TERRITORIAL CLUSTERING IN THE BLUE-BLACK GRASSQUIT: REPRODUCTIVE STRATEGY IN RESPONSE TO HABITAT AND FOOD REQUIREMENTS?

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Abstract. A phenomenon currently not well understood is the reproduction of some species in clustered territories. We evaluated two ecological hypotheses (material-resources and predation hypotheses) that could explain cluster formation during reproduction of the Blue-black Grassquit (*Volatinia jacarina*), a socially monogamous bird with a high rate of extra-pair fertilization. Additionally, we considered the breeding synchrony of females, since synchronization may serve as a means of diluting predation. To this end, we compared the breeding synchrony of females in clusters to that of those in solitary territories. We found support for the material-resources hypothesis in terms of vegetation structure and food availability: territories were clustered in habitat with more food and a more complex vegetation structure. Breeding synchrony of females in clusters was higher than that of females in solitary territories, but probably not as a mechanism to dilute predation: pairs within clusters suffered lower reproductive success because of elevated predation. The advantages gained by reproducing in clusters in areas of more complex vegetation structure and more food may offset the disadvantages due to predation, especially over a longer temporal scale. Our results suggest that the aggregation of Blue-black Grassquit territories could be explained by habitat heterogeneity in terms of vegetation and food, but these results do not exclude other hypotheses related to sexual selection and/or competition leading to aggregation.

Key words: aggregation, *Blue-black Grassquit*, *breeding success*, *extra-pair copulation*, *predation*, Volatinia jacarina.

Agrupación de Territorios en *Volatinia jacarina*: ¿Estrategia Reproductiva como Respuesta a los Requerimientos de Hábitat y Alimento?

Resumen. Un fenómeno poco entendido hasta ahora es la reproducción con territorios agrupados en algunas especies. Evaluamos dos hipótesis ecológicas (la de material-recurso y la de depredación) que podrían explicar la formación de agrupaciones durante la reproducción de *Volatinia jacarina*, una especie socialmente monógama con una alta tasa de cópulas extra-pareja. También consideramos la sincronía reproductiva de las hembras, ya que la sincronización podría servir para diluir el riesgo de depredación. Para esto, comparamos la sincronía entre hembras en grupos con la sincronía entre hembras en territorios solitarios. Encontramos evidencias que corroboraron la hipótesis de material-recursos en términos de estructura de la vegetación y disponibilidad de alimento: los territorios se encontraban agrupados en hábitats con más alimento y con una estructura de la vegetación más compleja. La sincronía reproductiva fue mayor entre hembras de territorios agrupados que entre las de territorios solitarios, pero probablemente no por un mecanismo para diluir el riesgo de depredación: las parejas en territorios agrupados tuvieron un menor éxito reproductivo debido a una depredación más elevada. Las ventajas de reproducirse en territorios agrupados en áreas de vegetación con estructura más compleja y con más alimento pueden contrarrestar las desventajas por depredación, especialmente a lo largo de escalas temporales mayores. Nuestros resultados sugieren que la agrupación de territorios de *V. jacarina* podría ser explicada por la heterogeneidad del hábitat en términos de la vegetación y alimento, pero estos resultados no excluyen otras hipótesis relacionadas a selección sexual y/o a competencia que puede llevar a la agrupación.

INTRODUCTION

Territoriality and its effects on populational variables such as density and spatial distribution have always attracted the attention of researchers (Adams 2001). An interesting pattern of territorial distribution observed in some species is the clustering of territories, where animals confine all their reproductive activities within territories adjacent to other breeding territories within a homogeneous habitat while leaving apparently suitable habitats unoccupied (Stamps 1988, Brown et al. 1992, Tarof and Ratcliffe 2004). This pattern has been reported for several birds including the European Robin (*Erithacus rubecula*; Lack 1968), Pied Flycatcher (*Ficedula hypoleuca*; Alatalo et al. 1982), *Phylloscopus* warblers and Goldcrest (*Regulus*

regulus; Tiainen et al. 1983), and Least Flycatcher (*Empidonax minimus*; Sherry and Holmes 1985).

Studies of avian clustered territoriality usually assume that birds are responding to some variation in habitat quality, aggregating in areas where the combination of habitat variables is particularly favorable (Haila et al. 1993, Brown et al. 1995). However, males may be attracted not only by habitat characteristics but also by conspecifics because of females' being likely to settle in places with higher densities of territorial males (Collias and Collias 1969, Wagner 1993, Stamps 1994). Male Wood Warblers (*Phylloscopus sibilatrix*), for instance, maximize their chances of breeding success by settling near neighbors (Herremans 1993).

As many as eight hypotheses have been proposed for clustering in birds and other animals (see Tarof and Ratcliffe 2004). Among the traditional explanations for clustered territories ecological factors prevail, particularly those related to the distribution of material resources (Kiester and Slatkin 1974, Wittenberger and Hunt 1985). The two most common hypotheses invoked to explain clustering are the material-resource hypothesis and the predation hypothesis. The former proposes that animals cluster in response to the patchy distribution of resources in the habitat, which may include aspects of vegetation, food, or nesting sites, among others (Kiester and Slatkin 1974). In this context, some studies suggest that animals settle near conspecifics because their presence may indicate the availability of resources and an adequate habitat (Stamps 1987, 1988, Danchin and Wagner 1997). For example, Black-capped Vireos (*Vireo atricapilla*) use the presence of other individuals as a way to locate suitable nesting sites (Ward and Schlossberg 2003).

The predation hypothesis suggests that clustering of territories reduces predation through the dilution effect or other antipredation strategies (Hamilton 1971). In the latter category are tactics such as communal defense against predators (Pulliam 1973, Wittenberger and Hunt 1985, Wicklund and Anderson 1994) or behaviors such as territory owners alerting close neighbors to predators nearby (Stamps 1994). A study of the Least Flycatcher found a higher response to predators inside clusters, showing that in clusters individuals may take advantage of collective vigilance, spending less time watching for predators and devoting more time to foraging or pursuing extra-pair partners (Perry and Andersen 2003). Breeding synchrony (i.e., the clustering of reproductive activities in time; Gochfeld 1980) may also be associated with the dilution of predation risk by swamping predators with an overabundance of prey within a brief interval (Findlay and Cooke 1982).

Other explanations for clustered breeding territories are based on sexual selection. The hidden-lek hypothesis suggests that the clustering of territories results from female pursuit of extra-pair copulations from high quality males that are already socially paired (Wagner 1997). Some studies show that in extra-pair copulations females mate with neighboring males (Westneat 1993, Stutchbury et al. 1994), emphasizing

the importance of understanding the spatial dynamics of territoriality for species that breed in clusters. Additionally, many authors have suggested that high breeding densities should promote extra-pair copulation (Morton et al. 1990, Birkhead and Møller 1992).

We studied a socially monogamous passerine, the Blue-black Grassquit (*Volatinia jacarina*), to evaluate the social dynamics of clustered and isolated nesting. The Blue-black Grassquit is a small (~10 g), granivorous passerine that migrates seasonally within the neotropics (Sick 1997). The males demarcate exceptionally diminutive (13.0 to 72.5 m^2) territories through vigorous and persistent displays. These multimodal displays encompass a visual component, in the form of vertical leaps, and an acoustic element, a short, whistle-like vocalization (Weathers 1986, Sick 1997). The displays are executed from perches, usually shrubs or small trees, which enhance the male's prominence above the surrounding savanna grasses. The territories are frequently arranged in discrete clusters (Almeida and Macedo 2001). In contrast to other species whose territories are clustered, the Blue-black Grassquit defends an "almost all-purpose territory," in which all breeding activity and part of the food supply are found within the territory, but individuals also stray outside the territory to forage. The species' complex breeding system has some characteristics of a lek (Murray 1982, Webber 1985), but the Blue-black Grassquit is socially monogamous (Almeida and Macedo 2001), though its high rate of extra-pair fertilizations is high (63% of clutches and 50% of chicks; Carvalho et al. 2006).

We tested some of the predictions of the material-resources and predation hypotheses (see Tarof and Ratcliffe 2004), including (1) the vegetation in areas of clustered territories should be more complex structurally than where solitary individuals defend territories. This prediction is based on a study showing that Blue-black Grassquits tend to select areas with complex vegetation structure (Aguilar et al. 2008). Therefore, males should prefer such areas, leading to territorial aggregation. If the availability of food influences settlement patterns, we expected that (2) the availability of seeds should be higher within clusters than in territories of solitary males. If clustering reduces nest predation, we predicted that (3) predation rates should be higher for solitary males than for those in clusters. Finally, if breeding synchrony is a mechanism to dilute predation in clusters, then (4) females within clusters should be highly synchronized but isolated females should not be synchronized.

Our study also allowed us to describe general characteristics of Blue-black Grassquit territories in clusters and in isolation. In addition to the ecological hypotheses that attempt to explain territorial aggregation, there are individual behavioral and physiological costs and benefits associated with these hypotheses that should be considered. Therefore, we evaluated differences among males in their morphology, territory sizes, and rates of visitation by females. We might expect that males

in clusters are of higher quality, are visited more frequently by females, and have better overall chances of mating than do isolated males. Considering the costs in defending territories that have close neighbors versus those in isolation, we believed that it was critical to assess how often males were involved in agonistic interactions as well as whether their display rates differed, since displays may have an important intrasexual component in signaling territorial exclusivity.

METHODS

FIELD METHODS

We conducted this study on the campus of the University of Brasília (15° 46′ S, 47° 52′ W) in central Brazil from December 2005 to March 2006. The study site is characterized by altered tropical savanna (cerrado) mixed with exotic grasses. Using mist nets, we captured 226 individuals, of which 128 were males and 98 were females. The birds were marked with unique combinations of color bands, and we measured body mass (to the nearest 0.5 g) and length of beak, tail, right wing, and tarsus (to nearest 0.02 mm). For males we visually estimated the percentage of nuptial black plumage over the whole body (0 to 100%). Of captured males, 40 remained and nested at the study site.

We monitored 41 territories, of which 36 were distributed in three clusters (9, 13 and 14 territories) and five were of solitary males. Isolated territories are uncommon, precluding larger sample sizes. We defined clusters as aggregations of more than three territorial males whose territories were contiguous but separated from other territories or similar clusters by sufficient unoccupied habitat that prevented visibility or direct acoustic exchange by the birds (at least 40 m). Although male grassquits usually display from the tops of shrubs and small trees, these are always located within the male's small territory. And although the grassland component of the savanna vegetation attains a height of only about 1 m, the high density of shrubs and small trees constitutes an effective visual barrier for individuals even at short distances. We defined solitary males as those with territories at least 100 m from other conspecifics. Thirteen (36%) of 36 paired males in clusters and four (80%) of the five solitary males were marked. Because territory boundaries (see below for method) remained stable throughout the study, we had high confidence in the continuity of the same individuals within each territory. For example, all 13 marked males in clusters as well as the four isolated territorial males remained in their territories throughout the entire study.

To evaluate the area of clusters, we observed each of the peripheral territories for intervals of 3 min (four to six intervals per territory; average 5.27 ± 0.12 min) to determine the perches used by territorial males for their displays in addition to points of agonistic encounters. We used the Global Positioning System (GPS) to locate the points outlining the territories with Universal Transverse Mercator coordinates. This method works well for the Blue-black Grassquit because males are easily seen in the habitat, have small territories, conspicuous displays and songs, and frequent agonistic interactions. To determine the sizes of individuals' territories, within clusters or isolated, we observed the males for three 20-min intervals to locate the positions where they displayed and engaged in agonistic interactions. In this case, however, the GPS was not used because the territories are so small, making estimates imprecise. Territory size was calculated geometrically by the method of the minimum polygon convex, which consists of joining the outermost points of the territory to form a polygon, from which the area is calculated.

To compare the vegetation structure and food availability in clusters to those in isolated territories we demarcated grids (quadrats 50 × 50 m), the midpoints of which we placed in the estimated center of the areas. For sampling, within each grid we used 25 1-m^2 plots separated by 10 m, totaling 75 plots for clusters and 75 for isolated territories.

We examined the vegetation's structural complexity by comparing plots within clusters with plots in areas of solitary territories. For this we used five characteristics: (1) the percentage of grass coverage within each 1-m^2 plot, estimated visually, (2) the average height of grasses, determined by measuring the shortest and tallest grass stalks and averaging these for each plot, (3) a count of all shrubs rooted within each plot, (4) the heights of the shrubs within each plot, and (5) the amount of available food, estimated by the proportion of grasses within each plot that was either producing seeds or gave evidence of recent seed production (empty dry caroypses).

In addition to evaluating vegetation structure and food within the plots we also used the quadrats for 10-min observations to assess the number of agonistic interactions among males and number of intruding females. We determined the display rate (number of leaps per 20 min) of territorial males by averaging the number of displays during the three 20-min focal observations made during territorial demarcation. All observations took place between 0600 and 0800 am, and the order of observations was defined randomly within each day's observation period.

To evaluate if clustering provides better protection against predators, we modeled the daily survival of Blue-black Grassquit nests to investigate the effect of territorial distribution on nest success. We found the nests by actively searching within the vegetation and displacing the parents from the nest, after which we monitored them every 2 or 3 days. We found 36 nests, of which five were subsequently deserted or damaged by inclement weather. The remaining 31 nests were monitored and used in analyses, and these included 26 nests in clustered territories and five in isolated territories. We considered nests successful when at least one chick fledged and depredated if the nest failed completely, with eggs or nestlings disappearing in addition to some evidence of predation (nest destroyed or disappeared). We also recorded the position of the nest within the cluster (center or edge).

We used a breeding-synchrony index (Kempenaers 1993) to calculate and subsequently compare the breeding synchrony

of females in clusters and in solitary territories. The index expresses the average percentage of females that are fertile per day during the breeding season. We defined a female's fertile period as extending from 5 days before the beginning of laying until the day of laying of the penultimate egg (Stutchbury and Morton 1995). We pooled results from females in the three clusters to calculate an average "cluster" breeding-synchrony index and compared this to the average breeding-synchrony index for the pooled females from isolated territories.

STATISTICAL ANALYSES

For all parametric tests we checked the data for normality and homoscedasticity. Data were transformed when needed; however, when assumptions were not met, nonparametric tests were applied. For vegetation characteristics we used principal-component analysis (PCA) to reduce the number of variables in the analysis. Subsequently, we used a nested ANOVA to evaluate differences in vegetation and food availability in relation to territory type (clustered or solitary). We used a multivariate analysis of variance (MANOVA) to evaluate differences in territorial males' morphometry relative to territory type. For this analysis the percentage of nuptial black plumage was arcsine-transformed. We used Student's t-tests to compare the territory size, display rate, and number of intruding females of clustered and solitary territorial males. Territory size was log-transformed prior to the analysis. We used the Mann–Whitney U-test to compare the breeding synchrony of females in clustered versus solitary territories. All tests were two-tailed and the means are expressed $\pm$ SE. These data were analyzed with the statistical software R 2.8.1 (R Development Core Team 2008).

We used the nest-survival approach in MARK (White and Burnham 1999, Rotella et al. 2004) to compare nest-survival models and to obtain estimates of daily nest survival as a function of continuous, categorical, and time-varying factors (Dinsmore et al. 2002) on the basis of a priori hypotheses. We used a hierarchical modeling approach to model daily nest survival (Dismore and Disnmore 2007). We first identified the most appropriate time-varying factor by fitting models with constant, linear, and quadratic time trends and then included nest age to evaluate if daily nest survival varies within nesting stages (Cooch and White 2007). Finally, we added the covariate for territory type only to the best models, since this variable should have the same general effect on any particular model when temporal variation and nest age are controlled for (Dinsmore et al. 2002). In a second stage, to assess the effect of position (center vs. edge of cluster) on nest fate, we evaluated nest survival of nests within clusters only. We repeated the steps described above for the time-varying factors and nest age and included the covariate nest position within the cluster in the best models (which are the only ones presented). For those nests within clusters we carried out a preliminary analysis in which we included the identity of the cluster as a factor, since cluster identity could possibly have a differential effect on nest survival. However, since the model with cluster identification performed poorly in relation to the null model, we did not to include it in further analyses. Following Dinsmore et al. (2002) we did not standardize individual covariates. Models were assessed by Akaike's information criterion for small sample sizes (AIC_c) and sorted by ΔAIC_c, the difference between the AIC_c value for a given model and the top model (Burnham and Anderson 2002). Estimates were obtained by model averaging when the best model carried <90% of the AIC_c weight.

RESULTS

CLUSTERS AND SOLITARY TERRITORIES

The three clusters (36 territories) were separated from each other by 56.0 ± 16.0 m, had an average size of 3582.4 ± 302.9 m^2 and contained 12.0 ± 1.5 territories. During the study each cluster yielded 11.0 ± 1.1 nests. There were no significant phenotypic differences between males within clusters and solitary males (MANOVA, Wilks' $\lambda = 0.85$, $P = 0.93$), and, despite clustered males' territories being twice the size those of the solitary males (approximately 87 m^2 vs. 40m^2), the two groups did not differ significantly in this parameter either (Student's t-test, $t_{15} = 1.62$; $P = 0.13$). All males, whether clustered or in solitary territories, obtained mates.

Obviously, the number of female intrusions inside the 50×50-m quadrats within clusters was significantly higher (3.12 ± 0.26 females per 10 min) than that for quadrats within solitary territories (0.87 ± 0.17; $t_6 = 7.53$; $P < 0.001$), but this difference was not significant when we applied a correction for the male:female ratio in the two areas (Student's t-test, $t_6 = 1.45$; $P = 0.20$). Solitary males displayed at twice the rate (75.50 ± 24.40 per 20 min) of clustered males (35.65 ± 7.86), a large though not quite significant difference ($t_{13} = 2.08$; $P = 0.06$). In addition, we observed more agonistic interactions between males in clusters than between solitary male (males in clusters = 2.59 ± 0.31 vs. isolated males = 0.45 ± 0.09; $t_6 = 8.29$; $P < 0.001$).

PREDICTIONS OF MATERIAL-RESOURCES AND PREDATION HYPOTHESES

The PCA combined five vegetation-structure variables into three components that together explained 80% of the total variance in the original variables. The first principal component explained 38% of the total variance and was loaded with the percentage of grasses and ground coverage. The second component explained 22% of the total variance and was loaded strongly with an inverse relation between the height of grasses and the height of shrubs. The third component explained 19% of the total variance and was loaded strongly with number of shrubs. Thus the three components corresponded to (1) percentage of grasses and ground vegetation coverage, (2) height of grasses and shrubs, and (3) number of shrubs. Areas within clusters and areas of solitary territories did not differ in the first principal component's scores (nested ANOVA, $F_{1,4} = 4.09$; $P = 0.11$). However, clusters had taller
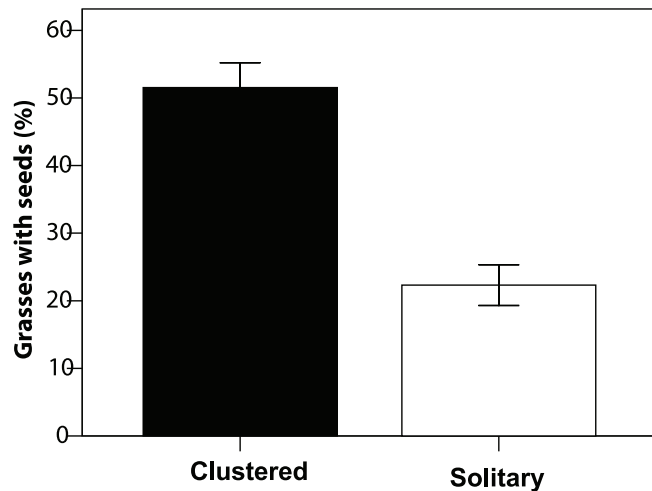
FIGURE 1.   Percentage of grasses bearing seeds in areas with clustered versus with solitary territories.
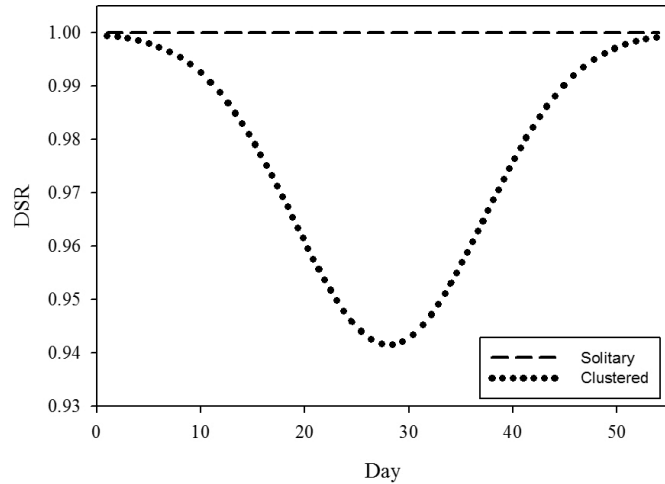

FIGURE 2.   Effects of territorial distribution on the daily survival rates (DSR) of Blue-black Grassquit nests as a function of season. Day 1 corresponds to 16 January, day 55 to 11 March.

grasses and smaller shrubs than did solitary territories (nested ANOVA, $F_{1,4} = 10.99$; $P = 0.03$). Moreover, areas within clusters also had more shrubs (nested ANOVA, $F_{1,4} = 7.49$; $P = 0.05$). In agreement with the prediction of food availability, areas within clusters had a higher percentage of grasses with seeds and dry caryopses than did areas within solitary territories (nested ANOVA, $F_{1,4} = 7.71$; $P = 0.05$, Fig. 1). This result is probably related to the fact that the areas within clusters contained taller grasses, in a more advanced stage of seasonal growth, and therefore had borne more and earlier seeds.

Model-selection results indicated that daily survival of Blue-black Grassquit nests was a function of seasonal effect and territory-distribution type, and models with quadratic trends for nest survival during the breeding season received strong support (Table 1, Fig. 2). Because all solitary nests

survived, that is, they had a daily survival rate of 100% (Fig. 2), the daily survival rates of solitary nests were higher than those of clustered nests. The evidence ratio indicates that the first model is 1.93 times more likely to be the best model than the model with the inclusion of nest age. When we evaluated only nests within clusters we observed the same seasonal effect, and in addition we found that nests at the edge of clusters suffered more predation than central nests (Table 2). The evidence ratio suggests that the model including the quadratic trend and position within cluster is 2.24 times more likely than the model with nest age included. Because the multiple models had a high degree of uncertainty due to similar model weights, we estimated the parameter β through model averaging. For the models considering both clustered and solitary individuals we observed a significant negative effect of distribution type on nest survival (Table 3). However, the same was not true for the effect of nest placement within the cluster after model averaging (β = –1.172, 95% CI = –2.654 to 0.308). In terms of breeding synchrony, females in clusters were significantly more synchronous (27.55 ± 3.91%)

TABLE 1.   Summary of model-selection results for daily survival rates of Blue-black Grassquit nests for both clustered and solitary pairs.

Model[a]	K[b]	ΔAIC_c[c]	w_i
$S_{(TT + distribution)}$	4	0.00	0.293
$S_{(TT + distribution + nest age)}$	5	1.31	0.152
$S_{(TT)}$	3	1.32	0.151
$S_{(distribution)}$	2	1.95	0.110
$S_{(TT + nest age)}$	4	2.14	0.100
$S_{(.)}$	1	2.57	0.081
$S_{(nest age)}$	2	2.62	0.079
$S_{(T)}$	2	4.38	0.033

[a] Model factors included linear seasonal trend (T), quadratic seasonal trend (TT), nest age, territory distribution (clustered or solitary), and a model with constant daily nest survival (.).
[b] Number of parameters.
[c] The lowest $AIC_c = 65.58$.

TABLE 2.   Summary of model-selection results for daily survival rates for Blue-black Grassquit nests within clusters.

Model[a]	K	ΔAIC_c[b]	w_i
$S_{(TT + position)}$	4	0.00	0.414
$S_{(TT + position + nest age)}$	5	1.60	0.185
$S_{(TT)}$	3	1.87	0.162
$S_{(position)}$	2	1.98	0.153
$S_{(TT + nest age)}$	4	3.18	0.084

[a] Model factors included quadratic seasonal trend (TT), nest age, and nest position (on the edge or in the center of the cluster).
[b] The lowest $AIC_c = 61.67$.

TABLE 3.   Model-averaged estimates of the parameter β and 95% confidence intervals (CI) for models of daily nest-survival rate of the Blue-black Grassquit for both clustered and solitary pairs.

| Parameter | β | 95% CI | |
		Lower	Upper
Intercept	15.019	−2.193	32.232
Distribution	−8.964	−16.770	−1.158
Quadratic time	0.004	−0.079	0.087
Linear time	−0.237	−0.881	0.406
Nest age	0.023	−0.149	0.196

than females mated with solitary males (5.80 ± 3.37%) ($U = 2.00$; $n_1 = 13$; $n_2 = 4$; $P < 0.01$).

DISCUSSION

A major result of this study is that we found support for the two predictions of the material-resource hypothesis. First, we found that there are differences in vegetation structure between areas occupied by clusters and those occupied by isolated territories. Clusters had more shrubs and taller grasses, pointing toward a more complex vegetation structure. This result reinforces previous studies of this species, which found that areas uninhabited by grassquits differed in type of vegetation from occupied areas (Almeida and Macedo 2001), that nest were built in structurally more complex vegetation, and that nests were built in only 20% of the grass species available in the area (Aguilar et al. 2008). It thus appears that males in clusters are occupying areas that may have favorable vegetation characteristics (e.g., for nest placement or protective cover, among other possibilities), and isolated males occupy less structurally complex habitat. Although males in clusters did not differ phenotypically from those in isolation, all males cannot occupy the most favorable areas. Exclusion from such areas may not depend upon a male's quality but could result from timing of arrival in the area, since these birds migrate within the neotropics. Our results differ from a few studies that have found little support for the material-resource hypothesis in terms of vegetation characteristics (Sherry and Holmes 1985, Perry and Andersen 2003, Tarof and Ratcliffe 2004). In the case of the Least Flycatcher, although Perry and Andersen (2003) found that the vegetation of clusters and scattered territories differed, they did not consider the differences to influence clustering patterns.

We also found support for the material-resource hypothesis in terms of food availability. Areas with clusters had a percentage of grasses with seeds greater than in areas with solitary territories, suggesting that one reason leading to dense aggregations of Blue-black Grassquits may be patchy food availability. Few studies have evaluated food availability as a reason for clustering, and those that have done so

evaluated arthropod abundance, arthropods being the most common food for birds (Perry and Andersen 2003, Tarof and Ratcliffe 2004). Those studies showed that variation in arthropod biomass did not influence individuals' patterns of settlement. However, the authors pointed out that several vegetation characteristics (e.g., plant species, foliage structure, vertical strata) could influence arthropod diversity (Tarof and Ratcliffe 2004), making the interpretation of the relation between clustering and food availability more ambiguous. When food availability is based on seed production, there are fewer associations with vegetation characteristics other than the occurrence of specific species of grasses in certain areas. Therefore, granivorous birds may cluster more frequently as a result of the distribution of seed-producing plants.

The predation hypothesis proposes that clustering reduces predation through collective anti-predator behavior (Hamilton 1971). We found no support for this hypothesis. Contrary to expectation, we found that the daily predation rate of nests in clusters was higher than that of solitary nests. A possible explanation for this result is that clusters may be more conspicuous and attract more predators, seriously reducing the benefits of reproducing in high densities (Wittenberger and Hunt 1985, Clode 1993). This may be particularly true for species such as the Blue-black Grassquit, which has very small territories, so that once a predator detects a cluster it will likely find many nests. Aguilar et al. (2008) found that Blue-black Grassquit nests were more successful when located farther from conspecifics. Thus nests in isolated territories may be less vulnerable to predation than nests in clusters. We also found a seasonal effect on nest survival with a decrease in daily survival rate for clustered nests in the middle of the breeding season, suggesting that the increment in number of active nests may be a factor in attracting more predators, predation decreasing at the end of the season when there are fewer nests.

However, the relation between predation and agglomeration is complex and possibly species-specific, and one important consideration concerns the position of a territory within the cluster. Some studies suggest that higher-density nesting may be associated with more intense predation (Krebs 1971, Page et al. 1983, Hoi and Hoi-Leitner 1997), whereas others suggest that aggregated territories confer protection against aerial predators (Hernández-Matías et al. 2003). These varied results probably reflect the fact that the comparison of reproductive success of nesting in clusters and in isolation is not straightforward. Nests at the periphery of clusters may be much more susceptible to predation than nests in isolation, since the cluster attracts predators; however, peripheral nests do not benefit from the dilution effect that benefits nests in the center of the cluster. In this study we found that the daily predation rate of nests at the edge of clusters was higher than that of nests in the center, as did Perry et al. (2008). Thus, nesting in clusters may indeed be advantageous for protection against predators, but only nesting in a more central position.

In theory, as discussed above, males may actively search for dense breeding clusters if these are advantageous. Active searching could occur, for example, if clustering were associated with specific and required habitat characteristics or benefits such as food or access to females for extra-pair copulations. Under such conditions, it would be expected that only competitive males of high quality join aggregations successfully (Morton et al. 1990). Although Blue-black Grassquits may defend solitary territories, they tend to occur in clustered territories, leading to high population densities in some areas. However, we found no support for the expectation that males in aggregations should be superior to ones in isolation: clustered males were similar to solitary males in morphological characteristics and territory size. A lack of phenotypic difference between males breeding in clusters versus isolated situations has been found for other birds as well, such as the Bearded Tit or Reedling (*Panurus biarmicus*; Hoi and Hoi-Leitner 1997), but in some species solitary males are unable to obtain mates (Perry and Andersen 2003). In our study, however, all males, whether in clusters or defending isolated territories, were successful in acquiring mates. This lack of difference may reflect our finding that females' intrusions into males' territories, clustered or solitary, were equally frequent, once corrected for the number of paired males and females in each category.

We found a strong tendency for solitary males to display at higher rates than those in clusters, suggesting that males in isolation may attempt to compensate for the smaller number of females in their habitat. Although this result seems biologically meaningful, it is not statistically significant, probably because of lack of power, since the sample was small. Further studies with larger samples may indeed find a significant difference in display rates between solitary males and those that are clustered, as well as in a few other attributes for which we found no significant differences were found (e.g., territory size, morphology). One other behavioral difference that we found was that males in clusters were involved in more agonistic interactions than those in isolation. The elevated rate of agonistic interactions among neighbors in clusters may be due to males attempting to obtain extra-pair copulations from neighboring females (Wittenberger and Hunt 1985). Hence, for the Blue-black Grassquit there may be costs associated with breeding in isolation, in the energy expended to attract mates, but there also seem to be costs in terms of agonistic interactions in clusters. Despite these differences, however, males in the two types of territories do not appear to differ in quality.

We evaluated breeding synchrony among females as a possible mechanism for diluting predation, predicting that synchrony in clusters should be higher than that for females in isolated territories. Although we confirmed that breeding synchrony was higher for females in clusters (28%) than for females in isolated territories (6%), the predation rate for the latter group was lower, implying that breeding synchrony in this species does not lower predation, contrary to the findings of some authors (e.g., Findlay and Cooke 1982).

There are other possible explanations for clustering in the Blue-black Grassquit. One alternative not tested in our study is that clustering could be due to competitive exclusion (Getty 1981, Sherry and Holmes 1985). This hypothesis suggests that in communities where several species share similar habitat requirements the dominant ones should aggregate in resource-rich areas to deter the exploitation of the resource by heterospecifics. In addition to the Blue-black Grassquit there are two other species of seedeaters in the study area, the Double-collared Seedeater (*Sporophila caerulescens*) and the Yellow-bellied Seedeater (*S. nigricollis*). All three species share similar morphology and foraging behavior and presumably occupy similar niches (Sick 1997). Although we did not test this hypothesis, we have rarely detected these species of *Sporophila* in areas with high densities of grassquits, leading us to conclude that although competitive exclusion is a possibility, it probably is not the best explanation for the breeding aggregations of the Blue-black Grassquit.

Another possibility also involving competition is that solitary males may be able to exclude other individuals from their vicinity if they settle in less than optimal habitat, since this choice may lead to reduced predation and perhaps a lower risk of cuckoldry. These benefits may outweigh the females' lower visitation rates and lower-quality habitat. The exclusion of males may lead to their aggregation in areas of better habitat. Thus different types of benefits may be associated with each strategy. The hypothesis we outline here recalls Van Horne's (1983) classic allegation that density is a misleading indicator of habitat quality. For the Blue-black Grassquit, habitat quality may include not only food availability but other less obvious features such as risk of predation and cuckoldry.

The Blue-black Grassquit may be an ideal candidate for testing the "hidden-lek hypothesis" (Almeida and Macedo 2001), which proposes that socially monogamous males should cluster their territories around particular high-quality males (Wagner 1997). Females attempt to obtain extra-pair copulations with these males, in a behavioral pattern somewhat similar to that of females targeting specific males for copulation in traditional leks. Our results strengthen the necessity of testing Wagner's hypothesis as an alternative explanation for the Blue-black Grassquit's pattern of clustering.

The hypotheses that attempt to explain the clustering of territories through females' pursuit of extra-pair copulations are not mutually exclusive of hypotheses of other naturally selected benefits of breeding in high densities. Indeed, the results of this study suggest that many factors, both ecological and sexual, appear to influence the of Blue-black Grassquit's settlement patterns. We propose that for this species the average benefits associated with aggregated reproduction prevail over the observed costs. Benefits include optimal habitat associated with specific vegetation structure and food abundance,

while costs are reflected in higher rates of nest predation and competition, seen in the higher rates of agonistic interactions among males within clusters.

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