multi-species groups with *Sporophila* (Antas and Cavalcanti, 1988). During the breeding season, which lasts from November to April in central Brazil, males become solitary and defend small, clustered territories. They exhibit a distinctive display, which consists of repeated, short, vertical leaps executed from elevated perches while emitting a short buzzing vocalization and exposing the white parts under the wings. The display is executed in a repetitive sequence throughout the day (Sick, 1997). Such elaborate displays are considered to be a result of sexual selection, particularly in non-monogamous species, where males have the tendency to compete for females and there is a greater variance in individual reproductive success (Payne, 1979).

The reproductive behavior of the Blue-black Grassquit is very distinctive in some ways, resembling a lek mating system in many aspects as suggested by Murray (1982) and Webber (1985). In a lek mating system there is no monopoly of either females or resources and the males form aggregations to execute displays and attract females. After mating and copulation, females leave the lek area to incubate the eggs and rear the nestlings. Males do not offer any resources to females other than their gametes (Bradbury, 1981; Höglung and Alatalo, 1995). However, some previous studies concerning the behavior and biology of the Blue-black Grassquit suggest that males provide some degree of parental investment (Carvalho, 1957; Alderton, 1963; Almeida and Macedo, 2001) and, therefore, the exact nature of the species' mating system remains unclear.

In this study we add to the information that exists concerning the reproductive biology of the Blue-black Grassquit by detailing some aspects of reproduction associated with morphology, territoriality, behavior and nesting. These data provide the first opportunity for comparison of results with previous studies carried out in other areas.

2. Material and Methods

2.1. Study site

The field sites were located in Fazenda Água Limpa (15° 57' S and 47° 56' W), an experimental farm of the Universidade de Brasília located approximately 18 km from Brasília, Brazil. We collected data during two breeding seasons, from November to March 1999-2001. During the first breeding season the study was conducted in an old tomato/pumpkin field of approximately 3000 m^2 (about 100 m from the farm headquarters) surrounded by typical "Cerrado" vegetation (tropical savanna) and, during the second breeding season, the study site comprised an area (about 400 m from the first site) of about 4000 m^2 of low savannah vegetation partially invaded by non-native grassland. We collected data in two different areas due to the birds' preference to aggregate in specific places during breeding seasons of different years.

2.2. General methods

We caught grassquits with mist nets within the study sites from the beginning of December, when birds were already aggregated and displaying. We marked the birds with permanent metal bands (issued by the Brazilian bird banding institution, CEMAVE) and unique combinations of three colored plastic bands. We took several measurements, including weight, wing, tail, tarsus and bill length, depth and width.

We conducted behavioral observations from November to March at random times throughout the day in order to record the first and last occurrence of events related to reproduction. The time of the observations was adjusted after the end of DST in Brazil (February). The first observed display and the fate of the last nest found during each breeding season were considered the first and last reproductive event, respectively. We recorded the first female in a male's territory, first nest found, first egg laid and first hatching in both reproductive seasons. We also conducted behavioral observations with territorial males to assess the time expenditure with different activities and display characteristics. The activity was assessed by 30 minutes focal samples (every 15 days) with banded males, where each minute a behavioral category was chosen from the following: 1) absent from the territory; 2) on the ground out of sight (foraging most of the time); 3) displaying; 4) perched; 5) fighting or pursuing other males; and 6) parental investment (building the nest, feeding the nestlings, feeding the female and guarding the nest, considered when the bird was positioned not farther than 1 m from the nest). Number and identity of females in the territories were recorded during the observations. We assessed display characteristics by observing banded males during 5 minutes (every 15 days) continuously at different times of the day, where we counted: 1) the number of displays executed; 2) the height of the leaps; and 3) the height of the perches used to execute displays. Perches were measured with a tapeline and leaps were estimated with a translucent scale. With measurements (through the scale) of leap height and perch height from a given distance, and the real perch height (measured with the tapeline), it was possible to calculate the leap height.

Throughout the reproductive seasons, individual territories were marked with plastic tags along the borders, which were identified by the observation of agonistic interactions between males and perches used for the execution of displays (Parish and Coulson 1998). We demarcated the area defined by the outermost plastic tags with a wire and, by measuring the sides and angles of the resulting polygon, calculated the area of territories. In each territory we recorded the number and height of perches that potentially could be used by males to display and assessed the structural characteristics of the vegetation. These were assessed by extending two perpendicularly-placed tapelines across each territory, at their widest points and, along the tapelines, recording the percent cover of different types of substrates: 1) exposed soil; 2) herbaceous; 3) low grassland (<40 cm); 4) tall grassland (>40 cm); and 5) grassland sparsely covered with shrubs. The total percent was then extrapolated for each territory. Because territories marked during the first reproductive season were located in an agricultural area that was homogeneous, we only recorded the number of perches in each territory in that area.

During the study each territory was thoroughly searched for nests. For each nest found we measured: 1) distance from the ground to the top rim; 2) internal diameter; 3) external diameter; and 4) internal depth. We also took measurements of the eggs found in the nests, including length, width and weight. Nests containing eggs or nestlings were checked regularly in order to determine the length of incubation, time to fledging and predation rates (predation was considered the cause of any destroyed or missing egg). Incubation and time to fledging were calculated considering the time elapsed between laying of the last egg to hatching of the last young, as suggested by Nice (1954).

2.3. Statistical analyses

All statistical analyses were performed using SYSTAT 5.0 for Windows (Systat, Inc. Evanston). For data that had normal distribution we applied parametric statistics. Sexual dimorphism in morphological characters, difference in the number of perches and size of territories between males in two different areas of the study site were assessed with two-tailed Student *t*-tests. We conducted Mann-Whitney U tests to evaluate whether males with and without active nests in their territories varied in terms of time invested in different activities. To determine whether height of the display leap was associated with perch height, we used a Pearson correlation analysis. We asked whether display rate in the population varied throughout the day and throughout the breeding season; for this we conducted an ANOVA with ranked data, using display rates of 21 individuals observed during one entire breeding season. Data are presented as means ± SD.

3. Results

Biometry of 174 males and females showed that sexes have some dimorphic characteristics (Table 1). Males had larger wings (t_{144} = 7.5, p < 0.001) and tails (t_{143} = 3.1, p = 0.003) while females weighed more (t_{140} = –3.7, p < 0.001). There were no differences for other variables.

Table 1. Biometry of Blue-black Grassquits captured in Fazenda Água Limpa Experimental Farm, Brasília, Brazil.

Variable	Mean ± SD (n)	
	Males	Females
Right wing (mm)[a]	51.0 ± 1.8 (88)	48.9 ± 1.4 (58)
Tail (mm)[a]	42.0 ± 2.7 (87)	40.6 ± 2.4 (58)
Tarsus (mm)	12.7 ± 1.2 (88)	12.7 ± 1.3 (58)
Bill length (mm)	9.2 ± 0.5 (88)	9.1 ± 0.5 (58)
Bill width (mm)	5.5 ± 0.5 (88)	5.5 ± 0.4 (58)
Bill depth (mm)	5.8 ± 0.2 (88)	5.8 ± 0.2 (58)
Weight (g)[a]	10.7 ± 1.0 (84)	11.4 ± 1.1 (58)

[a] p < 0.05 (two-tailed Student´s *t* test).

The beginning of the breeding seasons, defined as when the first display was recorded, occurred at the end of November and the beginning of December of 1999/2000 and 2000/2001, respectively. During the 1999/2000 breeding season, the last nest found, containing one nestling, was predated and destroyed at the end of February. The two nestlings of the last nest found during the 2000/2001 breeding season were also predated at the end of February. Reproductive events are summarized in Table 2.

During the first reproductive season, when territories were located in an agricultural area, mean territory size was 47.39 ± 16.25 m^2 (n = 5), with a mean of 40.4 ± 18.9 (n = 5) potential perches. During the second breeding season, when territories were located in the savannah area, the mean size was 72.36 ± 25.46 m^2 (n = 15), with a mean of 13.6 ± 10.2 (n = 15) potential perches. The difference between territories in the number of perches from the two breeding seasons was significant (t_{18} = 4.1, p = 0.001). Territories were on average about 50% larger in the savannah area, approaching significance (t_{18} = –2.0, p = 0.06). This may be due to the small sample size of territories in the agricultural area. The territories marked during the second breeding season (n = 15) were composed of 56 ± 26% tall grassland, 21 ± 22% grassland with shrubs, 17 ± 21% exposed soil, 4 ± 6% low grassland, and 3 ± 6% herbaceous.

During the two breeding seasons we found a total of 34 nests (29 nests were or became active and five nests remained inactive). The nests were cup-shaped, with an average internal diameter of 5.6 ± 0.7 cm (n = 25), average external diameter of 6.9 ± 0.7 cm (n = 25) and average internal depth of 4.7 ± 0.9 cm (n = 24), and were composed of interlaced grassy branches and small roots. They were usually hidden in the middle of the savannah grass at a height of 41.8 ± 25.7 cm (n = 25) above the ground. On two occasions, when the nest was discovered during construction we observed that both sexes participated actively in the construction. It took pairs approximately five days to complete the nest.

The 45 eggs found during the study were whitish with small reddish spots. Their mean weight was 1.49 ± 0.06 g (n = 12), mean length was 16.71 ± 0.67 mm (n = 11) and mean diameter was 12.43 ± 0.20 mm (n = 11). In the nests where it was possible to determine with cer-

Table 2. Breeding phenology of Blue-black Grassquits during two breeding seasons at Fazenda Água Limpa Experimental Farm, Brasília, Brazil. Categories listed refer to the first record of the event.

Year	Display observed	Female in a territory	Nest found	Clutch initiation	Hatching
1999/2000	3 Dec 1999	12 Dec 1999	13 Jan 2000	26 Dec 1999[a]	6 Jan 2000[a]
2000/2001	23 Nov 2000	6 Dec 2000	17 Jan 2001	4 Jan 2001[a]	15 Jan 2001[a]

[a] Because the first nest found in each season already had nestlings, hatching date was estimated. Clutch initiation was estimated considering a period of 10 days for incubation to hatching.

tainty the end of laying and the beginning of incubation (n = 18), the typical clutch size was of two eggs per nest (n = 16). In only two cases we found three eggs in the same nest. The observation of nests discovered before laying (n = 6) showed that eggs were laid with 24 hours intervals and hatched after 10 (n = 5) or 11 (n = 1) days of incubation. In one case we observed that the female removed the eggshells from the nest soon after hatching. In the cases where it was possible to observe eggs from hatching until the independence of the nestlings (n = 2), we verified that nestlings fledged after 10 days. After leaving the nest, they were observed in the vicinity of the nest being fed by the parents for 4-5 days. During the two breeding seasons, mortality rates of eggs and nestlings were very high. According to Mayfield´s method (1961; 1975), the daily mortality rate (DMR) was 14.2% for eggs and 12.9% for nestlings. The estimated survival was 18.6% (considering an 11-day period) for eggs and 25.3% for nestlings (considering a 10-day period), and the final success was 4.7%.

Through 62 observation sessions (30 minutes each) with 15 territorial males, we assessed the percentage of time spent in different activities throughout the two breeding seasons. The analysis of the data clearly shows that males with nests in their territories dedicated part of their time to parental investment (Table 3). Behavioral comparisons between males who had nests in their territories with those that did not showed differences only in the percentage of time spent in the execution of displays (Mann-Whitney U = 404, n = 52 males with nests and 10 males without nests, p = 0.006). Males without nests in their territories were more active. Additional observations showed that, on average, females were present inside male territories 34 ± 30% of the time (n = 52). In every case where it was possible to identify females, they always were the mates of the territory owner.

For a sample of 559 display leaps executed by 24 different individuals during the two breeding seasons, the mean leap height was 32.3 ± 13.8 cm. The mean height of the perches used for execution of such leaps was 166.9 ± 88.8 cm. Leap and perch heights were inversely correlated (r = –0.33, n = 559, p < 0.001). To assess display execution rate, we obtained a sample of 66 independent observations (5 minutes each) of 21 different individuals (randomly observed throughout the day). The average display execution rate was 13.5 ± 3.5 displays per minute. For the second season, only, we analyzed and found significant differences among display rates throughout the day ($F_{12, 35} = 4.9$, $p < 0.001$) and also among the months throughout the breeding season ($F_{7, 40} = 8.0$, $p < 0.001$). There were two peaks of activity during the day, early in the morning and another late in the afternoon (Figure 1). Similarly, considering all the months of the breeding season, we observed a peak of display activity between January and February, approximately in the middle of the breeding season (Figure 2).

4. Discussion

The breeding period of the Blue-black Grassquit coincides with the rainy season in the central Cerrado

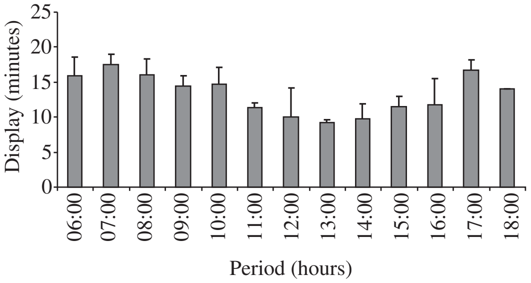

Figure 1. Average diurnal variation in male Blue-black Grassquit display rates (n = 48).

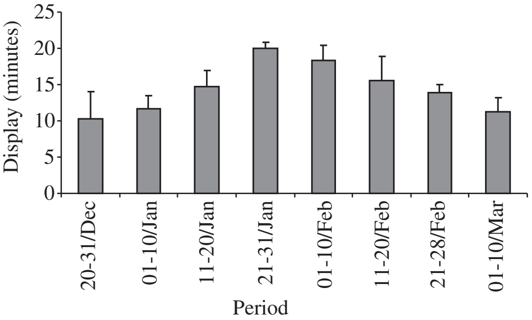

Figure 2. Average male Blue-black Grassquit display rates exhibited throughout the breeding season (8-12 day periods, n = 48).

Table 3. Comparative analysis of percentage of observations spent in different activities of Blue-black Grassquit males with and without nests in their territories, in Fazenda Água Limpa Experimental Farm, Brasília, Brazil.

Activity	Mean ± SD	
	Nesting males (n = 52)	Non-nesting males (n = 10)
Absent from territory	19.81 ± 19.42	17.67 ± 14.06
Ground (out of sight)	23.78 ± 18.04	18 ± 9.59
Displaying[a]	19.42 ± 10.54	31.33 ± 11.24
Perched	17.70 ± 10.61	23.33 ± 9.69
Fighting	8.72 ± 6.80	9.67 ± 7.28
Parental investment	10.58 ± 10.35	0

[a] $p < 0.05$ (Mann-Whitney U-test).

region of Brazil. It was notable that, although individuals of both sexes arrived in the area in November, mating and nesting was concentrated in the months of January and February. Probably, this delay is related to the process of obtaining territories and selecting mates. An additional factor is that the rains also produce a delayed peak of grassland seed maturation later in the season. There may also be an advantage to nesting later in the season due to the greater height of the grassland, which is an added protection factor for nests.

Males and females are dimorphic with regards not only to their plumage color, but also in some morphometric characteristics, in a pattern similar to that of most members of the Emberizinae (Sick, 1997). Sexual dimorphism is more conspicuous in polygynous species, although due to competition for reproductive partners and the possibility of extra-pair copulations, it can also be evident in species where monogamy is the predominant mating system (Andersson, 1994). The dimorphism found in certain size variables of the Blue-black Grassquit, with males having larger wings and a lighter body mass, may be related to their capacity to execute the display. Larger wings and low body weight may be associated with more vigorous displays and higher leaps. Another possibility is that females had higher body mass because during the reproductive season, measurements of females may reflect the mass of unlaid eggs.

Territorial analysis showed that, although territories are small, there is a great variation in size and vegetation structure among them. Studying this species in Costa Rica, Murray (1982) also found great variation in the size of territories and suggested that they are among the smallest of any Passeriformes. In our study, individuals were frequently spotted foraging outside their territories, suggesting that feeding activity is not restricted to the defended areas. Concerning the number of perches, a significant difference was found between territories in the two distinct areas within the study site, and also among territories within each area. Differences in habitat characteristics can result in competition between reproductive males for territories of better quality. Our results indicate that in the savannah area, territories were approximately 50% larger in size, but contained fewer perches than the much smaller territories in the agricultural area, which had a larger number of perches. Thus, the number of potential perches for display may be one important factor that influences the size of the territory. Larger territories or those with a greater number of perches can be more advantageous for many reasons, among them, a higher availability of nesting and foraging sites and, perhaps, the production of more conspicuous displays. Another aspect that must be considered is the height of the perches in the territories. The negative correlation between leap and perch heights strengthens the idea of competition for areas with specific characteristics. Through selecting higher perches, males could guarantee the conspicuousness of their signals while minimizing energetic expenditure, since the height of the leaps could be reduced.

The aspect and the location of the nests, usually built among grassy branches, are in accordance with previous studies (Carvalho, 1957; Alderton, 1963; Marcondes-Machado, 1988; Almeida and Macedo, 2001). The observation that both sexes participate actively in the construction of the nest confirms the male role in parental investment observed in previous studies (Carvalho, 1957; Alderton, 1963; Almeida and Macedo, 2001).

Although there are some differences concerning the color of the eggs, in general, the information relative to morphologic characteristics of eggs, laying interval, and length of incubation, was not distinct from previous studies (Carvalho, 1957; Alderton, 1963; Marcondes-Machado, 1988). The pattern of two eggs per nest differs from that described by Alderton, (1963) in Panama, where most of the nests contained three eggs. The number of eggs per nest presumably reflects parental capacity to invest in egg production and subsequent ability to provide parental care (Gill, 1995). This variation in the number of eggs per nest is probably related to characteristics of the habitats where the species has been studied. The average period of permanence of the nestling in the nest did not differ from previous studies (Carvalho, 1957; Alderton, 1963; Marcondes-Machado, 1988).

The mortality rates of eggs and nestlings found in this study were higher when compared to those found by Alderton (1963) in Panama, where mortality rates were about 26 and 23% for eggs and nestlings, respectively. In fact, a study with *Neothraupis fasciata* in the same area where the present study was conducted also found very high mortality rates, suggesting that predation is an important factor acting on different species in the study area (Alves and Cavalcanti, 1990). Risk of predation is considered one of the main causes promoting the formation of flocks, colonies and lek systems in some bird species (Page and Whitacre, 1975; Wittenberger, 1978; Beehler and Pruett-Jones, 1983; Robinson, 1985). Possibly, this is a factor that contributes to the grouping of Blue-black Grassquits, decreasing individual chances of predation and enhancing predator detection.

This study shows that males provide parental care, a pattern not compatible with the lek reproductive system mentioned as a possibility by Murray (1982) and Webber (1985). In fact, the studies of Alderton (1963), Carvalho (1957) and Almeida and Macedo (2001), confirm that males provide resources in the form of parental care and nesting sites, since nesting occurs within male territories. In this study, as well as in Almeida and Macedo (2001), only one female was habitually found per territory, suggesting social monogamy as the reproductive system of the species, but with some assimilated lek-like characteristics. The Blue-black Grassquit system greatly resembles the system recently described for the Least Flycatcher (*Empidonax minimus*), in that males are socially monogamous, form dense territorial clusters and exhibit paternal behavior (Tarof et al., 2005).

The role of the distinct parts of the reproductive display (vocalization, leap, white underwing patch flashing) exhibited by the Blue-black Grassquit are not yet known. However, the behavioral data in this and previous studies suggest that the display, in its totality, functions in the acquisition and maintenance of territories and, consequently, in attracting potential mates (Carvalho, 1957; Alderton, 1963; Murray, 1982; Webber, 1985; Almeida and Macedo, 2001).

Differentiated activity rates throughout the day are common in many bird species that adapt their behavior as a function of metabolic rates to regulate temperature and water consumption (Gill, 1995). Thus, the peaks of display execution found in this study are not surprising. Periods of higher activity early in the morning and late in the afternoon could prevent the excessive loss of liquids and salts that would occur during the hottest part of the day. Another possible explanation has been suggested by Møller (1991) for male Passeriformes, which usually have two periods of higher activity, one in the beginning of the morning and another one at the end of the afternoon. These activity peaks would be compatible with the periods of higher fertility of the female and would function in mate guarding, as well as in attracting other potential mates. Through this behavior, males could guarantee their paternity and increase reproductive success through extra-pair copulations.

Differentiated display execution rates throughout the breeding season appear to be circumstantial and associated with specific reproductive activities that change over the season. In the beginning of the breeding season, when males concentrate in the area and females are still scarce, competition for resources is probably still weak, and lower display execution rates are to be expected. Displays, in this period, can be directed only toward other males. During the breeding season, with increasing competition for reproductive territories and mates, an increase in the display rate is advantageous and likely. Therefore, in this period, displays could have the double function of territorial defense and the attraction of females. This would explain the peak of activity found during the end of January and beginning of February, when the breeding season reaches its peak. The subsequent reduction of display rates can be attributed to the fact that many individuals are nesting, resulting in a reduction of the time that can be dedicated to the execution of displays. However, even males with active nests in their territories continue executing displays, though at more reduced rates. There could also be a possible association between the fertile period of females with the peak of execution of displays in the middle of the breeding season (sensu Møller, 1991).

Although there are differences in the display execution rates between nesting and non-nesting individuals, the data showed that even nesting individuals dedicate a considerable part of their time to displaying. Since the energy cost for such activity is probably high, we presume that the continued execution of the display has an important role in the species' mating system. One explanation for the persistence of song throughout the breeding season by individuals that are nesting is related to the maintenance of the territory (Hanski and Laurila, 1993). Singing would function as a warning of territorial ownership directed to other males and, in the case of predation of eggs or nestlings, the couple could quickly start to build a new nest. The display could also be used by males to indicate status and genetic quality and, possibly, to obtain reproductive benefits by means of extra-pair copulations. In fact, the use of mixed reproductive strategies, where males and females of apparently monogamous species engage in extra-pair copulations, appears to be common in birds (Petter et al., 1990; Westneat et al., 1990; Kempenaers et al., 1992; Venier et al., 1993).

The results presented here indicate that the Blue-black Grassquit is a socially monogamous species, with males playing an important parental role. However, the displays exhibited by males persist both through the season and throughout nesting activities, suggesting a role in inter-sexual selection, in addition to territorial defense. Genetic analyses of kinship between nestlings and potential biological parents are essential to evaluate the occurrence of extra-pair copulations in the species and to attribute a social or genetic nature to the system. New studies considering territorial, morphological and behavioral differences among males, as well as the reproductive physiology of males and females, would be useful to clarify the factors that lead to the grouping and the execution of the display in this species.

Acknowledgments — We thank Verônica Borges, Laura Muniz, Fabio Costa and Valeria Saracura for their help in the field and Guarino Colli, Miguel Marini, Maria Alice Alves, Helena Morais, Mariana Cariello and an anonymous referee for reviewing the original manuscript. Research was funded by: the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES with a graduate scholarship to Carlos B. V. Carvalho, and the Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq with a fellowship for R. Macedo. We thank the Center for the Study of Tropical Birds (Clark Franzier Memorial Grant) for providing research funds, and the Universidade de Brasília for logistic support.

References

ALDERTON, CC., 1963. The breeding behavior of the Blue-black Grassquit. *Condor*, vol. 65, p. 154-162.

ALMEIDA, JB. and MACEDO, RHF., 2001, Lek-like mating system of the monogamous Blue-black Grassquit. *Auk*, vol. 118, p. 404-411.

ALVES, MAS. and CAVALCANTI, RB., 1990, Ninhos, ovos e crescimento de filhotes de *Neothraupis fasciata*. *Ararajuba*, vol. 1, p. 91-94.

ANDERSSON, M., 1994, *Sexual selection*. Princeton University Press, Princeton.

ANTAS, PTZ. and CAVALCANTI, RB., 1988. *Aves comuns do planalto central.* 1rst edn. Editora Universidade de Brasília, Brasília.

BEEHLER, B. and PRUETT-JONES, SG., 1983. Display dispersion and diet of birds of paradise: A comparison of nine species. *Behav. Ecol. and Sociobiol.*, vol. 13, p. 229-238.

BRADBURY, JW., 1981. *The evolution of leks*, p. 138-169. In ALEXANDER, RD. and TINKLE, DW. (eds.), Natural selection and social behaviour. Chiron Press, New York.

CARVALHO, CT., 1957. Notas ecológicas sobre *Volatinia jacarina* (Passeres, Fringilidae). *Bol. Mus. Para. Emílio Goeldi N. S.*, vol. 2, p. 1-10.

DOUCET, SM., 2002. Structural plumage coloration, male body size, and condition in the Blue-black Grassquit. *Condor*, vol. 104, p. 30-38.

GILL, FB., 1995. *Ornithology*. 2nd edn. FREEMAN, WH. and Company, New York.

HANSKI, IK. and LAURILA, A., 1993. Variation in song rate during the breeding cycle of the Chaffinch *Fringilla coelebs. Ethology*, vol. 93, p. 161-169.

HOGLUND, J. and ALATALO, RV., 1995, *Leks.* Princeton University Press, Princeton.

KEMPENAERS, B., VERHEYEN, GR., VAN DEN BROECK, M., BURKE, T., VAN BROECKHOVEN, C. and DHONDT, AA., 1992. Extra-pair paternity results from female preference for high-quality males in the Blue Tit. *Nature*, vol. 357, p. 494-496.

MARCONDES-MACHADO, LO., 1988. Comportamento reprodutivo de *Volatinia jacarina jacarina* (Linnaeus, 1766) em cativeiro (Passeres, Emberizidae). *Rev. Bras. Zoo.*, vol. 4, p. 319-330.

MAYFIELD, H., 1961. Nesting success calculated from exposure. *Wilson Bull.*, vol. 73, p. 255-261.

-, 1975. Suggestion for calculating nest success. *Wilson Bull.*, vol. 87, p. 456-466.

MØLLER, AP., 1991. Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. *Amer. Nat.*, vol. 138, p. 994-1014.

MURRAY JR., BG., 1982. Territorial behavior of the Blue-black Grassquit. *Condor*, vol. 84, p. 119.

NICE, MM., 1954. Problems of incubation periods in North American birds. *Condor*, vol. 56, p. 173-197.

PAGE, G. and WHITACRE, DF., 1975. Raptor predation on wintering shorebirds. *Condor*, vol. 77, p. 73-83.

PARISH, DM. and COULSON, JC., 1998. Parental investment, reproductive success and polygyny in the lapwing, *Vanellus vanellus. Anim. Behav.*, vol. 56, p. 1161-1167.

PAYNE, RB., 1979. Sexual selection and intersexual differences in variance of breeding success. *Amer. Nat.*, vol. 114, p. 447-452.

PETTER, SC., MILES, DB. and WHITE, MM., 1990. Genetic evidence of mixed reproductive strategy in a monogamous bird. *Condor*, vol. 92, p. 702-708.

ROBINSON, SK., 1985. Coloniality in the Yellow-rumped Cacique as a defense against nest predators. *Auk*, vol. 102, p. 506-519.

SICK, H., 1997. *Ornitologia Brasileira*. Editora Nova Fronteira, Rio de Janeiro.

TAROF, SA, RATCLIFFE, LM., KASUMOVIC, MM., and BOAG, PT., 2005. Are least flycatcher (*Empidonax minimus*) clusters hidden leks? *Behav. Ecol.*, vol. 16, p. 207-217.

TUBELIS, DP. and CAVALCANTI, RB., 2001, Community similarity and abundance of bird species in open habitats of a central Brazilian cerrado. *Ornit. Neotrop.*, vol. 12, p. 57-73.

VENIER, LA., DUNN, PO., LIFJELD, JT. and ROBERTSON, RJ., 1993. Behavioural patterns of extra-pair copulations in Tree Swallows. *Anim. Behav.*, vol. 45, p. 412-415.

WEBBER, T., 1985. Songs, displays, and other behavior at a courtship gathering of Blue-black Grassquits. *Condor*, vol. 87, p. 543-546.

WESTNEAT, DF., SHERMAN, PW. and MORTON, ML., 1990. The ecology and evolution of extra-pair copulations in birds. In POWER M. (ed), *Current ornithology.* Plenum Press, New York, vol. 7, p. 331-369.

WITTENBERGER, JF., 1978. The evolution of mating systems in grouse. *Condor*, vol. 80, p. 126-137.