

Universidade Federal de São Carlos
Campus São Carlos
Programa de Pós-Graduação em Ecologia e Recursos Naturais

Daniel Fernandes Perrella

Seleção de habitat para nidificação por aves em uma
área preservada da Mata Atlântica do sudeste do Brasil

Orientador: Dr. Mercival Roberto Francisco

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Orientador: Dr. Mercival Roberto Francisco

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sentem-nos ceder, mas cantam. Eles sabem que possuem asas”.

(Victor Hugo)

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RESUMO

Aves naturalmente apresentam determinadas exigências ecológicas para sobreviver nos ambientes complexos existentes nos habitats onde vivem e a capacidade de selecionar locais adequados e seguros para construção de ninhos tem se mostrado um fator adaptativo particularmente importante no ciclo de vida desses animais. Há décadas naturalistas têm relatado que em florestas Neotropicais diversas espécies de aves, mesmo não-aquáticas, nidificam próximo a corpos d'água. No entanto, estudos empíricos de seleção de locais de nidificação, bem como sobre a influência das características de riachos para o sucesso reprodutivo são escassos. Entre 2016 e 2018, foram estudados ninhos de aves de sub-bosque no Parque Estadual Carlos Botelho, São Miguel Arcanjo, SP e a influência dos riachos na seleção de locais de nidificação foram abordadas em três capítulos. No primeiro capítulo, a densidade de ninhos próximos a riachos presentes no interior da floresta primária foram comparadas com trajetos distantes de qualquer corpo d'água. No segundo e terceiro capítulos, para três das espécies que demonstraram selecionar locais de nidificação próximos às margens ou sobre os riachos (*Chiroxiphia caudata*, *Rhopias gularis* e *Onychorhynchus swainsoni*), variáveis como largura dos riachos, profundidade, velocidade da água, dentre outras, foram comparadas com pontos aleatórios para testar se estas espécies poderiam selecionar trechos de riachos com características específicas e para verificar se estas variáveis ambientais poderiam interferir no sucesso reprodutivo. Além disso, observou-se também para *O. swainsoni*, passeriforme ameaçado de extinção, outros parâmetros reprodutivos importantes para o entendimento da raridade da espécie, como medidas dos ninhos, ovos, períodos, fenologia reprodutiva, sucesso reprodutivo e densidade de casais ao longo dos riachos. Foram encontrados 63 ninhos de 18 espécies de aves próximos a riachos, onde a densidade foi de 5.3 ninhos/ha, enquanto longe deles houve apenas um ninho, representando uma densidade de 0.1 ninhos/ha. Foi demonstrado que nenhuma das três espécies estudadas selecionou os locais de nidificação com base nas características dos trechos dos riachos, sendo a densidade da vegetação ao redor dos ninhos o que determinou a escolha dos locais de nidificação para *C. caudata* e *O. swainsoni*. Com relação à influência das variáveis para a sobrevivência dos ninhos, para *R. gularis* foi demonstrado que a profundidade do riacho e distância da margem poderiam influenciar no sucesso reprodutivo. Foi evidenciado que *O. swainsoni* seleciona apenas riachos de maior porte para reprodução, apresenta baixa taxa reprodutiva e baixa densidade de territórios reprodutivos, o que deve contribuir com a raridade da espécie. O

presente estudo compreende o primeiro realizado na região Neotropical a fornecer informações sobre a densidade de ninhos em um remanescente preservado de Mata Atlântica e os riachos que permeiam suas florestas parecem compor um habitat significativo para diversas aves se reproduzirem, embora mecanismos envolvidos nessa seleção tenham se demonstrado diferentes para cada espécie estudada.

Palavras-chave: Ninhos; Riachos; Sub-bosque; Sucesso reprodutivo; Variáveis ambientais.

ABSTRACT

Birds naturally present a number of ecological requirements to survive in complex habitat environments where they live and the ability to select suitable and safe nesting sites has been shown to be a particularly important adaptive factor in the life cycle of these animals. In Neotropical forests, naturalists have long suggested that even non-aquatic birds often do reproduce near water bodies, which however, is still poorly addressed. From 2016 to 2018, nests of understory birds were studied at Carlos Botelho State Park, São Miguel Arcanjo, SP, and the influences of forest streams for nest site selection and nest survival were investigated, which is presented here in three chapters. In the first chapter, nests were searched near forest-streams and far from any watercourse in an attempt to compare nest density between these two situations. In the second and third chapters, nests of *Chiroxiphia caudata*, *Rhopias gularis* and *Onychorhynchus swainsoni*, which nested near or above forest streams, were monitored and we tested if these species could select specific stretches of the streams to build their nests, and we tested if stream characteristics, i.e. stream width, water depth, and water speed could interfere with their reproductive success. Further, in the third chapter, other reproductive parameters of *O. swainsoni*, which is endangered, were observed, such as nest and eggs measurements, incubation and nestling periods, breeding phenology, nesting success, and density of reproductive pairs along streams. We found 63 nests of 18 species along streams and only one far from them. We revealed that nest density was much higher near forest streams (5.3 nests/ha), than far from water (0.1 nests/ha). We showed that none of the stream covariates explained nest site selection for the three studied species, although water depth and distance to water were correlated to nest survival for *R. gularis*. In the third chapter we showed that *O. swainsoni* selected only the largest forest streams to establish their reproductive territories, and that their reproductive rates and breeding territory densities were low compared to other forest understory passerines, which is likely involved in its rarity. This study comprises the first carried out in the Neotropical region to provide information on nest density in a well-preserved Atlantic Forest remnant, and the streams that permeate this forest seem to provide important reproductive habitats for several bird species, although the mechanisms involved in nest site selection varied among the different species.

Key-words: Breeding success; Environmental variables; Nests; Rainforest; Streams; Forest Understory.

1. INTRODUÇÃO GERAL

As aves naturalmente apresentam determinadas exigências ecológicas para que possam sobreviver em meio aos ambientes complexos existentes nos habitats onde vivem (Temple 2004, Cintra & Cancelli 2008, Lees & Peres 2010) e a habilidade de selecionar locais capazes de oferecer abrigo, alimento e locais para reprodução têm sido considerada um elemento adaptativo relevante na evolução desse grupo de animais (Lack 1933, Mägi et al. 2009, Bailey et al. 2015). De fato, diversos estudos têm avaliado os efeitos da seleção de habitats sobre a história de vida das diferentes populações e comunidades de aves, uma vez que determinadas espécies apresentam-se bastante exigentes quanto à escolha de ambientes ideais para sua sobrevivência, enquanto outras são mais flexíveis ou mais influenciadas por um tipo de recurso específico do que pelo tipo de habitat em si (Lack 1933, Hildén 1965, Mägi et al. 2009, Rajpar & Zakaria 2011). Essa capacidade está envolvida com o reconhecimento das variáveis ambientais que instruem a ave em suas decisões, mecanismo inicialmente intrínseco em cada espécie, porém sujeito ao aprendizado após a experiência de vida de cada indivíduo (Hildén 1965; Dukas 2013).

Uma vez selecionado um habitat adequado para determinada espécie se estabelecer, espera-se que este forneça a ela condições, locais e material propícios para nidificação (Temple 2004). Há anos esse tema tem sido explorado e analisado em várias partes do mundo com foco em diferentes espécies (Hildén 1965, Jones 2001, Chalfoun & Schmidt 2012). Tais estudos costumam avaliar a seleção de habitat para nidificação em uma ou mais escalas diferentes, das quais a escala local (*nest site*), ou seja, aquela que considera o ponto específico onde o ninho está posicionado, frequentemente é a mais abordada (Aguilar et al. 2008; Murray & Best 2014). Há ainda a escala da mancha de habitat escolhida para construção do ninho (*nest patch*), onde se considera um espaço maior ao redor do local (Rodrigues 1994;

Mezquida & Marone 2002; Boves et al. 2013; Sánchez et al. 2013) e ainda a escala de paisagem (*nest landscape*), onde a avaliação é feita ao longo de todo o território onde determinada espécie se estabelece para exercer suas atividades reprodutivas (Boves et al. 2013; Sánchez et al. 2013).

Escolher um local apropriado e seguro para construção de um ninho é uma estratégia essencial adotada pelas aves para proteger suas proles e garantir (ou pelo menos aumentar) seu sucesso reprodutivo (Hansel 2000), afinal a fase de nidificação reflete um momento de sedentarismo temporário, onde ovos e filhotes estão extremamente vulneráveis às intempéries do tempo e a serem descobertos por predadores ou parasitas de ninho (Gjerdrum et al. 2005, Aguilar et al. 2008, Chalfoun & Schmidt 2012). De fato, diversos estudos envolvendo este tema demonstram que algumas características ambientais podem influenciar significativamente na taxa de sucesso dos ninhos (Rodrigues 1994; Aguilar et al. 2008; Sánchez et al. 2013; Murray & Best 2014). Em áreas abertas do Brasil Central, Aguilar et al. (2008) verificaram que para o tiziu, *Volatinia jacarina*, passeriforme comum que nidifica à pouca altura do chão (Sick 1997), as variáveis ambientais mais importantes na seleção do local de construção do ninho são a largura de arbustos, cobertura e altura da vegetação do entorno, ou seja, características que provavelmente ocultam o ninho contra predadores visualmente orientados (Aguilar et al. 2008). Murray & Best (2014) encontraram um resultado semelhante em seu estudo com *Geothlypis trichas*, um pequeno Paridae da América do Norte. Entretanto, a densidade da vegetação não foi relacionada à menor taxa de predação sobre a população da espécie, mas sim à menor frequência de ninhadas parasitadas por outras aves como *Agelaius phoeniceus* (Murray & Best 2014). Além da predação e do parasitismo, há outros fatores que podem influenciar o sucesso reprodutivo e exigir a seleção de características ambientais favoráveis, como as variações físicas dos pântanos de água salobra habitados por *Ammodramus maritimus* e *A. caudacutus* na América do Norte, onde há

inundações periódicas provocadas pela maré que forçam essas aves a posicionar seus ninhos em locais altos ou iniciar as atividades reprodutivas precocemente para garantir o sucesso de suas ninhadas (Gjerdrum et al. 2005).

Incoerências também fazem parte do cenário de estudos envolvendo seleção de locais apropriados para nidificação por aves. Existem casos nos quais se verificam que determinadas espécies selecionam variáveis ambientais que não corroboram com sua aptidão reprodutiva, ou seja, essas espécies estabeleceram seus territórios e construíram ninhos preferencialmente em habitats onde há menor chance de produzirem ninhadas bem sucedidas (Arlt & Pärt 2007; Mägi et al. 2009). Dessa forma, frente à elevada quantidade de material disponível sobre preferências de locais para nidificação, Chalfoun & Schmidt (2012) realizaram uma revisão dos estudos envolvendo aspectos relacionados à seleção de habitats reprodutivos, objetivando descrever e analisar os mecanismos que podem levar a tais incoerências entre as variáveis ambientais selecionadas pelas espécies e sua aptidão reprodutiva. Os autores ressaltaram que um dos principais problemas encontrados é a grande quantidade de estudos desenvolvidos em áreas alteradas por atividades humanas (Chalfoun et al. 2002; Chalfoun & Schmidt 2012), que poderia alterar a taxa de predação de ninhos e conduzir a conclusões equivocadas (Oniki 1979; Robinson & Sherry 2012).

Entre os tópicos levantados por Chalfoun & Schmidt (2012) sobre o que poderia acarretar na falta de congruência entre o habitat de nidificação preferencial das espécies e o sucesso reprodutivo, a influência de fatores ecológicos e/ou evolutivos foram frequentemente sugeridas como causadoras de tais discrepâncias em diversos estudos. Entre esses fatores, está a pressão seletiva exercida sobre a reprodução de espécies coexistentes que utilizam locais semelhantes para nidificar, acarretando na formação de agrupamentos de ninhos localizados a pouca distância uns dos outros (Martin 1996; Schmidt & Whelan 1998; Martin & Martin 2001). Tais agrupamentos aumentam a densidade de ninhos em um mesmo local e

consequentemente, a taxa de encontro por parte de potenciais predadores que estejam forrageando nas proximidades também aumenta (Schmidt & Whelan 1998). Um resultado que reforça este argumento foi obtido pelo experimento conduzido por Martin & Martin (2001) no sudoeste do EUA, pelo qual se verificou que a reprodução de duas espécies de Parulidae que nidificam em substratos semelhantes era mais bem sucedida quando a espécie coexistente era removida das imediações. Quando *Vermivora virginiae* foi removida, a taxa de sucesso reprodutivo de *V. celata* aumentou, enquanto a remoção de *V. celata*, além de aumentar o sucesso de *V. virginiae*, ainda induziu estas a construir seus ninhos em pontos idênticos aos usados pela outra espécie (Martin & Martin 2001). Algo similar parece acontecer entre os sabiás norte-americanos *Hylocichla mustelina* e *Turdus migratórios*: a probabilidade de falha nas tentativas de reprodução aumenta significativamente para a primeira espécie quando a segunda nidifica em coexistência (Schmidt & Whelan 1998).

Outra hipótese proposta para a incoerência entre habitats preferenciais e sucesso reprodutivo tem maior relação com a parte metodológica dos estudos conduzidos (Chalfoun & Schmidt 2012) e diz respeito à escolha das variáveis ambientais, cuja correlação pode ser prejudicada devido à negligência de uma ou mais variáveis que seriam importantes serem mensuradas para se entender os mecanismos de seleção de habitat (Conover et al. 2010). Entre as variáveis ambientais potencialmente relevantes, destaca-se a presença de corpos d'água, responsáveis por influenciar a distribuição de muitas espécies de aves relacionadas a ambientes aquáticos e consequentemente seus hábitos reprodutivos (Gjerdrum et al. 2005; Rajpar & Zakaria 2011). Nesses ambientes, merece destaque principalmente a vegetação ribeirinha presente ao longo de lagos, rios e riachos, uma vez que exercem um papel importante no estabelecimento e sobrevivência de determinadas comunidades de aves, principalmente em ambientes florestais (Stauffer & Best 1980, Knopf & Samson 1994, Darveau et al. 1995, Iwata et al. 2003). A estrutura dessa vegetação, bem como sua

composição florística, pode fornecer microclimas favoráveis para a distribuição de diferentes espécies (Rajpar & Zakaria 2011), além de locais adequados para posicionar e esconder seus ninhos durante a reprodução (Gjerdrum et al. 2005, Linhares et al. 2010). Além disso, margens de riachos no interior de florestas geralmente sustentam uma alta abundância de insetos aquáticos emergentes, os quais compreendem importante fonte de recursos alimentares para espécies de aves insetívoras que forrageiam e exibem preferência por habitats ribeirinhos (Murakami & Nakano 2002, Iwata et al. 2003).

Corpos d'água são abundantes em florestas neotropicais, formando diversos tipos de habitats úmidos que as espécies podem explorar, como igapós, brejos, rios e riachos (Haddad & Prado 2005, Harris et al. 2005). A grande variedade de ambientes é um atributo importante das florestas tropicais e subtropicais e reflete na alta diversidade de espécies de aves que elas abrigam (Naka et al. 2006, Anjos et al. 2007), representando uma biomassa até cinco vezes maior do que pode ser encontrada em florestas do Hemisfério Norte (Terborgh et al. 1900). Neste cenário, algumas espécies de aves que vivem no sub-bosque dessas matas, principalmente representantes das famílias Pipridae, Thamnophilidae, Parulidae e Furnariidae, adaptaram-se a utilizar a vegetação ribeirinha e explorar recursos presentes ao longo das margens de riachos presentes no interior das florestas (Ridgely & Tudor 1994, Sick 1997) e conseqüentemente, também possuem suas atividades reprodutivas relacionadas a esses ambientes (Snow 1985, Aguilar et al. 1999, Armacost 2004, Perrella et al. 2015, Zima et al. 2017).

No caso de espécies diretamente vinculadas ao ambiente aquático, como gaivotas, trinta-réis e garças, é esperado que a presença de corpos d'água tenha grande influência sobre a escolha do local para construção de ninhos (Sick 1997, Borboroglu & Yorio 2007; Aguilera 2010; Raynor et al. 2012). Entretanto, no caso de passeriformes florestais adaptados a nidificar ao longo de riachos no interior de matas, os critérios que influenciam na seleção

desses locais são pouco compreendidos, embora não faltem exemplos de espécies com esses hábitos (Snow, 1985, Aguilar et al. 1999, Armacost 2004, Linhares et al. 2010, Perrella et al. 2015, Zima et al. 2017). Uma característica importante desses ambientes é que eles podem apresentar consideráveis variações ao longo de seus leitos (Cetra et al. 2017), apresentando diferentes dimensões no que se refere a largura, profundidade, velocidade do fluxo da água, entre outras que poderiam interferir na decisão das aves ao selecionarem locais para nidificar. Teoricamente, algumas dessas características poderiam evitar que certos tipos de predadores tivessem acesso aos ninhos, especialmente animais terrestres como roedores (Zoellick et al. 2004, Ocampo & Londoño 2015). Por outro lado, o som produzido pela correnteza de um rio poderia sobrepor, por exemplo, os chamados dos ninhegos pedindo comida aos pais, os quais poderiam potencialmente chamar a atenção de predadores auditivos (McDonald et al. 2009, Husby 2018). Estudos envolvendo seleção de locais para nidificação e sua influencia sobre a taxa de sobrevivência de ninhos tradicionalmente costumam abordar principalmente variáveis como ocultação do ninho, densidade da vegetação ao redor dele, altura do substrato de sustentação do ninho em relação ao solo e algumas vezes também a influencia da simples presença de corpos d'água para explicar as preferencias das espécies ao construir seus ninhos em determinados locais em detrimento de outros (Borboroglu & Yorio 2007, Aguilar et al. 2008, Politi & Hunter Jr. 2009, Michalski & Norris 2014, Cockle et al. 2015, Méró et al. 2015). Contudo, as características específicas presentes ao longo dos riachos que são utilizados pelas aves como habitat para nidificação e como elas afetam seu sucesso reprodutivo, ainda permanecem muito pouco investigadas ou mesmo desconhecidas.

Um dos problemas para se estudar esse tipo de tema com aves florestais na região Neotropical é que, embora esse ecossistema detenha uma enorme diversidade de espécies (Ridgely & Tudor 1994), existe grande dificuldade em encontrar ninhos nesse tipo de ambiente. O naturalista David Snow foi talvez o primeiro a relatar o quão difícil é encontrar

quase qualquer tipo de ninho em florestas Neotropicais, com exceção apenas daqueles pertencentes a algumas poucas espécies que têm preferência por construí-los próximos a riachos (Snow 1985). De fato, esta é uma percepção comum entre muitos ornitólogos que trabalham na região tropical e há algumas hipóteses para tentar justificar os motivos que levariam às maiores densidades de ninhos próximos a corpos d'água. Primeiramente, diversos trabalhos têm demonstrado que a diversidade de aves tende a ser alta em ambiente próximos a corpos d'água (Knopf & Samson 1994, Naka *et al.* 2006, Anjos *et al.* 2007), o que poderia resultar em concentrações mais altas de ninhos nas imediações desses habitats. Entretanto, esta poderia ser uma percepção equivocada, uma vez que ornitólogos frequentemente utilizam riachos como trilhas, o que facilitaria encontrar mais ninhos próximos à água (Aguilar *et al.* 1999, Armacost 2004, Lima & Roper 2016). Uma segunda alternativa seria o fato de muitas espécies serem aparentemente adaptadas a nidificar próximo a riachos (ou mesmo outros ambientes aquáticos), como já foi documentado para passeriformes de sub-bosque como a choquinha-de-garganta-pintada *Rhopias gularis* e o tangará *Chiroxiphia caudata* no sudeste do Brasil (Perrella *et al.* 2015, Zima *et al.* 2017). Por outro lado, estes dois exemplos compreendem justamente duas das espécies de aves florestais mais abundantes na área estudada em questão (Antunes *et al.* 2013), e esta condição poderia trazer a impressão de que um grande número de ninhos de poucas espécies pode ser encontrado perto de cursos d'água, quando na verdade elas apenas concentram seus ninhos ao longo dos riachos florestais, seu habitat de nidificação específico.

O conhecimento envolvido com os fatores e condições ambientais que determinam a seleção de locais apropriados para as aves construírem seus ninhos também pode ser utilizado em prol da conservação de espécies (Rodrigues 1994; Gjerdrum *et al.* 2005). Entre as principais ameaças atuais à biodiversidade está a destruição de habitats naturais, que requer ações não só de proteção, mas também de restauração (Primack & Rodrigues 2001). Dessa

forma, para restaurar um ambiente degradado, entre outros fatores, é necessário saber quais características ambientais precisam ser recuperadas para que espécies de aves tenham condições de construir seus ninhos e criar suas proles (Rodrigues 1994). Outra ameaça que pode afetar diretamente a reprodução das aves é o processo de fragmentação florestal, responsável por aumentar consideravelmente as taxas de predação de ninhos em pequenos fragmentos de mata (Small & Hunter 1988, Yahner & Scott 1988), causando extinções locais de populações de aves dependentes de florestas, que passam a ter taxas de sucesso muito baixas em suas tentativas de nidificação (Karr 1982, Galetti et al. 2009). Outro exemplo é o declínio provocado sobre populações de espécies migratórias, que chegam para reproduzir em locais onde antes havia florestas e hoje existem apenas fragmentos insuficientes para sustentá-las (Wilcove 1985, Donovan et al. 1995), ou mesmo nos próprios locais de descanso reprodutivo, que são alterados e deixam de ser capazes de oferecer os recursos necessários para as atividades futuras (Norris et al. 2004).

Mesmo sendo um tema que ainda detém muitas lacunas dentro do conhecimento envolvendo as aves Neotropicais e que possui potencial para ser aplicado inclusive na conservação de espécies, estudos envolvendo seleção de habitats para nidificação ainda são escassos no Brasil (Aguilar et al. 2008; Pichorim et al. 2009; Chalfoun & Schmidt 2012; Franz & Fontana 2013, Bernardon et al. 2014, Repenning & Fontana 2016). Mais carente em informações sobre o assunto está a Mata Atlântica, Bioma predominantemente florestal (Oliveira-Filho & Fontes 2000) e listado como um dos grandes *hotspots* de biodiversidade do planeta devido ao elevado número de endemismos que abriga (Myers et al. 2000). Alvo de extensa e contínua devastação nos últimos séculos, este bioma já perdeu a maior parte de sua cobertura vegetal e atualmente resta apenas entre 11,4 e 16% de sua vegetação original, colocando-a em um patamar preocupante do ponto de vista da conservação (Ribeiro et al. 2009). Paralelamente, a Mata Atlântica abriga a segunda maior diversidade de aves do país

(Marini & Garcia 2005) e ainda assim, praticamente não há estudos sobre seleção de habitat para nidificação dessas espécies.

Dessa forma, os principais objetivos do presente estudo foram verificar se há maior densidade de ninhos de aves de sub-bosque em margens de riachos em uma área preservada da Mata Atlântica do sudeste do Brasil, bem como quais seriam os parâmetros ambientais que influenciariam nesta seleção. Considerando a hipótese de que os riachos assumem um papel significativo enquanto habitat utilizado para abrigar ninhos de diversas espécies, foram selecionadas três passeriformes intimamente relacionados a esse tipo de ambiente (*Chiroxiphia caudata*, *Rhopias gularis* e *Onychorhynchus swainsoni*) a fim de verificar se haveriam características ambientais específicas relacionadas aos riachos que seriam selecionadas por essas espécies para nidificação. Caso essas espécies selecionem de fato características dos riachos para construir seus ninhos, estas devem ter influência direta ou indireta sobre seu sucesso reprodutivo. No caso de *O. swainsoni*, espécie ameaçada de extinção, o conhecimento sobre tais características também poderia ajudar a compreender os motivos pela qual ela não tolera fragmentação ou alterações em seu habitat natural.

2. CAPÍTULOS

2.1. Streams promote higher nest densities of understory birds in a well-preserved Neotropical forest

Riparian vegetation along streams and other water bodies has been considered important habitats for the establishment and survival of bird communities, mainly in forested environments (Stauffer and Best 1980, Knopf and Samson 1994, Darveau *et al.* 1995, Iwata *et al.* 2003). The structure of this vegetation, as well as the floristic composition can provide favorable microclimate for the distribution of different species of birds (Rajpar and Zakaria 2011), and desirable microhabitats to support and hide their nests during reproduction (Gjerdrum *et al.* 2005, Linhares *et al.* 2010). Furthermore, stream edges usually hold high abundances of emergent aquatic insects, which can be important food resources for some insectivorous bird species that forage and exhibit preference for this kind of habitat (Murakami and Nakano 2002, Iwata *et al.* 2003).

In Neotropical forests, water bodies are abundant and allow the formation of several humid habitats that species can explore, including wetlands, marshes, rivers, and streams (Haddad and Prado 2005, Harris *et al.* 2005). This is an important attribute of tropical and subtropical environments, and is part of the explanation for the high diversity of birds there (Naka *et al.* 2006, Anjos *et al.* 2007), which presents a biomass sometimes five times greater than the forests from the Northern Hemisphere (Terborgh *et al.* 1900). In this scenario, some understory species became adapted to explore and to live in edges of streams and in the riparian vegetation inside forests (Ridgely and Tudor 1994, Sick 1997) and consequently have their nesting activities related to these environments (Snow 1985, Aguilar *et al.* 1999, Perrella *et al.* 2015).

Despite the large diversity of birds in Neotropical forests (Ridgely and Tudor 1994), nests are not easily found in these habitats. The naturalist David Snow was one of the first to report this difficulty for almost any nest in Neotropical forests, highlighting exceptions only for some species that prefer to construct nests in stream edges (Snow 1985). This is a common perception among many tropical ornithologists and there are some hypotheses that could explain the higher densities of bird nests near water. First, a number of works have demonstrated that birds diversity tend to be high riparian habitats (Knopf and Samson 1994, Naka *et al.* 2006, Anjos *et al.* 2007), which could result in higher nest concentrations in these habitats. However, this could be misleading because ornithologists frequently use streams as trails, which would facilitate finding nests near water (Aguilar *et al.* 1999, Armacost 2004, Lima and Roper 2016). Secondly, many species are apparently adapted to nest near streams, as were observed for the understory passerines Star-throated Antwren *Rhopias gularis* and the Blue Manakin *Chiroxiphia caudata* in southeastern Brazil (Perrella *et al.* 2015, Zima *et al.* 2017), which are very abundant (Antunes *et al.* 2013) and could cause the false impression that nests in general can be more common near water.

Here, we predict that if understory birds from a well-preserved Atlantic Forest continuum select stream edges and its riparian vegetation for nesting, nest density and diversity should be higher in these habitats than in trails inside forest and far from any watercourse. The confirmation of this prerogative would reinforce the high relevance of streams for the conservation of communities of Neotropical understory birds.

METHODS

STUDY AREA.—Fieldwork was conducted at Carlos Botelho State Park (PECB, 24°04' S 47°58' W, 20–1000 m a.s.l.), an Atlantic Forest remaining at state of São Paulo, Brazil, with

37,644 ha of protected area. Together with other three adjacent large conservation units, the PECB comprises one of the most important continuous Atlantic Forest areas from southeastern Brazil (Mattoso *et al.* 2008). The native vegetation in this park is highly preserved and classified mostly as submontane rain forest (Oliveira-Filho and Fontes 2000). The average temperature varies from 18 to 20°C (Ferraz and Varjabedian 1999), and climate is considered *Cfb* type according the Köppen classification, featured by temperate climate without dry season and with warm summer (Peel *et al.* 2007, Alvares *et al.* 2013). Rainfall varies annually from 777 to 2264 mm (average 1676 mm) with a marked wet season in October–March, with a rainfall peak in January, and a drier season in April–September, which presents a dried peak in August (Beisiegel and Mantovani 2006). The study was conducted in areas where the elevation ranges from 700 to 875 m.

FIELD PROCEDURES.—We searched for nests along three streams and two transects designed to be visually and audibly far from any watercourse.

We sampled parts of two larger streams, totaling 770 m in one and 1234 m in another. These streams were 4.56 ± 1.62 m wide (range 2.74 – 7.67 m, $N = 10$ random points), and 29.9 ± 16.7 cm deep (range 9.5 – 65 cm, $N = 10$ random points). In addition, we sampled 987 m from a narrower stream approximately 1.58 ± 0.5 m wide (range 1.12 – 2.93 m, $N = 10$ random points), and 9.25 ± 5.4 cm deep (range 3 – 18.5 cm, $N = 10$ random points). Their channels were composed predominantly by pebbles and thin sand. The two wider ones were more opened overhead, with points of sunlight crossing the trees canopy, while the third stream was completely shaded by the forest. The transects far from watercourses summed 1100 m. We delimited a 20m stripe width for each side to each track and stream for nest searching, and the entire area inside these limits was sampled.

Nests were found mainly by simply searching the appropriate locations, but some nests were also located when birds showed intense vocalizations for territory defense and we searched nearby for nests (Martin and Geupel 1993). Streams and tracks far from streams were sampled weekly from September to January during two different breeding seasons: one stream in 2014/2015, and two streams and two tracks in 2017/2018 breeding season. Each active nest found during field procedures was marked and the perpendicular distance to stream edge or transect was measured.

ENVIRONMENTAL VARIABLES.—We measured two environmental variables near and far from water that often can explain nesting site preference: canopy cover and vegetation density. These variables were obtained in ten random points along each transect, and totalized 20 random points in the margin of streams and 20 far from any watercourse.

Forest canopy cover was measured using a spherical densitometer held in front of the body of the observer, at chest height, to reflect the light penetration in a convex mirror. We made four readings per point facing North, West, South and East. The values were averaged and multiplied by 1.04 to obtain the percent of overhead area not occupied by canopy. Thus, the difference between each value and 100 was an estimation of over story vegetation density (Lemmon 1957). Vegetation density was obtained by passing a measuring tape horizontally from the randomly chosen point in the four cardinal directions and also over and under this point. We use only the first 50 cm of the measuring tape and considered only one contact with vegetation per each 10 cm interval. These hits were counted and the vegetation density was calculated as the number of 10 cm intervals contacts divided by all intervals (Mezquida 2004).

STATISTICAL ANALYSES.—The relative density of understory bird nests was estimated by the perpendicular distances between stream edge or transect and nests, using the model selection procedure implemented in the Program Distance Version 7.1 (Thomas *et al.* 2010). All of the 16 possible models were tested and the best model was selected by Akaike's Information Criteria- AIC (Buckland *et al.* 2001). As model parameter estimates perform better with 60 or more records (Buckland *et al.* 2001), and nest density in tropical forests is low, we pooled all transects of a target treatment together, as well as the data obtained across the several times each transect was surveyed. Then, the resulting nest density per hectare was subdivided by the number of times transects were surveyed to obtain the final nest density estimate (Bernardo *et al.* 2011).

Forest canopy and vegetation density data were analyzed using the T-Test in R software 2.15.3 (R Development Core Team 2013). Previously, the values of the variables were equalized through logarithm transformation. We compared the values obtained from 20 random points in the tracks far from watercourses with other 20 random points localized directly in the margins of the streams (margin sides were also selected randomly) to collect data from riparian vegetation.

RESULTS

We found 63 active nests from 18 different species of birds across the three streams and only one nest from one species across the line transect (Table 1). Nests per stream averages 21 ± 1 (range 20 – 22 nests, $N = 3$ streams), from 8 ± 3.6 species of birds (range 4 – 11 nesting species). The nests from Star-throated Antwren *Rhopias gularis* and White-necked Thrush *Turdus albicollis* were present in all surveyed streams. Only two species were representative of 54% of the nests, the Blue Manakin *Chiroxiphia caudata* ($N = 18$) followed by *R. gularis* ($N = 16$).

Table 1. Number of nests by species recorded along tracks near/on streams and far from any watercourse:

Species	Nest shape	Tracks on streams			Tracks far from streams	
		S1	S2	S3	T1	T2
<i>Thalurania glaucopis</i>	Cup		2			
<i>Trogon rufus</i>	Tree cavity			1		1
<i>Baryphthengus ruficapillus</i>	Ravine cavity	1				
<i>Rhopias gularis</i>	Cup	7	4	5		
<i>Dysithamnus mentalis</i>	Cup		1			
<i>Sclerurus scansor</i>	Ravine cavity	1				
<i>Lochmias nematura</i>	Ravine cavity		1			
<i>Automolus leucophthalmus</i>	Ravine cavity	2	1			
<i>Philydor rufum</i>	Ravine cavity		1			
<i>Chiroxiphia caudata</i>	Cup		8	10		
<i>Onychorhynchus swainsoni</i>	Closed		1	3		
<i>Platyrinchus mystaceus</i>	Cup	3				
<i>Mionectes rufiventris</i>	Closed	2				
<i>Leptopogon amaurocephalus</i>	Closed	1				
<i>Tolmomyias sulphurescens</i>	Closed	1				
<i>Lathrotriccus euleri</i>	Cup	2				
<i>Turdus albicollis</i>	Cup	1	2	1		
<i>Habia rubica</i>	Cup	1				

Most of the nests were found over the water (35%, distance = 0 m) or very close to the streams' margins (33%, distance $0 < X < 2$ m), and only 14 percent were more than 10 m away (distance $10 < X < 20$). This data generated a decreasing pattern of detection probability with increasing distance.

The direct estimate of nest density near streams was 5.3 nests/ha and the density provided by Distance was 7.4 nests/ha. As the number of nests far from water was low, modeling could not be precisely performed. We also used a direct estimate of the area and

nest density, which was 0.1 nests/ha. Thus, the density of nests found was one order of magnitude greater near, than far from water courses. The Program Distance estimated a density of 78.8 nests/ha near streams (AIC = 234.57), and we divided this value for the average number of repetitions of the tracks in streams (10.7 ± 1.5 , $N = 3$ streams), resulting in 7.4 nests/ha. For tracks far of streams, the estimated density through the Distance not was done because the low number of nests found.

Canopy cover estimates near and far from water were not significantly different ($t = -0.76$, $P = 0.45$). In contrast, the vegetation density was significantly lower in the edges of streams ($t = -2.35$, $P = 0.02$) (Table 2).

Table 2. Comparison of environment variables at random points in tracks near streams and far of watercourses in Carlos Botelho State Park:

Variable	Near streams	Far streams	<i>t</i>	<i>P</i>-value
Forest canopy	92.6 ± 3.41	93.4 ± 2.82	-0.76	0.45
Vegetation density	0.14 ± 0.08	0.19 ± 0.07	-2.39	0.02

DISCUSSION

Our main finding was that nest density of understory birds in a tropical forest was much higher near streams than far from them, suggesting that the perception pointed out by some ornithologists that nests of forest birds are more common near water is not simply the result of the use of streams as trails (Snow 1985, Aguilar *et al.* 1999, Lima and Roper 2016). Based on nesting habits literature information and in the long-term bird survey performed in our study area by Antunes *et al.* (2013), we can estimate that we have found nests of about 15% of the species that could nest in the forest understory of PECB, considering all possible types of nests, from cavities (both in ravines and trees) to open cups and closed suspended

(Del Hoyo *et al.* 2018 and therein references). This is evidence that we have sampled the most common nests, while nests of the other non-sampled species may be difficult to be found mainly because of their lower population densities. We detected that 54% of all of the nests were represented by only two species, the Blue Manakin and the Star-throated Antwren. These birds are not only among the most abundant species in the area but they are also known to select stream borders to nest, with nests of the Blue Manakin being often constructed hung on the top of water (Antunes *et al.* 2013, Perrella *et al.* 2015, Zima *et al.* 2017). Thus, nests of these species may be concentrated near the streams. Although in lower numbers, the same explanation can be given to *L. nematura* and *O. swainsoni* (see Euler 1900, Kirwan 2009). It is important to note that none of the species in our list are aquatic birds, although some select stream borders for reproduction. The frugivore *C. caudata* and the insectivore *O. swainsoni* seem to have no other association with water courses than nesting site, while *L. nematura* and the Star-throated Antwren occur in humid niches, foraging in the leaf litter of stream edges all year round (Ridgely and Tudor 1994, Sick 1997).

Another feature that could favor some species to select the streams to breed is the formation of ravines in its edges. At least 28 percent of the breeding species recorded in our study are cavity-nesters that excavate galleries in vertical walls of ground to construct their nests inside (Sick 1997, Remsen 2003 and therein references) and this kind of habitat were much more common along watercourses, mostly created by erosion. On the other hand, no ravines were present across transects far from water. In a long-term nest monitoring work in this study area, we observed at least 11 nests of *Automolus* and *Sclerurus* in road ravines. It suggests that forest streams are important providers of ravines, for birds with behavioral aspects associated to water or not. Although not excavator, *Leptopogon amaurocephalus* construct their nests attached to structures under ravines, and the same principle is also applied for this species (Aguilar 2001). Nevertheless, we found nests of many other species

only near streams that apparently do not have any relationship with water or ravines, as *Dysithamnus mentalis*, *Turdus albicollis* and *Habia rubica* (Euler 1900, Willis 1961, pers. obs.).

Density of nests in forests has been studied around the world. In the primary semi-deciduous Atlantic Forest from Argentina, Cockle *et al.* (2008) found 0.8 active bird nests per hectare in a study conducted only with the community of cavity nester species, while in forests from Mongolia and Sweden the density of active cavity nests seemed to be a little higher, presenting nearly 2 nests/ha (Carlson 1998, Bai *et al.* 2003). However, the bird community of a Neotropical forest includes a large diversity of other nesting strategies (Euler 1900, Kirwan 2009, Londoño 2014), and consequently it is expected a higher density than found only for cavity nesters. Although we had not been able to consider nests in the canopy because of logistic reasons, e.g. from large hawks, and some groups of passerines (Rangel-Salazar and Enriquez-Rocha 1993, Francisco *et al.* 2008, De la Peña 2013), we found an expressive diversity of nests, from cavities (both in ravines and trees) to open cups and closed suspended.

The Distance sampling methodology uses modeling to estimate the probability of detection of an animal given the length from it to a sampled track. It is based in the conception that the probabilities to detect the studied object decreases with observer distance, providing a corrected density value in relation to the sampled area (Buckland *et al.* 2001). Thus, when detectability declines quickly and there is the heaping of observations with distances near or equal to zero, the result is an exaggerated density estimate as obtained in our analyses (Bibby *et al.* 2000). However, this was not a problem in detectability. Our search was distributed also in distances further the streams inside the sampling area and in the trails far from any watercourse, and nevertheless we found many nests near streams, mainly in short distances from water. Furthermore, differently to sampling free moving animals, nests remain

unmoved and are being accumulated in the same area during the breeding season, once different species of birds can share temporally and spatially their nesting territory (Martin and Martin 2001, MacDonald *et al.* 2015) or even have several reproductive attempts (Roper 2005, Styrsky and Brawn 2011). Thus, to access the nest density at a time, it was necessary to divide the amount value obtained by how often the streams were sampled, and resulting in a very close density we obtained for the found nests.

Neotropical Forests hold an expressive biodiversity of birds (Marini and Garcia 2005, Naka *et al.* 2006, Antunes *et al.* 2013) and many of these species are highly dependent of well-preserved environments, disappearing completely from disturbed areas or small and isolated fragments in a long-term (Gimenes and Anjos 2003, Antongiovanni and Metzger 2005, Ferraz *et al.* 2007). In our results the channel of the streams did not influenced the forest canopy cover in their margins, once there was no significant difference between this variable near and far streams. Thus, we believe the canopy cover could not influence the higher density of nests near streams. In contrast, the denser vegetation found along tracks far of the streams was not expected, once higher cover of scrubs and leaves could better protect nests visually and are usually the mainly variable selected by birds in their nesting sites (Aguilar *et al.* 2008, Sánchez *et al.* 2013, Murray and Best 2014). These results demonstrate that the vegetation characteristics measured could not explain the preference of forest understory birds for nesting. Thus, environmental variables related to the streams deserve more attention and need to be well investigated in future studies to better understand this interaction.

Forested streams are environments related to several key ecosystem activities and ecological processes, once it influences in the transport and uptake of important nutrients as nitrogen and ammonium, and can provide more natural benthic habitat for macroinvertebrates (Sweeney *et al.* 2004), which in turn are resources for larger animals adapted to live in these

habitats (Murakami and Nakano 2002, Iwata *et al.* 2003). The importance of the streams and its riparian vegetation for forest birds was just highlighted in previous studies both due to the avian biodiversity that it can hold (Naka *et al.* 2006, Anjos *et al.* 2007, Seaman & Schulze 2010, Mitchell *et al.* 2018) and the functional role it plays as dispersal corridors (Gillies and St. Clair 2008, Seaman and Schulze 2010). Our data suggest that the nest density may be in some way another important trait closely related to the forested streams and their riparian vegetation. Therefore, the conservation of watercourses and its associated forest environments must be a high priority concern in management of landscapes both for maintenance of bird diversity and for its reproduction.

In conclusion, this study is the first to our knowledge to provide comprehensive information and a general perception about the density of nests of a bird community in a well preserved remnant of Neotropical forest. Moreover, we demonstrate that the nest density is comprehensively higher near forested streams, highlighting the importance of the conservation of the riparian vegetation for bird reproduction. However, our results with vegetation variables analysis infer that the operation of nest habitat selection by understory Atlantic Forest birds still need to be better investigated taking into account mainly the characteristics of the streams.

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2.2. Do forest-dwelling passerines nesting near water select specific sites along streams extensions in a well-preserved Neotropical forest?

Birds naturally presents certain ecological requirements survive in the complex environments in the habitat where it lives (Temple 2004, Cintra and Cancelli 2008, Lees and Peres 2010), and the ability to select sites that can offer suitable resources for establishment, feeding and breeding has been considered a relevant adaptive element in evolution of birds (Lack 1933, Magi et al. 2009, Bailey et al. 2015). Indeed, numerous studies have been evaluated the effects of habitat selection in birds' life history, and reproductive issues in particular have interested researchers for a long time (Hildén 1965, Jones 2001, Chalfoun and Schmidt 2012) once the nesting stage represents period of sedentary, where eggs and nestlings are vulnerable to weather conditions to be discovered by predators and nest parasites, becoming essential to develop strategies to protect their brood for ensure success in reproduction (Gjerdrum et al. 2005, Aguilar et al. 2008, Chalfoun and Schmidt 2012).

Birds often choose to build their nests in the same environments in which they live and forage, reason why most aquatic birds, for instance, nest in supporting structures near or over water (Hansell 2000, Winkler 2004). In the Neotropics, however, many forest-dwelling non-aquatic passerines, including manakins, antbirds, warblers, flycatchers, and even ovenbirds have been reported to build their nests associated to water courses, especially along forest streams (Sick 1997, Aguilar et al. 1999, Armacost 2004, Linhares et al. 2010, Perrella et al. 2015, Zima et al. 2017). Theoretically, this habit could have evolved in terrestrial birds to reduce predator access to the nests, an idea that is based on the assumption that certain predators are unable or reluctant to swim (Robinson 1985, Noske et al. 2013, Ocampo and Londoño 2015). Noske et al. (2013) suggested this theory to be named "aqua-phobic nest predator hypothesis", and although it has been pointed out by ornithologists (Collias and

Collias 1984), their predictions have been rarely tested. Ocampo and Londoño (2015) showed that river islands in Andean forests provided refuges to nesting birds, likely because predators such as mammals and snakes were unwilling to cross the river channel. Noske et al. (2013) indicated that for the Large-billed Gerygone, *Gerygone magnirostris*, constructing nests hung over the tidal channels in mangroves from tropical Australia often resulted in loss of nests due to flooding, suggesting that nesting over water not always provide advantages.

It is not clear whether tropical forest understory passerines can indeed select stream borders for nest construction. Researchers often use forest streams for searching nests (Aguilar et al. 1999, Armacost 2004, Lima and Roper 2016), which could cause the false idea that nests of certain species are more frequently found near water, and to our knowledge comparisons of nest frequencies near and far from streams were never carried out for Neotropical birds. Further, studies involving nest site selection in Neotropics have traditionally focused on covariates such as vegetation density, canopy cover, nest height, but rarely in the influence of water bodies (Aguilar et al. 2008, Bernardon et al. 2014, Michalski and Norris 2014, Repenning and Fontana 2016). However, it is predictable that if birds select stream edges for nest construction, they might select river stretches with specific characteristics that could increase nest survival.

Here we investigated nest site selection in two different levels for two Atlantic Forest passerines, the Blue Manakin, *Chiroxiphia caudata*, and the Star-throated Antwren, *Rhopias gularis*, for which nests have been commonly found near or over streams present within forest areas. In the first level, we searched for nests along streams and in transects far from watercourses, both within primary Atlantic Forest, in order to test if these species do indeed select stream edges for nesting. In this step, we also compared vegetation variables between nest sites and random sites far from water in an attempt to detect variables that could explain nest site choice. In the second level, we compared a number of stream characteristics,

including width, depth, speed of water flow, and water sound between nest sites and random sites chosen up, or downstream to test if birds can select stream stretches with specific features, controlled to vegetation density, and forest canopy cover. Then, we addressed the power of stream variables, also controlled to other important covariates such as nest height, vegetation density, canopy cover, and temporal variables to explain daily survival nest's Daily Survival Rate (DSR).

METHODS

STUDY SPECIES.—The Star-throated Antwren *Rhopias gularis* (Spix, 1825) is a 9.5 cm sized bird, brown colored above, with face grizzled grey and black wing-coverts. They present a slightly sexually dimorphism, especially in the color of forehead (buffy in females and grey in males) and in the size of white spots on the black throat, larger in females (Ridgely and Tudor 1994, Zimmer and Isler 2003). These insectivorous antbirds usually forage 0-5 m above ground, mostly in dense growth and wet vegetation with abundant foliage, and also in ravines and edges of streams inside forests (Willis 1984, Sick 1997, Zimmer and Isler 2003). Nesting occurs in the same habitat, where they build pensile deep cup nests well hidden in saplings or shrubs near to the ground or above water (34–70cm height), and apparently always near streams (Perrella et al. 2015). In our study area, clutch size of the Star-throated Antwren is invariably two eggs, incubation last 16– 18 days (16.8 ± 0.6), and nestling period is 10–13 days (11.0 ± 0.86). The nest attendance is bi-parental, where the pair incubates eggs, brood and feed the nestlings in similr proportion, from September to January (Perrella et al. 2017).

The Blue Manakin *Chiroxiphia caudata* (Shaw & Nodder, 1793) is a medium-sized (15cm) bird, common in lower growth of humid forests, secondary woodlands and forest edges, in dense vegetation (Ridgely and Tudor 1994, Sick 1997). The diet is composed predominantly by several species of fruits from shrubs, lower trees and other understory angiosperms (Galetti

and Pizo 1996). Males of Blue Manakins have turquoise-blue body, with black in much of tail and head, with a red band from forehead to nape. On the other hand, females are dull green and paler below (Snow 2004). Colorful males are completely absent of any task during nesting cycle, while females take care of the all nest attendance. She build shallow cups camouflaged in forks of saplings or shrubs, directly above water or at 0.07–6 m (0.47 ± 1.31 m) from the edge of forest streams (Euler 1900, Zima et al. 2017). Nests of Blue Manakin also are usually built higher up than Star-throated Antwren, varying from 1.14 to 2.98m above the water or ground (Perrella et al. 2015, Zima et al. 2017). In our study area the clutch size of this species is two eggs, incubation period is 18 days, nestling period last 15–16 days (15.8 ± 0.45) and breeding season is from October to February (Zima et al. 2017).

Both species are endemic to the Atlantic Forest (Bencke et al. 2006) and are among the most frequent birds from Carlos Botelho State Park (Antunes et al. 2013). Besides, according to unpublished studies conducted by our team at PECB, these are the most common species nesting along forest streams.

STUDY AREA.— We conducted the fieldwork at Carlos Botelho State Park (PECB, 24°04' S 47°58' W, 20–1000 m asl) in state of São Paulo, Brazil. The PECB is a 37,644 ha protected Atlantic Forest remaining, which comprises one of the most important continuous areas from southeastern Brazil together with other three adjacent large conservation units (Mattoso et al. 2008). The local climate is classified as Cfb type according the Köppen parameters, featured by temperate climate without dry season and with warm summer (Peel et al. 2007, Alvares et al. 2013). The well preserved vegetation is classified mostly as submontane rain forest (Oliveira-Filho and Fontes 2000), average temperature varies between 18 and 20°C (Ferraz and Varjabedian 1999), and rainfall varies from 777 to 2264 mm annually (average 1676 mm). The wet season is marked from October to March, with a rainfall peak in January, and

the drier season is between April and September, with dried peak in August (Beisiegel and Mantovani 2006). This study was conducted in elevations from 700 to 875 m a.s.l.

FIELD PROCEDURES.—We searched for nests of both studied species along two forest streams and three transects visually and audibly far from any watercourse. Each transect was 1100 m long inside preserved forest, and were traveled weekly during one breeding season each (two in 2017/2018 and one in 2018/2019).

Streams were sampled weekly from September to February during 2016/2017 and 2017/2018 breeding seasons and from October to January during 2018/2019 breeding season. The stretches traveled in streams had 1200 and 2600 m, and were composed predominantly by pebbles and thin sand, which permeate the most preserved forested areas of the Carlos Botelho State Park. The channel of these streams were from 2.74 to 7.67 m wide (4.56 ± 1.62 m, N = 10 random points), and from 9.5 to 65 cm deep (29.9 ± 16.7 cm, N = 10 random points).

Nests were located by investigating forks of bushes, shrubs or saplings with slender branches, where Blue Manakins and Star-throated Antwrens used to nest (Perrella et al. 2015, Zima et al. 2017). Some nests were found when parents showed intense vocalizations for territory defense, especially the Star-throated Antwren (Perrella et al. 2015, 2017), and then we searched nearby for nests (Martin and Geupel 1993). Once found, one or two camera traps Bushnell were positioned near each nest for success monitoring and set according described by Ribeiro-Silva et al. (2018). Nests and cameras were checked once a week and we assumed a nest depredated when eggs or nestlings disappeared prior to hatching or fledging age; abandoned when nests were no longer cared for or eggs became cold; and successful when we could detect fledging in videos or the time of monitoring correspond fledging time.

ENVIRONMENTAL VARIABLES.—For each nest point we measured six environmental variables that could influence nest site selection: stream width, stream depth, water speed, noise produced by the water flow, forest canopy cover, and vegetation density around the nest. In the nest sites we also measured the height of the nest above ground or water and its distance from the nearest stream edge (using negative numbers if nest were above water and positive numbers if nests were above ground).

In transects far from any watercourse, we measured only four variables in 20 random points: wind speed, noise, forest canopy cover and vegetation density.

Finally, at each nest point we designated a corresponding random point 30m down- or upstream, for measuring all of the seven covariates to compare then to the nest points.

Width of stream was considered as the length between the margins directly below the nest (or random point), while the depth was the value found in the middle of the stream. The speed of water was obtained calculating the average time a fluctuating standardized plastic object took to travel a distance of 5 meters starting from nest or random point.

The noise was estimated using a digital decibel meter (range 30dBA – 130dBA; accuracy ± 1.5 dB) positioned parallel to the observer chest directly besides the nest or random point, and averaged the sound level during three minutes in each point. This equipment measures the maximum and minimum average noise, but we considered only the second value because the running water usually produced the lower and only continuous sound in the environment, while the sounds produced punctually by birds and frogs were higher and can generate abrupt peaks counted in the maximum average.

Forest canopy cover was measured with a spherical densitometer following the manufacturer instructions (Convex Model-A, Forest Suppliers, Inc.) (Lemmon 1957).

Vegetation density was obtained by passing a measuring tape horizontally from the borders of the nest to four cardinal directions and also over and under it. We used the first 50

cm of the measuring tape and considered only one contact with vegetation per each 10 cm interval. These contacts were counted and the vegetation density around nests or random points were calculated as the number of 10 cm intervals hit by vegetation, divided by 30, the total number of intervals (Mezquida 2004).

STATISTICAL ANALYSES

Nest site selection.—This part of the statistical analyses had two steps. Firstly we compared the points with active nests to the random points on transects far from watercourses and then, to verify if the birds have selected nesting sites based on stream edges characteristics, we compared the environmental variables between nest and random points along the forest streams.

For both nest site comparisons cited above, we performed a Principal Component Analysis (PCA) with data corrected using z-score and correlation matrix, to reduce the number of variables. Then, the new scores obtained for the main axis were used on a t-test to access the level of significance with 95% confidence using the software Past3 (Hammer et al. 2001).

To verify if environmental variables could explain the nest site selection we performed a model selection procedure using a Logistic Regression Analysis with logit link-function. For the binary distribution, nest points were coded as 1 and random points coded as 0. The generated models, including the null model, were exploited using the function dredge provided by the R-package “MuMIn” (Bartoń 2018). Auto-correlation between variables was verified through Pearson correlation test using the function rcorr provided in R-package “Hmisc” (Harrell Jr et al. 2019). We considered variables auto-correlated when $r \geq 0.7$ or when a significant correlation was found ($P \leq 0.05$). Then, the variable with less capacity to explain the data was removed from the subsequent analyses. Models support were evaluated

using Akaike's Information Criterion corrected to small samples (AICc), but also by the ΔAICc and Akaike weight (w) values. We selected models presenting $\Delta\text{AICc} \leq 2$, which indicates substantial support evidence for them (Burnham and Anderson 2002). The parameter estimates of the select models, as well their standard errors (se) and upper and lower limits of 95% confidence were reported to demonstrate the validity of the explanation of each variable for the models. Further, we carried out Z-tests to verify if each variable within the selected models was differed significantly from zero.

Nest survival.—We calculated Daily Nest Survival Rates (DSR) for the studied species separately, using the binominal Generalized Linear Model approach proposed by Dinsmore et al (2002) with maximum likelihood parameter estimates, as an interface of the Program Mark (White & Burnham, 1999), implemented by the R-package “RMark” 2.2.6. (Laake 2013). Fates of the nests were coded as 0 when successful or 1 when depredated, and the considered variables included were stream width, stream depth, water speed, noise of water flow, canopy cover and vegetation density around the nest, height of the nest from the ground or water, it distance from the margin, and year of the breeding season. We also included two time dependent covariates commonly used for Mark analysis: “AgeFound”, which is how old the nest was when found in days, and “AgeDay1”, which is the day in Mark chronological time where the nest began to be active -1. All continuous covariates were standardized using score-z, and the corrected variables were tested for autocorrelation as described above for previous analysis. We pooled samples from the three breeding seasons to improve analysis effectiveness. Similarly to what we used for the Logistic Regression we generate models and evaluated their support using Akaike’s Information Criterion (AICc) (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.

For this approach, the cumulative probability of overall nest success can be estimated raising DSR to the power corresponding the duration of the nesting cycle. Statistical analyses were conducted using Software R version 3.4.2 (R Development Core Team 2017).

RESULTS

We found a total of 42 active nests of Blue Manakins and 30 active nests of Star-throated Antwrens across the three studied breeding seasons. For nest site selection analysis (PCA and Logistic Regression), all nests were considered from both species, however, for overall survival rate analysis due to predation we excluded nests were abandoned or we could not determine the precise fate. Thus, for the analysis to verify the influence of the predation over nest site selection (using Mark), we considered 29 nests of Blue Manakin and 24 nests of Star-throated Antwren.

All of the nests were found over or a few meters far from water, being -335 to 1300cm for the Blue Manakin and -44 to 267cm for Star-throated Antwren. No nests were found during searches in trails far from water, suggesting that these species do indeed select stream edges to construct their nests.

NEST SITES VS. SITES FAR FROM STREAMS FOR BLUE MANAKIN.—The PCA comparing the parameters canopy cover, vegetation density environmental sound in nest site with random sites far from water indicated that 82% of the variation was explained by the two main axes, with the first axis explaining 44.4% (Fig. 1). The t-test comparing the new scores of the main axis was highly significant ($t = -6.709$, $P < 0.0001$).

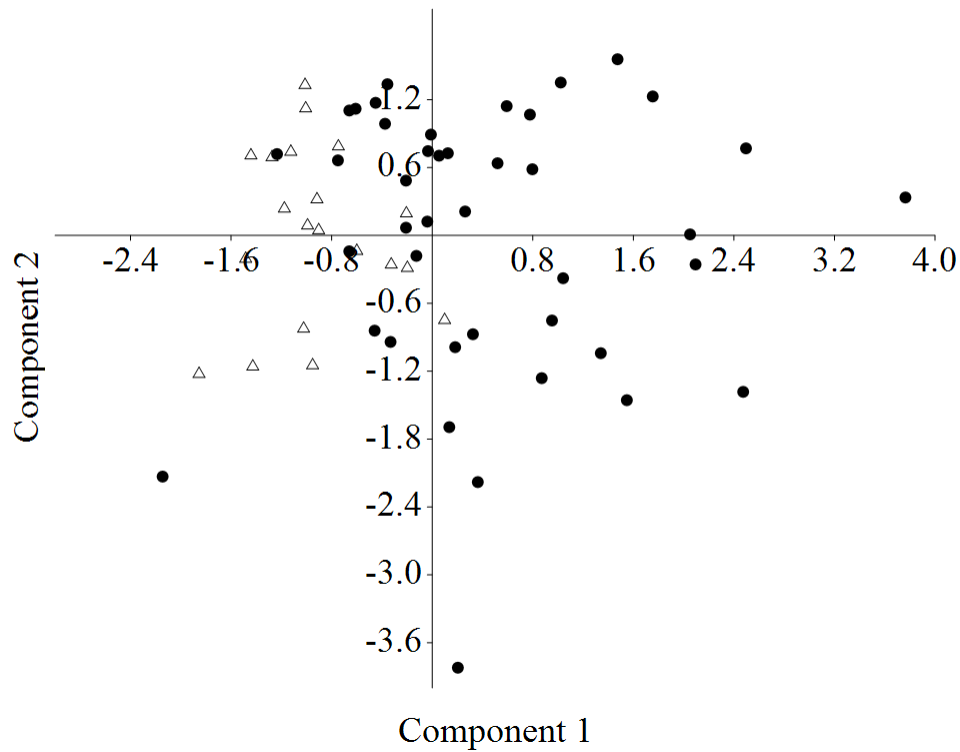


Fig. 1. Principal Component Analysis (PCA) addressing the variables canopy cover, sound, and vegetation density obtained in nest sites and in random sites far from water for the Blue Manakin. Black circles are nest sites and white triangles are the random sites.

The model selection procedure returned three models with $\Delta\text{AICc} < 2.0$ (supplemental table 1). The best model contained canopy cover and environmental sound; the second best model was the complete model, and the third best model included only the covariate sound. In these models intercepts were always positive, never overlapped zero and always differed significantly from zero. The variable environmental sound was present in the three best models and also was always positive, never overlapped zero and was always highly significantly different from zero, while the upper and lower 95% CI always overlapped zero for the other variables and they were never significant.

NEST SITES VS. SITES ALONG STREAMS FOR BLUE MANAKIN.—The PCA carried out to compare nest sites to random sites chosen up or down-stream, including vegetation density, canopy closure, stream depth, stream width, water speed, and sound did not result in any clustering evidence (fig. 2). The two main axes explained 42% of the variation obtained by the data of nest site selection along the streams, being 23% of it explained by the main axis. Then, T-test carried out with the new scores from PCA was non-significant ($t = 0.2956$, $P = 0.3841$).

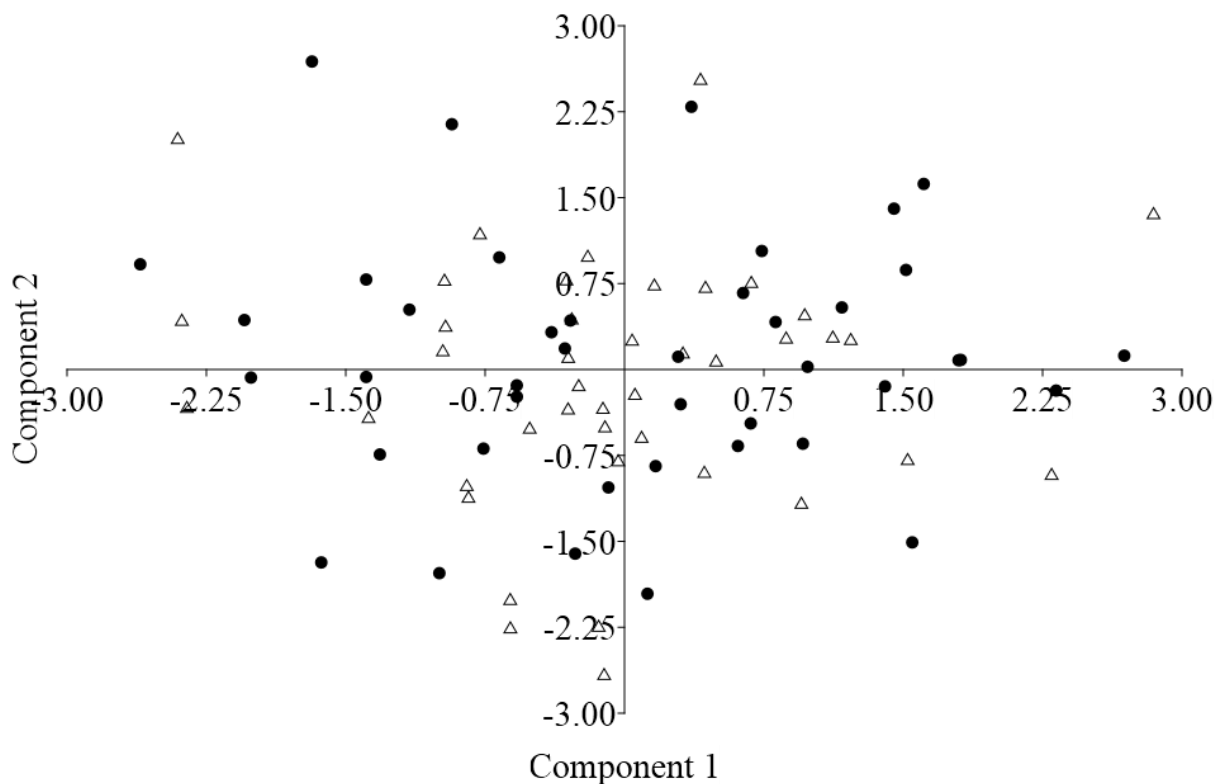


Fig. 2. Principal Component Analysis (PCA) used to compare nest sites and random sites along streams for the Blue Manakin. Black circles are nest sites and white triangles are the random sites.

From the 64 models resulted of the glm, six presented $\Delta AICc < 2$, receiving substantial support (supplemental table 2). None of them included the null model. Within all of these models vegetation density was always present, its lower and upper 95% CI never

overlapped zero and it was highly significant in all of the models according to the Z-test. Maximum likelihood estimates of all of the other parameters overlapped zero in all of the top-ranked models, and they were never significant.

NEST SURVIVAL FOR BLUE MANAKIN.—For Blue Manakin, 17 nests were successful (40%), 12 nests were lost by predation (29%), six were abandoned during incubation (14%) and for seven we could not determine fate with precision (17%). The rate of daily nest survival (DSR) was 0.975, SE=0.006 (0.957-0.986 of 95% IC) using Mark.

Nest survival pre-modeling using only the variables related to the streams returned four models with $\Delta AICc < 2$, including the null model (supplemental table 3). The only variables present in these models were distance of the nest from water and speed of water flow. Although they presented small values and their 95% IC always overlapped zero, they were maintained for the general modeling, as they were the only variables present in the pre-modeling.

The general modeling indicated six potential models, with the best model including the covariates canopy cover, distance of the nest from water, “AgeFound”, and year of breeding season (supplemental table 4). The covariates canopy cover, distance from water and year were present in all of the models. Canopy was positively, while year was negatively correlated to DSR, with 95% IC values never overlapping zero. Distance from water was also negatively correlated to DSR and 95%IC overlapped zero in only one model. The other variables (AgeFound, height of the nest from the ground/water, AgeDay1, water speed, and vegetation density), in addition of being present in only a few models, had 95% IC values always overlapping zero. Then, canopy cover, distance from water and year were main covariates explaining DSR for the Blue Manakin.

NEST SITES VS. SITES FAR FROM STREAMS FOR STAR-THROATED ANTWRN.—The parameters of canopy cover, vegetation density and sound compared using the PCA in sites with nests and in random sites far from watercourses demonstrated that 81% of the variation in the data was explained by the two main axes, which 45% comprises the value explained by the first axis (fig. 3). The t-test comparing the new scores of the main axis was highly significant ($t = 8.5022$, $P = 3.888e-11$).

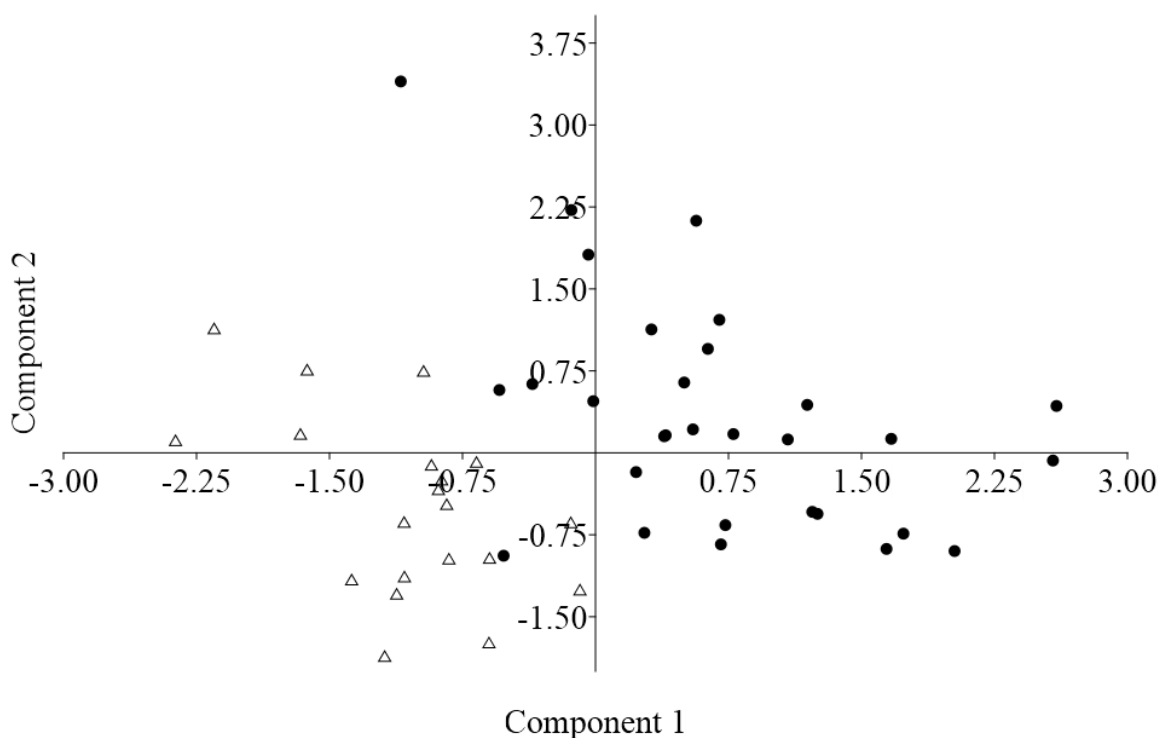


Fig. 3. Principal Component Analysis (PCA) addressing the variables canopy cover, sound, and vegetation density obtained in nest sites and in random sites far from water for the Star-throated Antwren. Black circles are nest sites and white triangles are the random sites.

The procedure for selection of models provided only two with $\Delta AICc < 2.0$, and the best of them provided vegetation density and environmental sound as variables that could explain the selection (supplemental table 5). The intercepts of these models were positive and

no overlapped zero. Both vegetation density and environmental sound was present in the two best models, had positive values, were always highly significantly different from zero and their upper and lower 95% IC never overlapped zero.

NEST SITES VS. SITE ALONG STREAMS FOR STAR-THROATED ANTWREN.—No clustering evidence was found through PCA (Fig. 4), where 43% of the variation in the data was explained by the two main axes, being 24% explained by the main one. Principal component scores used in subsequent T-test resulted in non-significant values ($t = 0.9871$, $P = 0.163$).

Modelling resulted on 64 models of which seven revealed values of AIC and delta smaller than two and thus received stronger support. Therefore, the better model obtained in this analysis was the null model, and neither was significant in relation to the other variables when using the Z-test (supplemental table 6), indicating that any measured environmental characteristic could explain the nest site selection of the Star-throated Antwren along sampled forest streams.

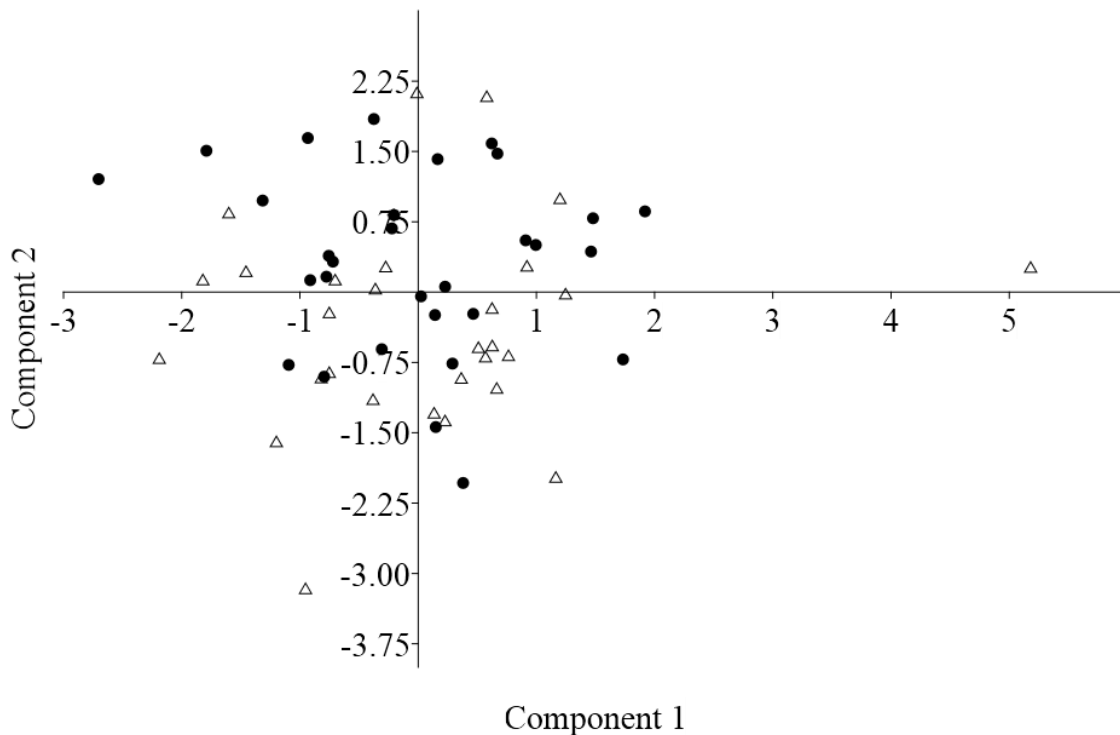


Fig. 4. Principal Component Analysis (PCA) addressed to compare nest sites and random sites along streams for the Star-throated Antwren. Black circles are nest sites and white triangles are the random sites.

NEST SURVIVAL FOR STAR-THROATED ANTWREN.—For Star-throated Antwren, 15 nests were successful (50%), nine nests were predated (30%), one nest were lost by stream flooding (3%), three were abandoned during incubation (10%) and for two we could not determine a precise fate (7%). The rate of daily nest survival (DNS) was 0.972, SE=0.008 (0.950-0.985 of 95% IC) using Mark.

The AIC model ranking returned three models with $\Delta AICc < 2.0$ when we used only variables related to the streams, and the best of them provided stream depth and distance of the nest from water as variables that could better explain the DSR. These two variables were also present on two other selected models, had positive values, and their upper and lower 95%

IC never overlapped zero (supplemental table 7). Sound of the water flow also was included in the best model, but its upper and lower 95% IC overlapped zero, then we discard this variable. The intercepts of all three models were positive and no overlapped zero.

In the following analysis, considering the variables selected above (depth and distance from water) and those that had not yet participated in modeling, we obtained seven models with $\Delta AICc < 2.0$ (supplemental table 8). The best model, presented again positive beta values for stream depth and nest distance from water, together the variables canopy cover, nest height, year of the breeding season and “AgeFound”. However, only the variables stream depth, nest distance from water and “AgeFound” had their upper and lower 95% IC overlapping zero, both in the best and in the other six selected models, then we disregard the other variables. In these seven models, the intercepts were positive and their IC no overlapped zero.

DISCUSSION

Our findings pointed out that Blue Manakins and Star-throated Antwrens selected edges of streams for nesting, once we could not find active nests of these species far from them. To our knowledge, this is the first empirical evidence that Neotropical non-aquatic forest birds can indeed select stream edges for nesting. However, only for antwren we found denser vegetation being selected in nest sites near streams compared to sites far of any watercourse. Comparing variables of nest and random sites along streams, only Blue Manakins seem to select any specific variable related to the stream margins, the vegetation density around the nests, but when we compared variables among successful and depredated nests, the forest canopy closure and the position of the nest over water for manakins, and the stream depth together the position of the nest far from the margin for antwrens were environmental variables that well explained their DSR.

Previous studies have been demonstrated that both in environments from Temperate and Neotropical regions, water bodies can be a consistent barrier or at least hamper access for bird nest predators (Robinson 1985, Willms and Crawford 1989, Zoellick et al. 2004, Ocampo and Londoño 2015). In a study conducted along a stretch of the Kcosñipata River in Peru, Ocampo and Londoño (2015) found higher daily survival rates for nests localized on small river islands than for nests on river edges, both for artificial and natural nest experiments. Similarly, the nest success observed for the endemic Black Catbird (*Melanoptila glabrirostris*) on some locations of the Yucatán Peninsula in Mexico, was significantly lower on mainland sites than found on Cozumel Island, separated by ~60km of water (Roldán-Clarà et al. 2012). Thus, the preference of Blue Manakins nest frequently above water, behavior that influences over her DSR, could be related to a strategy to avoid terrestrial predators as mammals and snakes. This suggestion can be corroborated due to the low frequency of records of snakes preying nests in Atlantic Forest (Cockle et al. 2016, Ribeiro-Silva et al. 2018), even with high diversity of species in these environments (Forlani et al. 2010), besides the main Blue Manakin nest predators reported at PECB are birds (Ribeiro-Silva et al. 2018), forcing adaptation ways to defend her nest against them. On the other hand, the DSR of Star-throated Antwren was influenced by the increase in the distance of the nest in relation to streams, probably because over the water there would be less vegetation in the stratum where antwrens build nests, which would leave the nest exposed to predators (Michalski and Norris 2014). Besides that, this antwren usually constructs on small scrubs or saplings whose branches above water do not move so far from the edges (Perrella et al. 2015), which does not significantly avoid access by terrestrial predators.

Neotropical forests have a striking diversity of potentially nest predators (Cockle et al. 2016, Menezes and Marini 2017, Ribeiro-Silva et al. 2018), probably higher than in Temperate regions (Ricklefs 1989), but tactics used by them to search and detect bird nests

are in general restricted for visual or olfactory ways (Martin 1987, Ricklefs 1989, Söderström et al. 1998). In this context, to select sites with high vegetation concealment for nest construction seen to be a positive strategy to protect it from visually oriented predators (Colombelli-Négrel & Kleindorfer 2009, Michalski and Norris 2014). Studies developed in Neotropical forests have revealed that birds are the main predators over *Chiroxiphia* Manakins' eggs and nestlings, while losses due to terrestrial mammal attacks are rarer (Reidy 2009, Ribeiro-Silva et al. 2018). In this way even for female Blue Manakins, which have a cryptic green plumage, to select locations with higher vegetation density around could increase improve camouflage of their nests. However, our results suggest that the closing of the forest canopy and its consequent increasing in lightless, could protect better their nests against visually-oriented predators, a strategy probably efficient, given its high nest survival rate when compared to other forest manakins (Ferreira and Lopes 2018, Ryder et al. 2008). On the other hand, nest concealment does not seem to confer protection and are technically inefficient against olfactory-oriented predators, represented mainly by terrestrial mammals (Remes 2005, Colombelli-Négrel and Kleindorfer 2009). Some studies where nest predators could be identified have been demonstrated that mammals play a significant role in predation over lower and ground nests, while birds are responsible by failure in nests positioned in taller sites (Söderström et al. 1998, Colombelli-Négrel and Kleindorfer 2009). Star-throated Antwrens construct nests frequently near to the ground, from 34 to 70cm (Perrella et al. 2015) on a habitat that apparently comprises the foraging stratum of both birds and terrestrial mammals with climbing skills that can depredate nests (Ribeiro-Silva et al. 2018). Nevertheless, we observed a high nest survival rate for the antwrens in the study area, which bring to the light some possible inferences about our results with nest site selection. The depth of the streams was a variable influencing in DSR of Star-throated Antwren nests, and as we discussed above, the construction of nests near deeper sites of the streams probably help to

avoid little terrestrial mammals and snakes, that would spend more energy trying to swim across a deeper site if was foraging randomly around.

Many studies have demonstrated that vegetation density is an important variable on the nesting site selection by birds, and this choice is mostly attributed to the protection against predators (Aguilar et al. 2008, Colombelli-Négrel and Kleindorfer 2009, Michalski and Norris 2014, Reppening and Fontana 2016). However, for some species the selection of a nesting site can be motivated by other characteristics of the habitat, as to avoid flooding in salt marshes selecting taller nest sites (Gjerdrum et al. 2005), or to search for sites with higher abundance of food for nestlings (Mägi et al. 2009). The sites where antwrens nest in the margins of the streams have denser vegetation than sites in forest far from watercourses, and although we could not test if this selection occur to avoid nest predation (because there were not nests of Star-throated Antwrens far from streams) this possibility cannot be ruled out. Along the streams, we did not find any variable that could explain nest site selection by the Star-throated Antwren, and based on what was discussed above, this findings can be attributed to: 1) the edges of forest streams had a vegetation somewhat homogeneous or presenting less variation in the height where antwrens build nests; 2) the low nest predation pressure in the study area results in other priorities influencing the decision of the antwrens for nest site selection, as for places with higher abundance of insects, an important resource during nestling attendance stage. Is it known that the vegetation along forest streams hold higher biomasses of insects which can support and directly influence the distribution of insectivorous birds (Murakami and Nakano 2002, Iwata et al. 2003), thus our inference of a possible bottom-up mechanism of selection by the antwrens due to high survival rate in the PECB could be well sustained; or 3) the selected variables were not able to describe the phenomena.

In conclusion, we could observe that both Blue Manakins and Star-throated Antwrens indeed selected some stretches of the streams to build their nests, though these variables

variables are clearer when we compare nest sites to sites far from watercourses for Star-throated Antwren. We verified the two studied species have different habitat requirements and priorities for select nesting sites, as well different pressures over their DNS, probably due to the different strategies of nesting used by these species. In this way, study the several species that use this kind of habitat for nesting could be the better way to start to understand its importance for bird reproduction in Atlantic Forest.

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Supplemental table 1. Best candidate binomial generalized linear models for comparisons of the variables canopy cover, vegetation density, and sound level between nest sites of the Blue Manakin and random sites determined far from any water course. Asteristics indicate the level of significance of the Z-statistics used to test if the parameters have differed significantly from zero and in parenthesis there is the lower and upper 95% confidence interval:

Model	AICc	ΔAICc	w	Intercept	Canopy	Vdens	Sound
Canopy+Sound*	36.1	0.0	0.422	5.479 (2.566-10.575)	-0.886 (-2.078-0.019)	-	8.087 (4.155-14.770)
Canopy+Sound*+Vdens	37.4	1.28	0.223	5.392 (2.527-10.452)	-0.939 (-2.288-0.105)	7.850 (-0.440-1.668)	0.474 (3.949-14.565)
Sound*	37.6	1.46	0.203	4.543 (2.171-8.549)	-	-	6.673 (3.504-11.767)

Supplemental table 2. Best candidate binomial generalized linear models for comparisons of the variables canopy cover, vegetation density, sound, stream depth, stream width, and water speed between nest sites of the Blue Manakin and random sites determined up or down-stream. Asterisks indicate the level of significance of the Z-statistics used to test if the parameters have differed significantly from zero and in parenthesis there is the lower and upper 95% confidence interval:

Model	AICc	Δ AICc	w	Intercept	Canopy	Vdens	Sound	Depth	Width	Speed
Vdens*	112.2	0.00	0.125	0.024 SE=0.230 (-0.427-0.480)	-	0.722 SE=0.277 (0.218-1.314)	-	-	-	-
Canopy+Vdens*	112.3	0.04	0.122	0.006 SE=0.233 (-0.452-0.467)	0.024 SE=0.019 (-0.008- 0.0736)	0.719 SE=0.277 (0.217-1.310)	-	-	-	-
Vdens*+Speed	113.5	1.32	0.064	0.022 SE=0.231 (-0.432-0.480)	-	0.725 SE=0.278 (0.221-1.318)	-	-	-	0.203 SE=0.229 (-0.238-0.674)
Canopy+ Vdens*+Speed	113.7	1.46	0.060	0.008 SE=0.234 (-0.452-0.472)	0.025 SE=0.0195 (-0.008-0.075)	0.723 SE=0.277 (0.220-1.316)	-	-	-	0.205 SE=0.231 (-0.247-0.672)
Canopy+Vdens* +Width	113.8	1.54	0.058	0.005 SE=0.234 (-0.455-0.468)	0.2631 SE=0.019 (-0.007-0.077)	0.732 SE=0.279 (0.226- 1.327)	-	-	0.197 SE=0.236 (-0.263-0.674)	-
Vdens*+Width	113.9	1.68	0.054	0.024 SE=0.231 (-0.429- 0.481)	-	0.731 SE=0.279 (0.225-1.326)	-	-	0.159 SE=0.232 (-0.294-0.624)	-

Supplemental table 3. Results of Daily Survival Rate model selection for Blue Manakin, involving the variables related to stream characteristics in nest sites: distance form water, width, depth, sound level and water speed:

Model	AICc	ΔAICc	w	Intercept	DistH2O	Sound	Depth	Width	Speed
DistH2O	106.8	0.0	0.138	3.517 SE=0.298 (2.933-4.102)	-0.851 SE=0.480 (-1.792-0.091)	-	-	-	-
Null	107.6	0.78	0.093	3.684 SE=0.292 (3.111-4.257)	-	-	-	-	-
DistH2O+ Speed	107.9	1.12	0.079	3.572 SE=0.312 (2.959-4.184)	-0.800 SE=0.474 (-1.728-0.128)	-	-	-	0.303 SE=0.323 (-0.331-0.936)
Speed	108.4	1.63	0.061	3.733 SE=0.306 (3.132-4.331)	-	-	-	-	0.337 SE=0.319 (-0.289-0.964)

Supplemental table 4. Results of Daily Survival Rate model selection for Blue Manakin, involving the variables distance of the nest from water and water speed returned from the pre-modeling and including the variables canopy cover, vegetation density, nest height, “AgeFound”, “AgeDay1” and Year of the breeding season:

Model	AICc	ΔAICc	w	Intercept	Canopy	DistH2O	AgeFound	Height	AgeDay1	Vdens	Speed	Year
Canopy*+ DistH2O*+ AgeFound+ Year*	102.0	0.0	0.068	6.674 SE=1.344 (4.039-9.309)	0.909 SE=0.357 (0.208-1.611)	-1.209 SE=0.555 (-2.297-(-0.121))	-0.066 SE=0.039 (-0.144-0.012)	-	-	-	-	-1.332 SE=0.559 (-2.4280-(-0.236))
Canopy*+ DistH2O+ Year*	102.8	0.9	0.044	5.194 SE=0.887 (3.455-6.933)	0.718 SE=0.313 (0.103-1.333)	-1.056 SE=0.574 (-2.181-0.069)	-	-	-	-	-	-1.179 SE=0.549 (-2.257-(-0.103))
Canopy*+ DistH2O*+ AgeFound+ Speed+ Year*	103.3	1.3	0.034	6.901 SE=1.412 (4.134-9.667)	0.848 SE=0.369 (0.125-1.572)	-1.275 SE=0.598 (-2.447-(-0.103))	-0.064 SE=0.039 (-0.142-0.014)	-	-	-	0.347 SE=0.417 (-0.469-1.164)	-1.489 SE=0.627 (-2.719-(-0.259))
Canopy*+ DistH2O*+ AgeFound+ Height+ Year*	103.5	1.5	0.031	6.715 SE=1.366 (4.036-9.394)	0.858 SE=0.372 (0.128-1.588)	-1.155 SE=0.526 (-2.186-(-0.123))	-0.071 SE=0.041 (-0.153-0.010)	-0.010 SE=0.014 (-0.037-0.017)	-	-	-	-1.233 SE=0.561 (-2.331-(-0.134))
Canopy*+ DistH2O*+ AgeFound+ Vdens+ Year*	103.8	1.8	0.027	6.789 SE=1.371 (4.103-9.477)	0.944 SE=0.379 (0.201-1.687)	-1.157 SE=0.538 (-2.213-(-0.101))	-0.066 SE=0.039 (-0.144-0.012)	-	-	-0.218 SE=0.464 (-1.128-0.692)	-	-1.441 SE=0.598 (-2.614-(-0.267))
Canopy*+ DistH2O*+ AgeFound+ AgeDay1+ Year*	103.9	1.9	0.026	7.144 SE=1.899 (3.420-10.868)	0.973 SE=0.405 (0.179-1.766)	-1.189 SE=0.552 (-2.272-(-0.106))	-0.064 SE=0.040 (-0.144-0.015)	-	-0.004 SE=0.009 (-0.023-0.016)	-	-	-1.409 SE=0.594 (-2.573-(-0.245))

Supplemental table 5. Best candidate binomial generalized linear models for comparisons of the variables canopy cover, vegetation density, and sound level between nest sites of the Star-throated Antwren and random sites determined far from any watercourse. Asteristics indicate the level of significance of the Z-statistics used to test if the parameters have differed significantly from zero and in parenthesis there is the lower and upper 95% confidence interval:

Model	AICc	ΔAICc	w	Intercept	Canopy	Vdens	Sound
Sound*+Vdens*	18.0	0.0	0.672	2.859 SE=1.759 (0.666-8.406)	-	3.738 SE=1.529 (1.551-8.022)	4.771 SE=2.351 (1.891-2.077)
Canopy+Sound*+Vdens*	19.4	1.44	0.328	2.764 SE=1.631 (0.609-8.124)	1.199 SE=1.307 (-1.152-4.354)	4.217 SE=1.950 (1.683-10.249)	4.590 SE=2.157 (1.777-11.463)

Supplemental table 6. Best candidate binomial generalized linear models for comparisons of the variables canopy cover, vegetation density, sound, stream depth, stream width, and water speed between nest sites of the Star-throated Antwren and random sites determined up or downstream. Asterisks indicate the level of significance of the Z-statistics used to test if the parameters have differed significantly from zero and in parenthesis there is the lower and upper 95% confidence interval:

Model	AICc	ΔAICc	w	Intercept	Canopy	Vdens	Sound	Depth	Width	Speed
Null*	85.2	0.0	0.087	2.867e-17	-	-	-	-	-	-
Sound	85.6	0.33	0.074	0.002 SE=0.262 (-0.514-0.519)	-	-	0.357 SE=0.271 (-0.161-0.915)	-	-	-
Canopy	85.7	0.50	0.068	-0.002 SE=0.262 (-0.519-0.513)	0.341 SE=0.271 (0.178-0.903)	-	-	-	-	-
Canopy+Sound	86.8	1.55	0.040	-0.0002 SE=0.264 (-0.521-0.521)	0.275 SE=0.278 (-0.263-0.846)	-	0.297 SE=0.278 (-0.240-0.865)	-	-	-
Speed	86.9	1.64	0.038	-0.004 SE=0.259 (-0.516-0.507)	-	-	-	-	-	-0.207 SE=0.326 (-1.245-0.349)
Vdens	87.0	1.71	0.037	-0.016 SE=0.259 (-0.529- 0.495)	-	0.007 SE=0.013 (-0.014- 0.049)	-	-	-	-
Canopy+Speed	87.0	1.75	0.036	-0.007 SE=0.264 (-0.529- 0.514)	0.395 SE=0.279 (-0.136- 0.976)	-	-	-	-	-0.289 SE=0.340 (-1.379-0.280)
Sound+Speed	87.1	1.87	0.034	-0.0009 SE=0.264 (-0.523-0.519)	-	-	0.377 SE=0.273 (-0.145-0.941)	-	-	-0.242 SE=0.334 (-1.319-0.319)

Supplemental table 7. Results of Daily Survival Rate model selection for Star-throated Antwren, involving the variables related to stream characteristics in nest sites: distance from water, width, depth, sound level and water speed:

Model	AICc	ΔAICc	w	Intercept	DistH2O	Sound	Depth	Width	Speed
Depth*+Sound+ DistH2O *	90.3	0.0	0.180	4.146 SE=0.503 (3.161-5.132)	0.2022 SE=0.075 (0.055-0.349)	-0.607 SE=0.345 (-1.283-0.069)	1.222 SE=0.581 (0.083-2.360)	-	-
Depth*+DistH2O*	91.2	0.89	0.115	3.996 SE= 0.428 (3.156-4.835)	0.148 SE=0.066 (0.019-0.277)	-	1.004 SE=0.465 (0.093-1.915)	-	-
Depth+Sound+ DistH2O*+Width	92.0	1.68	0.078	4.056 SE= 0.501 (3.075-5.037)	0.193 SE= 0.073 (0.049-0.336)	-0.736 SE= 0.405 (-1.530- 0.058)	0.994 SE= 0.657 (-0.293-2.281)	0.236 SE= 0.382 (-0.514-0.985)	-

Supplemental table 8. Results of Daily Survival Rate model selection for Star-throated Antwren, involving the variables distance of the nest from water and stream depth returned from the pre-modeling and including the variables canopy cover, vegetation density, nest height, “AgeFound”, “AgeDay1” and Year of the breeding season:

Model	AIC	ΔAICc	w	Intercept	Height	Canopy	Depth	DistH2O	AgeFound	AgeDay1	Vdens	Year
Height+Canopy+ Depth*+DistH2O* +AgeFound*+Year	87.2	0.00	0.067	9.008 SE=2.181 (4.733-13.283)	0.159 SE=0.125 (-0.084-0.404)	-0.599 SE=0.352 (-1.289-0.089)	2.649 SE=0.784 (1.112-4.186)	0.227 SE=0.072 (0.085-0.369)	-0.116 SE=0.053 (-0.219-(-0.013))	-	-	-1.033 SE=0.597 (-2.203-0.138)
Canopy+Depth*+ DistH2O*+ AgeFound*	87.4	0.23	0.060	6.244 SE=1.249 (3.794-8.694)	-	-0.588 SE=0.334 (-1.242-0.066)	2.070 SE=0.710 (0.678-3.462)	0.215 SE=0.074 (0.069-0.361)	-0.102 SE=0.049 (-0.198-(-0.005))	-	-	-
Depth*+DistH2O* +AgeFound*+Year	87.7	0.54	0.051	8.487 SE=2.096 (4.381-12.593)	-	-	1.990 SE=0.732 (0.555-3.424)	0.198 SE=0.073 (0.055-0.341)	-0.111 SE=0.051 (-0.212-(-0.010))	-	-	-0.856 SE=0.517 (-1.869-0.157)
Canopy+Depth*+ DistH2O*+ AgeFound*+Year	87.7	0.55	0.051	8.312 SE=2.172 (4.054-12.569)	-	-0.469 SE=0.343 (-1.141-0.202)	2.278 SE=0.759 (0.789-3.766)	0.218 SE=0.075 (0.072-0.364)	-0.118 SE=0.053 (-0.222-(-0.015))	-	-	-0.697 SE=0.544 (-1.763-0.369)
Height+Canopy+ Depth*+DistH2O* +AgeFound*	88.3	1.15	0.038	6.189 SE=1.252 (3.736-8.642)	0.071 SE=0.104 (-0.134-0.276)	-0.669 SE=0.342 (-1.339-0.0002)	2.231 SE=0.722 (0.816-3.646)	0.219 SE=0.074 (0.074-0.363)	-0.101 SE=0.050 (-0.199-(-0.003))	-	-	-
Height+Depth*+ DistH2O*+ AgeFound*+Year	88.4	1.20	0.037	8.843 SE= 2.054 (4.818-12.869)	0.107 SE=0.113 (-0.115-0.329)	-	2.187 SE=0.741 (0.735-3.639)	0.204 SE=0.071 (0.065-0.343)	-0.106 SE=0.052 (-0.207-(-0.004))	-	-	-1.069 SE=0.553 (-2.154-0.016)
Depth*+DistH2O* +AgeFound*	88.7	1.51	0.031	5.966 SE=1.204 (3.607-8.326)	-	-	1.398 SE=0.547 (0.328-2.469)	0.165 SE=0.067 (0.033-0.297)	-0.099 SE=0.049 (-0.197-(-0.002))	-	-	-

2.3. Nest site selection and reproductive parameters of the threatened Atlantic Royal Flycatcher, *Onychorhynchus swainsoni*, and its significance for conservation

Patterns of rarity of animal species can be explained mainly by large body size, low reproductive rates, large home range, requirement of pristine and stable environments, high habitat specificity, and high levels of endemism (for review, Primack 2006). Then, knowledge on these parameters is essential for understanding the levels of vulnerability of the taxa, and for generating guidelines for conservation planning (Primack 2006). In birds, important characteristics determining annual productivity involve clutch sizes, reproductive phenology, nest survival and renesting rates (Gilpin and Soulé 1986, Cuthbert et al. 2004, Pacifico et al. 2014), while nest site selection and habitat specificity can determine the density of reproductive pairs and the fate of the nests (Fondell and Ball 2004, Gjerdrum et al. 2005, Ocampo and Londoño 2015).

In the last years many of the megadiverse environments in the world are disappearing, losing its original vegetation to anthropic landscapes (Ratter et al. 1997, Myers et al. 2000, Ribeiro et al. 2009, He et al. 2014). The Brazilian Atlantic Forest is one of the five main world's hotspots of biodiversity (Myers et al. 2000), concentrating high levels of endemisms, and at the same time high levels of habitat loss, with only about 20% of its primary cover remaining (Ribeiro et al. 2009). It holds more than 830 species of birds, of which 217 are endemic, and and most of them are vulnerable to extinction (Bencke et al. 2006, Hasui et al. 2018). However, even basic information needed for conservation planning are lacking for most species.

One such a case is the Atlantic Royal Flycatcher, *Onychorhynchus swainsoni*. Formerly classified as *O. coronatus*, it was subsumed to *O. swainsoni* due to the disjunctive distribution, smaller body size, and divergences in body color and voice, with the Atlantic

Royal Flycatcher restricted to humid montane forests of east Brazil, from Minas Gerais and Rio de Janeiro to Santa Catarina states, while the Amazonian Royal Flycatcher is distributed throughout the Amazon region, including Venezuela, Guianas, Colombia, Ecuador, Bolivia, and almost all of Brazilian Amazon (Del Hoyo et al. 2019a, Farsworth et al. 2019). This species is remarkable due to its crest, scarlet in male and orange in female, with spots of black and steel-blue at the tips, which gives it a symbolic appeal (Sick 1997, Fitzpatrick et al. 2004). It inhabits exclusively humid montane forests and seems to be closely related to the streams present in this type of environment (Sick 1997, Mallet-Rodrigues et al. 2006, IUCN 2016). The current conservation status of the Atlantic Royal Flycatcher is "vulnerable" according to the International Union for Conservation of Nature, but mainly due to habitat loss, it is suspected that the population is decreasing, and the need for studies on its ecological requirements has been emphasized (IUCN 2016). However, information on reproductive aspects for this species is limited only to nests (Von Ihering 1914, Descourtiz 1983, Kirwan 2009), and eggs descriptions (Von Ihering 1914, Sick 1997, Mallet-Rodrigues et al. 2006).

Here we investigated nest site selection, breeding territorial density, nesting success, and annual productivity of the Atlantic Royal Flycatcher in a well-preserved Brazilian Atlantic Forest continuum. Besides, we provide additional information on nests and eggs characteristics, and we present aspects of the breeding phenology, descriptions of the nestlings, incubation and nestling periods. We reveal that nests are built only above forest streams with very specific characteristics. This level of nesting habitat specificity combined with a long reproductive cycle, low renesting rate, low annual fledgling productivity, and very low reproductive territorial density may explain the rarity of this species even in well-preserved habitats. We believe that these data will be helpful to delineate conservation strategies for this Atlantic Forest endemic bird.

METHODS

STUDY AREA.—Nests were searched in Carlos Botelho State Park (PECB, 24°04'S 47°58'W, 20–1,000 m a.s.l.) which is part of one of the biggest and better preserved continuous tracts of Atlantic Forest from southeastern Brazil (Mattoso et al. 2008). PECB is a 37,644 ha Atlantic Forest remnant located at São Paulo State, Brazil, where the predominant vegetation is primary Atlantic Forest (Oliveira-Filho and Fontes 2000). The local average temperature is between 18 and 20°C (Ferraz and Varjabedian 1999) and the climate in the region is classified as Cfa according the Koppen-Geiger (Kottek et al. 2006, Peel et al. 2007). The annual average rainfall is 1,676 mm (varying from 777 to 2,264 mm) with a marked wet season from October–March, with a rainfall peak in January, and a dry season from April–September, with a drought peak in August (Beisiegel and Mantovani 2006). The study was conducted in an area where the elevation ranges from 700 to 760 m, and the vegetation is classified as submontane Atlantic Forest. We also included in our analyses one nest found at Trilha dos Tucanos Lodge (TTL) (24°00'17"S 47°33'45"W), a private and well-preserved reserve dedicated to nature conservation and birdwatching ecotourism, which is close to Carlos Botelho and belongs to the same forest continuum.

FIELD PROCEDURES. —We conducted nest searches during five breeding seasons at PECB, from September to February in 2013/2014, 2014/2015, 2016/2017 and 2017/2018, and from October to January in 2018/2019. In this area, we used 10 trails, totaling 9.4km, and four streams, totaling 6 km, as transects. Each trail or stream was surveyed weekly during the whole reproductive season, but not necessarily all of these paths were analyzed every year (supplemental table 1). At TTL, we performed only one visit in 2017/2018, when we located one nest. Nests were found by searching appropriate locations while walking in trails and

streams (Martin and Geupel 1993), mainly by inspection of structures similar to nests of Royal Flycatchers (Pinto 1953, Kirwan 2009).

NEST SITE SELECTION.—We measured six covariates to access the nesting site preferences of the Atlantic Royal Flycatcher, of which two were related to vegetation (forest canopy cover and vegetation density around nest) and four were related to the characteristics of the streams where we found nests (width and depth of streams, water flow speed and sound produced by it). We measured these variables at each nest site during 2016/2017, 2017/2018 and 2018/2019 breeding seasons, and also in a random site at 30 m down- or upstream of each nest.

We measured canopy cover using a spherical densitometer, following the instructions of manufacturer (Convex Model-A, Forest Suppliers, Inc.). This equipment has a convex mirror that reflect over story vegetation when hold in front of the observer chest. Then four readings were taken per point in the mirror, facing cardinal directions (N, S, E, W) according to the suggested by Lemmon (1957). Each value was multiplied by 1.04 to obtain the percent of over story area with no vegetation in the canopy, and the difference between these values and 100 were calculated. Thus, the resulted numbers averaged was the estimation of canopy cover (Lemmon 1957).

The measuring of vegetation density around the nest was obtained by passing a measuring tape horizontally from outer surface of the nest through the surrounds for directions north, south, east, west, up and down. We use only the first 50 cm of the tape and considered only one contact with vegetation each 10 cm interval. These hits were counted and the vegetation density was calculated as the number of 10 cm intervals contacts divided by all 30 intervals. At the random point, measurements were obtained using the same procedure, at the same height of the reference nest (Mezquida 2004).

To estimate the sound produced by the water flow we used a digital decibel meter (range 30dBA – 130dBA; accuracy ± 1.5 dB). Sound level was obtained during a 3 min session in each nest and random up- or downstream point, with the microphone pointed to the water. As the water sound is constant, and interferences, including the sound of the wind or of animals are punctual, only the minimal minimum average values obtained during each session were used in our analysis.

Water depth was measured at nests and random sites right in the middle of the streams. For the width of streams, we measured the length between the margins directly below the nest and random site. Water speed was obtained by calculating the time that a standardized fluctuating plastic object took to travel a distance of 5 m, starting from the nest or random site.

BREEDING BIOLOGY DATA.—To provide further information on the reproductive aspects of the Atlantic Royal Flycatcher, nests were monitored both by focal observations and with one or two camera traps. Camera types, settings, and field procedures are described in Ribeiro-Silva et al. (2018). We used the classifications proposed by Winkler (2004) for nest type and eggs shape. Measurements of eggs and nests were taken with a metal caliper accurate to 0.5 mm, and eggs were weighed with a 0.1 g spring scale.

Nests were checked at least once a week, but to access incubation and nestling periods we performed daily nest checking during late incubation and late nestling stages. We avoid handle or touch nestlings on the nest to not interfere nestling period duration (Skutch 1945). We obtained clutch initiation dates from nests found in construction stage and incubation initiation was determined by the presence of an incubating female or by the presence of warm eggs. The period of incubation was considered from the first day the eggs became warm to the day before hatching, and we considered nestling period from the day of hatching to the day

before fledging (Winkler 2004, Oliveira et al. 2010). Nest predation was assumed when eggs or nestlings disappeared from the nest before fledging age, and abandonment was considered when eggs were cold and parents were not seen attending the nest for more than two consecutive observation sessions. Nests were considered successful when fledging was recorded by the cameras or when well-developed young disappeared from a nest in consecutive monitoring days, with no records of predators in the cameras.

DENSITY OF REPRODUCTIVE PAIRS.—For estimating the density of breeding pairs along the streams in which nests were found, we divided the number of territories by the total extension of rivers searched in each breeding season. Then, these values were averaged across the five breeding seasons to generate an estimate of numbers of nests per km, and its standard deviation (SD).

STATISTICAL ANALYSES

Nest site selection.—Nest site selection was addressed in three different levels. First, as nests were searched along streams and also in transects far from water, we evaluated if water courses are selected by our studied species. Second, considering only the water courses, we compared the characteristics of the streams where we found nests with the characteristics of the streams without nests. To achieve this purpose we first performed a Principal Component Analysis (PCA) with data corrected using z-score and correlation matrix, using the variables stream width, water depth, and canopy cover. Then, we applied a t-test with the new scores obtained for the main axis to access the level of significance with 95% confidence using the software Past3 (Hammer et al. 2001). To assess what variables were contributing with the potential differences between these two stream categories, we compared each variable independently using simple t-tests.

Third, we addressed nest site selection within the streams in which nests of the Atlantic Royal Flycatcher were found. A PCA was performed following the same above procedures to compare the variables stream width, depth, water speed, water sound, and canopy cover between nests and random sites. To elucidate which variables could explain nest site selection, we performed two model selection procedures using Generalized Linear Models, with binary distribution and logit link-function, where nest points were coded as 1 and random points coded as 0 in the binary distribution. In the first Logistic Regression, we considered only the variables related to the streams (depth, width, water speed and sound), and then, we performed a second analysis using the most important stream variables together with vegetation density and canopy cover. The generated models, including the null model, were exploited using the function dredge provided by the R-package “MuMIn” (Bartoń 2018). We tested for auto-correlation between variables using Pearson correlation test with the function rcorr provided in R-package “Hmisc” (Harrell Jr et al. 2019). We considered variables auto-correlated when $r \geq 0.7$ or when a significant correlation was found ($P \leq 0.05$). One or more variables with less capacity to explain the data (when $r \geq 0.7$ or when P-value of correlation was ≤ 0.05) were removed from the subsequent analyses. Models support were evaluated using Akaike's Information Criterion corrected to small samples (AICc), and also by the $\Delta AICc$ and Akaike weight (w) values. We selected models presenting $\Delta AICc < 2$, which indicates substantial support for them (Burnham and Anderson 2002). We also reported the parameter estimates of the select models and their standard errors, with upper and lower 95% confidence limits, to demonstrate the validity of the explanation of each variable for each model. Further, we carried out Z-tests to verify if each variable within the selected models were significantly different from zero.

Nest survival.—The Daily Nest Survival Rate (DSR) was calculated for the Atlantic Royal Flycatcher using the binominal Generalized Linear Model as proposed by Dinsmore et al. (2002), with maximum likelihood parameter estimates, with the interface of the Program Mark (White and Burnham 1999), implemented by the R-package “RMark” 2.2.6. (Laake 2013). Fates were coded as 0 for successful nests or 1 for the depredated ones, and we pooled samples from all breeding seasons to improve analysis effectiveness. Due to reduced sample sizes, only the null model of constant DSR was addressed. For comparative purposes with other previous works related to reproductive parameters of birds, we also calculated the DSR using the method proposed by Mayfield (1961). In both approaches, the cumulative probability of overall nest success can be estimated by raising DSR to the power corresponding the duration of the nesting cycle. Statistical analyses were performed using the Software R version 3.4.2 (R Development Core Team 2017).

RESULTS

NEST SITE SELECTION.—During the five breeding seasons we found 23 active nests. All of the nests were placed over water, but we found nests in only two of the four sampled streams. The two streams in which nests not found were 1.51 ± 0.3 m wide (range 0.98 – 2.31 m, N = 15 random points), and 8.2 ± 3.5 cm deep (range 4.5 – 16 cm, N = 15 random points), while the other two, where we found the nests (excepted from TTL), were 4.28 ± 9.8 m wide (range 2.6 – 5.74 m, N = 15 random points) and 21.4 ± 10.4 cm deep (range 8 – 41 cm, N = 15 random points). The PCA including the characteristics of the streams with and without nests revealed a significant divergence, with 64% of the variation explained by the first axis and 28% by the second (fig. 1). The t-test with the new scores of the main axis was also highly significant ($t = -8.43$, $P < 0.0001$). T-tests of the independent variables also have differed

significantly: forest canopy cover ($t = 2.68$, $P = 0.006$); stream width ($t = -10.29$, $P < 0.0001$), and depth ($t = -4.67$, $P = 0.0001$) (fig. 2).

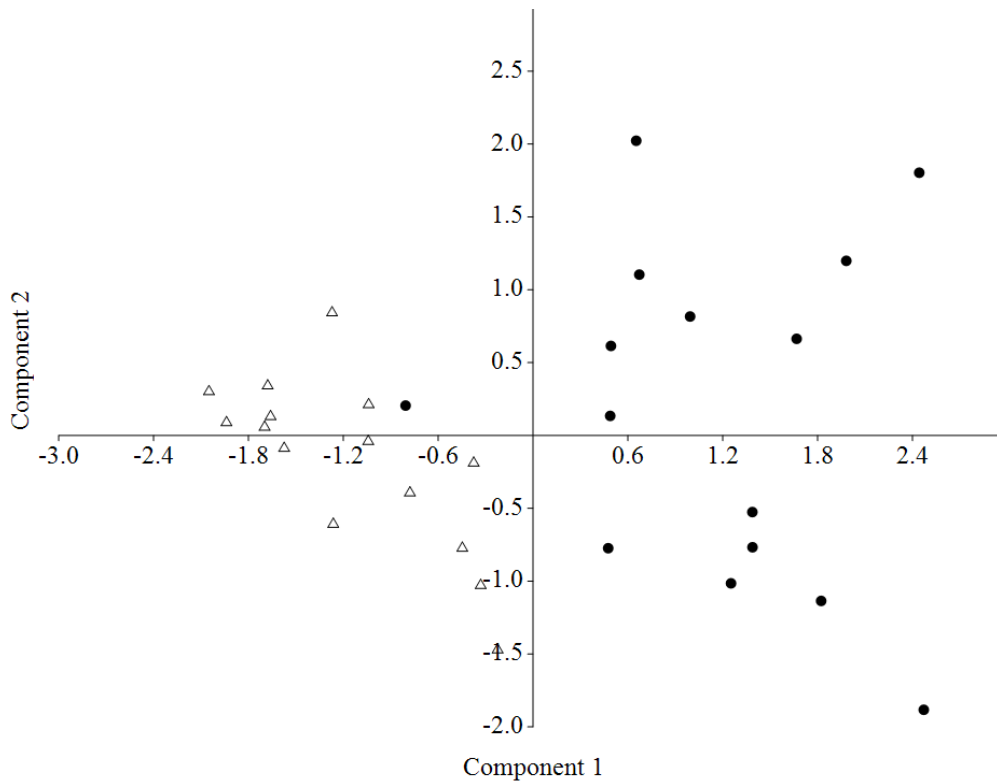


Fig. 1. Principal Component Analysis addressing the variables canopy cover, streams width and depth obtained in random sites along streams with (black circles) and without (white triangles) Atlantic Royal Flycatcher nests.

Sixteen nests found in the last three breeding seasons were used to address nest site selection within the rivers in which nests were found. The PCA analysis performed to compare the variables vegetation density, canopy cover, stream depth, stream width, water speed, and sound between nest and random sites demonstrated that 52% of the variation could be explained by the main two axes, where 27% of it was explained by the main one (fig. 3). The t-test carried out with the new scores of the main axis was significant ($t = 2.4495$, $P = 0.02$).

In the first block of GLM modeling including only covariates related to stream characteristics (depth, width, water speed, and sound) revealed 11 models with $\Delta AICc < 2.0$. However, the z-test indicated lower and upper 95% intervals overlapping zero for almost all of the variables, excepted for water speed, which was then selected for the second block of analysis (supplemental table 2). For the second GLM, in which the best stream variable (water speed) was modeled together with canopy cover and vegetation density, only four models presented $\Delta AICc < 2.0$, and only vegetation density was present in all of the models and had 95% CI not overlapping zero, with a negative value (supplemental table 3).

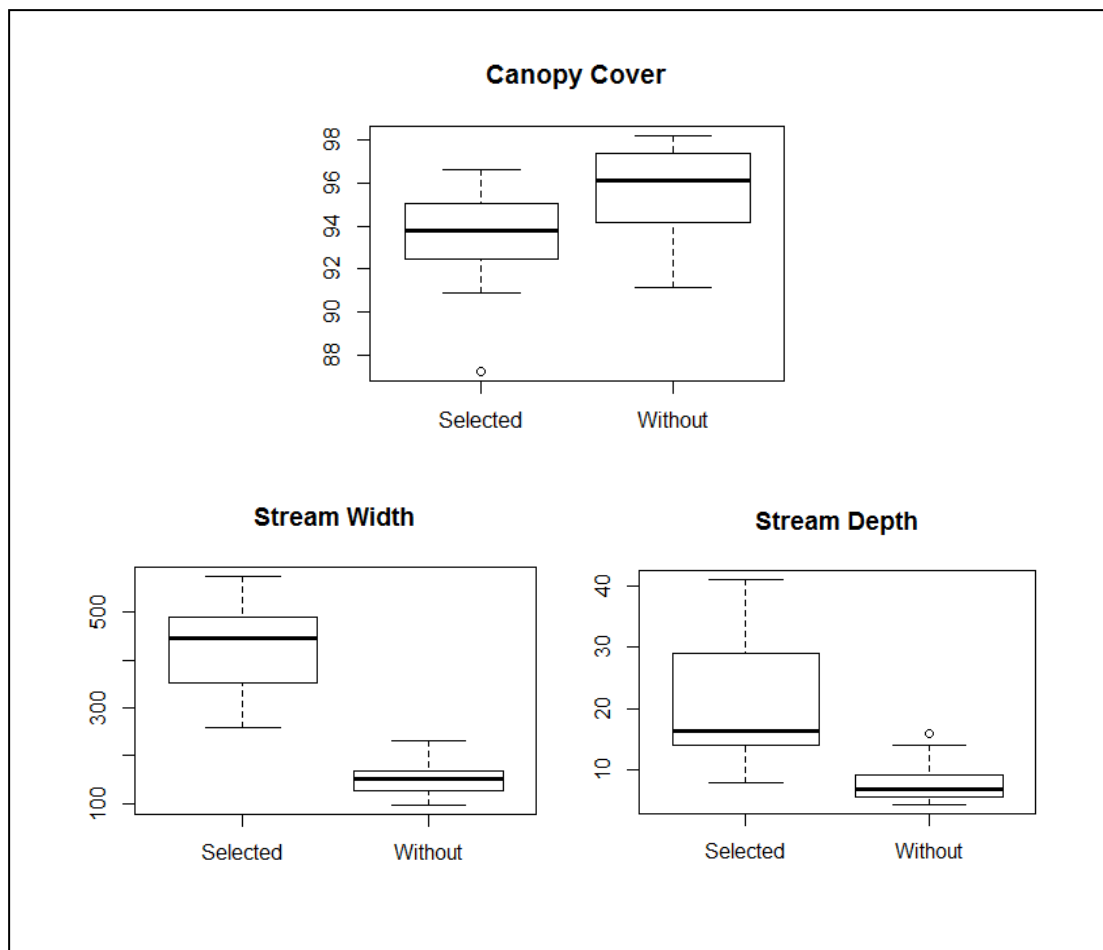


Fig. 2. Boxplots comparing Canopy cover, width, and depth of the streams selected (Selected) by the Atlantic Royal Flycatchers for nest construction, and those not used by the birds (Without).

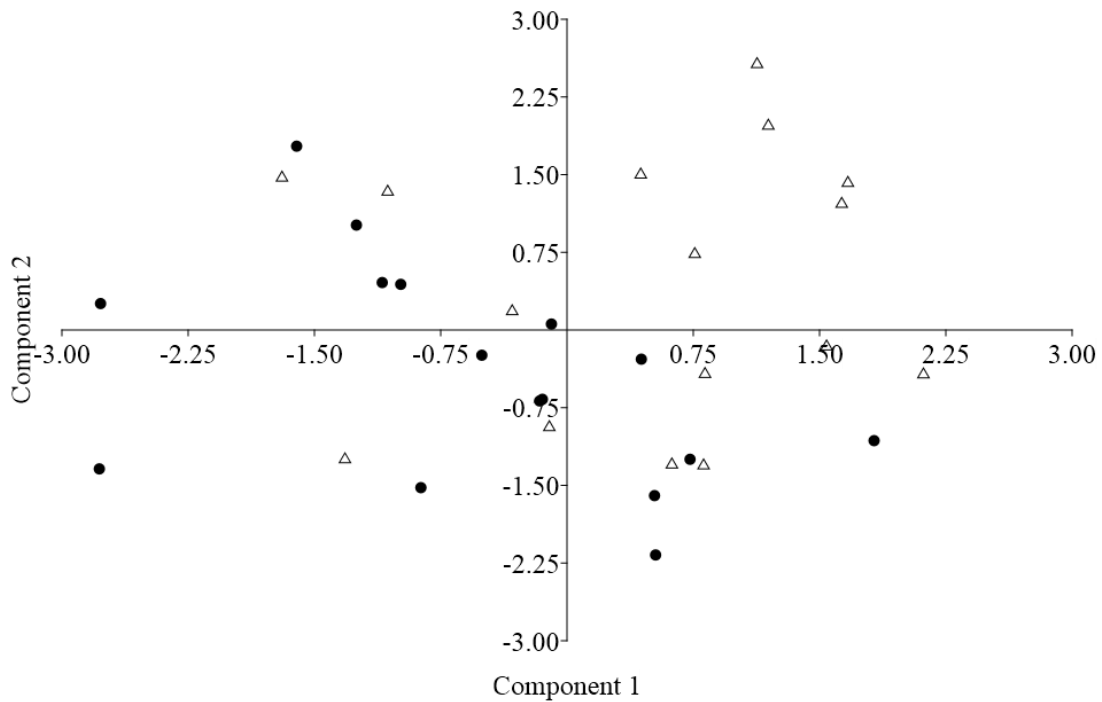


Fig. 3. Principal Component Analysis addressing the variables canopy cover, vegetation density, stream width, depth, water speed, and sound used to compare nest sites (black circles) and random sites (white triangles) within rivers used by the Atlantic Royal Flycatcher for nesting.

DENSITY OF REPRODUCTIVE PAIRS.—Considering only the streams in which nests were found, the average number of reproductive pairs in the study area was 1.62 ± 0.065 pairs/km (1.56 – 1.73 pairs/km), and we found one nest or territory every 618.4 ± 24.04 m (577 – 640 m).

Although we would have not marked the birds to determine the breeding territories precisely, active nests were found very distant each other on a same breeding season, indicating this species has a large home range. However, among the years, new nests were found relatively close of nests from previous breeding season, providing security to determine the territoriality of the breeding pairs.

NESTS, EGGS AND NESTLINGS. —In 2013/2014, the first nest was found during construction on 25 October 2013 and the last nestling fledged around 16 February 2014. In 2014/2015, the first nest was found on 7 October 2014 in construction stage, and the last nestling fledged on 22 January 2015. In 2016/2017, the first nest was found on 28 October during the initiation on material deposition for nest construction and the last fledging was early March. In 2017/2018, the first nest was found during construction in 19 September and the last nest with nestlings was successful in late January. In 2018/2019, the first nest was found in 16 October during construction and the last nest was predated in 30 December. However in this last season, we found two renestings from nests from successful nests with eggs in incubation stage in 31 January 2019, but that did not be monitored longer.

Nests were 1.88 ± 0.38 cm (range 0.93–2.44, N = 18) above water and they had no vegetation hidden them. Nests were elongated pendulous domes with untidy appearance, and attached to slender malleable branches with large green leaves. The material deposition was done around these branches, which were incorporated to the nest architecture and left their live leaves in evidence (fig. 4A). The whole structure averaged 56.4 ± 17.7 cm (range 30–104 cm) in length, and the nest chamber was positioned in its lowest portion. Outer diameter of nest chamber was 88.1 ± 16.6 mm (range 52.9–117.8 mm), inner cup diameter was 74.3 ± 11.5 mm (range 53.3–87.7 mm), cup depth was 41.6 ± 9.9 mm (range 30.3–70.5 mm), and the lateral entrance measured on average 72.3 ± 8.2 mm (range 56.6–81.8 mm) per 52.3 ± 8.1 mm (range 42.9–69.9 mm). The outer nest layer was composed by long and fine brown rootlets, small dried fern leaves, and some green leaves. The surface was adorned by hung large dried fern leaves, dried and twined leaves, and loose tufts and filaments of green moss sometimes exceeding the bottom of the structure and forming a “tail” averaging 31.3 ± 14.9 cm (range 10–60 cm) (fig. 4A). Nest chamber was composed by finest rootlets loosely interwoven and with no inner lining, in order to be possible to see eggs through chamber wall. A pronounced

roof of the same material of the outer layer was deposited over the nest entrances, making the incubatory chamber hidden from above.

Clutch size was two eggs (N = 16) or nestlings (N = 2), except for one nest in which we found only one hatchling. In two nests found during construction, the laying could be accompanied. In these nests, the second egg was laid with one or two days interval, and incubation began in the morning of the second egg was laid. Incubation period was 22 days (2 eggs from one nest). Eggs were chalky textured and elliptical-shaped, averaging 20.5 ± 0.7 mm (range 19.2–22 mm) per 15.2 ± 0.4 mm (range 14.2–15.7 mm), and weighed 2.2 ± 0.4 g (range 1.5–2.8 g, N=14 eggs from seven nests). Eggs were pinkish brown or reddish brown in background color, and wreathed with darker rufous scratches (fig. 4B).

Hatching was synchronous in one nest and asynchronous in two nests, with an interval of approximately one day. For four young from two nests, nestling periods were 24 days, and for one young from one nest, nestling period was 27 days. Hatchlings had pink skin, yellowish upperparts, closed eyes, and were devoided of down. Commissures were bright orange, the same color of the bill, which was grizzly in the upperparts (fig. 4C). When nestlings became feathered, their heads and bodies upperparts were strongly streaked and the crest could already be noted. Nestlings always exposed their crests when an observer approached, a behavior that is common in the adults when they are mistnetted.

REPRODUCTIVE SUCCESS.—Of the 20 nests monitored for nest predation, six were lost to predation (30%, two during incubation and four during nestling stages), one was abandoned during construction (5%), and 13 were successful (65%). DSR estimated using RMark was 0.988 ± 0.004 (0.975-0.995 of 95% IC), and the survival probability from incubation initiation to fledging was 62.3% (DSR=0.990; 0.992 during incubation stage; 0.988 during nesting stage) using Mayfield method.



Fig. 4. A- Nest of Atlantic Royal Flycatcher; B- Eggs; C- Hatching (Photos: Daniel Perrella and Michele Viana).

NESTING ATTEMPTIVENESS AND RENESTING.—We observed only two cases of second nesting attemptiveness after predation of the first nest. One nest was predated during incubation stage on 18 November 2014, and the construction of a second nest was detected on 23 November, with incubation initiation in early December, and fledging in 21 January 2015. In the second case, a nest also in incubation stage was depredated between 10 and 15 November 2017. The second nest was found in 23 November in construction, but it was abandoned a few days later and no more attempts of reproduction were detected for this pair in this season. For the other four failed nests, predated during nestling stage, no attemptiveness was verified.

Nest reuse was observed only during the last studied breeding season (2018/2019). Two reproductive pairs that were successful in their first nesting attempt, with fledging in late December 2018, were observed with eggs being incubated on 30 January 2019, but they were no longer monitored.

DISCUSSION

Our main finding was that Atlantic Royal Flycatchers were selective in relation to nesting site characteristics in the three levels of analyzes addressed here. In the first level, birds have built their nests hung over water, in detriment of river edges and forest areas far from water. In the second level, nests were found in only two of four analyzed rivers, and the rivers used by the birds for reproduction presented a set of divergent characteristics in relation to the non-used ones, and in the third level, nest sites differed from random sites within the used streams in at least one of the six analyzed environmental covariates.

The streams used for nest construction were the two larger ones, which were similar, but were much bigger than the two non-used streams. It is important to note that although used and non-used streams have differed in canopy openness, even the larger streams were typical "forest streams", mostly covered by forest canopy. Although we could note that they excluded the smaller forest streams, we are unaware if they could construct nests, for instance, along the biggest Atlantic Forest rivers that are, for instance, 10-15m wide, and have forest canopy presenting large gaps.

The only significant variable indicated by within-streams nest site selection modeling was vegetation density, which was negatively correlated to the presence of nests. The construction of the nests in descending branches in the middle of the rivers, far from the edges where the vegetation is denser, is the first predictive of low vegetation density around the

nests of the Atlantic Royal Flycatchers. Since we have adopted for random sites the nearest descending branch chosen from the middle of the streams, we are certain that this result is not a byproduct of obtaining vegetation parameters from sites that were closer to the stream edges than were the real nests. As our vegetation density estimates were in a scale of 30 cm, this finding suggests that the birds have selected nesting branches with less ramifications and foliage densities.

Despite the taxonomic problems involved to the *Onychorhynchus* complex (Fitzpatrick et al. 2004), the usually recognized species seen to construct nests very similar to Atlantic Royal Flycatcher. The scarce nest observations reported for Pacific Royal Flycatcher *O. occidentalis* (Sclater, 1860) and for Northern Royal Flycatcher *O. mexicanus* (Sclater, 1857) confirm that these species also build their pensile closed nests over forest streams, although higher in relation to water (Tashian 1952, Skutch 1960, Whittingham 1994). However, for the Amazonian Royal Flycatcher *O. coronatus* (Müller, 1776), there are reports about nests both over and far from watercourses (Pinto 1953, Kirwan 2009). Then, at least the Pacific and Northern Royal Flycatchers appear to have a close interaction with forest streams for nesting, as was observed for *O. swainsoni*. This specificity for habitat selection is dangerous for species with a so small distribution range, because any environmental disturbance could reduce their breeding activity and compromise the entire population (Primack 2006), so much that *O. occidentalis*, that occurs in a restricted area from Ecuador and Peru, is also considered a threatened species while *O. mexicanus*, that occurs along almost all Central America, is least concerned (IUCN 2016, Del Hoyo et al. 2019b).

The Atlantic Royal Flycatcher is endemic of humid forests from east Brazil (Sick 1997), but their habitat requirements are possibly much more complex than it. Firstly because the majority of the forests where it lives are actually restricted to small fragments (Ribeiro et

al. 2009), which may have contributed to the species decline (IUCN 2016), once several inventories and monitoring conducted in no continuous remnants along its distribution range, did not find populations of Atlantic Royal Flycatchers (Willis 1979, Ribon et al. 2003, Antunes and Eston 2008, Schunck et al. 2016, Perrella et al. 2018). Besides that, we found a very low density of breeding pairs along the sampled streams, even the PECB been one of the larger and most preserved areas of Atlantic Forest (Mattoso et al. 2008). Comparing the density of breeding Atlantic Royal Flycatchers to another bird that use stream margins for nest and are more common, the Star-throated Antwren *Rhopias gularis*, we found a density more than three times lower for the flycatcher (average 5,35 nests/km or a breeding pair each 197 m for *R. gularis*, pers. obs.). In this way, it would be impossible a small fragment, with limited extensions of forest streams, offer enough resources for a viable population of breeding Atlantic Royal Flycatchers.

The process of fragmentation can be highly damaged for forest-dwelling bird populations (Ferraz et al. 2007, Oliveira Jr. et al. 2011). Among its negative effects, there is the increasing nest predation rates in smaller size forest remnants (Small and Hunter 1988, Yahner and Scott 1988), reducing significantly the potential success of nesting attempts of birds (Karr 1982, Galetti et al. 2009). The Atlantic Royal Flycatcher presented a comprehensive longer nesting cycle, totalizing at least 46 days without counting days of laying and nest construction. This scenario, besides the low rate of renesting and attemptiveness if the nest is predated in late stage of the breeding season, become this species more vulnerable to disappear from small patches of forest, even if it hold streams with good environmental characteristics for nesting.

Although the absent of streams could be a limiting factor for this species survive in most of remnants, select this kind of habitat for nesting have been considered an efficient strategy against nest predators (Robinson 1985, Ocampo and Londoño 2015), once some

terrestrial species as small mammals are unable or have difficulty to cross streams and reach a nest (Noske et al. 2013). Thus, the decision to select wider and deeper streams could be related to maintain the security of the nest isolated over water, even along the stream no variables related to water have been demonstrated strong power for selection explanation. By other side, the selection for sites with less vegetation density around the nest is probably related to decrease access for climbing terrestrial predators, as the Grey Slender Mouse Opossum (Lund, 1840) recorded by Ribeiro-Silva et al (2018) preying an Atlantic Royal Flycatcher nest. Visual oriented nest predators as birds, would not be affected by this strategy because can detect and access the nests flying (Remes 2005, Roldán-Clarà et al. 2013, Ocampo & Londoño, 2015), and maybe camouflage of the nests play a more effective role in this aspect considering the high DSR (Collias and Collias 1984, Fraser et al 2007), but this possibility would have to be better investigated.

In conclusion, we could verify that the Atlantic Royal Flycatchers indeed select certain kinds of forest streams for nesting, being highly specialists in these environments. However, their long nesting cycle, the low density of breeding pairs along streams even on a well preserved reserve, and low productivity become them dependent of the high DNS found in undisturbed remnants of forest, with low rates of nest predation. This factor, besides the association to streams, does not allow Atlantic Royal Flycatcher occurs in small fragments, which can threaten seriously the population of this species, once large remnants of Atlantic Forest are scarce and restricted today.

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Supplemental table 1. Streams and trails travelled during the five breeding seasons for searching nests of Atlantic Royal Flycatcher, the length (m) of each transect is presented in parenthesis:

		Breeding season				
		2013/2014	2014/2015	2016/2017	2017/2018	2018/2019
Streams (5911m)	Santuário (1250)	X	X	X	X	X
	Braço (1000)	X	X			
	Forno (987)	X	X	X		
	Ribeirão (2674)				X	X
Trails (9407m)	Forno (1300)	X	X	X		
	Uru (362)	X				
	Cano (380)	X	X			
	Braço (1700)	X	X			
	Rota (165)	X				
	Canela (1900)	X				
	Caqui (200)	X				
	Quiosque (1100)				X	
	Aceiro (1100)				X	
	Bifurcação (1200)					X

Supplemental table 2. Best candidate models from Logistic Regression for comparisons between nest and random sites determined for Atlantic Royal Flycatcher. Asteristics indicate the level of significance of the Z-statistics used to test if the parameters have differed significantly from zero:

Model	AICc	ΔAICc	w	Intercept	Sound	Depth	Width	Speed
Speed	45.5	0.0	0.130	-0.010;SE= 0.373 (-0.754-0.728)	-	-	-	-0.691;SE=0.408 (-1.583-0.057)
Width+Speed*	46.3	0.75	0.090	-0.014;SE=0.383 (-0.780-0.746)	-	-	0.518;SE=0.413 (-0.253-1.402)	-0.790;SE=0.425 (-1.716-(-0.013))
Null	46.5	0.97	0.080	0.00	-	-	-	-
Depth	46.5	0.98	0.080		-	-	-	-
Sound+Speed	46.6	1.07	0.076	0.014;SE=0.381 (-0.746-0.773)	-0.457;SE=0.400 (-1.308-0.301)	-	-	-0.638;SE=0.408 (-1.525-0.121)
Sound+Depth	46.6	1.07	0.076	0.064;SE=0.384 (-0.689-0.841)	-0.599;SE=0.411 (-1.490-0.161)	0.697;SE=0.484 (-0.124-1.823)	-	-
Depth+Speed	46.7	1.21	0.071	-0.002;SE=0.381 (-0.760-0.757)	-	0.452;SE=0.429 (-0.336-1.440)	-	-0.612;SE=0.429 (-0.760-0.757)
Sound	46.8	1.31	0.068	0.0272;SE=0.365 (-0.694-0.754)	-0.517;SE=0.385 (-1.339-0.205)	-	-	-
Depth+Width +Speed	46.9	1.37	0.066	-0.012;SE=0.397 (-0.808-0.778)	-	0.607;SE=0.464 (-0.225-1.693)	0.649;SE=0.436 (-0.155-1.596)	-0.713;SE=0.455 (-1.706-0.124)
Depth+Width	47.0	1.49	0.062	0.023;SE=0.379 (-0.727-0.785)	-	0.764;SE=0.483 (-0.062-1.879)	0.537;SE=0.398 (-0.216-1.382)	-
Sound+Depth +Speed	47.5	1.95	0.049	0.024;SE=0.393 (-0.760-0.809)	-0.563;SE=0.428 (-1.491-0.234)	0.575;SE=0.472 (-0.266-1.686)	-	-0.556;SE=0.435 (-1.496-0.262)

Supplemental table 3. Best candidate models from Logistic Regression for comparisons between nest and random sites considering the best variable related to the streams (water speed) with canopy cover and vegetation density. Asteristics indicate the level of significance of the Z-statistics used to test if the parameters have differed significantly from zero:

Model	AICc	ΔAICc	w	Intercept	Canopy	Vdens	Speed
Vdens*+Speed	41.9	0.0	0.267	-0.028;SE=0.414 (0.868-0.794)	-	-0.997;SE=0.446 (-1.993-(-0.192))	-0.664;SE=0.449 (-1.658-0.158)
Vdens*	41.9	0.02	0.265	-0.029;SE=0.397 (-0.829-0.756)	-	-1.053;SE=0.451 (-2.058-(-0.247))	-
Canopy+Vdens*	42.4	0.50	0.208	-0.051;SE=0.412 (-0.892-0.759)	-0.590;SE=0.448 (-1.591-0.224)	-1.066;SE=0.465 (-2.111-(-0.236))	-
Canopy+Vdens*+Speed	43.3	1.37	0.135	-0.049;SE=0.425 (-0.918-0.791)	-0.527;SE=0.493 (-1.617-0.379)	-0.989;SE=0.454 (-2.011-(-0.174))	-0.582;SE=0.459 (-1.594-0.271)

3. CONSIDERAÇÕES FINAIS

O presente estudo compreende o primeiro realizado na região Neotropical a fornecer informações sobre a densidade de ninhos de uma comunidade de aves de sub-bosque em um remanescente preservado de Mata Atlântica. Além disso, verificou-se que tal densidade é significativamente mais alta nas proximidades de riachos que permeiam o interior da floresta, salientando a importância de proteger e garantir a conservação dessas áreas com vegetação ribeirinha para garantir a reprodução de determinadas espécies de aves que parecem estar intimamente relacionadas a esses ambientes. Entretanto, os resultados obtidos considerando variáveis ambientais da vegetação, indicam que os mecanismos relacionados com a seleção de locais para nidificação pelas aves de sub-bosque podem ser diferentes de uma espécie para outra, e para entender melhor essas particularidades, são necessários estudos que investiguem melhor cada caso, considerando em especial variáveis relacionadas aos próprios riachos.

Dessa forma, ao utilizar como modelos de estudo *Chiroxiphia caudata* e *Rhopias gularis*, para avaliação de quais variáveis ambientais diferentes populações teriam preferência em selecionar para construir seus ninhos em determinados locais ao longo de riachos, chegou-se à conclusão que de fato pressões diferentes parecem ser exercidas sobre cada espécie que nidifica nesse tipo de ambiente. Tais variações poderiam diferir de acordo com o local e estrato onde cada ave faz seus ninhos, o que os expõe a diferentes tipos de predadores e dessa forma exigem estratégias diferentes de proteção para obter sucesso. Por outro lado, a seleção de trechos do riacho também poderia ser influenciada por outros fatores ambientais, como disponibilidade de alimento, quando o próprio ambiente em questão favorece taxas de sobrevivência mais altas.

No caso de *Onychorhynchus swainsoni*, pudemos verificar que embora haja espécies com alta especificidade para nidificar ao longo de riachos em detrimento de outros locais no

interior da matriz florestal, as características desses ambientes palustres também influenciam na seleção de habitat, de forma que nem todo tipo de riacho parece favorecer a nidificação dessa espécie. Para *O. swainsoni*, o equilíbrio entre disponibilidade de riachos adequados e ambientes contínuos e preservados que favoreçam seu ciclo reprodutivo longo e pouco prolífico devido à baixa abundância natural de casais reprodutivamente ativos, torna ainda mais significativa a insistência na manutenção de longos trechos de riachos preservados ao longo de grandes remanescentes de Mata Atlântica.

Por fim, os riachos que permeiam o interior da Mata Atlântica parecem compor um habitat ideal para diversas espécies de aves construírem seus ninhos e atingirem taxas de sucesso promissoras, embora mecanismos que interfiram nessa seleção claramente não sejam os mesmos para todas as espécies e ainda demandem estudos mais profundos para serem mais bem compreendidos.

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