

LEK-LIKE MATING SYSTEM OF THE MONOGAMOUS BLUE-BLACK GRASSQUIT

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ABSTRACT.—In this study, we investigated the role of display and mating system of the little known Neotropical Blue-black Grassquit (*Volatinia jacarina*). Males form aggregations and execute a highly conspicuous display, resembling traditional leks. Number of displaying males declined throughout the study period, though displaying intensity during the season showed no variation. Individual males had significantly different displaying rates and also defended territories of very different sizes, ranging from 13.0 to 72.5 m², but we found no association between territory sizes and the average displaying rates of the resident males. There also is no association between displaying rates of males and size and vegetation structure of their territories. Four of seven nests were found within male territories and observations indicated that both sexes invest equally in caring for nestlings. Results suggest that the Blue-black Grassquit does not fit into the traditional lek mating system, contrary to what has been proposed in the scarce literature available. However, it is clear that these apparently monogamous birds behave like a lekking species. We speculate about the possibility that aggregation of nesting territories in this species may be due to sexual selection pressures, and suggest that the Blue-black Grassquit may be an ideal candidate to test Wagner's (1997) hidden-lek hypothesis. Received 2 August 1999, accepted 17 October 2000.

SEXUAL SELECTION in lekking species has been the object of much attention during the last decades. A lek can be broadly defined as any aggregation of males visited by females for mating purposes (see review in Höglund and Alatalo 1995). Lek mating systems—where males are clustered but still maintain fairly large territories—are sometimes called exploded leks (Emlen and Oring 1977), as opposed to classical leks, where males are tightly clumped. Males may choose to display at sites associated with resources used by females. For example, epauleated bats court females from within territories with resources females need, but do not control access to these resources as a way to obtain females (Bradbury 1981, 1985). In cases where resources are located within male territories, it is possible that female choice is based upon the quality of resources, and not upon quality of the male. Thus, difference between a lekking species and one with territorial polygyny may be difficult to discern, for in certain species, such as some hummingbirds (Stiles

and Wolf 1979), females do not nest within male territories, but may depend upon resources within them. It is possible that in some species, male aggregations function like typical leks: individuals form a monogamous pair bond while displaying in a lek close to the nesting site (Höglund and Alatalo 1995).

In this study, we addressed questions related to the lek-like mating system and function of the conspicuous display exhibited by a little-studied, small, Neotropical bird, the Blue-black Grassquit (*Volatinia jacarina*). This common species has a geographical range extending from Mexico throughout most of South America. It typically occurs in open savanna grasslands, usually involving some degree of human disturbance. During the breeding season, adult males are easily distinguished from brownish females and juveniles by their glossy black plumages and white wing underparts. They are easily spotted in the field due to their distinctive display, which consists of repeated vertical flights of about 50 cm, from elevated perches. During these short vertical flights, the males expose the white underwing area and emit a short buzzing vocalization (“teez-wee”). Males are generally found executing their displays in a clustered manner, quite similar in appearance to leks.

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Very little information is available concerning the Blue-black Grassquit's mating system or the males' attention-calling display. A description of the display is provided by Sick (1997), and early observations suggested that the display could be related to pair formation (Alderton 1963). Some experimental work concerning the acoustic part of the display was done by Wilczynski et al. (1989). The display rate is approximately 12 to 14 leaps per minute (Carvalho 1957) at a speed of 1.13 m/s (Weathers 1986). On the basis of very short field observations (3–4 days), Murray (1982) and Webber (1985) suggested that the Blue-black Grassquit had a lek mating system, solely on the basis of the fact that males display in aggregations.

Bradbury (1977, 1981, 1985) specified four criteria for distinguishing traditional lekking species from those using alternative lek-like mating systems. These criteria are: (1) no paternal care; (2) the aggregation of males in an arena, to which females come for mating; (3) the arena contains no resources for females other than the males themselves (e.g. no food, nesting sites, water, etc.); and (4) females are free to choose a mate when visiting the arena. In this study we analyzed male territorial dispersion, habitat preferences, and nesting behavior of the Blue-black Grassquit to see how well Bradbury's (1977, 1981, 1985) criteria for characterizing lekking behavior were satisfied.

METHODS

Study site and general methods.—Our study took place at an experimental farm belonging to the Universidade de Brasília (Fazenda Água Limpa) located approximately 30 km from Brasília, Brazil (15°56'S and 47°55'W). The study site comprised an area of typical "cerrado" vegetation, which varied from a low savanna grassland sparsely covered with bushes to a denser form of "cerrado", consisting of grassland, bushes, and small trees. This area was divided into a grid (100 × 50 m) of 50 quadrants of 100 m² each, with the 66 intersection points marked with identifying flags. The grid was bounded on one side by a dirt road, by a cultivated area on its second side, a small cliff on the third side, and shrubby grassland on the fourth side.

The study was conducted within the rainy season, from September 1995 to April 1996. From mid-November 1995 until early April 1996, we captured 66 male and 38 female grassquits with mist nets within the study plot, marked them with unique combinations of colored plastic bands, and took several mea-

surements of each individual (weight; and bill, tarsus, right wing, and tail lengths).

Behavioral observations.—Observations were conducted between the second week of November and third week of April, almost always between 0600 and 1100 h (GMT-3 h). After this time period, displaying activity markedly declined until late afternoon, when displaying resumed in a more subdued form. Observations were made with binoculars, at distances ranging from 15 to 20 m from grassquits, which did not disturb their displaying. Display perches used by males were marked with an identifying tag to allow the demarcation of territorial boundaries. Other observations included agonistic dominance interactions among males, feeding, courtship, and nesting. Three categories of parental care were considered: (1) visitation, which is the number of times the adult entered the nest; (2) permanence, which is the time the adult spent inside the nest; and (3) proximity, which is the time the adult spent within a 2 m radius of the nest. Observations also included 5 min focal samples of banded males to record the number of display leaps executed (at least two samples per male). To analyze how number of displaying males varied within the breeding season, we calculated a display sighting rate, that is, the number of displays counted in a week divided by the total time spent in the field that week (number of displays divided by sum of minutes in the field). That rate reflects the frequency with which grassquits were encountered in display, because the time spent in the field involved both focal observations and time spent searching for individuals. A different measure assessed the variation in intensity with which males displayed along the season, and that was calculated by taking into account only the 5 min focal periods, disregarding time spent between focal observations (number of displays divided by sum of minutes of focal observations). We also registered the causes of display interruption, which could be due to factors considered neutral, such as leaving the territory without apparent reason and interruption by external elements (such as cars or people on the road), or agonistic factors, such as the intrusion of other males. Displaying males were occasionally interrupted by other males, often causing the resident to approach the intruder and, sometimes, to pursue him. When a female approached a male, he continued his display while getting closer to the female. Copulation was only observed once because most of the time, after courtship was initiated, the pair flew to the ground beneath the vegetation and was lost to sight.

Vegetation structure and resource availability.—We assessed local vegetation structure, which could be associated with suitability of the area for nesting, and also availability of food (grassland seeds) in territories identified within the grid. That was done by extending two perpendicular tapelines within each grid quadrant, producing four identical 25 m²

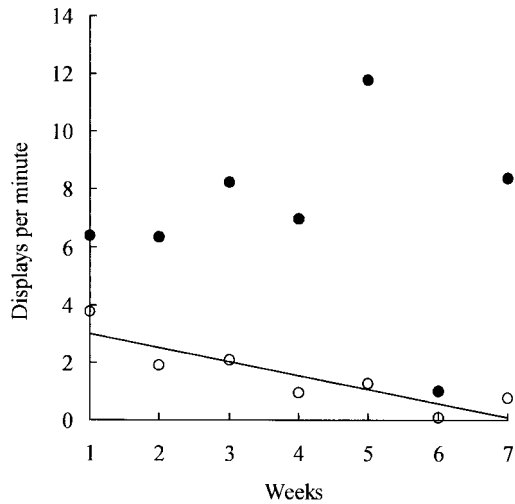


FIG. 1. Weekly variation in the intensity (solid circles) and sightings (open circles) of displays in Blue-black Grassquits. Weeks in 1996: 1 = 5 to 11 February; 2 = 12 to 18 February; 3 = 26 to 29 February; 4 = 11 to 17 March; 5 = 18 to 24 March; 6 = 25 to 31 March; 7 = 1 to 7 April.

squares. Along the tapeline we determined the percent cover of different types of substrate: (1) exposed soil; (2) herbaceous (excluding savanna grassland); (3) "campo sujo" (savanna grassland sparsely covered with bushes); (4) tall savanna grassland (>30 cm); and (5) low savanna grassland (<30 cm). Thus, each 25 m² square had the vegetation along two of its sides assessed. With that we extrapolated the percent of each vegetation type for each 25 m² square. To determine the percent cover of each vegetation type within territories, we multiplied the percentages of each vegetation type by the area each respective square occupied within a territory. For comparison purposes, areas of each vegetation category within territories were converted to percent of territory.

RESULTS

Display seasonality, individual rates, and interruptions.—The first sighting of grassquits in the study area occurred on 30 September 1995, when we observed three males, only one of which had already acquired a complete black plumage. On 4 October 1995, we observed a group of 15 individuals; however, it was not until mid-December, after the rainy season was well underway, that we observed displaying males. By the end of December, a large number of displaying males occurred within the study plot, sometimes separated by only 2 m. Display

TABLE 1. Average display rates, agonistic interruptions, and territory sizes of *Volatinia jacarina* males.

Male	Average displays per minute	Agonistic interruptions per minute	Territory size (m ²)
M1	4.8	0.1	72.5
M2	5.2	0.1	51.0
M3	7.2	0.1	49.0
M4	8.0	0.2	—
M5	3.4	0.1	21.0
M6	6.2	0.0	—
M7	6.4	0.1	36.0
M8	10.8	0.1	39.0
M9	9.3	0.0	61.5
M10	6.1	0.0	55.0
M11	12.3	0.0	34.0
M12	5.7	0.1	—
M13	1.8	0.0	—
M14	—	—	22.0
M15	—	—	13.0
M16	—	—	46.5

perches usually were tree branches or shrubs located well above the surrounding grassland vegetation. Display activity initiated at around 0600 h (average of 8 displays per min), peaked at 0945 h (average of 11 displays per min) and practically ceased by 1100 h (less than 1 display per min; counts taken during 17 days).

There was a significant negative relationship between the display sighting rate with regard to the weeks of observation ($r = -0.87$, $n = 7$ weeks, $P = 0.012$; Fig. 1), indicating that fewer grassquits were displaying as the season progressed. On the other hand, intensity of displays did not vary with the season ($r = 0.03$, $n = 7$ weeks, $P = 0.95$), even when leaving out week 6, where only one display sighting occurred ($r = 0.58$, $n = 6$ weeks, $P = 0.23$; Fig. 1).

A total of 13 individuals were observed within the grid for at least two, 5 min focal samples. A one-way ANOVA was used to compare the displaying rates (number of displays per min) among these individuals. Average displaying rates were significantly different between males ($F = 4.38$, $df = 12$ and 95 , $P < 0.001$; Table 1). During the 5 min focal observations of these males, display interruptions caused by intruding males were also noted. A one-way ANOVA showed that the number of interruptions per minute did not vary significantly among these individuals ($F = 1.35$, $df = 12$ and 95 , $P = 0.20$; Table 1).

Territory size and quality.—We identified 12 territories within the grid area, 9 of which were

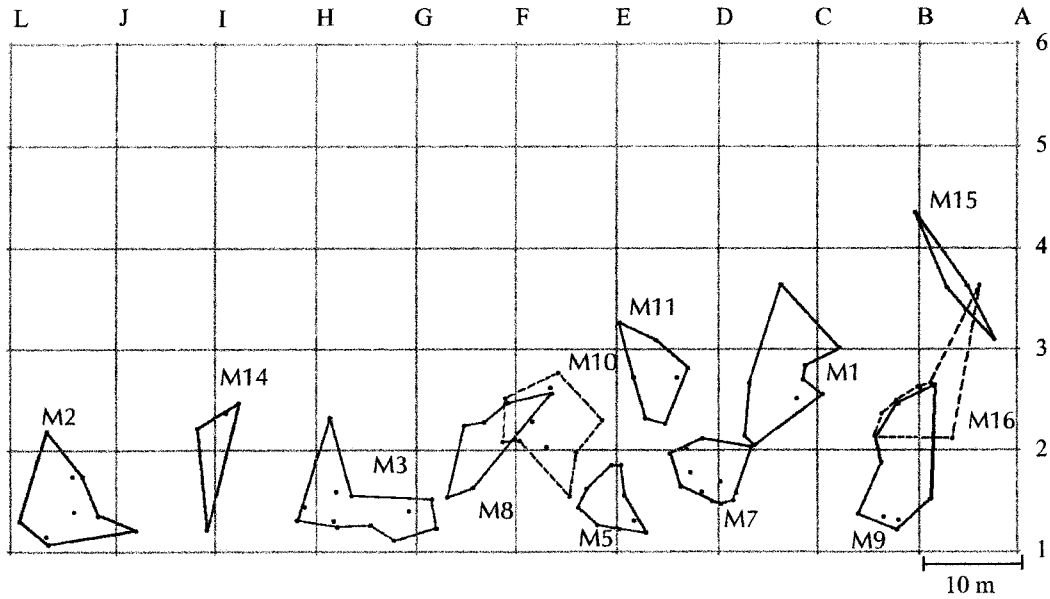


FIG. 2. Location of territories within the study grid. Territories, identified by the male codes (see Table 1) are in continuous black or broken lines; broken lines indicate spatial overlap.

of focal males (Table 1 and Fig. 2). Territory sizes varied from 13.0 to 72.5 m². Individual males did not defend their territories throughout all of the weeks of the study, but remained for varying periods ranging from three to 22 weeks; two males were present for more than four months (Fig. 3). The territories were clustered between lines one and three of the grid, whereas within other grid areas, even encountering a grassquit was a rare event (Fig. 2).

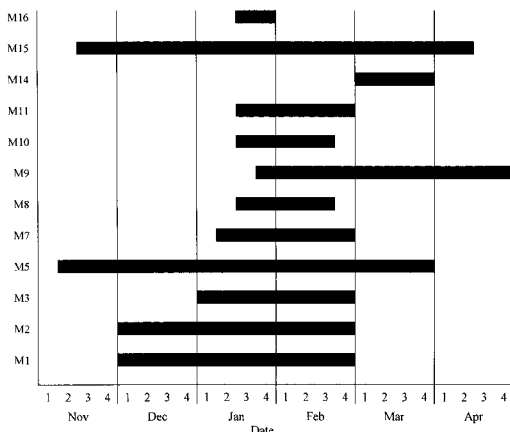


FIG. 3. Territorial occupation from the day each male was banded until the last day observations occurred (codes as in Table 1).

There was no significant correlation between territory sizes and the average displaying rates of their residents ($r = -0.094, n = 9, P = 0.805$).

Within the grid, we compared the vegetation structure of the 25 m² squares that overlapped with grassquit territories ($n = 89$ squares, mainly between lines one and three of the grid) with those without overlapping territories ($n = 111$, mainly between lines three and six of the grid; Fig. 2). We found a significant difference for the following vegetation categories: low savanna grassland (Mann-Whitney U -test: $U = 5,963.5, P = 0.011$); tall savanna grassland ($U = 1,900.0, P < 0.001$); and herbaceous ($U = 6,874.0, P < 0.001$; Fig. 2). The greatest difference found was for the percentage of tall savanna grassland which, in the area occupied by the birds, accounted for 45% of ground cover, as opposed to only 14% in the unoccupied area. With a multiple-regression test, we also examined the possibility of an association between displaying rate of a territorial male, and size and vegetation structure of his territory, but found no significant relation among these variables.

Nesting and parental investment.—Seven nests were found during the study period (four within the grid) in different nesting stages; four of the nests were observed for periods that ranged

from 3.5 to 12.5 h. In three of these nests, observations were conducted on a single day (from 3.5 to 5.5 h). In one nest, observations totaling 12.5 h were spread out over five days. Nests are small (diameter approximately 7.5 cm) and round, composed mostly of roots, and are attached to the herbaceous vegetation from 10 to 50 cm off the ground. In five of the nests, two nestlings were present. The other two nests had one single egg, which had apparently been deserted. We compared male and female parental investment in the number of visits, time spent within (minutes per hour), and in the proximity of the nest. There was no difference in male and female parental behavior for any of the categories measured ($n = 4$ nests): (1) average number of visits (per hour) for males = $2.06 \pm \text{SD of } 1.72$, average number of visits (per hour) for females = 1.22 ± 0.70 : $t = 0.912$, $df = 3$, $P = 0.429$; (2) average permanence (minutes per hour) in the nest for males = 1.40 ± 0.62 , average permanence (minutes per hour) in the nest for females = 4.84 ± 8.12 : $t = -0.88$, $df = 3$, $P = 0.442$; and (3) average time (minutes per hour) near the nest for males = 6.66 ± 8.11 , average time near (minutes per hour) the nest for females = 11.12 ± 9.98 : $t = -7.68$, $df = 3$, $P = 0.192$. In two nests, the male parents were banded. This allowed us to examine the relation between their displaying activities and nesting. In nest #1, found on 30 January 1996 with two nestlings, the male parent (M5) was observed executing displays from the second week of November until the fourth week of March. In nest #7, found on 17 April 1996, displaying by male M9 lasted from the fourth week of January to the end of April.

DISCUSSION

The role of the Blue-black Grassquit male display may be assessed by analyzing the context in which it occurs and its variation throughout the day and breeding season. Wilczynski et al. (1989) proposed that the aerial part of the display (i.e. the leap itself) is not associated with visual conspicuousness, because in their study the grassquits used perches lower than the surrounding vegetation. Thus, they reasoned that the leap would be visible only to nearby individuals. On the basis of experiments with vocalizations broadcast from speakers at various heights, they concluded that the leap was exe-

cuted to augment the radius of vocalization reception by other individuals. In our study, however, perches used by the grassquits emerged above the surrounding grassland vegetation, and displaying males were visible when resting, but became more conspicuous to us when they executed their displays. It is probable that both the visual and auditory components of the display are important to increase perception by other individuals.

Grassquits had their peak display activity in the morning, as is common for many other birds. The reasons for this appear to vary depending upon the species. Birkhead and Møller (1992) suggest that male singing in the morning is related to greater female fertility during this time period, and that singing could function as a pair-guarding mechanism while simultaneously attracting other females for copulation. In a study of Chiffchaffs (*Philloscopus collybita*), Rodrigues (1996) argued that early morning singing could be used by males to determine whether females have survived increased predation risk imposed by nighttime, and could facilitate acquisition of a new mate when predation does occur. To determine reasons for the peak in early morning display with some degree of certainty for Blue-black Grassquits, it would be necessary to pinpoint the females' fertile period. The gradual decrease in displaying throughout the season reveals that that activity is more important in the beginning of the season when males are establishing territories and determining dominance hierarchies. On the other hand, display intensity did not vary throughout the season, and different males occupied the area for varying periods. Consequently, there appears to be some asynchronous breeding in the population, possibly allowing males excluded from the area in the initial part of the season to obtain copulations.

For song birds, male competition for territory acquisition occurs mostly through singing (Krebs 1977, Krebs et al. 1978, Westcott 1992). The intensity, frequency, and quality of the song are associated with territorial parameters, such as size, resource quality, or both; additionally, the physical condition and age of the individual will also affect song components (Westneat 1988, Dale and Slagsvold 1990, Westcott 1992, Chapman and Kramer 1996). Territorial intrusions are frequently executed by individuals occupying lower quality territories

(Matthysen 1990) or by satellite males without territories (Smith 1978, Westcott 1992). The greater capture rate of grassquit males in that study and Webber's (1985) observation of a 10:1 ratio of males to females in the field support the idea that the display area is occupied by a small percentage of the male population, whereas many more transient males occur in the area.

Territories vary greatly in size, the largest one more than five times the size of the smallest one. However, even the largest territory (72.5 m²) is exceptionally small by most standards. Territories are unmistakably used only for reproductive purposes—given their diminutive sizes, the fact that grassquits were seldom seen feeding within them, and that territorial displays practically ceased at the end of February.

Within the grid area, grassquits only occupied areas with tall savanna grassland, completely ignoring the remaining available space. Because some of the nests found were within territories in the grid, it is possible that this type of vegetation is an important determinant of quality in the form of adequate nesting sites. Other more subtle habitat characteristics not measured in this study may also be important. However, there is no relation between display rate of individuals with the size or specific vegetation structure of territories, or both, nor is there any difference in vegetation structure among territories. Hence, females do not choose males on the basis of individual territory characteristics. However, territories are established only within areas with appropriate vegetation characteristics, which may limit the number of males occupying a given region.

Female choice may be the result of male-male competition (passive choice), or it may occur through active selection of some male characteristic (Halliday 1983, O'Donald 1983, Partridge and Halliday 1984). Benefits resulting from female choice may be direct (e.g. territorial resources such as food or nesting sites); or indirect, involving genetic quality that will produce attractive and viable offspring (Andersson 1994, Møller and Thornhill 1998). The evidence from Blue-black Grassquits points to variable types of benefits that can be gained by females through their choice: nesting site, paternal care, and, possibly, genetic quality for offspring. In addition to mate attraction, males may also use displays in territorial defense.

Lack of difference in vegetation structure among territories implies that females are not choosing among males on the basis of resource parameters. Although females were seen only with territorial males, thus excluding part of the male population, characteristics other than territorial ones must be important in determining female choice. The expressive paternal investment found may be crucial for offspring development and survival, thus limiting female reproductive success. In this case, females would benefit greatly by being able to evaluate a male's paternal-care potential. This does not exclude other phenotypic traits that could be indicative of overall male quality.

The small territory sizes associated with conspicuous displays prompted Murray (1982) and Webber (1985) to consider a lek-mating system for the Blue-black Grassquit. In leks, males aggregate and display in a given area and, typically, territories are very small (Westcott 1992, Andersson 1994, Höglund and Alatalo 1995). Because aggregations of animals may occur for reasons other than mating (Bertram 1978, Danchin and Wagner 1997), specific criteria have been suggested to define leks (Bradbury 1977, 1981, 1985), the most relevant of which are that males do not participate in caring for offspring, and that the lekking arena contains no resources needed by females. In effect, upon visiting a lekking arena, females must choose a mate on the basis of factors other than territory quality and paternal care (Höglund 1989, Westcott 1992, Andersson 1994, Johnsgard 1994, Prum et al. 1996). Male traits that may be used in female choice are not limited to plumage or size, for example, but may be acoustic or behavioral characters as well.

In Blue-black Grassquits, despite male aggregations being very similar in form to lekking arenas, other characteristics lead us to conclude that their mating system is not that of a typical lek. Females, at least in the cases monitored within the grid, build their nests within male territories; additionally, some and perhaps all males exert parental care. We do not have substantial data to determine whether males typically continue to display after nest initiation, or whether they dedicate all their time and energy to the nesting attempt. In two nests, display activities were carried out well before, during, and after nesting activities occurred. Although males had significantly dif-

ferent display rates, the number of interruptions by intruding males did not differ among focal males. Thus, displays can function to attract additional copulations for males, but that does not rule out the possibility that males may use displays in territory maintenance.

In species where food, nesting sites, or egg-laying sites are located within male territories, lek systems simply do not apply (Höglund and Alatalo 1995). There are other examples of species showing complex mating strategies that defy a clearcut definition. In colonially nesting Razorbills (*Alca torda*), a seabird traditionally viewed as monogamous with biparental care, both sexes attend mating arenas to obtain extrapair copulations (EPCs) (Wagner 1992).

Wagner (1997) proposed the hidden-lek hypothesis to explain how territorial clustering could evolve in monogamous birds. In essence, a hidden lek could operate because in monogamous species, only a single female pairs with the highest quality male within a certain area. However, other females can attempt to obtain EPCs from this high-quality male. This would lead to a clustering of territories because females would prefer to socially pair with those males whose territories provided them with easier access to the high quality male. Although a loss of paternity could ensue for these males, this would still be better than not gaining a breeding partner.

Thus, the hidden-lek hypothesis predicts that aggregations in monogamous birds may occur through sexual selection. Although Blue-black Grassquit territories are highly clumped, in our study site unoccupied areas were composed of different vegetation. However, within the occupied area territories were homogeneous for characteristics evaluated. Thus, it is unclear from this system how much aggregated territories may be the result of habitat constraints versus lek mechanisms.

Nonetheless, existence of pair bonds and paternal care in Blue-black Grassquits is surprising considering the energy-consuming and conspicuous display of males in aggregations, which leads to the suspicion that EPCs may occur. Should that be the case, it would be enlightening to identify whether more attractive males obtain a greater proportion of EPCs, a situation approaching the hidden-lek hypothesis. Additionally, this species provides promising circumstances in which to explore interplay between

male displays, EPCs, paternal investment, and certainty of paternity.

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