



Experimental Evidence that Sexual Displays are Costly for Nest Survival

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Abstract

Nest predation is one of the most significant limitations for successful breeding of tropical passerines. Thus, parental strategies may include choosing appropriate nest sites and behaving in ways that minimize predation. Habitat characteristics that may influence nest success include degree of nest concealment, proximity to habitat edge, plant architecture as well as several others cited in the literature. However, few studies have examined display behavior as a factor that could also influence nest survival. We experimentally tested whether sexual motor displays served as a cue for visually oriented predators to locate artificial nests in a population of blue-black grassquits *Volatinia jacarina*, a Neotropical passerine that exhibits a complex sexual display and is subjected to elevated rates of nest predation. We also evaluated the effect of nest substrate on survival. Predation rate was higher for nests within territories of displaying males relative to areas without displaying males and for nests placed in shrubs relative to grasses. Predation increased sharply in the third experimental replicate, at the end of the breeding season, which suggests that predators may develop a search image for nests or may become more abundant during specific periods of the season. Avian predators appear to be the most important nest predators. Results suggest that there may be a trade-off between the increase in fitness derived from sexual displays of males to attract potential mates and the decrease owing to predation of active nests within their territories.

Introduction

Nest predation is a primary cause of egg and chick losses for many passerine species, generating a diversity of life history traits dependent upon the degree of predation risk (Ricklefs 1969; Lima 2009; Martin & Briskie 2009). Therefore, parents can be expected to select a safe nest site and behave in a way that reduces the possibility of losing their eggs and offspring to predators. By selecting safe nest sites, parents can decrease nest encounter rate for both incidental predators (Schmidt et al. 2001) and those that actively search for nests. Several parameters are

known to affect nest success, some of which may facilitate nest detection by predators. Among them, nest-site characteristics are thought to determine nest fate, and these may include nest concealment (Schieck & Hannon 1993; but see Götmark et al. 1995), distance to habitat edge (Winter et al. 2000) or even differences at the macrohabitat scale (Tarvin & Garvin 2002; Fraser & Whitehead 2005). Another factor that seems to be important but that has been poorly studied is nest substrate, which can provide protection against both predators as well as climatic factors (Best & Stauffer 1980; Collias & Collias 1984; Young et al. 1990; Murphy et al. 1997). Several

studies have examined predation risk for species that use different nesting substrates (reviewed in Martin 1993). In one study, it was found that artificial nests with quail eggs placed on the ground were more vulnerable to predation than those placed at 1–2 m above ground (Wilcove 1985). Although there is different evidence pointing toward greater predation on ground nests (see Ricklefs 1969), patterns may not be similar across different habitats. For instance, some studies have shown that natural nests on the ground in shrub and grassland habitats suffer less predation than off-ground nests but that this pattern differs for forest habitats (Martin 1993). Thus, the study of nest predation patterns suffers from several confounding elements, owing to occasional pooling of results for nests across different heights, substrates (ground, shrub, canopy), habitats and species. Hence, generalizations concerning nest predation rates relative to type of substrate still lack substantial support.

Several authors have also suggested that some behaviors may attract predators to nests, including begging by nestlings and parental feeding activity (Skutch 1949; Haskell 1994; Leech & Leonard 1997; Martin et al. 2000). An experimental study using playback of tree swallow (*Tachycineta bicolor*) begging calls in artificial nests demonstrated that nests with nestling begging calls were depredated before those without playbacks, suggesting that predators possibly used chick vocalizations to locate nests (Leech & Leonard 1997). Similarly, parental movements to and from the nest could attract predators and increase the probability of nest loss, although the effect of such activity may be masked by nest-site characteristics, as demonstrated by recent studies (Martin et al. 2000; Weidinger 2002; Muchai & du Plessis 2005). Similarly, a study with the Siberian jay (*Perisoreus infaustus*) showed that parents can modify their behaviors in a situation of high predation risk, increasing feeding effort when predators are less active (Eggers et al. 2004).

It is well known that conspicuous secondary sexual characters involved in mate attraction and competition with conspecifics (Darwin 1871; Andersson 1994) may be costly in terms of enhanced risk of predation and brood parasitism (Zuk & Kolluru 1998; Garamszegi & Avilés 2005). Such ornamental traits include mating displays that are commonly used by males to attract females and that can encompass an assortment of vocal, motor, visual and tactile signals. Sexual signals tend to be wide-ranging and non-directional, thus lending themselves easily to eavesdropping by illicit receivers such as predators

or competitors (Bradbury & Vehrencamp 1998). In a study that evaluated predation risk during singing, it was found that birds with the most exposure owing to singing had the highest risks of predation by sparrowhawks (*Accipiter nisus*) (Møller et al. 2006). Conspicuous coloration is another high-risk trait. For example, brighter pied flycatcher (*Ficedula hypoleuca*) males were more easily detected and were victimized more successfully by sparrowhawks (Slagsvold et al. 1995). Nest predation was also found to pose a constraint on female plumage brightness for warblers and finches, in which only females incubate eggs and brood young. As predicted for these species, variation of female but not male plumage was correlated with variation in nest predation (Martin & Badyaev 1996). Thus, it is clear that acoustic signals, bright coloration and, possibly, parental behavior can attract the attention of predators. To our knowledge, however, no studies have evaluated whether mating motor displays may also be used by predators to locate nests.

We investigated whether visually oriented nest predators use sexual multi-modal displays as a cue to locate nests of a passerine species that inhabits the savanna habitats of central Brazil. A second objective of the study was to assess another component of nesting success, which is the impact of nest substrate type (grass or shrub) on nest survival. The species used in our study was a small, Neotropical bird, the blue-black grassquit (*Volatinia jacarina*), which exhibits highly conspicuous multi-modal displays and nests in both shrubs and grasses and was thus particularly well suited to answer our questions. We used artificial nests for this experiment and predicted that nests located in areas associated with male display activity would have higher nest predation than nests in areas without male display activity. A prior study with this species showed that although the grassquits nest both in grasses and in shrubs, most of the nests are placed in grasses (66% of 101 nests; Aguilar et al. 2008). Thus, we predicted that artificial nests located in shrubs could be more easily detected and suffer a higher predation rate than nests located in grasses, as the latter may typically be better camouflaged by surrounding vegetation.

Methods

Study Species

The blue-black grassquit is a small passerine widely distributed throughout most of South America and

northwards to Mexico (Sick 1997). The species is socially monogamous (Almeida & Macedo 2001), but certain characteristics are particularly noteworthy, such as the defense of one of the smallest territories found for passerines and the repeated execution of a conspicuous display by males, composed by a vertical leap accompanied by a short vocalization (Murray 1982; Webber 1985; Weathers 1986; Sick 1997). During the breeding season, males acquire a nuptial blue-black iridescent plumage (Maia et al. 2009), defend very small territories (13.0–72.5 m²; Almeida & Macedo 2001) and exhibit a striking multi-modal display that encompasses motor and acoustic elements. Video filming in the field indicates that the motor part of the display includes at least six complete beatings of the wings, which allows good visualization of the white underwing patches. Also, birds may either maintain an upright posture during the leap or rotate forward at the peak of the leap. These conspicuous displays are executed continuously throughout the day during the breeding season, ranging approximately from 15 displays/min during peak hours (early morning and late afternoon) to 10 displays/min at midday; display rates also peak in mid-season, with an average display execution rate of 18–20 displays/min in January–February (Carvalho et al. 2007).

Females build their nests within male territories, and both sexes care for the offspring. Paired males execute their displays after acquiring mates and during the period of egg laying, incubation and nestling care, a behavior that probably leads to extra-pair fertilizations. Analyses have shown a very high rate of extra-pair paternity: 50% of chicks resulted from extra-pair matings (Carvalho et al. 2006). The grassquits use both grasses and shrubs as nest substrate, and there appears to be specific selection of plant species for nest placement (Aguilar et al. 2008). Grassquit nest predation rate is high in the study area (approximately 70% of nests; see Aguilar et al. 2008), which is typical of tropical regions (Stutchbury & Morton 2001). However, it is important to note that predation rates can vary among different habitats within the tropics (Noske et al. 2008) and that it is probable that in many regions, the most likely predators are birds, which are visually oriented and active during the day (Mezquida et al. 2004). The most common nest predator for passerines in the region where the study was conducted (*Cerrado* savanna of central Brazil) is the curl-crested jay (*Cyanocorax cristatellus*; M. Marini, unpub. data).

Study Area

The study was conducted in central Brazil, in a 4500-hectare reserve called Fazenda Água Limpa (FAL; 15°57'S, 47°56'W), located 32 km from the city of Brasilia. This study site features areas of natural and altered Cerrado (savanna) vegetation, which is highly favored for grassquit nesting. The study was carried out from October 2007 to March 2008, which is the rainy season and coincides with the grassquit breeding period.

General Field Procedures and Use of Artificial Nests

Artificial nest experiments have been broadly used to test hypotheses in ecology and evolution. Because artificial nests can be monitored in large numbers, they enhance sample sizes and present obvious advantages (Robinson et al. 2005), including the possibility to control nest location, clutch size and parental activity. Similar to other methods, artificial nest experiments also have some drawbacks (Major & Kendal 1996; Thompson & Burhans 2004), which we attempted to address and minimize in this experiment.

Our intention was to determine whether the motor and acoustic traits of the sexual display could attract predators. Thus, we wanted to maximally restrict predators to those that are visually oriented and that could use the display activity of the grassquits to find nests. Hence, it was important to minimize olfactory and/or temperature-related cues that could be used by non-visually oriented predators. We baited artificial nests with Japanese quail (*Coturnix coturnix*) eggs because (1) predators may learn to avoid nests containing clay eggs (Nour et al. 1993); (2) small-mouthed mammals appear to be unable to depredate quail eggs (Roper 1992; Haskell 1995; DeGraaf & Maier 1996; Fulton & Ford 2003); and (3) snakes do not seem to depredate quail eggs at ambient temperature, as demonstrated experimentally by Marini & Melo (1998). Additionally, we also wanted to exclude cues associated with nestling begging behavior and parental activities around the nest, so that results could be clearly associated with sexual display activity. For this reason, the testing protocol involved exposure only of eggs in the nest.

Artificial nests of grasses were sewn together to resist severe climatic factors, and gloves were used during their construction to reduce human scent. Artificial nest size was as similar as possible to that of natural nests (Aguilar et al. 2008), with an

external diameter of 5 cm and an external height of 4 cm. To increase the degree of camouflage of the nests, we attached metal frames to the underside of the nests, and these held the nests approximately 30 cm above the ground [natural nests (mean \pm SD): 41.8 ± 25.7 cm; Carvalho et al. 2007]. Artificial nests were placed in an area of homogeneous vegetation covering approximately 120 ha, encompassing territories with displaying grassquit males and, within the same habitat, areas not occupied by territories, therefore lacking displaying males. The breeding density of males in the total area was estimated at approximately 20 males/ha. Distance between natural nests in the field is 22.3 ± 2.4 m (mean \pm SE) (Aguilar et al. 2008), and for this experiment, a minimum distance of 30 m was maintained between artificial nests. For those artificial nests in areas with active territories, we attempted to place the nest close to the spot where the territorial male most frequently displayed, although males change display perch frequently. In natural conditions, nests are located within the small breeding territory, usually a few meters from perches where males execute displays. These procedures were repeated for artificial nests placed in areas without territories, the only difference being the absence of a displaying male.

Both grasses and shrubs were selected as substrates for the artificial nests, similar to what is found for natural nests. To control for possible differences in nest concealment, both types of nest substrate and the surrounding vegetation (1 m radius) were trimmed to a standard height of 50 cm. Areas for nest placement were selected so that the percentage of ground vegetation cover was an average of 70%, corresponding to what has been described for natural nests (Aguilar et al. 2008). During the study period, 360 artificial nests were set up during three trials (replicates). In each trial, a total of 120 artificial nests were used, with 30 nests in each of the following categories: (1) in grasses within a territory; (2) in shrubs within a territory; (3) in grasses outside a territory; and (4) in shrubs outside a territory.

Nests contained a single quail egg and were checked every two or 3 d and then removed after a 12-d sampling period, independent of their fate. The period of 12 d replicates the normal exposure time of blue-black grassquit clutches during incubation. Ten days after removal of the nests, they were used in a subsequent trial and placed in the immediate vicinity (within 3 m) of the former site, but using another substrate (shrub/grass). Nests were classified as depredated if the egg was missing or damaged. In

the latter case, the type of damage was recorded (egg perforated or cracked).

Statistical Analyses

The free software R 2.7.2 (R Development Core Team, 2008) was used for all computations. All statistical tests were two-tailed, and the null hypothesis was rejected at $p < 0.05$. To estimate the fixed effects of substrate type (grass or shrub) and territory type (display or non-display) on occurrence of predation (response variable), generalized linear mixed models (GLMM, 'lmer' in R package 'lme4', version 0.999375-28) were fitted considering a log link function and a binomial error distribution. This GLMM framework was applied to account for the repeated usage of artificial nests in different trials through the breeding season, by including the identity of the nest in the model as a random effect. Parsimonious models were achieved using a stepwise approach, sequentially removing the variables from relatively more complex models, starting with interactions. The variables with lowest explanatory power were removed and likelihood ratio tests (LRT) were used to compare nested models, using the change in deviance as a chi-square approximation. The simplified model was preferred whenever the removal of a variable caused no significant decrease in model fit. Values reported are means \pm standard error. For significant terms, parameter estimates β (\pm SE) are given on the logit scale.

Results

Of the 360 nests exposed throughout the breeding season, only 11% (38) were depredated, the majority of which (79%) were within the territory of a displaying male. On average, 12.66 ± 1.76 nests were depredated during each trial, and predation increased along the breeding season with the last trial accounting for 42% of total predation (Fig 1 and 2). When evaluating depredated nests, we found that most eggs disappeared from the nest ($N = 21$; 55%) with no signs of vegetation disturbance; in 14 nests, the egg was perforated, and in three the egg was cracked.

None of the interactions between nest placement area (within or outside a territory) and substrate or period in the breeding season (trial number) significantly predicted the occurrence of predation events (GLMM, all LRT $p > 0.05$) (Table 1). Nevertheless, we found a significant effect of nest placement area ($\chi^2_1 = 14.56$, $p < 0.001$, $\beta = 1.49 \pm 0.42$; Fig. 1) and substrate type ($\chi^2_1 = 7.88$, $p = 0.005$,

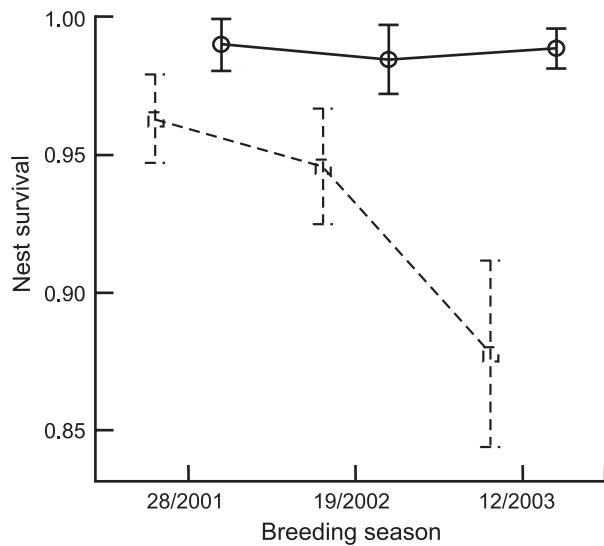


Fig. 1: Proportion of days the nests survived for the three trials through the breeding season relative to the activity of displaying males, or lack thereof. For illustrative purposes (only on the graph), the response variable was transformed into a proportion, so that 1.0 represents nests that survived for the whole 12-d period. Dashed lines represent nests within territories, and solid lines nests outside territories.

$\beta = -1.04 \pm 0.38$) on predation (Fig. 2). These results indicate that nests near displaying males suffered more predation than nests not associated with displaying males. Additionally, results indicate that nests placed in shrubs were depredated at higher rates than those placed in grasses.

Discussion

Our results confirm that display activity of male grassquits was the key factor used by predators as a cue to find nests. This is consistent with hypotheses described in the literature suggesting that activity of the parents around the nest may affect survival of eggs and nestlings and could potentially be useful for predators (Skutch 1949; Martin et al. 2000). Moreover, we showed that there is an effect of nest substrate on predation risk, as nests placed in shrubs were depredated at higher rates than those in grasses.

These results imply that adult behaviors not associated with offspring care, such as songs and/or displays, can be used as cues by predators to locate nests. Indeed, the conundrum faced by animals that use conspicuous acoustic signals to attract mates has been documented for some vertebrates. For example, it has been documented that bats capture frogs at higher rates when the latter are vocalizing (Tuttle &

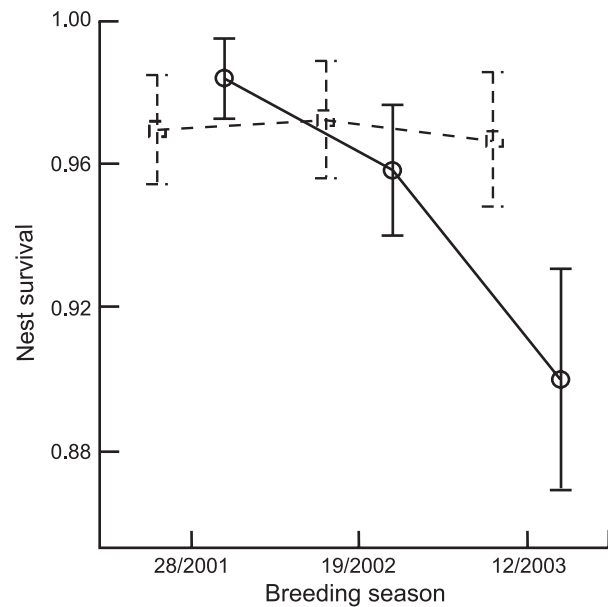


Fig. 2: Proportion of days the nests survived for the three trials through the breeding season relative to nest placement type. For illustrative purposes (only on the graph), the response variable was transformed into a proportion, so that 1.0 represents nests that survived for the whole 12-d period. Dashed lines represent nests placed in grasses, and solid lines represent nests placed in shrubs.

Ryan 1981). Acoustic sexual advertisement in birds may also be constrained by the risk of predation: the mate attraction call of the blue petrel (*Halobaena caerulea*) can be used by skuas (*Catharacta antarctica*) as a cue for locating and preying on calling individuals (Mougeot & Bretagnolle 2000). Our study, however, additionally advocates that sexual motor displays can significantly increase the risk of predation not only to the calling individual but also to eggs and, possibly, to offspring. Male displays of blue-black grassquits, used to attract females and defend territories from other males, probably entail a trade-off between sexual advertisement and predator avoidance. Past field observations revealed that displaying males are subject to predation during display execution (R. Dias, unpublished data). We suggest display activity has a non-trivial effect on nest predation risk in species with small territories containing nests and where males execute prominent motor displays during the incubation and nestling periods.

Nevertheless, there are other possible explanations for the higher nest predation in placement areas associated with male activity. Potentially, at least part of the higher predation in territories with male displays reflects a density-dependent effect because some of the territories with displaying males could

Table 1: The likelihood ratio tests compare each model with that in the row above it

Model	Deviance	χ^2	p
Full model	214.6		
Minus period in breeding season * nest placement area	215.2	0.65	0.42
Minus nest substrate * nest placement area	217.9	2.66	0.10
Minus period in breeding season	219.6	1.71	0.19
Minus nest substrate	227.5	7.87	0.005
Minus nest placement area ^a	234.2	14.56	0.0001

There is one degree of freedom for all cases, and they are for the χ^2 statistic in the likelihood ratio test. We started model reduction with interactions. Eligible terms were removed one at a time, and their contribution to model explanatory power assessed using likelihood ratio tests.

^a The removal of the variable is in relation to the model two rows above it.

also contain one additional grassquit nest. Studies using both natural and artificial nests have demonstrated that predation can increase in high nest-density areas, because predators may intensify their search behavior in response to the higher number of nests found (Martin 1988a,b, 1996). However, this explanation does not adequately explain our results. The density-dependent effect was probably attenuated in this study owing to the small size of grassquit territories (<100 m²; Almeida & Macedo 2001) as well as the 30-m distance between artificial nests (similar to the distances between natural nests). These factors lead us to believe that both treatments were exposed to almost equivalent nest density. Moreover, during the grassquits' breeding season, many other bird species with similar nesting habitat reproduce within the same area. Thus, it is likely that nest placement areas without displaying individuals also contained active nests belonging to other species. In the case of the blue-black grassquit, we can speculate that a density effect may occur not for nests, but for displaying individuals, so that a predator may focus on a specific area because of the high number of males executing displays.

Despite an observed increase in predation rate at the end of the breeding season and associated with the third experimental trial, we did not find significant support for an effect of time on predation along the breeding season, which we had expected (see Schiegg et al. 2007). There is considerable support for an increase in efficiency of visually oriented predators because of the development of search images for a resource, prey or nests (Persson 1985; Lewis 1986; Martin 1988a,b, 1996), or even of markers

used to flag nests (Picozzi 1975). In our case, larger sample sizes of nests within active territories would possibly show that predators may develop a search image for nests or may learn to associate the displaying male phenomenon with the reward of a clutch of eggs. An alternative though less likely explanation is that predator abundance may vary throughout the season and was somewhat higher at the end of the breeding period.

Among other factors, nest substrate is a characteristic that is thought to affect survival by influencing predator ability to detect or to access the nest (Best & Stauffer 1980; Filliater et al. 1994; Mezquida & Marone 2002). We found that artificial nests placed in shrubs were more depredated than those in grasses. We did not estimate the proportion of both types of nest substrate in the study site, but all of the area is within open, grassy habitat where it is obvious that there is a higher abundance of grasses relative to shrubs. Although the grassquits also use shrubs, a study in the same study area revealed that most natural nests are found in grasses and that some species of grasses are used more or less than expected based on availability (only four of 20 grass species are used; Aguilar et al. 2008). This indicates that grassquits may indeed be choosing nest substrates associated with a lower predation risk. Why do grasses offer greater protection from predation than shrubs? A first possibility is that grasses simply provide better concealment for nests than shrubs (Burhans & Thompson 1998). A second explanation is that the high abundance of grasses relative to shrubs protects nests because it is more time-consuming and difficult for predators to find nests in this more plentiful type of habitat structure (Martin & Roper 1988). Nevertheless, we cannot exclude the possibility that in natural conditions, the selection of nest substrate could be opportunistic, with a higher selection for the most abundant type of substrate (see Isenmann & Fradet 1998).

Natural predation rates for grassquit nests are variable but usually higher than what we found in the present study, ranging from 71% to 95% in the same study area (Carvalho et al. 2007; Aguilar et al. 2008). Obviously, however, natural predation rates refer to the complete nesting cycle, which encompasses egg laying, incubation and nestling phases, which was not the case for artificial nests in our study. The nest predation rate of 11% that we found, however, was also lower than that for other studies in the Neotropics that used artificial nests (40%: Duca et al. 2001; 48%; 5%: Alvarez & Galetti 2007). The most probable explanation for this

difference is that using quail eggs in our nests, two sources of predation were probably excluded, that by small mammals and by snakes. This makes it more likely that we were successful in restricting predation to visually oriented predators. Additional explanation for the lower predation rate found is that because we simulated the period of nesting where only egg laying and incubation occur, we excluded parental feeding of nestlings and begging calls from the latter, both of which presumably can increase predation.

In most cases of predation, the eggs disappeared with no sign of disturbance around the nest or of the nest itself. Approximately, 37% of the depredated eggs had a single perforation, which suggests bird predation. Evidence resulting from an experimental study using artificial nests baited with quail eggs strongly suggests that in the Neotropical region almost all predation events occur during daylight hours, signifying a higher incidence of birds as nest predators (Mezquida et al. 2004). Söderstrom et al. (1998) also concluded that birds prevail over non-avian predators for shrub nests in comparison to ground nests. Our results may reflect this conclusion, because we only used nests above the ground both in shrubs and in grasses. We frequently observed several potential avian predators in the study area including squirrel cuckoos (*Piaya cayana*), smooth-billed anis (*Crotophaga ani*), guira cuckoos (*Guira guira*) and curl-crested jays (*Cyanocorax cristatellus*), among others.

Results from this study indicate that the signaling component of male display behavior may also be subjected to other forms of selection, which may generate variation in the patterns of mate choice. An important issue arising from these results relates to the costs versus benefits that females may gain by selecting males that display intensively, a behavior that may lead to a loss in fitness through nest predation. Additionally, if display intensity can effectively help males to gain extra-pair paternity and is indeed an honest signal of quality, one could expect that females paired with less intensively displaying males should search for extra-pair copulations with more vigorously displaying males. Females could thus integrate two important components for improved fitness, generating 'sexy sons' within safer nests.

In conclusion, we have shown through an experimental study using artificial nests that in addition to signaling behavior, sexual signaling that includes motor displays may entail a cost by increasing the risk of nest predation. Moreover, we can conclude that the mere placement of a nest in a vegetation

structure of one type, independent of nest height or surrounding concealing vegetation, may offer better protection from predators. Further investigations are needed to understand the role of predation in relation to display rate during the breeding season, whether nests of more actively displaying males suffer higher predation compared to those of less energetic males, the relative importance of the display compared to other male attributes that potentially allow a higher breeding success and how females may assess male quality through the display relative to nest predation risk.

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