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Percepção dos predadores de ninhos e estratégias anti-predação numa comunidade de aves da Mata Atlântica do estado de São Paulo.

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Dedico este trabalho a todas as pessoas que de alguma forma me apoiaram até aqui, principalmente à minha família, através de meus pais e avó e também à minha companheira que soube ser paciente e amorosa nos momentos mais difíceis dessa caminhada.

RESUMO

A principal causa da variação anual no sucesso reprodutivo das aves é a falha causada pela predação durante os períodos de nidificação. Os ovos expostos em ninhos abertos geralmente apresentam uma ampla gama de colorações e podem coincidir com a cor do material do ninho, o que é considerado uma estratégia de camuflagem para evitar a predação. Muitas hipóteses inferem que as características dos ninhos e de seu entorno também podem evitar a predação, mas muitas dessas hipóteses ainda são pouco testadas. Este trabalho teve como objetivos i) testar o efeito da cor dos ovos na vulnerabilidade dos ninhos à predação, usando ovos de plasticina com três padrões de cor, em ninhos naturais de *Chiroxiphia caudata* em uma área bem preservada da Mata Atlântica e ii) expandir os testes da "hipótese do local potencial de predação", que infere que estruturas semelhantes a ninhos nas proximidades dos ninhos naturais podem reduzir a probabilidade de predação por dificultar a formação da imagem busca nos potenciais predadores. Para o primeiro experimento, foram utilizados 78 ninhos abandonados de *C. caudata*, 26 com cada padrão de ovo proposto (todo branco, branco com manchas marrons e todo marron), sendo utilizados dois ovos por ninho. Onze ninhos (14,10%) foram predados por predadores visualmente orientados, (cinco com ovos brancos; quatro com ovos brancos com manchas marrons e dois com ovos marrons). Embora não tenha havido diferença significativa na probabilidade de predação para cada padrão de cor, há uma tendência crescente, em que o ovo branco teve a menor taxa de sobrevivência, seguido pelo branco com manchas marrons e, finalmente, os ovos totalmente marrons.

Para testar a ‘’hipótese do local potencial de predação’’ primeiramente foi investigado se *C. caudata* poderia selecionar locais de nidificação onde estruturas similares a ninhos estivessem presentes, como tufos de musgos e depósitos de detritos em forquilhas. Para isto, os números destas estruturas, bem como uma série de outras variáveis ambientais foram comparadas entre os locais dos ninhos e pontos aleatórios através de um procedimento de seleção de modelos utilizando-se Modelos Lineares Generalizados. Durante três estações de reprodução, foram analisados 42 ninhos ativos de *C. caudata* e a modelagem indicou que as estruturas similares a ninhos e a densidade da vegetação foram as variáveis que melhor explicaram a escolha dos locais de nidificação. No entanto, estes parâmetros não foram correlacionados com probabilidade de sobrevivência dos ninhos, corroborando apenas parcialmente a ‘’hipótese do local potencial de predação’’.

Palavras-chave: predação de ninhos, comportamento do predador, ovos de massinha de modelar, comunidade de predadores, local de nidificação, ninho críptico, comportamento de nidificação.

ABSTRACT

The main cause of annual variations in bird's reproductive output is the failure of nests resulted from predation. Eggs exposed in open nests, usually have a wide range of colorations, and may coincide with the color of the nest material, which can be considered as a mimetic strategy to avoid predation. Many hypotheses have predicted that nest characteristics and the characteristics of its surroundings also affect nest predation probability, but many of these hypotheses are still poorly tested. One such hypothesis is the "potential prey-site hypothesis". In this work we tested the effects of egg color in nest predation, using plasticine eggs with three color patterns, in natural nests of the Blue Manakin, *Chiroxiphia caudata*, and we extended the theory of the"potential prey-site hypothesis" by addressing nest-like structures in a Atlantic Forest well-preserved area.

For the first experiment we used 78 abandoned nests of the Blue Manakin, 26 with each egg pattern (all white, white with brown spots, and all brown), of which 11 (14.10%) nests were depredated by visually oriented predators: (five with white eggs; four with white eggs with brown spots; and twowith brown eggs). Although there were no significant differences in the probability of predation for each color pattern, there was a growing tendency, in which white eggs had the lowest survival rate, followed by white with brown spots, and finally the all-brown eggs. To address the "potential prey-site hypothesis" we first tested if the Blue Manakin could select nesting sites in which nest-like structures, such as tufts of moss and deposits of debris in horizontal forks, were in higher densities, controlled to a set of covariates. Then, we evaluated if the numbers of nest-like structures in nest surroundings were correlated to nest survival, using 42 active nests. Modelings using Generalized Linear Models indicated that nest-like structures and vegetation density were the main covariates explaining nest site choice in this species. However, we found no correlations of nest-like structures to nest survival, which corroborates only partially the "potential prey-site hypothesis".

Keywords: nest predation, predator behavior, clay eggs, predator communities, nest site, cryptic nest, nesting behavior, predation avoidance.

SUMÁRIO

1. INTRODUÇÃO GERAL

Reprodução em aves

Por ter uma heterogeneidade de relevos e climas que proporcionam uma grande diversidade de formações vegetais, a América do Sul é reconhecidamente o continente com mais quantidade de espécies de aves do planeta, sendo que mais de um terço das espécies são encontradas neste continente (Ridgely and Tudor 1994, Sick 2001). Grande parte deste continente é ocupado pelo território brasileiro, no qual estão inseridas a Floresta Amazônica e a Floresta Atlântica, duas das maiores formações florestais do mundo, além de outras formações vegetais importantes, como o Cerrado (Myers et al. 2000).

Mesmo com toda essa grande riqueza de espécies na América do Sul e no Brasil, ainda há uma grande defasagem de estudos com relação a informações básicas sobre os aspectos da biologia reprodutiva e características de vida da maioria das espécies de aves tropicais (Martin 1996, Stutchbury and Morton 2001), apesar de alguns livros (ex.: Hilty and Brown 1986, Belton 1994, Sick 2001) terem compilado descrições de hábitos reprodutivos de muitas espécies.

No século XX muitos autores (Euler 1900; Skutch 1945, 1985; Oniki 1979) publicaram descrições de ninhos, ovos e tamanho de ninhada para muitas espécies, no entanto dados refinados como extensão do período reprodutivo, taxas de sucesso dos ninhos, períodos de incubação dos ovos e permanência dos filhotes nos ninhos, e dados de cuidado parental não são conhecidos inclusive para espécies comuns e abundantes (Robinson et al. 2005b). Há a necessidade de aumentarmos nosso conhecimento acerca de informações básicas dos parâmetros reprodutivos de nossas espécies, não apenas para testarmos hipóteses sobre padrões naturais, mas também para nos auxiliar e embasar de tomadas de decisão de medidas conservacionistas (Boyce 1992, Reed et al. 1998), além de ajudar a esclarecer relações de parentesco (Sick 2001).

Riscos à reprodução

Considerando-se a história de vida das aves, sabe-se que estas estão sujeitas a “trade- offs” relacionados a diversas estratégias evolutivas (Ricklefs 1969). Um dos “trade- offs” mais conhecidos é a relação entre aumento da taxa de reprodução, que pode gerar uma redução na taxa de sobrevivência (tanto dos parentais quanto da prole). Por isso, essa mortalidade dos indivíduos norteia a maioria das diferenças entre as características de vida das aves (Martin 1996, Winkler 2004).

A principal maneira das aves aumentarem seu rendimento reprodutivo é aumentar a chance de sobrevivência da prole, assim, grande parte das características da biologia reprodutiva estão voltadas para esse objetivo (Skutch 1976, Winkler 2004). Segundo Skutch (1976) a predação é a principal causa da baixa taxa de sobrevivência obtida em ninhos na região neotropical. No entanto essa taxa poderia ser reduzida caso o número de ovos por ninhada fosse reduzido, havendo assim uma redução na probabilidade de um possível predador detectar um parental no momento da alimentação, pois as visitas dos adultos para este fim seriam menos frequentes. Trabalhos de Skutch (1949), Snow e Snow (1964), Ricklefs (1969) Ghalambor and Martin (2000) e Martin e colaboradores (2000) trazem mais elementos que apoiam essa teoria.

É raro os parentais serem predados durante o cuidado com a prole, porém a predação de ovos e ninhegos pode chegar a taxas bastante altas, muitas vezes acima de 50% (Martin 1992, Winkler 2004). Os predadores podem ser animais terrestres (como gambás), ter hábitos arbóreos (como saguís) ou aéreos (como tucanos), e o período do dia onde ocorrem essas predações também varia, por ação de animais diurnos, crepusculares e noturnos (Sick 2001, Winkler 2004, Colombelli-Négrel and Kleindorfer 2009).

No entanto poucos são os estudos com taxas de predação, que identificam quem são esses predadores, ou ao menos seu hábito de vida, informação essa importante para se testar uma das premissas da hipótese de Skutch (1949), de que os ninhos seriam predados principalmente por animais de hábitos diurnos e esses seriam predadores com grande acuidade visual. Considerando apenas os trabalhos realizados nos Neotrópicos, somente seis trazem informações de identificação sobre quem são os predadores dos ninhos (Robinson and Robinson 2001, Robinson et al. 2005a, Auer et al. 2007, Libish et al. 2008, França et al. 2009, Reidy 2009 e Menezes and Marini 2017). Quando ocorre essa identificação, por vezes são casuais, sem uma padronização, o que incorre em muitas identificações enviesadas no período diurno, já que é o período em que os pesquisadores passam a maior parte do tempo em campo (Robinson and Robinson, 2001).

Contudo, para compreender de forma mais detalhada as consequências da degradação ambiental sobre o sucesso reprodutivo das aves, e por meio disso, elaborar planos de manejo para essas áreas, e para que testes de hipóteses acerca da evolução da história de vida das aves sejam melhor compreendidos, a identificação desses predadores de ninhos trona-se fundamental. Porém, o número reduzido de estudos trazendo esta informação se dá principalmente por três fatores: a. A probabilidade de detecção de uma predação é reduzida, por ocorrerem em eventos muito rápidos; b. Podem ocorrer em qualquer horário do dia, inclusive no período noturno, quando os pesquisadores não estão no campo para observá-las e c. A maior parte dos meios de monitoramento constantes, que envolvem principalmente câmeras filmadoras apresentam muitas limitações (Thompson III et al. 1999, Robinson and Robinson, 2001). Atualmente, uma boa opção em relação às gravações contínuas, são os equipamentos de monitoramento acionados via infra- vermelho, onde as filmagens são ativadas somente quando há movimento (Bolton et al., 2007; Chiavacci et al. 2014), como ocorre com as câmeras *trap*.

As aves apresentam adaptação contra a predação em seus hábitos de nidificação, tanto para proteger os parentais como para proteger a prole, como por exemplo, construção de ninhos em penhascos ou entre rochas (Roper 2000), ovos camuflados, ninhos cobertos por vegetação

(Opermanis 2004) e até defesa direta onde os parentais combatem os invasores (Montgomery and Weatherhead 1988). Com isso, afastar ou iludir os predadores parece ser parte da evolução das estratégias de biologia reprodutiva das aves (Winkler 2004, Trnka and Prokop 2010).

Construção e função dos ninhos

A principal função de um ninho é assegurar à prole um local protegido para que estas se desenvolvam com segurança através da construção de um “ambiente” controlado (Skutch 1961, Hansell 2002, Healy et al. 2008). Estes podem auxiliar os parentais a manter os ovos e ninhegos nas temperaturas desejadas – próximo a 40º C (Calder and King, 1974), e podem reduzir os riscos de predação do seu conteúdo, uma vez que as aves desenvolveram uma série de adaptações para este fim (Young et al. 1990, Sick 2001).

Filhotes e ovos atraem predadores porque são uma fonte de recursos de alto valor energético, e essa predação pode causar grandes impactos na sobrevivência dos filhotes e por isso, as aves desenvolveram características peculiares na construção de seus ninhos (Snow 1976, Sick 2001). Dessa maneira, podemos considerar os ninhos como sendo uma extensão do cuidado parental (Skutch 1961). Com essa pressão sofrida principalmente pela predação, vários grupos dentro de Aves desenvolveram diversificados formatos de ninho, como, um buraco aberto no chão, ninhos em plataforma, ninhos em forma de taça (apoiada por baixo, suspensa, em pêndulo, entre outras), ninhos em forma de domo, globulares, ninho em montículos e cavidades (em oco ou barrancos) (Winkler 2004). Alguns padrões de adaptações anti-predação dos ninhos foram discutidos por Koepcke (1972): 1. Construção dos ninhos em locais de difícil acesso (ou até em plantas urticantes); 2. Aves de tamanhos pequenos fazendo ninhos muito grandes para o seu tamanho (podendo esconder a câmara de incubação ou acessos falsos); 3. Confecção de ninhos camuflados; 4. Comportamento de nidificação gregário; 5. Defesa ativa ou despistamento do ninho pelos parentais; 6. Ninhos em locais onde há atividade próxima de formigas ou vespas; e 7. Redução extrema do tamanho do ninho (Hansell 2000).

Uma das adaptações feitas efetivamente pelas aves para evitar a predação é o ato de camuflar seus ninhos (Collias and Collias 1984, Hansell 2000), por meio da inserção de materiais como pequenas porções de líquens e teia de aranha (Hansell 1996, Calvelo et al. 2006), fezes de carnívoros (Schuetz 2005), que não necessariamente fazem parte do conteúdo estrutural do mesmo, podendo assim, torna-lo críptico em relação ao micro-habitat (Flaspohler et al. 2000, Albrecht and Klvană 2004, Colombelli- Negrel and Kleindorfer 2009). Para que os ninhos sejam menos visíveis, as aves podem utilizar materiais que sejam mais homogêneos com o fundo do local onde o ninho está inserido (Stevens and Merilaita 2011), ou até utilizar materiais que buscam quebrar visualmente a forma geral de um ninho, conferindo falsos limites (Fraser et al. 2007)

Em um trabalho recente Bailey e colaboradores (2015) fizeram um experimento disponibilizando materiais de várias colorações para os indivíduos de Mandarin (*Taeniopygia guttata*) construírem seus ninhos para testar a teoria de utilização de matérias como camuflagem dos ninhos. O resultado obtido foi que as aves escolheram materiais com colorações próximas ao fundo de seus recintos, mostrando pela primeira vez, que os indivíduos escolhem ativamente materiais para a camuflagem dos seus ninhos.

Escolha de sítios de nidificação

Consideramos como sítio de nidificação a planta suporte do ninho, bem como o material vegetal usado no mesmo (Martin and Roper 1988). Segundo Martin (1993), o principal fator considerado pelas aves no momento da escolha do sítio de nidificação é a sua baixa susceptibilidade a predação (deixando em segundo plano fatores também importantes como limitação de alimento e competição). Diferenças entre as qualidades dos sítios de nidificação podem torná-los mais, ou menos suscetíveis a predadores de ninhos, podendo esconder a movimentação dos parentais nos mesmos (Martin 1998). Sítios de nidificação podem ser escolhidos por uma enorme gama de características desejadas pelas aves, seja tipo de solo/substrato e declive, para ninhos em cavidade, dossel e vegetação rasteira, que podem ser escolhidas para esconder melhor os adultos em suas visitas aos ninhos ou até topografia do terreno (Bancroft et al. 2005, Rodway et al. 1998, Buxton et al. 2015), locais de apoio propícios aos ninhos (Sándor 2015), cobertura vegetal do entorno, altura do ninho em relação ao chão (Martin et al. 1997, Vasseur and Leberg 2015).

Coloração e manchas dos ovos

A pigmentação dos ovos é adicionada à casca assim que esta é formada no oviduto, por glândulas de pigmento presentes em suas paredes, que conforme o ovo passa, vão depositando camadas de cor. Essas pigmentações podem variar muito, tanto em forma quanto em cores, podem ser escuros, lustrosos, arroxeados, com ou sem manchas, entre uma enorme variedade de padrões (Winkler 2004). No entanto, dentro de uma espécie os padrões de coloração são geralmente pouco variáveis (Jackson 1993).

Ovos expostos em ninhos abertos, geralmente possuem uma grande gama de colorações, muitas vezes coincidindo com a coloração do material do ninho, o que é considerado como uma estratégia desenvolvida para evitar a predação através da camuflagem dos ovos (Stoddard et al. 2011) e em muitos casos essa pigmentação está também relacionada com a proteção do conteúdo contra a intensa radiação solar (superaquecimento), onde possivelmente essa superfície pigmentada ajuda a dissipar o calor (Web 1987). Já ovos brancos geralmente são encontrados em ninhos de cavidades ou fechados (como domos) ou em ninhos onde os parentais, antes de deixarem o ninho, adotam como estratégia, cobrir os ovos (Oniki 1979), e como esses ovos sofrem menos ameaças de predadores visuais, não há a necessidade da pigmentação de camuflagem, considerando ainda que esses pigmentos devem ser custosos energeticamente para serem produzidos (Winkler 2004).

De acordo com Kilner (2006), essa grande gama de padrões de coloração de ovos foi principalmente gerada por influência da predação, onde a camuflagem dos ovos foi de grande importância como estratégia anti-predação. Alguns trabalhos buscaram testar essa relação entre a pigmentação e a camuflagem: Nguyen e colaboradores (2003) viram que os padrões de manchas em *Charadrius semipalmatus* ajudam a tornar os ovos mais camuflados; Lee e colaboradores (2010) utilizaram *Larus crassirostris* como modelo para avaliar a influência da variação de manchas entre ovos, relacionado à taxa de predação, e concluíram que ovos que possuíam a coloração base mais próxima a do fundo do ninho obtiveram maior sucesso. Essa relação também foi encontrada por Skrade e Dinsmore (2013). Lovell e colaboradores (2013) analisaram a escolha do micro-habitat de nidificação pelas fêmeas e viram que estas escolhem os lugares dos ninhos de acordo com o padrão de manchas dos seus ovos (buscando melhor camuflagem), e analisaram a visibilidade dos ovos em relação aos ninhos através de uso de um software computacional e concluíram que ovos em substratos mais escuros possuíam mais manchas escuras, tornando-os mais crípticos.

Westmoreland (2008), testou a camuflagem dos ovos em ralação ao ninho, utilizando ovos de três espécies diferentes (*Agelaius phoeniceus*, *Euphagus cyanocephalus* e *Xanthocephalus xanthocephalus*) em ninhos de *Turdus migratorius* e viram que os ovos que eram mais chamativos ao olho humano (menos camuflados) foram os encontrados mais rapidamente pelos predadores (apesar das taxas de sucesso entre os ovos das três espécies utilizadas terem sido equivalentes).

2. CAPÍTULOS

2.1. Can the pigmentation of the eggs be a good camouflage to avoid visually oriented predators? A test with natural nests and plasticine eggs.

INTRODUCTION

Egg color and patterns of markings are highly variable among bird species, and the function of these pigmentations is one of the most basal questions in ornithology (Montevecchi 1976, Harrison 1985, O'Connor 1985, Kilner 2006, Cassey et al. 2010). Potential explanations include protection of egg content against intense solar and UV radiation (overheating) (Lack 1958, Montevecchi 1976, Bakken et al. 1978, Oniki 1985, Shafey et al. 2002, Maurer et al. 2011, Maurer et al. 2015, Lahti and Ardia 2016), and the gain of egg-shell resistance provided by pigments (Solomon, 1991, Gosler et al. 2005), but the most commonly argued hypothesis is that color patterns may provide camouflage to avoid detection by visual predators (Nguyen et al. 2003, Kilner 2006, Stoddard et al. 2011, Lovell et al. 2013). Egg pigmentation is more common among open-nester species, while white is the predominant color in closed-nester birds, which is thought to be a result of lower nest predation rates in closed nests (Ricklefs 1969, Oniki 1979a, 1979b, Christman and Dhondt 1997, Winkler 2004), and because in closed nests eggs are not visually exposed, eliminating the need of mimetic anti-predatory strategies (Lack 1958, Underwood and Sealy 2002). This tendency *per se* is an evidence for the anti-predatory function of eggs background color and markings, but experimental studies have provided mixed evidences for this hypothesis (Nguyen et al.2003, Westmoreland 2008, Lee et al. 2010, Lovell et al. 2013, Skrade and Dinsmore 2013).

Despite this theoretical and empirical background, the anti-predatory hypothesis of egg color is still surprisingly unresolved due to the following reasons: i) most of the studies were performed with artificial nests and quail eggs, known to attract more easily predators and do not have the anti-predatory strategies of natural nests (Götmark 1992, Jokimäki and Huhta 2000, Weidinger 2001, Purger et al. 2008, Purger et al. 2012); ii) many studies do not consider the effect of covariates related to the nesting site, which frequently explain predation, such as vegetation density, nest height, canopy cover (Götmark 1992, Weidinger 2001, Purger et al. 2008, Purger et al. 2012); iii) because it is a defense against visual predators, nests depredated by nocturnal olfactory predators should not be considered in the analyses, however, only a few studies have used predators detection devices (Götmark 1992, Larivière 1999, Weidinger 2001, Lahti 2009), and predators identification based on indirect evidences, like bite marks, is imprecise (Marini and Melo 1998). Identification of these predators is important because they affect the interpretation of the results due to their foraging strategies (Benson et al. 2010, Ibáñez-Álamo et al. 2015); and iv) at least some works have been done in altered areas where predators communities and nest predation rates are not natural (Weidinger 2001, Purger et al. 2008, Purger et al. 2012). In addition, the vast majority of the existing works were performed in temperate environments, where the visual component may be different compared to the shadowed rainforest environments (but see Zanette 2002, Lewis et al. 2009, Oliveira et al. 2013, Rodrigues et al. 2018).

In this work we add knowledge to this caveat by testing the effect of egg color on nest predation rate, by using natural nests of the Blue Manakin, *Chiroxiphia caudata* (Shaw and Nodder, 1793), as a model species, and plasticine eggs. Our study was conducted in a preserved area of Atlantic Forest; nests were full-time monitored for predators identification using camera traps, and the joint effect of a number of covariates commonly known to affect nest predation was addressed.

METHODS

Study Area

Field work was conducted at Carlos Botelho State Park, PECB (24.0655° to 24.1441°S, 47.4718° to 48.0717°W), São Paulo State, southeastern Brazil. This Park holds 37,644 ha of Atlantic Rain Forest, and together with a set of adjacent conservation units, it comprises one of the largest Atlantic Forest remnant in Brazil, with more than 1 million ha. This is one of the few tracts of Atlantic Forest left in which the whole assemblage of large carnivores still persists and in which the original elements of this ecosystem are still preserved (Brocardo et al. 2012). Altitude varies from 30 to 1,003 m and annual rainfall varies from 777–2,264 mm (average 1,676 mm) (Beisiegel and Mantovani 2006).

Model Species

The Blue Manakin (*Chiroxiphia caudata*) is common in both primary and secondary humid Atlantic Forest in southeastern Brazil, northeastern Argentina and eastern Paraguay (Ridgely and Tudor 1994). Nests are shallow cups attached at their rim to horizontal forks in bushes or saplings with slender branches and they are usually built over or close to forest streams. Reproductive activities can be recorded from October to February and clutches invariably consist of two eggs, with background color varying from beige to light-brown. Egg markings consist of light or dark brown round or elongated blotches, that can be concentrated in the large end or form a crown near the large end (Figure 1A). The incubation period is 18 days and nestling periods vary from 15 to 16 days (Zima et al. 2017).

We considered the nest of this species as a good model because they construct open nests in forest understory, where it is one of the most abundant bird species. Further, their nests persist in the field in good conditions for up to two years, are abundant, and are not reused (Zima et al., 2017).

Field Procedures

The experiment was conducted between September and March to coincide with the reproductive period of Blue Manakin (Zima et al., 2017). We searched for nests during two breeding seasons, 2016/2017 and 2017/2018, by monitoring approximately seven kilometers of trails, and three kilometers of streams, in a sub-montane area varying in altitude from 680 to 850 m (Oliveira-Filho and Fontes 2000). The search for nests, and consequently the experiment, were carried out on the bank of three rivers within the PECB: Ribeirão Grande, Ribirão de Pedras, and Rio Taquaral. Nests were located when the females left the nest with our approach, or by chance, since manakins do not exhibit territorial behavior.

The nests used in this work were nests of the previous breeding season, and when nests of the same season were used, a minimum interval of two months between the last registered activity was respected.

For the experiment, plasticine eggs were made in three color patterns: all white (Figure 1B), white with brown spots (Figure 1C), and all brown (Figure 1D). For this, we used atoxic plasticine with the necessary colors. In each nest, a pair of eggs of the same pattern was placed, and for that, the sequence above was adopted for the definition of which egg pattern would be placed in each nest. The eggs were exposed for a period of 18 days, which coincides with the incubation period of this species. Predation was considered when eggs disappeared from a nest or when potential predators were filmed (see methods bellow) removing or biting the eggs.

Figure 1. (**a**) Nest and natural eggs of Blue Manakin; (**b**) All white plasticine eggs; (**c**) White with brown spots plasticine eggs; (**d**) All brown plasticine eggs.

Nests Monitoring

For nests monitoring, in order to identify predators, we used 68 digital camera traps Bushnell TrophyCam, model 119437C (Bushnell Outdoor Products, Kansas, USA). Cameras were positioned 1–3 m from each nest, according to the availability of natural supports like trunks or branches to support the camera-trap. Videos of 30 seconds were used in the monitoring, as they are better than photos to identify real predators, and to distinguish animals that only examine the contents of the nests without causing damage to them, besides the precise identification that allowed us to separate visual and olfactory predators (Ribeiro-Silva et al. 2018).

To measure the density of vegetation around the nest, we used the first 50 cm of a metal measuring tape passing it horizontally from the nest border to the four cardinal directions, as well as up and down the nest, and we counted the number of 10 cm stretches that were touched by the vegetation. The vegetation density was calculated as the number of 10 cm intervals contacts divided by all intervals (*n* = 30) (Mezquida 2004, Davis 2005).

To measure forest canopy cover we used a spherical densitometer. The same observer positioned the equipment close to its chest, in front of the nest, and the numbers of grids with light reflects in the convex mirror were obtained in the four cardinal directions. A mean was calculated for each nest multiplying each value by 1.04 to have the measure of the area not covered by the vegetation and later that value was subtracted from 100, to obtain the area a relative value of canopy cover. Distance from water was treated as a categorical factor, i.e. on the top of water or not. To make these variables comparable, they were all *ln*-corrected.

Statistical Analyses

The effect of egg color on nest predation was modeled using Logistic Generalized Linear Models (GLM) with Logit Link-Function. For the binary response variable, 0 represented nest success and 1 nest predation. To control for potential explanatory variables other than egg color, we also considered the following covariates: vegetation density, canopy cover, height above ground, and distance to the nearest water course.

Nest success was estimated using the method of Mayfield (1961), to have the daily survival rate of each color pattern, and we used the formula presented by Hensler and Nichols (1981) to compare the survival rates between the different egg patterns.

We used the R package MuMIn (Bartón 2013) to generate all possible candidate GLM models. This package was also used to rank the models according to corrected Akaike Information Criterion (AICc) (Burnham and Anderson 2002), and to calculated ΔAICc, which is a measure of each model relative to the best model, i.e. AICc of model *i* minus the AICc value of the best model, and Akaike weights (*w*), which is the probability that a target model is the best among all candidate models. Selected models were those presenting ΔAICc ≤ 2, which indicates substantial evidence for the model (Burnham and Anderson 2002). Then, a Log-Likelihood test was used to test model fit, by comparing each model to a reduced model in which explanatory variables are omitted, and *p* values were obtained using chi-square distribution.

RESULTS

The experiment involved 78 nests of Blue Manakins, being 26 for each treatment. Four nests were eliminated from the analyses because they were: depredated by a nocturnal marsupial (one nest with white with brown spots eggs); the eggs fell down during a heavy storm (one nest with natural pattern eggs); the eggs fell down because of the passage of a group of coatis (*Nasua masua*) that used the nest branch to jump from one three to another (one nest with all-brown eggs), and in one case (all-white eggs) the eggs disappeared but the videos did not permitted to detect the reason. Of the remaining 74 nests, 11 (14.86%) were depredated by visually oriented animals (Figure 2), being five with white eggs (20%), four with the natural pattern (16%), and two with the brown color (8.33%). Nests were attacked by six bird species (Table 1), and The Red-breasted Toucan (*Ramphastos dicolorus*) was main predator (four of 11 predations; 36.4%), and the only that attacked the three egg patterns (Table 1).

Figure 2. (**a**) White-eyed Foliage-gleaner; (**b**) Greenish Schiffornis; (**c**) and (**d**) Red-breasted Toucan.

Table 1. Visual predators of each type of egg pattern and quantities of predation events for each predator.

Egg color pattern	Potencial predators	Nº of events
All white	Buff-fronted Foliage-gleaner (*Philydor rufum*)	1
	Red-breasted Toucan (*Ramphastos dicolorus*)	2
	White-eyed Foliage-gleaner (*Automolus leucophthalmus*)	1
	Eastern White-throated Spadebill (*Platyrinchus mystaceus*)	1
White with brown spots	Red-breasted Toucan (*Ramphastos dicolorus*)	1
	Red-crowned Ant-tanager (*Habia rubica*)	1
	Greenish Schiffornis (*Schiffornis virescens*)	2
All brown	Uniform Finch (*Haplospiza unicolor*)	1
	Red-breasted Toucan (*Ramphastos dicolorus*)	1

Probabilities of survival during the time of the experiment using the Mayfield (1961) method were: 81% for white eggs, 85% for the natural pattern, and 92% for the brown eggs. White eggs were depredated on average 7.2 days after the beginning of the exposure (1 - 15 days), while average time to predation was 9.5 days for the natural pattern (1 - 18 days), and 9.5 days (2 - 17 days) for the brow eggs. Considering the two groups with the greatest difference probability of survival, we did not find significant differences in predation rates (*p*-value = 0.111).

Seven of the 32 potential GLM models presented AICc values lower than two (Appendix), and egg color was present in two of them. However, the best model had a single parameter (distance from water), and its Akaike Weight value was an order of magnitude higher than the second model. Distance from water was also the most frequent covariate, present in four of the seven models. The only covariate not present in the seven selected models was nest height above ground. (Table 2).

Table 2. Ranking of the models with the best Akaike weight values (*w* ≤ 2). χ2 represent the value of the Likelihood Ratio Test (χ2), *P* represent its significance.

Model Rank	**Model**	**AICc**	**ΔAICc**	***w***	**Res Dev**	**χ2**	***P***
1	Pred ~ - 1.7093 + 0.3877 X $DistH_2O$	68.1	0.11	0.102	63.945	2.0059	0.1567
2	Pred ~ - 1.756 + 0.3879 X DensVeg	68.9	0.89	0.069	64.729	1.225	0.2691
3	Pred ~ - 1.764 - 0.4277 X DensVeg + 0.4009 X $DistH_2O$	68.9	0.91	0.069	62.572	3.3782	0.1847
4	Pred ~ - 1.686 - 0.2894 X Dossel	69.4	1.37	0.054	65.21	0.7418	0.3891
5	Pred ~ - 1.740 - 0.2898 X Cor + 0.4143 X $DistH_2O$	69.5	1.50	0.051	63.16	2.7879	0.2481
6	Pred ~ - 1.679 - 0.2467 X Cor	69.5	1.51	0.051	65.35	0.5984	0.4392
7	Pred ~ - 1.734 + 0.3722 X $DistH_2O$ + 0.2749 X Dossel	69.7	1.67	0.047	63.34	2.6137	0.2707

DISCUSSION

Despite the lack of significance in nest survival probabilities among egg color treatments, there was a tendency predation reduction with increasing egg pigmentation. One potential explanation for the lack of statistical support is the lower nest predation rate in general.

Mayfield nest survival estimate for 16 natural nests of the Blue Manakin in incubation stage was 85% (Zima et al. 2017), which was similar to the same estimates for natural pattern eggs. In Ribeiro-Silva et al. (2018), who worked in the same area, the diurnal predators observed attacking nests of the Blue Manakin were White-necked Hawk (*Amadonastur lacernulatus*), Red-breasted Toucan, Barred Forest-Falcon (*Micrastur ruficollis*) and Buff-fronted Foliage-gleaner. In our experiment White-eyed Foliage-gleaner, Eastern White-throated Spadebill, Red-crowned Ant-tanager, Greenish Schiffornis and Uniform Finch were added to the list of predators. These are small birds that probably were not detected in natural nests because they could be easily displaced by the parental females. The fact that the work was carried out in a well preserved area, and therefore with low rates of predation in other studies conducted in the same location, it may have been preponderant to the low number of predations obtained in this work.

Another thing that may have contributed to the lack of significance is the fact that Red-breasted Toucans were the most frequent predators. This was already expected because in a work on active natural nests, in the same locality, Ribeiro-Silva et al. (2018) had already registered the Red-breasted Toucan as the main predator of Blue Manakin nests. As they were registered depredating nests with the three egg patterns, it suggests that this is a specialized nest predator, which can be guided by the image of the nests *per se* (Croze 1970, Martin 1988, Martin 1995, Langley et al. 1996, Šálek and Zámečník 2014), rather by the view of its contents.

It is important to note that we are confident that our cameras have not missed predation events for two reasons: first because these cameras were proved to be able to record all of the nest predators present in the study area (Ribeiro-Silva et al. 2018), and second because egg markings were never present in the eggs from nests for which predators were not detected by the cameras.

In summary, although some models were selected with good AICc values, no variables were significant enough to be considered the cause of the predations presented in this study. This may be due to the fact that visual predators may base their searches directly on the nests (Møller 1988, Cresswell 1997, Martin et al. 2000), which may be seen before the contents of the nests.

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P.V.Q.Z., D.F.P. and M.R.F. conceived the idea. P.V.Q.Z. and D.F.P. performed the experiments. P.V.Q.Z. and M.R.F. analyzed the data. P.V.Q.Z. and M.R.F. wrote the paper, with all authors contributing substantially to revisions.

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APPENDIX

```
Global model call: glm(formula = Pred ~ Cor + Altur + Dossel + DensVeg + 
DistHdO, 
    family = binomial(logit), data = data)
---
Model selection table 
   (Intrc)     Altur     Cor   DnsVg  DstHO  Dossl df  logLik AICc delta weight
1   -1.658                                           1 -32.975 68.0  0.00  0.108
9   -1.709                           0.3877          2 -31.972 68.1  0.11  0.102
5   -1.706                   -0.3879                 2 -32.365 68.9  0.89  0.069
13  -1.764                   -0.4277 0.4009          3 -31.286 68.9  0.91  0.069
17  -1.686                                  0.2894   2 -32.604 69.4  1.37  0.054
11  -1.740           -0.2898         0.4143          3 -31.581 69.5  1.50  0.051
3   -1.679           -0.2467                         2 -32.676 69.5  1.51  0.051
25  -1.734                           0.3722 0.2749   3 -31.668 69.7  1.67  0.047
10  -1.720 -0.178800                 0.4416          3 -31.840 70.0  2.01  0.039
2   -1.658 -0.015680                                 2 -32.974 70.1  2.11  0.038
15  -1.794           -0.2749 -0.4246 0.4233          4 -30.947 70.5  2.46  0.032
7   -1.727           -0.2371 -0.3865                 3 -32.097 70.5  2.53  0.031
21  -1.721                   -0.3452        0.2200   3 -32.148 70.6  2.63  0.029
29  -1.775                   -0.3882 0.3874 0.1937   4 -31.135 70.8  2.84  0.026
19  -1.709           -0.2566                0.3009   3 -32.284 70.9  2.90  0.025
14  -1.773 -0.156000         -0.4227 0.4447          4 -31.192 71.0  2.95  0.025
6   -1.706  0.008289         -0.3883                 3 -32.364 71.1  3.06  0.023
27  -1.769           -0.3017         0.3999 0.2919   4 -31.249 71.1  3.06  0.023
18  -1.686  0.016000                        0.2920   3 -32.603 71.5  3.54  0.018
12  -1.747 -0.132700 -0.2695         0.4533          4 -31.514 71.6  3.59  0.018
4   -1.679  0.040200 -0.2553                         3 -32.669 71.7  3.67  0.017
26  -1.738 -0.144400                 0.4154 0.2491   4 -31.587 71.7  3.74  0.017
23  -1.744           -0.2462 -0.3403        0.2325   4 -31.860 72.3  4.29  0.013
31  -1.808           -0.2856 -0.3803 0.4103 0.2124   5 -30.770 72.4  4.40  0.012
16  -1.802 -0.122600 -0.2615 -0.4246 0.4578          5 -30.892 72.7  4.65  0.011
8   -1.727  0.052260 -0.2460 -0.3877                 4 -32.085 72.7  4.74  0.010
22  -1.721  0.021160         -0.3454        0.2221   4 -32.146 72.9  4.86  0.010
30  -1.783 -0.141700         -0.3893 0.4275 0.1783   5 -31.059 73.0  4.98  0.009
20  -1.712  0.081750 -0.2746                0.3157   4 -32.255 73.1  5.08  0.009
28  -1.771 -0.088580 -0.2871         0.4254 0.2746   5 -31.221 73.3  5.31  0.008
24  -1.745  0.073240 -0.2597 -0.3384        0.2419   5 -31.838 74.5  6.54  0.004
32  -1.813 -0.100600 -0.2727 -0.3849 0.4386 0.1985   6 -30.734 74.7  6.70  0.004
Models ranked by AICc(x) 
```

2.2. Nest site selection near nest-like structures: an empirical test with the Atlantic Forest endemic Blue Manakin (Chiroxiphia caudata)

INTRODUCTION

Beyond the basal function of providing an adequate environment for eggs and young development, various aspects related to nest architecture and nesting sites have been attributed to nest predation avoidance (Collias 1997, Mainwaring et al. 2014, Noske et al. 2013). In face of the great amount of nest designs across taxa and habitats (Mainwaring et al. 2014) many anti-predatory strategies and hypotheses to explain their evolutions have been proposed, yet many of them are still poorly addressed (Mainwaring et al. 2014, Ibáñez-Álamo et al. 2015, Noske et al. 2013). The "potential prey-site hypothesis" (Martin and Roper 1988, Martin 1993) infer that predators efficiency to find sedentary preys, such as nest contents, using search images may decrease with increasing number of unoccupied sites to be searched. Chalfoun and Martin (2009) provided empirical support for this hypothesis by considering the numbers of potential nesting bushes in territories of the Brewer's Sparrow, *Spizella breweri*, as unoccupied sites, and they evidenced that these birds have selected nesting sites with higher numbers of unoccupied sites, and that survival was higher in these places. Noske et al. (2013) added to this idea by considering old nests present near the active ones as unoccupied prey-sites, and revealed that the Large-billed Gerygone, *Gerygone magnirostris*, constructed their nests near old nests, which resulted in lower predation probability likely because nest predators might give up foraging when surrounding nests are empty (Noske et al. 2013).

Here we extend this theory by addressing nest-like structures. In tropical forests ornithologists have long perceived that nests of many species can resemble clumps of vegetation or of debris, not only in composition but often also in shape (Hansell 2000, Noske et al. 2013). It is unclear, however, whether nests of certain species have evolved to match these structures or if the similarity is caused by the use of the materials available in each site, which could make them inconspicuous to human eyes simply by chance (see Bailey et al. 2015). Under the perspective of the potential prey-site hypothesis, it poses a question of whether these types of nests have evolved to imitate nest-like structures that could serve as unoccupied prey-sites.

To address this issue, we investigated nest site selection in the Blue Manakin, *Chiroxiphia caudata*, a forest-dwelling passerine endemic to the Atlantic Forest, which nests closely resemble depositions of debris, commonly found in its environment. As both nest site choice and the distribution of these structures might be influenced by multiple habitat parameters, we predict that if nest site selection and nest survival are correlated to the abundance of closely similar nest-like structures, then nest architecture in the Blue Manakin might have evolved to match these debris deposits to use them as unoccupied prey-sites.

We reveal a strong association between the numbers of nest-like structures, as well as vegetation density, and the choice of nest sites by the Blue Manakin, suggesting that nest architecture in this species could have evolved to match these structures. On the other hand, the numbers of nest-like structures surrounding the nests were not among the main covariates explaining nest survival, which may be a by-product of the strong selection *per se*, indicating the need of further experimental works involving the removal of the nest-like structures in control groups of nests.

We predict that if birds select nest sites with structures similar to their nests, than nest architecture may have evolved to imitate these structures.

METHODS

Study species

The Blue Manakin, *Chiroxiphia caudata* (Pipridae), is a small frugivorous passerine (23.4g) endemic to the Atlantic Forest, where they are common elements in the forest understory. Its distribution ranges from southeastern Brazil, in southern Bahia, Minas Gerais and southern Goiás to Rio Grande do Sul states, and eastern Paraguay and northeastern Argentina (Ridgely and Tudor 1994). They are remarkable for male's lekking pre-copulatory displays, and while males are brightly colored, females are olive green (see Ridgely and Tudor 1994 for descriptions). Like all of the members of the family Pipridae, only females construct the nests and provide parental care. Nests are shallow open cups with 7 - 9 cm in outer diameter, attached to their rim to slender horizontal forks of saplings ore shrubs, in which they typically lay two eggs (Zima et al. 2017). Nest wall consists of a variety of leaf rachises, tendrils, rootlets, and black fungal filaments, with outer surface often adorned with tufts of green moss and dry or green leafs. In general appearance they are brown with small spots of green materials, and at a distance they remind the agglomerates of debris that are often formed on the top of horizontal forks by the retention of materials that fall down from the top of the higher trees. The similarity is even more remarkable due to the amount of loose material that rung from the bottom of the nests, which forms a tail that can vary from 8 cm to 1.25 m in length (Fig 1).

Fig.1. Natural nest of the Blue Manakin (in blue) surrounded by nest like structures (in red)

We chose the nests of Blue Manakin as a model, being an abundant species in the work area, the easy access to the nests, their quantity, besides the fact that the nests remain for long period in good conditions (Zima et al. 2017).

Study area

Our study was conducted in Carlos Botelho state Park (24°06’55” to 24°14’41”S, 47°47’18” to 48 07’17” W), São Paulo state, Southeastern Brazil. The area of the park totals 37,644 ha, but together with a set of protected areas it composes one of the largest remaining Atlantic Forest continuous, with more than 1.1 million ha. For this reason, this is one of the few Atlantic Forest areas in which the original faunal composition is still preserved. (Brocardo et al. 2012). The vegetation in the park is mainly primary Atlantic Forest, and nest searches were conducted in a region in which altitudes range from 700 to 840 m a.s.l. and vegetation is classified as submontane rain forest (Oliveira-Filho and Fontes 2000). Average annual temperature ranges from 18 to 21°C, and the mean annual precipitation varies from 777–2,264 mm (Ferraz and Varjabedian 1999).

Field procedures

During three breeding seasons, nests were searched one to three times a week, from October to February, which corresponds to the reproductive period of the Blue Manakin (Zima et al. 2017). Nests were searched alongside two different forest streams, Ribeirão de Pedras and Ribeirão Grande, in the interior of primary forests. The sections of these rivers used by us summed 4 km, and in their closest portions, these searching areas were 4.5 km far from each other. As this species do not exhibit any territorial behavior, nests were located by the displacement of incubating females and by checking the surrounding vegetation. After found, nests were checked every 1-7 days, but checking was intensified near fledging age. In addition, all nests were also monitored with the aid of cameras-trap Bushnell TrophyCam, model 119437C (Bushnell Outdoor Products, Kansas, USA).

Nest site selection

To test the theory that the Blue Manakin can select nesting sites based on the amount of nest-like structures, we compared the numbers of these elements in a 3m radius surrounding natural nests and in random sites. We considered nest-like structures the agglomerates of debris present in branches, which resulted in platforms or a pack of vegetal material that reminded a nest cup, that were similar in color to the nests of the Blue Manakin, and had loose material forming a tail underneath. Tufts of green moss or of the pendant stems of the Spanish Moss, *Tillandsia* sp. (Bromeliaceae) with similar characteristics were not discarded when they had the above mentioned format, and had debris attached to them, giving them a predominantly brown coloration.

Random sites were established 30 m far from each natural nest, following the water course. To choose each site we assorted between up- or downstream, and right or left sides of the stream. Then, we adopted the same distance from the stream edge as the natural nest, inward or outward the water limits, and took the measurements from the nearest horizontal fork from the nearest sapling or shrub. To control to other covariates that often affect nest site choice, we also measured: vegetation density and forest canopy cover. To estimate vegetation density we used a 50 cm metal measuring tape that was pointed from nest border or from the random site (at the same height above ground or water) to the four cardinal directions, as well as up and down, and we measured the number of 10 cm stretches that were touched by the vegetation. Then, vegetation density was considered as the number of 10 cm interval contacts divided by the total number of intervals (n = 30) (Mezquida 2004, Davis 2005). To estimate forest canopy cover we used a spherical densitometer, Convex Model-A, Forest Suppliers, Inc., following the manufacturer instructions. The same observer positioned the equipment close to its chest, but distant enough to the observer head to be outside the grids, in front of the nest or in the random point, and the numbers of grids with light reflects (maximum of 96) in the convex mirror were obtained in the four cardinal directions. Then, this value was averaged across the four cardinal directions and this figure was multiplied by 1.04 to obtain an estimate of the area not covered by the vegetation. Finally, the resulting value was subtracted from 100 to obtain the relative estimate of canopy cover (Lemmon 1956).

To compare the variable estimates between nests and random sites, we first performed a Principal Component Analysis (PCA) to reduce the number of variables, with data corrected using z-score and correlation matrix. Then, the new scores obtained for the main axis were compared using t-test. These analyses were carried out using the software Past3 (Hammer et al. 2001), with 95% significance level. Then, to elucidate which variables were contributing to the potential difference we performed a model selection procedure using Generalized Linear Models, with binary distribution and logit link-function. Nest sites were coded as 1 and random sites were coded as 0, and all of the possible models and also de null model were exploited by using the dredge-function of the R-package MuMIn. Candidate models were ranked according to their relative support using the Akaike's Information Criterion corrected to small samples (AICc) (Burnham and Anderson 2002), as well as by the ΔAICc, which is a measure of each model relative to the best model, and Akaike weights (*w*), which is the probability that a target model is the best among all candidate models. Selected models were those presenting $\Delta\text{AICc} \leq 2$, which indicates substantial evidence for the model (Burnham and Anderson 2002). Model parameter estimates, their standard errors (se) and 95% confidence upper and lower limits are reported to indicate the importance of each variable to the selected models. Further, Z-tests were carried out to test the importance of each variable within the selected models, i.e. if they differed significantly from zero.

Nest survival

To address whether nest survival could be correlated to the abundance of nest-like structures, we modeled it by using the binomial generalized linear model approach of Dinsmore et al.

(2002) with maximum likelihood parameter estimates, as implemented in the R-package RMark 2.2.6. (http://www.phidot.org/software/mark/downloads/), an interface of the software MARK (White and Burnham, 1999). With this framework, Daily Survival Rates (DSR) are estimated as a function of time-dependent or other pre-defined variables (Rotella et al. 2004), and we used default sin-link and logit-link functions.

A nest was considered successful when it fledged at least one young, and predation was considered when eggs or young disappeared in early developmental stage, before fledging age. Nest fate was coded as 0 (successful) or 1 (depredated). As time dependent covariates we included "NestAge", to measure the effect of nest age in survival probability; "Time" to address the temporal effect of across the breeding season, and "Year" to address whether DSR can vary across different reproductive seasons. We also controlled to the following covariates that could affect nest survival: distance from water, canopy cover, nest height above ground or water, and vegetation density. All of these non-temporal covariates were standardized using score-z, and the corrected variables were considered as autocorrelated when they presented high Pearson correlation coefficient ($r \geq 0.6$), or significant correlation using Pearson correlation test, under a significance level of 0.05. To achieve an adequate sample size, we pooled samples from the three breeding seasons. As nest height was significantly correlated to water distance ($r = 0.4157$, $P = 0.0248$) and to nest tail length ($r = 0.4124$, $P = 0.0261$), then, they were not used in the same modeling, although they explained only 17% of the variation of one another.

RMark was used to generate all possible candidate models and to rank them according to their relative support using the corrected Akaike's Information Criterion (AICc) (Burnham and Anderson 2002), and to calculated ΔAICc, which is a measure of each model relative to the best model, and Akaike weights (w), which is the probability that a target model is the best among all candidate models. Selected models were those presenting $\Delta AICc \leq 2$, which indicates substantial evidence for the model (Burnham and Anderson 2002). Model parameter estimates, their standard errors (se) and 95% confidence upper and lower limits are reported to indicate the importance of each variable to the selected models. All statistical methods were conducted in RStudio 1.1.423 (RStudio Team 2016).

Nests that were abandoned; lost due to accidental fall, or had the fate undetermined were not used in these analyses. In three breeding territories old nests were present but due to the low frequency this was not included as a variable (see Noske et al. 2013).

RESULTS

Nest site selection

During three breeding seasons (2016/2017, 2017/2018, and 2018/2019) we found 42 active nests of the Blue Manakin. Numbers of nest-like structures, and values for canopy cover, and vegetation densities for nest and random sites are depicted in Fig. 2. The Principal Component Analysis indicated that the two main axes explained 73% of the total variation, with the first axis explaining 40% (Fig. 2). The t-test using the new scores of the main axis was highly significant ($t = 4.752$, $P < 0.0001$), suggesting that the values for the variables have differed between nesting and random sites. Model selection procedure indicated only one model of the eight candidate models as presenting $\Delta AIC < 2$. This model included the variables nest-like structures and vegetation density ($AICc = 99.7$; $w = 0.6$), with the two variables differing significantly from zero (Table 1).

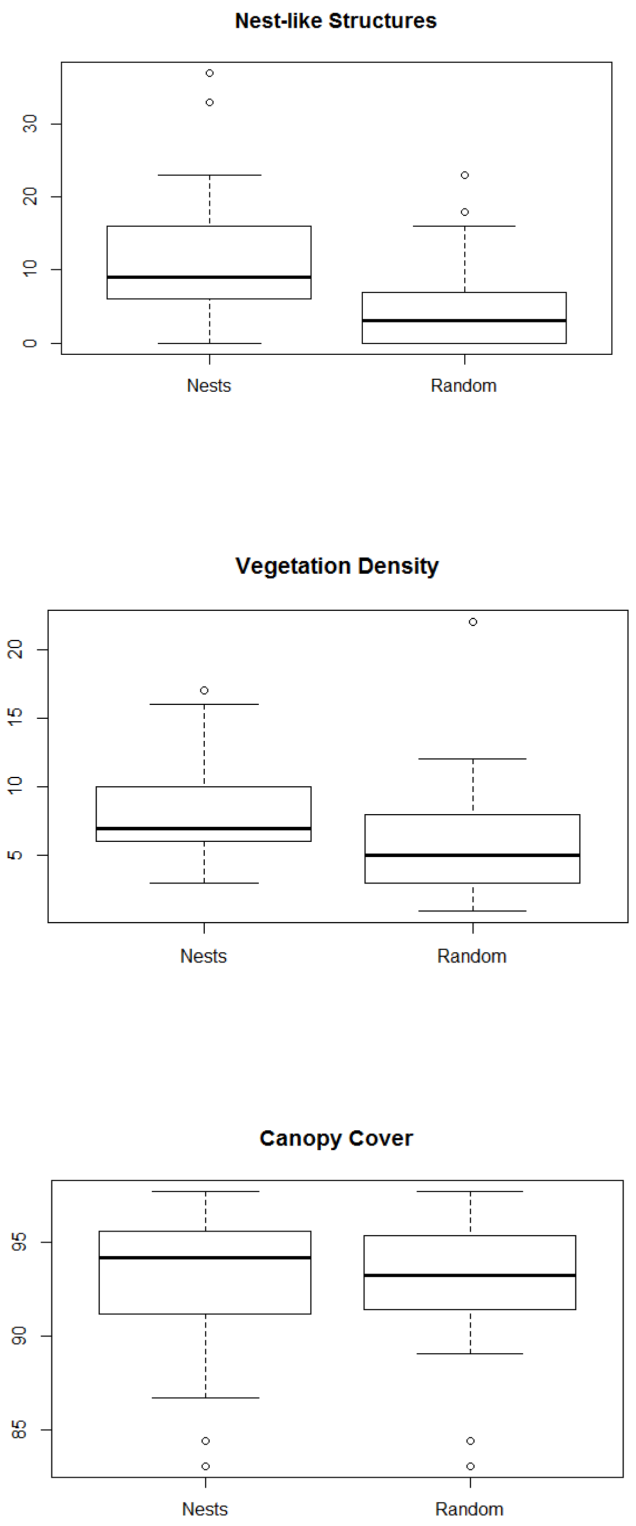

Figure 2. BoxPlots depicting values obtained in nest sites and at random sites for (A) numbers of nest-like structures; (B) vegetation density not divided by the number of 10 cm intervals, and (C) canopy cover.

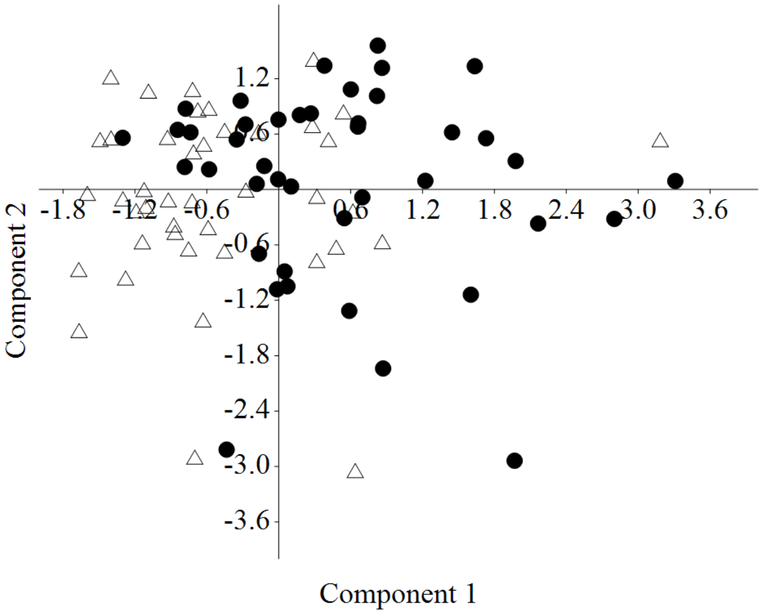

Figure 3. Principal Component Analysis (PCA) showing the distribution of nest sites (black dots) and randomly chosen sites (triangles) based on numbers of nest-like structures in a 3m radius, vegetation density, and canopy cover.

Table 1. Maximum likelihood parameter estimates, standard error (SE), lower and upper 95% confidence interval (IC), and value of the Z-statistic used to test whether parameters have differed significantly from zero (Z-value), and its significance (P) for the best candidate model to explain nest site selection in the Blue Manakin in a Brazilian Atlantic Forest area.

Model Parameters	**Estimate**	**SE**	**Lower/Upper 95% IC**	**Z value**	**P**
Intercept	0.0927	0.2566	-0.406 - 0.609	0.361	0.71790
Structures	1.0956	0.3341	0.495 - 1.819	3.280	0.00104**
Vdens	0.6169	0.3001	0.071 - 1.258	2.055	0.03984*

Nest survival modeling

Excluded six nests that were abandoned, two that feel down after heavy storms, and five for which fate was undetermined, the number of nests used in the modeling analyses dropped to 29. In the modeling containing nest height, AIC model ranking returned three models with

ΔAIC < 2, and the best model included the variables nest height, canopy closure, numbers of nest-like structures and the time-variables year and NestAge. The covariates canopy, year and numbers of nest-like structures were present in all of the three models and the covariates vegetation density and time were never present. Within these models, canopy closure was positive and its upper and lower 95% CI never overlapped zero, while the covariates year and numbers of nest-like structures were negatively correlated to DSR, but also with upper and lower 95% CI not overlapping zero. Although nest height and NestAge were present in the best model, they showed vary low parameter estimate values and their upper and lower 95% CI overlapped zero (Table 2). In the analyses from which nest height was excluded, six models presented ΔAIC < 2, being canopy closure and year the only variables present in all of the models, and nest tail length the only covariate absent from all of the top-ranked models. Like in the above modeling, the canopy closure was positively while year was negatively correlated to DSR, and the upper and lower 95% CIs of these covariates consistently never overlapped zero. All of the other parameters presented upper and lower 95% CI overlapping zero in all of the selected models (Appendix). Overall, our body of analyses suggests that year and canopy cover are the two most robust variables explaining nest survival.

Table 2. Results of Daily Survival Rate model selection involving the variables vegetation density, Nest Height, canopy closure, numbers of nest-like structures, and the time-variables Year, Nest Ages and Time.

Model	**Δ AICc**	***W***	**NestHeight**	**Canopy**	**Structures**	**Year**	**NestAge**
NestHeight+Canopy+Structures+Year+NestAge	0.00	0.097	-0.025;SE=0.015 (-0.055-0.004)	0.875;SE=0.387 (0.115-1.635)	-0.929;SE=0.351 (-1.618- -0.241)	-1.463;SE=0.647 (-2.732- -0.193)	-0.086;SE=0.04 (-0.171- -0.001)
Canopy+Structures+Year+NestAge	0.3	0.083	-	0.914;SE=0.356 (0.215-1.613)	-0.825;SE=0.341 (-1.494- -0.155)	-1.542;SE=0.631 (-2.779- -0.305)	-0.069;SE=0.039 (-0.147-0.007)
Canopy+Structures+Year	1.6	0.045	-	0.707;SE=0.309 (0.100-1.314)	-0.628;SE=0.307 (-1.23- -0.026)	-1.356;SE=0.619 (-2.569- -0.143)	-

DISCUSSION

Testing if bird's nests evolved to match certain structures present in their habitats is not straightforward, but in the present study a number of indirect evidences provides support for this idea. Birds could have chosen to build their nests near structures that remind their own nests just because they use these structures as sources of nest material, and being closer to them would reduce the energetic costs of nest construction. However, the close similarity between the Blue Manakin nests and the debris deposits is caused by the deposition of certain materials in the outer layers of the nests, while the materials used in nest walls and in the incubatory chamber are different, then, if Blue Manakin females are collecting nest materials directly from these nest-like structures, it would be in a smaller amount, reducing the support for this hypothesis. The presence of a nest-tail formed by loose materials can be hypothesized as a way to disrupt the nest image, breaking the nests outlines to confound nest identification by visual predators (Stevens et al. 2006, Bailey et al. 2015), and the similarities between Blue Manakin's nests and the debris deposits could occur because, by chance, these birds might have evolved to use similar materials in its nest's tails. The hypothesis of disruptive nest image caused by the nest tail cannot be discarded and might be addressed in future works, but alone it cannot explain the strong selection for nest sites in which the numbers of these nest-like structures are higher. Further, nest architecture in the Blue Manakin is poorly variable, suggesting that they are not simply using materials from structures that could be present in nesting areas by chance, but rather, they are actively seeking for places in which specific types of structures similar to their well-established nest formula are present. Then, our findings give support to a scenario in which the Blue Manakins selectively construct nests that match these deposits of debris in external shape, and are selected to build their nests near these structures, reflecting specialization rather than causality.

These findings corroborate partially the "potential prey-site hypothesis", as we found support for the prediction that birds might actively seek for places with higher numbers of unoccupied prey sites. Our modeling analyses also indicated support to an important prediction of the "total foliage hypothesis", that birds may actively seek for places with higher vegetation density, as our best model ranked by AICc also included vegetation density as second parameter explaining nest-site selection. However, we found no support for increased nest survival to explain the adaptive significance of such behaviors. Our modeling analyses revealed that other variables, i.e. year and canopy cover, are the main parameters influencing nest survival. Interannual variation in nest predation rates have been reported for many species from different environments, and it can result mainly from demographic fluctuations in predator populations, fluctuations in the types and amounts of resources available for these predators, influencing in their foraging decisions, or interannual variations in habitat characteristics, such as vegetation density (Dinsmore et al. 2002). In our first study season we evaluated only four nests, and the low number of nests was likely resulted from the most severe drought ever documented in southeastern Brazil, indicating that remarkable environmental variations can indeed occur in tropical forests in these latitudes. Further, the results of the modeling can be supported by our row data, as in 2017/2018, 29% (four of 14 nests) of the nests were depredated and in 2018/2019 a much higher percentage of nests was lost to predation (64%; seven of 11 nests). Canopy cover is another parameter that frequently can explain nest survival, and like in the present study, it can often be negatively correlated to survival. It can affect the visual component of predators, as more illuminated sites, such as in forest clearings, but it also can reflect the diversity of predators, such the faunal components that seek for natural clearings to forage (Martin and Roper 1988, Twedt et al. 2001). However, visual predators avoidance as potential causal explanation for nest architecture evolution and nest site choice in the Blue Manakin may not be yet discarded because in addition to the effects of Year and Canopy cover overcoming its effects, other potential scenarios also can explain the negative relationship and the lack of support for nest-like structures covariate reducing nest predation rate, and they must be investigated: First, there can be an effect of the olfactive predators in our nest survival modeling, although only one of seven predations in nests of Blue Manakins reported by Ribeiro-Silva et al. (2018) in the same study area was caused by a nocturnal mammal, being all of the others caused by diurnal birds, especially the Red-breasted Toucan, *Ramphastos dicolorus*. Second, with a so strong selection for sites containing nest-like structures, here only nests containing structures in a 3 m radius had their predation rates compared.

In summary, our nest site selection analyses gave support to the theory that nest architecture in the Blue Manakin has evolved to match the shape of the depositions of debris commonly found in saplings and shrubs from Atlantic Forest undergrowth. Although the theoretical background suggest that nesting near other nests, or as in the present case near nest-like structures, can be anti-predatory strategies, our nest survival modeling showed that the interaction between nest survival and habitat parameters can be complex and experimental studies involving the total removal of these structures from a controlled group of nests may be required for testing increased survival as the adaptive reason for this type of mimicry.

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P.V.Q.Z., D.F.P. and M.R.F. conceived the idea. P.V.Q.Z. and D.F.P. performed the experiments. P.V.Q.Z. and M.R.F. analyzed the data. P.V.Q.Z. and M.R.F. wrote the paper, with all authors contributing substantially to revisions.

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APPENDIX

Appendix. Results of Daily Survival Rate model selection for using the variables vegetation density, canopy closure, distance from water, tail length, numbers of nest-like structures, and the time-variables Year, NestAge and Time.

Model	**Δ AICc**	***w***	**Vdens**	**Canopy**	**DistH2O**	**Structures**	**Year**	**NestAge**	**Time**
Canopy+DistH2O+Structuress+Year+NestAge	0.00	0.075		1.058;SE=0.390 (0.293-1.824)	-1.017;SE=0.649 (-2.289-0.255)	-0.637;SE=0.355 (-1.333-0.059)	-1.63;SE=0.642 (-2.891- -0.375)	-0.080;SE=0.041 (-0.161-0.001)	
Canopy+DistH2O+Year+NestAge	0.77	0.051		0.909;SE=0.357 (0.208-1.612)	-1.209;SE=0.555 (-2.296-0.121)		-1.332;SE=0.559 (-2.427- -0.236)	-0.066;SE=0.039 (-0.144-0.012)	
Canopy+Structuress+Year+NestAge	1.22	0.041		0.914;SE=0.356 (0.215-1.613)		-0.824;SE=0.341 (-1.494- -0.155)	-1.542;SE=0.631 (-2.779- -0.305)	-0.069;SE=0.039 (-0.147-0.007)	
Canopy+DistH2O+Year	1.63	0.033		0.717;SE=0.314 (0.103-1.333)	-1.056;SE=0.574 (-2.181-0.069)		-1.179;SE=0.549 (-2.257- -0.103)		
Canopy+DistH2O+Structuress+Year+NestAge+Time	1.67	0.032		1.190;SE=0.459 (0.289-2.092)	-1.014;SE=0.656 (-2.299-0.271)	-0.670;SE=0.356 (-1.367-0.027)	-1.768;SE=0.672 (-3.086- -0.451)	-0.079;SE=0.042 (-0.162-0.004)	-0.006;SE=0.010 (-0.026-0.014)

Vdens+Canopy+DistH2O+Structures+Year+NestAge	1.87	0.029	-0.203; SE=0.469 (-1.123-0.716)	1.084;SE=0.409 (0.281-1.887)	-0.965;SE=0.612 (-2.164-0.235)	-0.624;SE=0.351 (-1.313-0.064)	-1.713;SE=0.653 (-2.994- -0.432)	-0.081;SE=0.041 (-0.162-0.000)

CONSIDERAÇÕES FINAIS

Apesar da baixa significância entre as probabilidades de sobrevivência dos tratamentos, parece haver uma tendência de dimiuição da probabilidade de predação conforme a pigmentação da casca aumenta.

A estimativa de probabilidade de sobrevivência de Mayfield para o experimento com ovos manchados foi a mesma para a encontrada em ovos naturais de *Chiroxiphia caudata* por Zima e colaboradores (2017).

Ramphastos dicolorus foi o predador mais frequente do experimento, predando ninhos com os 3 padrões de coloração, isso somado ao fato de também ter sido o principal predador no trabalho de Ribeiro-Silva e colaboradores (2018) mostra que ele é um predador de ninhos especialista, provavelmente se guiando pelo próprio ninho independente de seu conteúdo.

Apesar de alguns modelos terem obtido valores baixos de AICc, nenhuma variável foi significativa para ser considerada relevante para os valores de predação, e isso pode ser motivado pelo fato dos predadores buscarem diretamente os ninhos, já que o mesmo pode ser visto antes mesmo do conteúdo.

Nossas análises de seleção do local de nidificação deram suporte à teoria de que a arquitetura do ninho de *C. caudata* evoluiu para combinar com a forma dos depósitos de detritos comumente encontrados em mudas e arbustos de vegetação de sub-bosque da Mata Atlântica. Embora os fundamentos teóricos sugiram que nidificar próximo a outros ninhos, ou como no caso deste estudo, próximo a estruturas semelhantes a ninhos, possa ser uma estratégia anti-predatória, nossa modelagem de sobrevivência mostrou que a interação entre a sobrevivência dos ninhos e os parâmetros do habitat pode ser complexa e experimentos envolvendo a remoção total dessas estruturas com um grupo controle de ninhos pode ser necessário para testar o aumento da sobrevivência como a razão adaptativa para esse tipo de mimetismo.

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