UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS - RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA)

COMPORTAMENTO DE LEK, FRUGIVORIA E DISPERSÃO DE SEMENTES POR *MANACUS MANACUS* (LINNAEUS 1766, PIPRIDAE) EM ÁREAS DE RESTINGA NO SUDESTE DO BRASIL

CÉSAR CESTARI

Rio Claro
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Tese apresentada ao Instituto de Biociências da Universidade Estadual Paulista "Júlio de Mesquita Filho" campus de Rio Claro, como requisito para obtenção do grau de Doutor em Ciências Biológicas (Zoologia).

Orientador: Dr. Marco Aurélio Pizo Ferreira

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Dedico este estudo aos meus pais, aos meus avós, ao meu irmão, à Cris, ao Ílson e todas as pessoas que consciente ou inconscientemente me transmitiram o pouco conhecimento que adquiri até o momento.

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Lembro-me em 2003, quando eu estava há alguns anos formado em Biologia e trabalhando em um projeto com as aves no Pantanal, que comecei a conhecer pessoas influentes no meio científico e conservacionista. Fui apresentado ao professor Marco Aurélio Pizo, o então editor de uma de nossas mais famosas revistas sobre Ornitologia no Brasil, na época chamada Ararajuba. Expliquei para ele as minhas condições de vida, a propósito, que não era das melhores em termos de pesquisa, e minhas pretensões, pois apesar de ter vontade de continuar estudando as aves com mais seriedade, eu ainda não havia tido uma oportunidade realmente séria. Foi então que ouvi: você não quer fazer o mestrado comigo? Estou disponível a orientá-lo! A partir de 2004, com o início de meu mestrado, sem bolsa, participando de projetos conservacionistas durante 15 dias na planície pantaneira para me sustentar, e viajando nos outros 15 dias do mês para a Mata Atlântica para coletar os dados para meu mestrado, que realmente defini que gostaria de continuar a trabalhar com comportamento e ecologia de aves e que possivelmente uma vida será curta para isso! Esse entusiasmo ocorreu não somente porque sabia que gostava de estudar aves e poderia fazer alguma coisa para conhecê-las melhor e protegê-las, mas também por vários outros importantes motivos. Mesmo sem dizer isso diretamente, mas somente com trabalho, o professor Marco A. Pizo me ensinou que para se fazer ciência são necessários poucos ingredientes: humildade, transparência, seriedade, organização, dedicação e afinidade. Portanto Marco, muito obrigado! Hoje, posso dizer que você contribuiu para que estes quatro anos de meu doutorado, dedicados inteiramente à pesquisa com aves, fossem os mais produtivos e mais prazerosos até o momento!

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Por fim, às rendeiras (*Manacus manacus*), espécie alvo deste estudo, que exibem comportamentos magníficos de cortejamento sexual, transformando um ambiente outrora silencioso em um ambiente mágico, eletrificado e cheio de vida! Contrário muitas vezes do que acontece na vida acadêmica, a transição de meu mestrado para o doutorado marcou intencionalmente a mudança de minhas investigações em uma visão de comunidade para uma visão de populações de uma única espécie, pois achei que eu precisava desse maior detalhamento. Cada um dos indivíduos de rendeira que observei quase imóvel durante muitos

dias no meio da floresta ensinou-me que pouco se sabe sobre ecologia comportamental de aves, mesmo as mais abundantes. Estes indivíduos ensinaram-me também que realizam pontualmente a cada minuto e a cada dia, funções ecológicas relevantes para a conservação de seus hábitats e sobrevivência, desde que não molestadas pela ação destrutiva dos humanos. Depois de algum tempo observação, consegui identificar cada indivíduo de *M manacus* pelo seu comportamento. Desta forma, aprendi a valorizar e respeitar o indivíduo e a sua pequena, mas importante contribuição para a perpetuação da espécie e do hábitat onde sobrevive. Espero somente que daqui a algumas décadas eu volte em cada uma das áreas visitadas durante esse estudo e encontre a mesma vida exuberante e momentos mágicos que tive a oportunidade de presenciar.

"Aggressiveness and sociability of *Manacus manacus* are so balanced as to result in a compact group of constantly maintained, individual territories"

David W. Snow (1962)

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APRESENTAÇÃO

A tese está dividida em uma introdução geral no qual apresento as bases teóricas que me levaram a formular hipóteses ligando comportamento sexual de Piprídeos à ecologia de dispersão de sementes, que serão exploradas nos sete capítulos seguintes. A espécie alvo do estudo foi a rendeira (*Manacus manacus*, familia Pipridae), um passeriforme frugívoro comum em restingas do litoral paulista e que possui o sistema reprodutivo de *lek*. Cada capítulo está apresentado em forma de artigo científico, de acordo com as normas das revistas que foram publicados ou submetidos. Por objetividade e divulgação mais ampla dos resultados científicos, optei por escrever os capítulos em inglês. Adicionalmente, para a melhor compreensão e conforto do leitor, optei: (1) por manter as figuras em ordem sequencial ao texto, (2) por apresentar algumas figuras extras não publicadas nos artigos originais das revistas como apêndices no final do manuscrito, e (3) por apresentar as referências bibliográficas de todos os capítulos em uma única seção no final do manuscrito. Peço somente desculpas ao leitor pelas repetições de caracterização das áreas de estudo e biologia da rendeira na seção de Materiais e Métodos de alguns dos capítulos, mas isso foi inevitável dada a natureza dos capítulos acima mencionada.

Inicialmente, eu e meu orientador planejamos este projeto de doutorado para responder algumas questões sobre diferenças comportamentais e de deslocamento entre machos adultos, fêmeas e jovens, relacionando-as com possíveis diferenças destas categorias na dispersão de sementes de plantas na restinga, um ecossistema extremamente ameaçado pela ocupação humana desordenada. No entanto, com o decorrer das observações e trabalhos no campo, somados ao suporte literário do que já havia sido estudado a respeito desta espécie, percebemos que algumas lacunas e nuances sobre o comportamento de *lek* de *M. manacus* ainda não haviam sido abordados em estudos anteriores. Desta forma, este trabalho foi desenvolvido para responder questões inéditas relativas ao comportamento de *M. manacus*, tratados nos primeiros três capítulos. O primeiro capítulo refere-se ao acompanhamento do período anual da atividade de *lek* de *M. manacus* no sudeste do Brasil, indicando detalhes sobre o tempo de permanência de machos adultos em suas *courts* e territórios dentro do *display ground*, sua freqüência e duração de exibições (*displays*) nas *courts*. Adicionalmente, acompanhamos a freqüência de visitas de fêmeas e jovens às *courts* de machos adultos. Ao final, os dados acima são comparados com estudos realizados em

regiões mais setentrionais dos Neotrópicos. O segundo capítulo refere-se ao uso de *courts* auxiliares em adição à *court* "principal" por machos adultos, algo que ainda não havia sido reportado para a espécie. Discutimos as prováveis funções ecológicas e comportamentais relacionadas ao uso de *courts* auxiliares. O terceiro capítulo trata especificamente do acompanhamento anual do comportamento de limpar a *court* principal (*court cleaning behavior*) por machos adultos. Algumas hipóteses sugeridas por estudos científicos anteriores (i. e., aumento de contraste da plumagem colorida dos machos em atividade de *lek* e diminuição de predação por potenciais predadores terrestres e camuflados) foram testadas com experimentos no campo. No quarto capítulo, existe uma maior interação entre as áreas de comportamento, frugivoria e ecologia. O comportamento de formicar-se de *M. manacus* em *courts* foi abordado, associando-o: (1) à presença de formigas que procuram restos de frutos em sementes regurgitadas e defecadas nas *courts* e, (2) ao cuidado da plumagem por machos adultos para tornarem-se mais atraentes às fêmeas durante o intenso processo de competição sexual nos *leks*. O quinto capítulo destaca a frugivoria por *M. manacus* no ecossistema da restinga, com resultados que corroboram com o consumo de uma alta variedade de espécies de pequenos frutos pela maioria do píprideos. A partir do sexto capitulo, retomamos o planejamento inicial da tese, relacionando mais fortemente o sistema reprodutivo de *lek* da espécie com a dispersão de sementes das plantas na qual se alimenta. O sexto capítulo analisa a frugivoria por *M. manacus* comparando-a com outras espécies simpátricas que não se exibem em *lek*, com o objetivo de inferir sobre o serviço de dispersão de sementes de *M. manacus* e outras aves engolidoras de frutos no ecossistema de restinga. Por fim, no sétimo capítulo exploramos a capacidade de dispersão de sementes (incluindo chuva de sementes) de plantas de restinga por machos adultos e verdes (fêmeas e machos jovens) de *M. manacus*, acompanhando as distâncias que se movem (e potencialmente dispersam sementes) com a utilização da metodologia de rádio-telemetria durante períodos de *lek* e em períodos com pouca ou completa ausência de exibições da espécie.

RESUMO

A rendeira (*Manacus manacus*, Pipridae) é um pequeno (15 – 18 g) passeriforme frugívoro amplamente distribuído na região Neotropical e que apresenta o sistema reprodutivo de *lek*. Existem vários estudos sobre a história natural e comportamento de *lek* desta espécie e poucos estudos que se referem aos aspectos ecológicos relacionados à sua atividade de frugivoria. Nos primeiros capítulos, nos referimos a alguns aspectos comportamentais da espécie em atividade de *lek* que foram pouco explorados ou inéditos para a ciência. Do quarto ao sétimo capítulos, procuramos enfocar parte das funções e interações ecológicas que a espécie exerce considerando a frugivoria e dispersão de sementes de plantas de *restinga* no sudeste do Brasil. Os principais resultados sobre o comportamento de *lek* revelaram que a permanência dos machos adultos dentro de seus territórios em áreas de *lek* está positivamente correlacionada com o comprimento do dia. Dessa forma, diferenças no comprimento do dia entre regiões tropicais e subtropicais influenciam um padrão anual invertido de atividade de *lek* da espécie, ou seja, quando machos residentes estão mais ativos na região tropical, os machos da região subtropical estão menos ativos e vice-versa. Adicionalmente, a frequência e a duração de exibições de machos residentes em suas *courts* (locais de exibição) variaram ao longo do ano. No entanto, os machos jovens treinaram suas exibições em *courts* de machos residentes ao longo de todo o ano, sem variações significativas. As fêmeas visitaram mais freqüentemente os machos residentes que se exibiram por períodos mais longos. Nossas observações revelaram que machos residentes, principalmente os que estabeleceram territórios localizados na periferia de áreas de *lek*, podem utilizar mais de uma *court* dentro de seu território (denominadas *auxiliary courts*), fato ainda não descrito para a espécie. Nós sugerimos que este comportamento é uma estratégia para atrair as fêmeas visitantes de machos com territórios mais centrais em áreas de *lek*, geralmente com maior sucesso reprodutivo. O comportamento de limpar a *court*, retirando folhas e detritos, e puxando folhas vivas de plântulas que crescem ao redor, também foi experimentalmente investigado. Nós concluímos que este comportamento provavelmente esteja relacionado com o aumento da luminosidade na *court* e aumento na conspicuidade de machos durante as exibições, e não como um comportamento utilizado para evitar potenciais predadores terrestres que estejam em espreita próximos da *court*, tal como sugerido por outros pesquisadores. No quarto capítulo, nós descrevemos o comportamento de formicar-se

de machos adultos de *M. manacus*, relacionando-o com o hábito frugívoro e comportamento de *lek*. Machos residentes defecam e regurgitam uma grande quantidade de sementes em suas *courts* devido ao longo período que permanecem em seus territórios. Desta forma, sementes com resquícios de polpa aderidos atraem algumas formigas herbívoras (p.ex. *Solenopsis* spp.) para a *court*, que são capturadas pelos pássaros e esfregadas nas penas, provavelmente como uma ferramenta para manter a boa aparência das penas e saúde exibidos durante o cortejamento. As formigas possuem ácido fórmico, utilizado por várias espécies de aves para manutenção das penas e prevenção contra ectoparasitas. Considerando a frugivoria e dieta de *M. manacus*, nós registramos uma ampla variedade de pequenos frutos que esta espécie consome no ecossistema da *restinga*. A maioria desses frutos, maduros ou imaturos são engolidos inteiros, o que ressalta o potencial de *M. manacus* como dispersor de sementes. Em áreas de *lek*, nós também verificamos um maior serviço de dispersão de sementes de duas plantas (*Miconia rigidiuscula* e *Ocotea pulchella*) realizado por *M. manacus* em comparação com outras espécies de aves que engolem de frutos inteiros. Para finalizar, nós investigamos diferenças entre a riqueza e abundância de sementes depositadas em áreas com *lek* de *M. manacus* e áreas controles. Descobrimos que não existem diferenças na riqueza e abundância de sementes entre os dois tipos de áreas. No entanto, em uma análise mais refinada dentro das áreas de *lek*, encontramos uma maior abundância e riqueza de sementes em *courts* do que em áreas controle revelando que as sementes possuem uma distribuição mais agregada em *courts*, provavelmente pela atividade de defecação e regurgitos de machos residentes. Adicionalmente, com o uso de rádio-telemetria, nós verificamos que os machos residentes e verdes (i.e., fêmeas e machos jovens) alternam a extensão de deposição das sementes que potencialmente produzem durante os períodos da manhã e tarde, com os machos residentes espalhando mais amplamente as sementes pelo ambiente nos período da tarde enquanto os verdes o fazem no período da manhã, exercendo assim, atividades complementares de dispersão de sementes ao longo do dia.

Palavras-chave: aves, chuva de sementes, dieta, interação, rendeira.

ABSTRACT

The White-bearded Manakin (*Manacus manacus*, Pipridae) is a small frugivore passerine (15 – 18 g) that presents the lek breeding system. There are several studies about the natural history and lek behavior of this species, however, few studies focused on the ecological aspects related to its frugivorous diet. In the first chapters, we studied some aspects of the species' lek behavior that were underexplored before. From the fourth to seventh chapters, we focused on the ecological functions and ecological interactions of this species considering the frugivory on and seed dispersal of *restinga* plants in southeastern Brazil. Regarding lek behavior, the permanence of resident males in their lekking territories was positively correlated with day length. Thereby, differences in day length between tropical and subtropical regions resulted in an inverted annual pattern of lek activity, i.e., when males are more active in the tropical region, males from subtropical region are less active and vice-versa. Additionaly, the frequency and duration of display bouts of resident males varied along the year while juveniles did not. The females visited frequently courts of residents that displayed for longer bouts. Also, our observations revealed that resident males may use auxiliary courts to display; a behavior previously unknown for this species. We suggest that the use of auxiliary courts may be a strategy adopted mainly by peripheral males to attract females that visit more successful males with central territories in the lek area. The court cleaning behavior, which consists of the removal of leaves and debris from courts was also investigated. We concluded that instead of acting as a defensive strategy to avoid terrestrial lurking predators as argued by some authors, the court cleaning is related to the increase of luminosity on courts supposedly to augment the conspicuosity of males' plumages. In the fourth chapter, we described the anting behavior of lekking males of *M. manacus* and related it with its frugivory and lek behavior. Resident males defecate and regurgitate large quantities of seeds in the courts due to their long daily (and annual) permanence in their territories. In this way, seeds with pulp remains attract herbivore ants (e. g. *Solenopsis* spp.) to the courts that were captured by the birds. Birds then rubbed ants on its plumage supposedly as a way to maintain fitness and showy appearance during displays. Ants have formic acid that was used by several species of birds to maintain good healthy and prevent ectoparasites. Regarding the frugivory by *M. manacus*, we recordered a high variety of small fruits consumed in the *restinga* ecosystem. Most of these fruits were swallowed whole in ripe or unripe conditions,

thus highlighting the potential of *M. manacus* as seed disperser. We also noted a greater seed dispersal service by *M. manacus* to two plants (*Miconia rigidiuscula* and *Ocotea pulchella*) near lek areas compared with non-lekking birds in *restinga*. In the last chapter, we investigated differences in species richness and abundance of seeds between lek and control areas. We found no differences in the abundance and richnness of seeds, but in finer scale analysis, we found higher abundance and richness of seeds in courts than control areas within lek areas revealing a more aggregated distribution of seeds due to defecation and regurgitation activities of resident males. With radio-telemetry, we also noted that resident males and greens (females and juveniles males) alternated their ability to generate greater seed shadow in the afternoon and morning periods of the non-lek and lek seasons, highlighting their daily complementary roles as seed dispersers.

Keywords: birds, diet, interaction, seed rain, White-bearded Manakin.

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INTRODUÇÃO GERAL

A dispersão de sementes e o recrutamento das plantas é de particular importância para a manutenção e expansão de hábitats. O ponto central nos planos de conservação e manejo envolvendo espécies de plantas dispersadas por animais é a identificação dos estágios críticos do recrutamento (e.g., dispersão de sementes, formação de banco de sementes no solo, viabilidade de sementes para a germinação) nos quais a atividade dos animais frugívoros pode ser limitante (Jordano et al. 2006). As aves que possuem a maior parte da dieta constituída de frutos geralmente se deslocam sazonalmente por diversas áreas para satisfazer suas necessidades energéticas, podendo exercer importante papel como dispersoras de sementes e no recrutamento de plantas. Muitas vezes, populações de aves frugívoras de médio e grande porte revelam baixas densidades populacionais somadas às ações antrópicas (e.g., sobrecaça e alterações de caça) que comprometem a sua sobrevivência (Galetti et al. 1997; Jordano et al. 2006). Desta forma, estudos demográficos e de dispersão de sementes das plantas das quais estas aves se alimentam são difíceis de serem executados. No entanto, algumas aves frugívoras de pequeno porte não-cinegéticas que necessitam de menores áreas para sobrevivência podem concentrar vários indivíduos em rituais de cortejamento reprodutivo (p. ex. Pipridae, Beehler e Foster 1988) e modificar demograficamente a chuva de sementes e dinâmica do recrutamento das espécies de plantas que utilizam para se alimentar (Krijger et al. 1997).

A maioria das espécies pertencentes à família Pipridae são conhecidas por possuírem o sistema de acasalamento de *lek* no qual os machos residentes, geralmente com plumagens coloridas e ornamentadas, se exibem a maior parte do ano com manobras específicas para atrair e acasalar com as fêmeas, as quais geralmente possuem plumagem verde uniforme. De pequeno porte (8 – 30 g), os piprídeos se destacam por apresentar a dieta composta predominantemente por frutos e exercem importante função como vetores na dispersão de sementes na região Neotropical (Snow 2004). Os piprídeos consomem uma ampla diversidade de frutos (Loiselle and Blake 1991; Snow 1962; Worthington 1982), principalmente pertencentes às famílias Melastomataceae e Rubiacea (Blendinger et al. 2011; Haemig 2006; Krijger et al. 1997; Snow 1962). *Manacus manacus* (Linnaeus, 1766) é um piprídeo com massa corpórea de 15 a 18 g. Esta espécie possui ampla distribuição em

território brasileiro, podendo ser encontrado em áreas de matas contínuas e fragmentadas da Amazônia e Mata Atlântica (Sick 1997; Sigrist 2006; C. C, obs. pess.). Segundo (Snow 1962), *M. manacus* habita principalmente vegetações secundárias que ofereçam condições adequadas de espaço para exibição de machos, obtenção de recursos e locais para nidificação das fêmeas. A predominância de frutos na dieta de *M. manacus* foi confirmada por Snow (1962) e Théry (1990). No Brasil, *M. manacus* apresentou uma das maiores freqüências de visitas em árvores frutíferas entre piprídeos em áreas fragmentadas (Pizo 2007).

O cortejamento sexual de *M. manacus* pode concentrar elevado número de indivíduos machos (dois a 70 indivíduos!) durante quase todo o ano (exceto em períodos de troca de penas), com o propósito de atrair e acasalar com fêmeas em locais de exibição na floresta, chamados de *display grounds* (Snow 1962). Cada macho se exibe em sua própria *court* dentro do *display ground*. As *courts* estão distanciadas a poucos metros umas das outras (sistema denominado *lek* clássico), permitindo que machos vizinhos tenham contato visual e auditivo entre si. Assim, com a existência de uma competição sexual intensa característico do sistema de acasalamento de lek os machos estabelecem uma dominância poligínica enquanto permanecem agregados, pois não possuem habilidade de monopolizar recursos essenciais para as fêmeas, no caso os frutos (Emlen e Oring 1977). As fêmeas e jovens, por sua vez, visitam as *courts* dos machos adultos em *display grounds* com finalidade reprodutiva e prática esporádica de manobras de exibição, respectivamente. Dessa forma, baseado em diferenças no comportamento de côrte sexual entre machos adultos, fêmeas e jovens de *M. manacus*, provavelmente as fêmeas e jovens (daqui para frente chamados de “verdes” devido à coloração predominante de suas plumagens) tenham maior eficiência na dispersão de sementes por se deslocarem mais e por possuírem maiores áreas de vida em relação aos machos adultos (Krijger et al. 1997). No principal período de côrte reprodutiva (que geralmente se sobrepõe ao período de maior quantidade de chuvas), os machos adultos passam a maior parte do tempo de vida (aproximadamente 90%) se exibindo para as fêmeas e alimentando-se em *display grounds* que possuem de 15 a 20 metros de diâmetro (Théry 1992), ou áreas próximas (Snow 1962; Théry 1992). Segundo Théry (1990), os machos adultos investem curtas manobras de vôo para retirar frutos e utilizam pequena quantidade de tempo (2 a 5 minutos) para forragearem quando em atividade de exibição. No entanto, apesar da suposta falta de eficiência para a dispersão de sementes em distâncias maiores, os machos adultos podem contribuir favoravelmente para o armazenamento e concentração de sementes

no solo das áreas de *lek* e em áreas próximas, influenciando no potencial de regeneração da floresta destas áreas (Haemig 2006; Krijger et al. 1997).

De acordo com (Snow 1981), a evolução de sistemas sociais peculiares como o *lek* em Pipridae pode ser reflexo da especialização da dieta em frutos altamente nutritivos, que permitiram que indivíduos satisfizessem suas necessidades energéticas em curtos períodos, liberando a maior quantidade do tempo para atividades no *lek*. Outros autores comprovaram que algumas espécies de piprídeos exibem adaptações comportamentais e fisiológicas que permitem ter uma dieta "generalista" em frutos pouco ricos em nutrientes, tais como: rápida taxa de passagem de frutos no intestino, alta eficiência de digestão e hipotermia noturna (Bucher e Worthington 1982; Worthington 1989). Segundo Levey (1987b), os piprídeos aumentam a eficiência na dispersão pelo consumo de frutos pouco palatáveis (menos doces) e pelo comportamento de engolir frutos por inteiro. Algumas espécies de piprídeos, entre elas uma pertencente ao gênero *Manacus* (*M. vitellinus* e *Pipra mentalis*), defecam pequenas sementes em um intervalo de 12 a 15 minutos após a ingestão e passagem pelo sistema digestivo. Adicionalmente, regurgitam grandes sementes após sete a nove minutos (Worthington 1989). Considerando esses fatos, é possível que haja uma alta contribuição de *M. manacus* para a dispersão sementes e recrutamento de plantas da restinga brasileira, um ecossistema atualmente ameaçado especialmente pela crescente expansão urbana (Sampaio 2005).

A diversificada dieta baseada em frutos, a ampla distribuição em florestas neotropicais e a possível diferenciação na distribuição espacial e movimentação entre machos adultos e verdes de *M. manacus* fazem dessa espécie um importante objeto para estudos sobre frugivoria e dispersão de sementes.

OBJETIVOS GERAIS

No presente estudo investigamos (A) o comportamento de lek de *M. manacus* e (B) a atividade de frugivoria e dispersão de sementes no ecossistema de restinga do sudeste do Brasil. Considerando o primeiro aspecto, procuramos responder à seguinte questão: como se caracteriza a atividade anual em áreas de *lek* por machos adultos e verdes (jovens e fêmeas) na região sudeste do Brasil? Esta questão foi investigada com diversos temas específicos tratados dos capítulos primeiro ao quarto, tais como: atividade de *display* e tempo de

permanência de machos adultos e jovens em *courts*, visitas de fêmeas às *courts*, uso de mais de uma *court* (denominadas *courts* auxiliares) por machos adultos, comportamento de limpar a *court* da espécie e até mesmo observações que registraram o comportamento de formicar-se de machos adultos durante os intervalos em que se exibiam para as fêmeas (veja Apresentação). Considerando o segundo aspecto, as questões foram as seguintes: qual o número de espécies de frutos que *M. manacus* consome no ecossistema restinga? Quais as principais características relacionadas à frugivoria (e.g., grau de maturidade dos frutos, modo de manipular os frutos e manobras de forrageamento) desta espécie em plantas de restinga? Em uma análise comparativa entre espécies de aves e abordando o sistema reprodutivo de lek presente em *M. manacus*, nós também investigamos qual a contribuição na taxa de consumo de frutos e dispersão de sementes por *M. manacus* e outras espécies de aves que não possuem o sistema reprodutivo de *lek* na restinga. Além disso, considerando a movimentação de *M. manacus* e sua atividade de dispersão de sementes, e partindo do pressuposto de que a maioria das sementes de frutos ornitocóricos depositadas em áreas de *lek* (ou *display grounds*) seja proveniente de atividade de *M. manacus*, nós investigamos: (1) se existem diferenças quantitativa e qualitativa no número de sementes em áreas com e sem *lek* e (2) se existem diferenças na capacidade de dispersão de sementes entre os machos adultos e verdes de *M. manacus* em períodos com maior e menor atividade de *lek*?

CAPÍTULO 1

Lek phenology of the White-bearded Manakin (*Manacus manacus*, Pipridae) in a subtropical region

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Abstract

Descriptions of lek-breeding in White-bearded Manakins (*Manacus manacus*) first appeared 55 years ago from studies conducted in tropical Trinidad. No published studies on lek activity, however, exist from subtropical areas of the Neotropics. Herein, annual lek phenology of *M. manacus* in a subtropical region was analyzed and compared with studies conducted in Trinidad. Day-long observations were conducted in nine male territories from three leks. Permanence of lekking males in their territories was positively correlated with day length. When males are more active in subtropical region, males from Trinidad are less active and vice-versa. Additional new information about this manakin's lek activity were disclosed: residents stayed in their courts up to 7% of the day length, the frequency and duration of display bouts of residents varied throughout the year whereas those of juveniles did not, and females made more visits to courts of residents who displayed for longer bouts.

Keywords: behavior, day length, manakins, sexual selection, southeastern Brazil, temporal analysis.

Introduction

The lek behavior of the White-bearded Manakin (*Manacus manacus*), which occurs from tropical forests of Colombia and Trinidad and Tobago to subtropical forests in Brazil and Argentina, was first described by Frank M. Chapman and Jean Stolzmann in the late 19th century (Chapman 1935). Thereafter, Darnton (1958) revealed more information about this species during a month-long study in Trinidad. She briefly described the courts ("dancing rings" and "bare spaces" on the soil), behavior of males on leks, and some temporal aspects of male behavior, including the peak time of displays on courts and the gradual decrease of lek activity during the morning. Since then, long-term studies conducted by Snow (1962) and Lill (1974a, b) used different methodologies such as focal observations, bird capture, and video recording to disclose additional details about the natural history and lek behavior of *M. manacus* in Trinidad. Studies in Trinidad thus became the main source of information for other studies on this species in the Neotropics (Olson and McDowell 1983, Shorey 2002, Shorey et al. 2000, Berres 2002, Théry 1992, Krijger et al. 1997, Cestari 2010, Cestari and Pizo 2012).

Regarding lek phenology, Snow (1962) argued that although males of *M. manacus* display year-round in Trinidad, there is a notable molting period between July-December when displays are much reduced and some molting males stay out of their courts for nearly 80 days. During the breeding season, males may stay in lek areas up to 90% of the day, with brief absences for feeding and bathing in surrounding areas. Frequency of displays by resident males varied during the day, with peak periods of activity between 06:30 – 08:00 hrs and 13:30 – 15:00 hrs. The daily display cycle of males occurred independently of females' presence in lek areas (Snow 1962).

Six years after Snow's study, Lill (1974a, b) restarted investigations with *M. manacus* in the same locality, revealing new aspects about this species' biology. Males occupied individual territories for several years and, thus resident males had slow turn-over rates on lek areas. In addition, females were found to visit several courts to sample males before choosing a particular male for mating (Lill 1974a, b).

According to Snow (1962), sunrise and sunset times, including intrinsic luminosity, may be the main influence (besides climate and availability of food) on the daily pattern of display activity by *M. manacus* males on leks. Light conditions on courts are hypothesized to affect conspicuousness of males during their displays (Endler and Théry 1996, Heindl and Winkler 2003) and under optimal light conditions the number of matings may increase (Théry and Verhrencamp 1995). Given spatially and temporally heterogeneous light conditions found in forest environments (Chazdon and Pearcy 1991), longer days might increase the probability that males experience more optimal light conditions in which to display.

Taking advantage of the differences in day length between tropical and subtropical regions, we evaluated Snow's hypothesis on the relationship between sunrise/sunset times and lek attendance of male manakins. Specifically, we compared the annual pattern of daily attendance of male *M. manacus* on leks and the frequency of female visits to males' courts in a subtropical region to results reported from past studies in tropical Trinidad. We focused our test of Snow's hypothesis on *M. manacus* for two main reasons. First, this species has the broadest geographic distribution among manakins, occurring from tropical to subtropical areas of the Neotropics (Snow 2004), and thus may provide a robust test on how daily variation in day length may influence display activity. Second, extensive studies on the natural history of this species conducted in Trinidad allow a powerful comparison with our

data. If Snow's hypothesis is to be supported, then we would expect that differences in the day length between tropical and subtropical areas will result in different temporal patterns of male lek attendance. In subtropical areas, males would be expected to be active over longer period in austral summer than in Trinidad due to increased day length. Along the same reasoning, longer lek attendance of males is expected to Trinidad during the longer day length periods in the year. Additionally, the present study analyzes temporal aspects of this manakin's lek behavior that remained elusive in Trinidadian past studies, such as: (1) how do resident males and juvenile males differ in the frequency and duration of display bouts over the course of the year? (2) Is the duration of displays of resident males correlated with female visit to courts along of the year? And (3) does the frequency of female visit to courts vary along of the day?

Material and Methods

The studied species

The White-bearded Manakin, *Manacus manacus* (Linnaeus 1766), is a small (15 – 18 g) frugivorous bird commonly found in the understory of Neotropical lowland forests. It has a widespread geographic distribution from Colombia to NE Argentina and inhabits continuous and fragmented forests of Amazon basin and Atlantic forest of South America (Sick 1997, Snow 2004). Like most of manakins, it is a dimorphic species. Males have black cap, back, wing, and tail, grey rump, upper tail coverts, flanks and belly, and white neck, whereas females and juvenile males are olive above, greyer and paler below (Snow 2004; see Appendix 1). This manakin prefers secondary forest with a high abundance of fruits and small upright saplings (Snow 1962). Lek areas (or display grounds) are formed by adjacent territories of males. Each territory contains one main court, and auxiliary courts may exist (Cestari and Pizo 2012, see chapter 2). Lek areas may have from 2 to 70 main courts 0.9 to 82 m apart, and neighboring males are often in visual and aural contact with each other (Darnton 1958, Snow 1962, Lill 1974a, Olson and McDowell 1983, Shorey 2002). Each resident male displays at an oval court of 0.15 - 0.9 m in diameter delimited by two or more saplings (Darnton 1958, Snow 1962, Lill 1974a, Olson and McDowell 1983, Snow 2004; see Appendix 2). In the most frequent "snap–jump" display, male jumps between saplings of the court producing a loud snap caused by movements of modified secondary feathers (Snow 1962). During visits, females generally stay above the court accompanying the male's

performance and may dance with him (see more details in Snow 1962). Juveniles also practice display maneuvers in the courts during periods when resident males are less active (Snow 1962). According to Lill (1974a), most females copulate with a single mate per season, but a minority is promiscuous, mating with multiple males; females may make several nesting attempts per season. Males are reported to spend up to 90% of the day in lek areas, making brief excursions of less than 6 min to forage at nearby fruit sources (Snow 1962). Resident males may have a long lasting sexual life up to 14 years, and defend permanently the area immediately around their courts from intrusion by neighboring residents and other adult males without territories (Snow 1962, Lill 1974b).

Study area

This study was conducted in lowland *restinga* forests in Itanhaém (24°10'11.9"S; 46°55´32.81"W), and in Juréia Itatins Ecological Station (Iguape, 24°28´07.4"S; 47°07´13.17"W; see Appendix 3), São Paulo state, southeastern Brazil. Both areas are primarily covered with *restinga* vegetation, an Atlantic forest ecosystem threatened by urban expansion. *Restinga* is composed by structurally simple vegetation formed by halophytic herbs and shrubs close to the sea, and more complex vegetation in lowland and lower mountain forests as one moves further inland (Sampaio 2005). The most speciose plant families in *restinga* are Myrtaceae, Leguminosae, Rubiaceae, Melastomataceae, Lauraceae and Annonaceae (Mamede et al. 2004). In the study region, the climate is subtropical and humid. Mean annual rainfall is 2,278 mm with the rainy season occurring from October to April, and the dry season from May to September. Average annual temperature is 21.4ºC, with maximum average temperature of 25.8°C, and minimum average temperature of 19.0ºC (Tarifa 2004). Day length ranges from 639.3 min (June) to 817.25 min (December) (Time and Date 2012: http://www.timeanddate.com/).

Data collection

Daily activity of *M. manacus* were studied at three leks: LEK 2 (24°31'40.65" S, 47°11'40.85" W) with four male territories, LEK 3 (24°28'7.62" S, 47° 7'13.20" W) with 11 territories, and LEK 4 (24°10'11.9" S, 46°55'32.81" W) with nine territories; the first two leks are located in Juréia Itatins Ecological Station (JIES), while the latter is located in the

municipality of Itanhaém. Distances between leks ranged from 10 km (LEK 2 to LEK 3) to 38.5 km (LEK 2 to LEK 4). We conducted observations in a total of nine male territories (three territories from each lek) from November 2009 to October 2010. In each month, we observed the lek(s) from one study area (Itanhaém or JIES) for three days; each study area was visited six times over the year. Only one territory was observed at a time from a concealed location > 5 m from the main court. We observed three different territories at different periods along the day. We previously delimited the territory boundaries of males during exhaustive observations of their hierarchical interactions with neighbors at the limits of their territories, and by observing the perches that they used for preening or resting inside their territories (see Snow 1962, Lill 1974a, and Shorey 2002 for more details). Observations were conducted from sunrise to sunset on sunny days to minimize cloud and rain effects on behavior of the birds (between 05:00 – 18:00 hrs). All resident males from observed territories were individually color-banded.

The following parameters were recorded during focal male territory observations: (1) arrival and departure times of resident males from lek areas, (2) time spent by resident males within their territories and display courts, (3) frequency and duration of their display bouts in the courts, (4) frequency and duration of display bouts of visiting juveniles in the courts, (5) frequency of female visits to courts, and (6) frequency of copulations in the court. A male display bout was defined as one uninterrupted sequence of leaps on court saplings.

Day lengths of the study area and of Trinidad were calculated by subtracting time at sunset from sunrise. Sunset and sunrise times were accessed in a free online database (Time and Date 2012: http://www.timeanddate.com/). Molting period of individuals was defined according to the annual period of absence of the resident males from their territories (and courts) (see Snow 1962).

Data analyses

Data from different leks were pooled and analyzed bimonthly to obtain an overall view of the temporal aspects of the species' lek behavior over an annual cycle. We used Friedman's test to analyze seasonal variation in the average daily frequency and duration of display bouts of resident adult males and juvenile males during the year, and the frequency of female visits to courts. Mann-Whitney test was used to check for differences in the average

frequency and average duration of display bouts between resident adult and juvenile males. Spearman correlation was used to test the relationships between: (1) the average frequency and duration of male display bouts with the average frequency of female visit to courts, and (2) the average period of the resident males in their territories (and courts) with average day lengths of the study area and Trinidad.

To explore the variation in daily activity patterns, the frequency of display bouts of males (resident and juveniles), and the frequency of female visits to courts (dependent variables) were quantified every 30 min (independent variable) from 05:00 to 18:00 hrs. Friedman's test was used to analyze temporal variation along the day using these parameters. We employed the Bioestat software 5.0 (Ayres et al. 2004) for all analyses. Significance of test result was accepted at $p \leq 0.05$.

Results

Resident males, on average, stayed up to 54.8% and 7.3% of the day length in their territories and display courts, respectively (Table 1). If the arrival of the first males and departure of the last males from lek areas were considered, the period of permanence of males in lek areas reached up to 82% of the day length. The time spent by resident males in their territories was positively correlated with day length in the study area ($r_s = 0.94$; $n = 6$; $p = 0.005$), but negatively correlated with day length in Trinidad ($r_s = - 0.94$; $n = 6$; $p = 0.005$).

Table 1. Mean day length, mean arrival and departure times of nine resident males from three lek areas, and their mean annual period of permanence in territories and courts in the subtropical region. Nine territories and courts were observed at each two month intervals.

Months	Day length (min)	Males' arrival (hour ± min)	Males' departure (hour ± min)	Time in territory (min); [% day length]	Time in courts (min); [% day length]
Jan – Feb	789 ± 19.1	05:51 ± 47.2	16:19 ± 32	250 ± 273 [31.7]	19.8 ± 26.2 [2.5]
Mar – Apr	701.8 ± 21.8	07:18 ± 26.3	14:03 ± 51.5	37.5 ± 29.4 [5.3]	10.2 ± 14.3 [1.4]
May – Jun	646.7 ± 7.8	-	-	0 [0]	0 [0]
Jul – Aug	663.6 ± 13.1	07:04 ± 7.9	15:34 ± 27	187.9 ± 143.5 [28.3]	32.1 ± 25.2 [4.8]
Sep – Oct	745.1 ± 25.6	06:17 ± 27.3	15:06 ± 33.2	189 ± 69.4 [25.4]	20.5 ± 12.7 [2.7]
Nov – Dec	812.7 ± 4.9	05:20 ± 10.3	16:28 ± 39	445.1 ± 147.2 [54.8]	59 ± 45.5 [7.3]

Resident males displayed significantly more (14.47 ± 11.82 displays per day) than juveniles (0.86 ± 0.79 display per day) (U = 4, n = 6, p = 0.02). However, the average duration of displays bouts did not differ between resident males (12.47 ± 9.06 s) and juveniles (5.94 ± 2.1 s) (U = 7.5, n = 6, p = 0.09). Further, resident males varied in their frequency (H = 13.86, df = 5, p = 0.02), and duration of display bouts (F_r = 13.23, df = 5, p = 0.02) over the year, whereas juveniles did not (frequency: F_r = 2.92, df = 5, p = 0.71; duration: F_r = 2.69, df = 5, p = 0.75) (Figure 1).

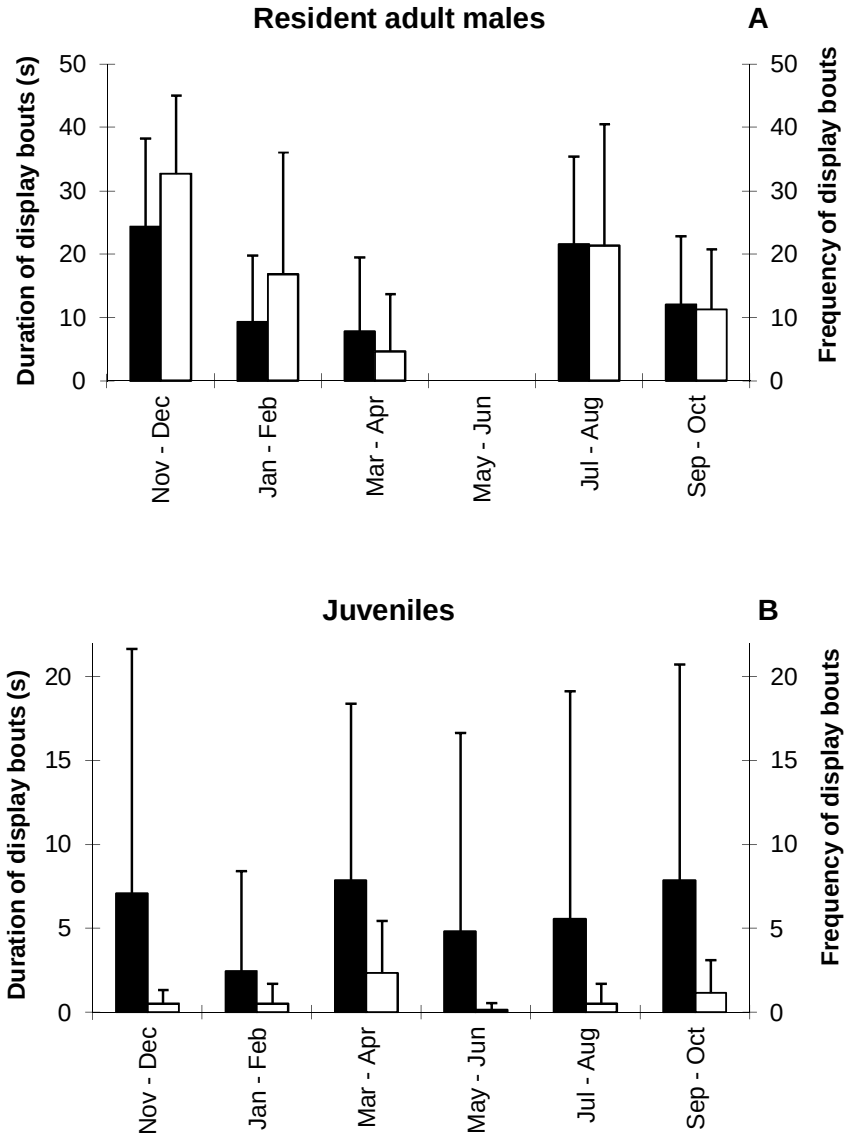

Figure 1. Annual variation in duration (black bars) and frequency of display bouts (white bars) of resident males (A) and juveniles (B) of *M. manacus*. A total of nine males were observed each at two month intervals. Vertical lines represent standard deviation.

Although the average frequency of female visits to courts was slightly higher from July to December (range: 2.5 – 3 visits per day) than from January to April (0.8 – 1 visits per day), there was no variation in the frequency of female visits over the course of the year (F_r = 8.02, df = 5, p = 0.15). No female visits were observed in May and June. Female visits were

not correlated with the frequency of display bouts of males (r_s = 0.62; n = 6; p = 0.19), but visits were positively correlated with the duration of display bouts of males over the course of the year (r_s = 0.82; n = 6; p = 0.04; Figure 2). Copulations were recorded only between September to December (range: 0.33 – 0.66 copulations per day).

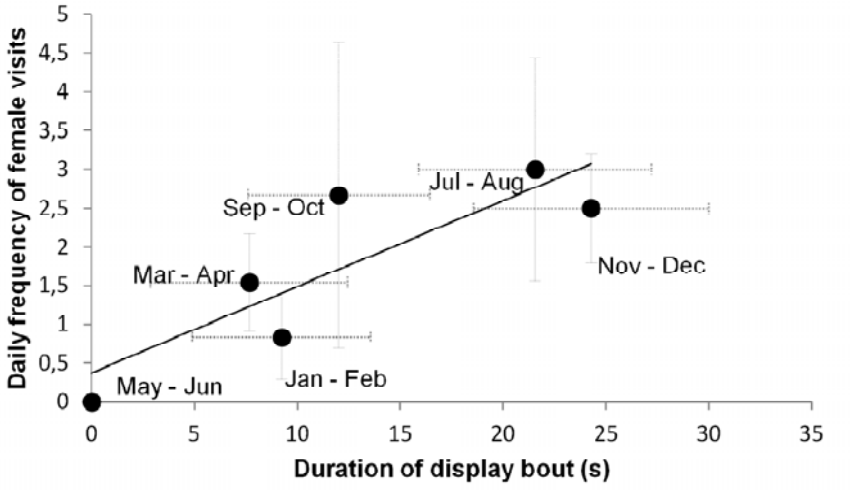

Figure 2. Correlation between the frequency of female visits and duration of display bouts of males of *M. manacus* across the year. Vertical and horizontal lines represent standard errors in the frequency of female visits and duration of display bouts of males, respectively. Nine resident males were observed each at two month intervals.

The frequency of display bouts of resident males varied over the course of the day (F_r = 40.94, df = 25, p = 0.02), with males displaying more frequently from 6:30 – 7:00 hrs. Such daily variation was not observed for juveniles (F_r = 1.12, df = 25, p = 1.00). The distribution of female visits was homogeneous throughout the day (F_r = 5.51, df = 25, p = 1.00) (Figure 3).

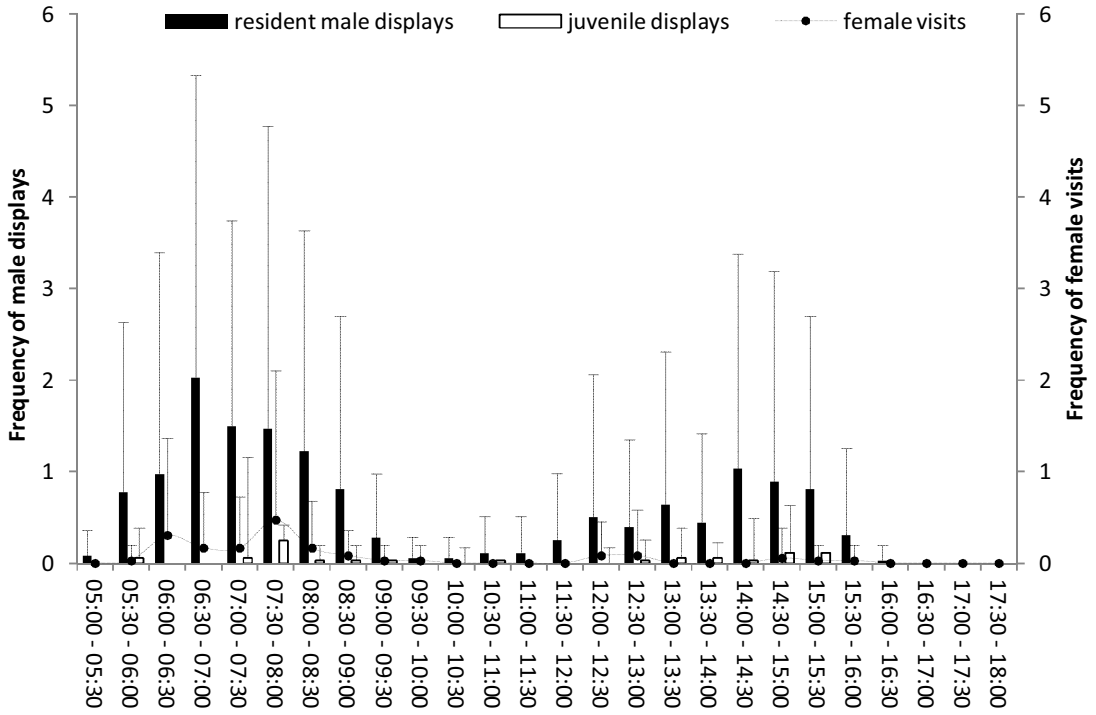

Figure 3. Within daily variation in the frequency of male displays (resident adults and juveniles) and frequency of female visits to courts of *M. manacus* over one year period. Vertical lines represent standard deviation. Nine courts were observed each at two month intervals.

Discussion

Lek activity of resident *M. manacus* males varied throughout the year in the study area. There was a sudden decrease in display during May and June due to the disappearance of resident males from their territories in lek areas (non-lekking or molting period, Snow 1962). Lek activity began again in July and August, followed by a peak period in duration and frequency of displays in November and December, and a decrease in March and April. Astor (1997) also found a decrease in lek activity of *M. manacus* between February and May in southeastern Brazil (22^{o}S; 42^{o}W). In Trinidad (10^{o}N; 62^{o}W) and Panama (09^{o}N; 79^{o}W), the lek activity of *M. manacus*, Golden-collared Manakin *Manacus vitellinus*, and Red-capped Manakin *Pipra mentalis* decreased markedly between July and December (Chapman 1935, Worthington 1982, Snow 1962), showing an inverted pattern of lek activity compared with our data from subtropical region. In our study, significant correlations between lek

attendance of resident males and day lengths in subtropical and tropical regions strengthen the idea that day length is one of the environmental factors (examples of other environmental factors: climate and availability of food resources) that mediates differences in lek attendance of *M. manacus* (Snow 1962). In both regions, higher lek attendance of males occurred on longer days during the year. Studies argued that male manakins may display under specific conditions of light in the forest which may influence mating attempts (Théry and Vehrencamp 1995, Endler and Théry 1996, Heindl and Winkler 2003, Anciães and Prum 2008). Thus, longer days may provide more opportunities to encounter suitable light conditions for males to display and attract females.

In the study area, during the longest days in November and December, resident males of *M. manacus* stayed in lek areas up to 82% of the day, which is similar to the 90% of lek attendance observed by Snow (1962) in Trinidad. However, the attendance of resident males on display courts was much lower (up to 7% of the day length) because they spent most of their lekking time out of their display courts defending territories against intruders, interacting with neighbors, preening, or calling the attention of visiting females with specific displays (e. g. rolled snap and fanning) to drive them to the court where short and intense exhibition occurs (see Snow 1962; Lill 1974a; Cestari and Pizo 2012, see chapter 2).

As in tropical region, resident males in the subtropics displayed more in the early morning from 06:30 to 08:00 hrs, decreasing gradually the lek activity from 08:00 to 11:30 hrs; a second peak in activity occurred between 14:00 to 15:00 hrs. The latest individual left the lek area close to sunset (see Darnton 1958, Snow 1962). Juvenile males practiced lek maneuvers in the courts sporadically, mainly during absence of adults. Juveniles did not show any clear pattern in either daily or annual display activity. Display bouts of juveniles, however, did not differ in their length from those of resident males. According to Coccon et al. (2011), adult males of *M. vitellinus* have individual dance choreographies with precise sequence of moves and use of court saplings that are learned during weeks of practice. Considering its close phylogenetic relationship, *M. manacus* juveniles probably have similar mechanisms for learning displays as do *M. vitellinus*. Thus, time in display practice may be important for juveniles to establish their individual dance choreographies before they display in its own court acquired later during the adult phase. In species with no pair bond such as *M. manacus*, a precise and synchronized dance between males and females is important for successful copulation once both sexes meet during brief periods for mating (Snow 1962).

In our study, no variation was found in female visits to courts over the course of the year. However, a slight increase in the average number of female visits occurred during July to December, which coincides in part with the period when copulations were recorded (September to December). In addition, two nests were found in the region in December and January (CC, pers. obs.). In Trinidad, Snow (1962) argued that females frequently visit males in the breeding season, which may last up to 5 months during any year and varies according to environmental factors (such as rainfall) that are important in affecting availability of food resources (arthropods and fruits) for manakins. In Panama, Worthington (1982) detected the beginning of breeding of *M. vitellinus* and *P. mentalis* when the fruit supply increased. In general, the first heavy rains marked the beginning of the species' breeding season in tropical as well as in subtropical region (Snow 1962; CC and MAP, pers. obs.).

Females of *M. manacus* have a "sampling period" of visits to courts, visiting several males before mating with one of them (Lill 1974a). Our results revealed that females tended to visit resident males more frequently during periods of the year with longer display bouts. Therefore, longer dances of males which occurred during July to December or January probably explained the female visitation to courts and mating choice. Lill (1974a) also demonstrated a positive correlation between female visit and males displays characteristics in Trinidad. Studies on individual level are needed to reveal how display duration of males translates to reproductive variance in male mate success and the opportunities for sexual selection. Several other traits may influence the male attractiveness to females, including: larger male size (Snow 1962), higher frequency of aggressive displays and territory defense (Lill 1974a), larger territory size (Olson and McDowell 1983), centrality of the court in the lek area (Shorey 2002), plumage maintenance (Cestari 2010), use of auxiliary courts (Cestari and Pizo 2012), and court clearing maintenance (Cestari and Pizo, unpubl. data, see chapter 3).

The temporal uniformity in the daily pattern of female visit to courts supports the hypothesis that the marked daily display cycle of males is related to the maintenance of the communal display ground, as pointed by Snow (1962). A compact group of constantly displaying males that maintain individual territories have high attractiveness to females than solitary males (Snow 1962). Also, compared with other types of display dispersions, communal displays may be preferable by lekking males by providing reduction of mate search costs and retention of receptive females in lek areas (Westcott 1997).

In summary, the present study confirmed several hypotheses about the temporal aspects of lek behavior of *M. manacus* first advanced in tropical Trinidad are also occurring in the subtropical region, including: (1) that day length has a positive on the lek attendance of resident males; (2) that males may spend long periods of up to 82% of day time in lek areas during the breeding season; and (3) that males have a daily cycle of lek activity, with peaks occurring between 06:30 – 08:00 and 13:30 – 15:00 hrs, irrespective of female visit to courts. Additionally, new aspects about lek phenology for this species were disclosed, including: (1) that there is an inverted temporal pattern in the lek activity of resident males between tropical and subtropical regions; (2) that up to 7 % of the day is spent by resident males in their courts during the breeding season; (3) that there is a clear variation in the frequency and duration of display bouts of resident males (but not juveniles) over the course of the year; and (4) a there is a positive correlation between duration of displays of resident males and the frequency of female visit to courts.

Studies of courtship behavior patterns of manakins in a regional scale are useful to understand their demography as well as relevant behavior strategies responsible for their mating success (Anciães et al. 2009). We expect that the consolidated and new aspects of courtship of *M. manacus* advanced here will be useful in comparative studies that concern the ecological and evolutionary basis of lek behavior in birds.

Acknowledgments

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CAPÍTULO 2

The use of auxiliary courts by the lek-forming White-bearded Manakin *Manacus manacus* (Aves, Pipridae)

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Abstract

The White-bearded Manakin is a passerine specially noted for elaborate courtship. Each resident male has a cleaned oval court delimited by saplings in leks. No study mentions the use of more than one court by a territorial male during the breeding season. We report the use of auxiliary courts by males in the lowland forest of southeastern Brazil and discuss its probable function in attracting females for mating. Additionally, we experimentally modified a male's main courts, testing that auxiliary courts serve as alternative display places. Twelve males from four different leks were observed for 145 h. Six males used from one to four auxiliary courts located 1.0 to 8.1 m from their main courts. The males that also used auxiliary courts displayed more than males that used only the main court. Nevertheless, the proportion of female visits per display time indicates that males that used only the main court have greater efficiency in attracting potential mates. Individual males responded differently to the experimental modification of their main courts, but one male avoided the modified court. The use of auxiliary courts may be a strategy adopted mainly by peripheral males to attract females that visit more successful males with central territories on the lek. In the short-term, auxiliary courts function as optional display places in cases of loss of the main court. In the long-term, the use of auxiliary courts may be involved in the temporal persistence of lek areas.

Keywords: Atlantic Forest, Brazil, courtship behavior, sexual competition

Introduction

Manakins form a neotropical bird family whose members frequently adopt the lek as a breeding strategy (Höglund and Alatalo 1995; Sick 1967). Apart from designating the breeding strategy per se, the term lek also refers to the area where males congregate with the purpose of attracting and stimulating females to mate, often generating intense inter-male competition for mating opportunities (Höglund and Alatalo 1995). In manakins, the spacing of lekking males varies greatly. In classical leks, males may be regularly spaced with visual contact with each other and separated by as little as a meter or less apart, whereas in exploded leks males are within a hearing distance but broadly dispersed with no visual contact with each other (Sick 1967; Snow 2004).

The lek behaviour of White-bearded Manakin (*Manacus manacus*) comprises the classical type and was first studied by Chapman in 1894 in Trinidad Island (Chapman 1935). According to the author's observation, "they (four individuals of *M. manacus*) were all uttering, in an excited way, their sharp, twittering call, at the same time they were jumping back an forth from bush to bush buzzing and whirring at every wing-stroke, and frequently, with each jump, making the sharp snapping sound". Afterwards, more detailed descriptions of the courtship behaviour of the species was reported based mainly on studies at the Trinidad Island and Suriname, northeast of South America (Darnton 1958; Lill 1974a; Olson and McDowell 1983; Snow 1962). Snow (1962), for instance, reported that "each bird displays on and around a small area of bare soil and rootlets", which he called court.

Studies on the lek system of the White-bearded Manakin focused mainly on the traits that influence the attraction of females by males, such as male's size, plumage maintenance of males, frequency of aggressive display and territory defense by males, male's territory size, and distance of a male's court to the lek centre (Cestari 2010; Lill 1974a; Olson and McDowell 1983; Shorey 2002; Snow 1962). In relation to the latter trait, it has been shown that central males attract more females and get more matings than peripheral males (Lill 1974a; Shorey 2002; Snow 1962).

In the present study, we recorded the use of more than one court (hereafter referred as auxiliary courts) during a breeding season by lekking males of *Manacus manacus gutturosus* in southeastern Brazil. The use of auxiliary courts has not been mentioned in the several studies conducted with the species. Snow (1962) referred to "practice display grounds" as areas where adult males not established on leks or young males practice courtship maneuvers. These males, however, were not resident and did not display in delimited territories located in leks areas as shown in the present study. We aimed to answer the following questions: (1) how many auxiliary courts a resident male uses? (2) Is the displaying time of a resident male in the main court greater than its displaying time in the auxiliary courts? By definition, we expected a greater displaying time in the main courts. Due to the absence of studies that reported the use of more than one court inside the territories of resident males, we presumed that all the studies that reported displays of resident males referred to main courts only (Berres 2002; Cestari 2010; Lill 1974a; Lill 1974b; Olson and McDowell 1983; Shorey 2002; Shorey et al. 2000; Snow 1962). We discussed the importance of the use of auxiliary courts as an extra trait involved on mate attraction. Therefore, we also asked (3) how lekking males that used only the main court compares to males that also use auxiliary courts in relation to

the efficiency in attracting females? We hypothesized that auxiliary courts increase the male attractiveness by providing optional places to stimulate female visits. As an additional effort to reveal causes for the use of auxiliary courts by lekking males, we experimentally tested if auxiliary courts may serve as alternative display places in cases of loss of the main court due to disturbances that lead to its disruption. Studies in Trinidad showed high longevity of leks (over 42 years), and low turnover of resident males (Berres 2002; Lill 1974b; Snow 1962). We then hypothesized that the use of auxiliary courts by resident males is important to maintain display places inside their territories over the years, thus contributing to the persistence of lek areas.

Material and methods

The species

The White-bearded Manakin, *Manacus manacus* (Linnaeus 1766), is a small (15 – 18 g) frugivorous passerine found in secondary forests with an abundance of small upright saplings that are used in its displays (Snow 1962). Males may spend up to 90% of their daylight time in leks, making brief excursions of less than 5 min to forage at nearby fruit sources (Snow 1962; Cestari and Pizo, in press, see chapter 1). Each resident male displays at an oval court of 0.15-0.9 m diameter delimited by two or more saplings (Darnton 1958; Lill 1974a; Olson and McDowell 1983; Snow 1962; Snow 2004). In the most frequent display, the bird with its head thrust forward and extended beard perches in a horizontal position across one of the saplings round its court, then suddenly with a loud snap leaps to another perch facing the way it came from (Snow 1962). The court is actively cleared from litter by the resident male because leaves and debris may reduce the court view by females and the visual contrast of the manakin body color against background during displays (Darnton 1958; Snow 1962; Uy and Endler 2004; Cestari and Pizo, unpubl. data, see chapter 3). The number of courts in a given lek, and the distances among courts of neighboring males, may vary from 2 to 70 and 0.9 to 82 m, respectively (Darnton 1958; Lill 1974a; Olson and McDowell 1983; Shorey 2002; Snow 1962). Resident males may have a long lasting sexual life (until 14 years), and defend permanently the area immediately around its court against neighboring residents and males without territories (Lill 1974b; Snow 1962).

Study site

The study was made in *restinga* forests of the State of São Paulo, southeastern Brazil (Fig. 1). The *restinga* ecosystem integrates the Atlantic forest biome, and it is distinguished by a mosaic of plant communities occupying the sandy plain between the sea and inland mountains. Halophytic herbs and shrubs compose the structurally simple vegetation close to the sea, while more complex vegetation composes the lowland and the lower mountain forests deeper into the continent (Sampaio 2005). Climate is subtropical and humid. Mean annual rainfall is 2278 mm with the rainy season occurring from October to April, and the dry season from May to September. Mean annual temperature is 21.4ºC, with maximum temperatures averaging 25.8ºC and minimum temperatures averaging 19.0ºC (Tarifa 2004).

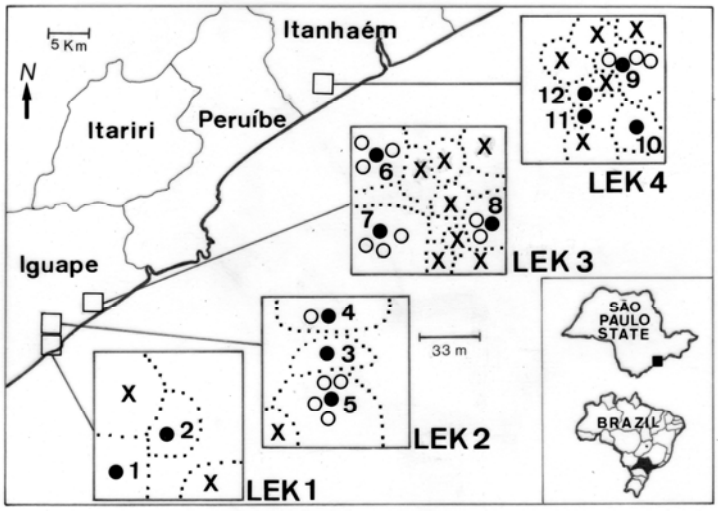

Fig. 1 Study lek areas along the coast in southeastern Brazil. Black circles indicate main courts of resident males. Empty circles indicate auxiliary courts. Dotted lines indicate approximate limits of male's territories. *X* symbols indicate males whose lek behaviour was not monitored.

Data collection

Twelve males from four different leks (LEK 1 to 4) were color-banded and observed from 1 to 36 h (mean 12.1 ± 3 h), totaling 145 h of observations. Leks were located in areas of secondary vegetation growing in old agricultural fields abandoned 15-30 years ago.

Distances between leks were 0.08 km from LEK 1 to LEK 2, 9.7 km from LEK 1 to LEK 3, and 37.9 km from LEK 1 to LEK 4. The maximum numbers of active resident males were four in LEK 1 and LEK 2, eleven in LEK 3, and nine in LEK 4 (Fig. 1). Observations were conducted between August 2009 and January 2010. Observations on the annual breeding behaviour of the species in the region confirmed that this is the main period of lek activity (Cestari and Pizo, in press, see chapter 1). Observations started at dawn (between 05:11 and 06:23) immediately after the arrival of males in their courts, and finished at late afternoon (between 15:23 and 17:42), when the males left the lek. Only one male were observed at a time from concealed positions distant at least 5 m from the focal court. Appropriated camouflaged clothes were adopted by the observer to minimize the influence on the birds' behaviour.

For each male observed, the following parameters were recorded: (1) the territory size in the lek, (2) the total displaying time spent by the male in its main and auxiliary courts, (2) the number of auxiliary courts used, (3) the distance between the main and auxiliary courts, and (4) the number of female's visit to the main and auxiliary courts. We delimited the territory boundaries of males during exhaustive observations of their hierarchical interactions with neighbors at the limits of their territories, and by observing the perches that they used for resting inside their territories (see Lill 1974a; Shorey 2002; Snow 1962). We considered the main court as the cleanest court used by a male. The White-bearded Manakin frequently cleans its main court picking up dead leaves and twigs from the soil to drop them nearby (Darnton 1958; Snow 1962; Cestari and Pizo, unpubl. data, see chapter 3). Other kinds of cleaning behaviour involve beating the wings to generate an air drift that dislodge soil debris in the court, and picking pending leaves that may obstruct the court view.

In the second breeding season (August to November 2010), we modified the main courts of three banded males that used auxiliary courts (males 5, 7 and 9) and three banded males that did not use auxiliary courts (males 10, 11 and 12) in the previous season (see Fig. 1 for locating the experimental courts of males). Few minutes before the arrival of the focal male, we added leaves and branches to its court in a manner that the bird could not remove them (Fig. 2).

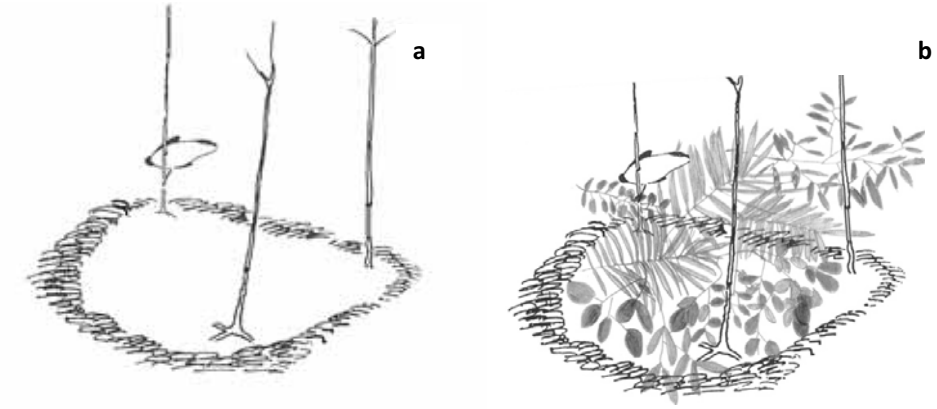

Fig. 2 Courts of White-bearded Manakins (area of bare soil surrounded by saplings) with no modification (a), and modified with experimentally added branches and leaves (b).

As soon as the male arrived, we started a 66-min period of observations recording the reaction of the male to the modification of its main court. The following parameters were considered: the displaying time spent by the male up to 20 cm above its modified court or up to 20 cm on the border of it, and the number of frustrated display attempts. We considered frustrated displays when the male did not snap more than twice, performing an incomplete display (see Snow 1962 for a complete description of the species display maneuvers). For male 7, which responded to the experiment using one of its auxiliary courts (see below), we conducted 112 min of additional observations following two consecutive interventions: (1) we moved the modification from its main court to the previously used auxiliary court and observed the male reaction for 66 min, and (2) we modified both the main and auxiliary courts additionally observing the male for 66 min.

Data analyses

For males with auxiliary courts, we compared the proportion of displaying time per total time of observation in the main and the auxiliary courts using Wilcoxon test. The territory size and proportion of displaying time of males that used only the main courts and the males that added auxiliary courts were compared with Mann-Whitney U test, which was also used to compare these two groups of males in relation to the rate of female visits per

total displaying time. We evaluated the efficiency in attracting females by the ratio between the rate of female visits and the proportion of displaying time. All the analyses were performed in Bioestat v. 4.0 (Ayres et al. 2004). The values presented are mean ± standard error.

Results

Use of auxiliary courts

Six to twelve males used from one to four auxiliary courts located 1.0 to 8.1 m (2.98 ± 1.88 m) from their main courts (Fig. 1 and Fig. 3). For males with auxiliary courts (males 4 – 9), there was no difference in the proportion of displaying time in auxiliary and main courts (Z = -1.36, N = 6, P = 0.17; Fig. 4).

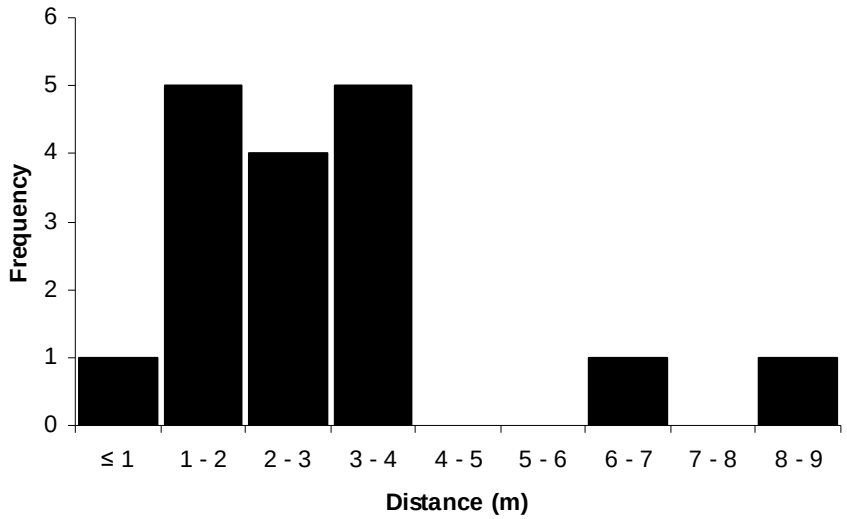

Fig. 3 Frequency of the distances of auxiliary courts from main courts of White-bearded Manakin males in lowland forest from southern Brazil.

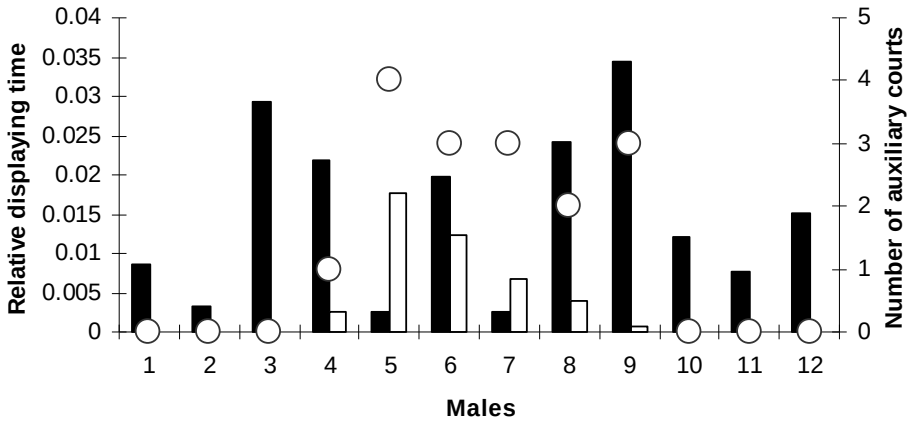

Fig. 4 Proportion of displaying time of lekking males of White-bearded Manakin. Black bars indicate main courts, white bars indicate auxiliary courts, and circles indicate the number of auxiliary courts.

Males with auxiliary courts had a higher proportion of displaying time than males that used only main courts (U = 1.92, N = 12, P = 0.05; Fig. 5). Territory size of the first group also was higher (270.15 ± 87.32 m^2) than the last group (91.52 ± 59.63 m^2) (U = 2.08, N = 12, P = 0.03). However, there was no difference in the rate of females visits between these two groups of males (U = 0.32, N = 12, P = 0.74). Therefore, considering the ratio between females attracted per displaying effort, males with auxiliary courts was nearly eight times less efficient in attracting females than males that used only the main court (Fig. 5).

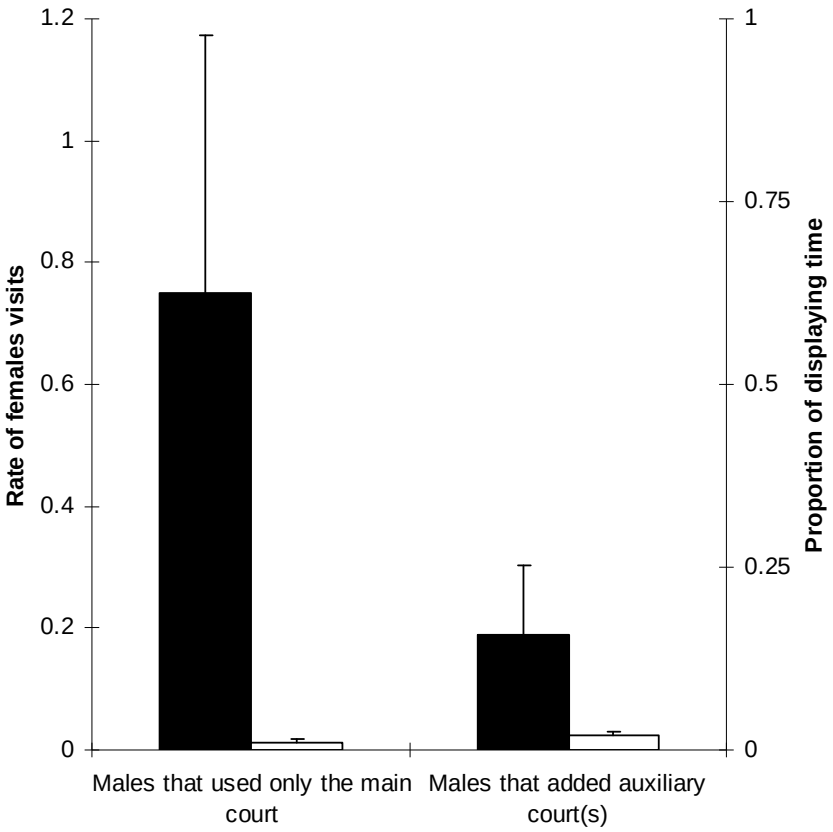

Fig. 5 Rate of females visits (black bars) and proportion of displaying time (white bars) of the group of six White-bearded Manakin males that used only the main court and the group of six males that added auxiliary courts. The vertical lines indicate the standard errors.

Experimental modification of courts

During the experiment, male 5 did not display in its auxiliary courts, but attempted to display eight times in the main court with no more than twice snaps, which characterized frustrated displays. Male 7 displayed most frequently in one of its auxiliary court (70.0% of the 1.4 min of displaying time) and less frequently at the border of its main court. Male 9 did not display in the auxiliary court, using exclusively the border of its main court in 2.40 min of displaying time. Among the males that did not have auxiliary courts, male 10 displayed 1.10 min above its court and made frustrated displays five times. Male 11 displayed either at the border (75.7% of the 1.03 min of displaying time) or above (24.3%) its court, while male 12 displayed 2.98 min only above its court.

With the auxiliary court modified, male 7 displayed mainly in its main court (84.7% of the 3.27 min of displaying time), and less frequently in the border of the auxiliary court. With both courts modified, male 7 only attempted to display once in the main court and displayed for 1.07 min in a previously unrecorded place 1.2 m from its main court.

Males received from one to seven female visits during the experiment, but there was no copulation. When male 7 had its main court modified, a female moved from the main to the auxiliary court, being followed by the male.

Discussion

This study adds a new behaviour to the lek system of White-bearded Manakin not yet described in long-term studies concentrated on northeast of South America (Berres 2002; Darnton 1958; Lill 1974a; Lill 1974b; Olson and McDowell 1983; Shorey 2002; Sick 1967; Snow 1962). The use of more than one display site within a male territory was also cited for other manakin species (e.g. *Lepidothrix serena, Corapipo gutturalis, C. heteroleuca, C. altera, Masius chrysopterus, Ilicura militaris*; see Anciães and Prum 2008, Prum 1985), but no function has been proposed for the use of such extra display sites. Snow (1962) described the use of more than one display site as "practice display grounds" by non lek-established males and juveniles of White-bearded Manakin in Trinidad. In this case, however, the individuals did not present territoriality.

The group of males that used auxiliary courts displayed equally at their main courts and auxiliary courts. We did not record any apparent effort of males to clean the auxiliary courts, but male 7 maintained one of its auxiliary courts as clean as its main court. Probably, the "gardening" work of this male was one more trait that favored the attraction of a female to its auxiliary court. Uy and Endler (2004) suggested that behavioral modification of the court's background by males of Golden-collared Manakin (*Manacus vitellinus*) increase their conspicuousness, and may explain why manakins build and clean courts (see also Cestari and Pizo, unpubl. data, chapter 3).

Contrary to the expected, our results indicated a higher efficiency in the attraction of females by males that used only the main court. Combined biological features (e.g., court-cleaning, plumage maintenance, higher frequency of aggressive display and defense of territory, larger territory size, and the centrality of the male's courts) may contribute for

individual attractiveness to females and mating success of *Manacus* species (Cestari 2010; Lill 1974a; Olson and McDowell 1983; Shorey 2002; Uy and Endler 2004; Cestari and Pizo, unpubl. data, chapter 3). Furthermore, in a local population perspective, the number of individuals in a lek is suggested to increase the male's attractiveness (Snow 1962). We propose two explanations for the use of auxiliary courts by males: the centrality of the male's courts and the male's territory size.

Resident males of White-bearded Manakin that occupy central territories in leks were preferred by females, sometimes leading to a non-random distribution of mates among lekking males (Lill 1974a; Shorey 2002; Snow 1962). Usually, these successful males are more aggressive with conspecifics in order to maintain its territories. They establish a dominance hierarchy in ritualized agonistic encounters during territory invasion attempts by less successful males that are settled on the periphery of the lek (Lill 1974a; Shorey 2002; Snow 1962). This fact suggests a permanent competition between males for space in the lek. As more males are recruited to the lek, more space in its periphery is required, and the areas of central territories have the tendency to decrease depending on the male's dominance and aggressiveness. This situation leads to the existence of smaller territories dominated by successful males on the centre of leks, and larger peripheral territories dominated by subordinated males that attempt to parasitize the success of the former. Four (#6, 7, 8, 9) out of the six males that used auxiliary courts had higher territory sizes than males that did not, and tend to be settled at the periphery of the leks, while three males (#3, 11, 12) that displayed only in the main courts on the lek centre had smaller territory sizes (< 40 m^2) (see Fig. 1). In this context, the use of auxiliary courts by these males might be a behavioral strategy to attract females that visit mainly the successful males with central territories in the lek. Usually, when a female visited a central territory, a peripheral male moved to the limit of his territory and displayed in its nearest auxiliary court supposedly to call the attention of the female. A male did not approach a female visiting a neighboring territory until she is within his own territory a few meters from his court (Snow 1962; C. C., pers. obs.). Once the female entered his territory, the male promptly flew to the main court to display.

Individual males had different responses to the experimental modification on their main courts, exhibiting frustrated display attempts, displaying at the border and above the courts, and also at auxiliary courts. Male 7 showed a particular malleability during the experiment, avoiding its modified court and displaying at the auxiliary court. In one instance, it was also followed by the visiting female to its auxiliary court. This fact suggests that in the

short-term, auxiliary courts function as optional display places in cases of loss of the main court. In the long-term, the use of auxiliary courts allied with the high longevity of males (Lill 1974a) might be one more trait that made possible the persistence of lek areas (Berres 2002; Lill 1974a) even in case of small forest disturbances. For instance, Berres (2002) suggested that the dissolution of lek areas in Trinidad was due to major disturbances on forest caused by human invasion. In our experiment, we avoided to prolong the period of perturbation on courts or totally destroy the courts by cutting its saplings due to ethical reasons. According to Snow (1962), one main upright sapling growing around the court is more important than the others and some of the main displays and the mating itself take place on it. Furthermore, the abandonment of successful males from the lek due to a definitive modification of their courts might destabilize the lek as a whole.

In conclusion, we suggest that the use of auxiliary courts is likely related to the avidity of subordinated males to attract potential mates. By functioning as alternative display sites when the main court is for some reason disrupted, auxiliary courts may contribute to the persistence of lekking territories and the lek area as a whole. Future studies attempting to understand the mechanisms involved in the use of auxiliary courts, and the consequent additional energetic costs associated with their use by a lekking male of White-bearded Manakin or any other manakin species are welcome.

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CAPÍTULO 3

Court cleaning behavior of the White-bearded Manakin (*Manacus manacus*) and a test of the anti-predation hypothesis

Submetido para Emu – Austral Ornithology

Abstract. Cleaning of courts is used by several forest lekking birds. Increase of the conspicuousness of displaying males and prevention of lurking predators on court areas are suggested to explain its function. We investigated the annual court cleaning of White-bearded Manakin (*Manacus manacus*) and tested it as a sexual success mechanism correlating with females' visits, duration of males' displays and biomass of fallen debris on courts. We also conducted an experiment to test the reaction of 21 lekking males to a replica of pit viper (*Bothrops jararaca*) placed on the court and in adjacent leaf litter area. Two main annual peaks of court cleaning were positively correlated with females' visits, duration of males' display bouts, and biomass of debris on courts: soon after the non-lekking period in which courts were filled with debris and females were assessing males, and in the main lekking period when females started mating. Males perceived the snake replica in the court and the adjacent area, refuting the anti-predation hypothesis as an explanation for the court cleaning. We suggest that sexual exhibition driven by the optimization of light on court but not predation is related to the court cleaning in *M. manacus*.

Additional keywords: arena, conspicuousness, lek, luminosity, manakins.

Introduction

Forest lekking birds such as manakins, cock-of-the-rocks, peacock pheasants, and birds of paradise may clean debris and pluck leaves from their courts on or near the forest floor (Johnsgard 1994). Among manakins, all species of *Manacus* remove leaves and twigs from their ground courts and pluck leaves surrounding it (Snow 2004). White-throated Manakin *Corapipo gutturalis* remove leaves and twigs from their log display areas (Endler and Théry 1996), and some species of *Pipra* and *Chiroxiphia* also pluck leaves around and above their display branches (Gilliard 1959; Sick 1967).

A cleared court presumably signals ownership of a delimited display area by a resident male and the quality of the court owner for conspecifics (Uy and Endler 2004). Other probable functions of court cleaning include: predation avoidance (Gilliard 1959), and optimization of light incidence on courts with improvement of males' plumage contrast against background during displays (Uy and Endler 2004).

Gilliard (1959) suggested that some birds clean leaves from arboreal perches and ground courts as a predator defense mechanism to better locate predators that lurk on or near

their courts such as lizards and snakes. However, few instances of predation upon forest lekking birds were observed during long-lasting studies in the Neotropical region (Lill 1974a; Lill 1974b; Lill 1976). Raptors were the main predators in leks of the Guianan Cock-of-the-Rock *Rupicola rupicola* (Trail 1987). This conspicuous bird used spooks and alarm calls as antipredator behaviors that apparently were efficient with raptors, but it has no known defensive mechanism against terrestrial predators, such as snakes (Trail 1987).

Forest structure has been shown to affect the quality and intensity of light reaching the courts of lekking birds, thus influencing the appearance of plumage coloration and the movements of displaying birds (Endler 1993; Endler and Théry 1996; Théry and Vehrencamp 1995). Strong evidences showed the importance of physical factors in conspecific communication of lekking birds, and that selection had favored optimal use of the dim light available in the forest understory (Endler and Théry 1996; Heindl and Winkler 2003; Théry and Vehrencamp 1995). Moreover, the plumage brightness, a factor that depends of light incidence, is considered a good predictor of mating success of Golden-collared Manakin *Manacus vitellinus* (Stein and Uy 2006). Even Gilliard (1959), who proposed the predator defense hypothesis, pointed out the importance of light to Blue-backed Manakin (*Chiroxiphia pareola*) displays when he described the species' cleaning behavior in perches during "the hottest and driest period of the year…when many of the deciduous trees shed their leaves and permits a great deal of light to penetrate to the forest floor at the season when basal vegetation is used by the displaying birds".

Uy and Endler (2004) argued that there are at least three ways in which displaying birds can behaviorally enhance the conspicuousness of their color patches: incorporating postures that highlight specific color, choosing to display in locations or times of day that best complement their color signals, and modifying the existing visual background by building or cleaning courts to enhance optimal contrast of colors. These authors proved that the court cleaning behavior in *M. vitellinus* increases the males' visual contrast against the background of the court during displays. Therefore, it would be possible that court cleaning is used to optimize light incidence on court and improve males' display performance to attract females. According to Snow (1962), males of White-bearded Manakin *Manacus manacus* frequently clean their courts during displays bouts, and cleaning bouts become longer in duration before the peak period of breeding. Chapman (1935) noted that the preparation of the court together with cleaning behavior in *M. vitellinus* indicates the arrival of the breeding season.

The court cleaning behavior was well described for the genus *Manacus* (Chapman 1935; Darnton 1958; Sick 1967; Snow 1962), but there was no study that monitored it through time or properly investigated its function. Individual males of *Manacus* species have high longevity, slow rate of turn-over, and extended periods of residency in lek areas (maximum of 11.5 years reported by Lill 1974b), which suggests that the predation pressure is low in lek areas or that the anti-predatory strategy of lekking males is efficient. On the other hand, these birds present high sexual competition and the use of cleaning behavior may improve the display performances of competing males. Therefore, males of *Manacus* may use the court cleaning behavior as an anti-predation strategy (as hypothesized by Gilliard 1959) and/or to improve the visual contrast of their plumage (as supported by Uy and Endler 2004). In the present study we confront these two hypotheses to determine the function of court cleaning behavior by males of *M. manacus*. For this, we address the following questions: (1) how does the frequency of court cleaning vary throughout the year? (2) Is court cleaning correlated with the frequency and duration of display bouts? (3) Is it correlated with the frequency of females' visits to courts? Finally, (4) is court cleaning a behavior used to avoid terrestrial predators such as snakes?

Methods

Species

Manacus manacus (Linnaeus 1766) is a small (15-18 g) frugivorous passerine that preferentially inhabits secondary forests of South America (Snow 1962). It is the most widespread manakin with its distribution extending from Colombia to NE Argentina (Snow 2004). Similarly to the majority of manakins, it is a dimorphic species: males have black on cap, back, wing, and tail, grey on rump, upper tail coverts, flanks and belly, and a white neck. Females are olive above, greyer and paler below (Snow 2004). Males display in classical leks from two to 70 individuals (Olson and McDowell 1983; Snow 1962). Each lekking male has an individual oval court of 0.15–0.9 m in diameter set on the ground and delimited by saplings which males actively clean from litter (Darnton 1958; Snow 1962). During displays, adult males make loud snaps with wings while leaping among the saplings that surround its court. At times, males may extend his white beard and expand the white collar. Females generally stay above the court accompanying a male's performance and may sometimes display with it (Snow 1962). Snow (1962) pointed a well-defined molting period of *M.*

manacus following breeding, during which displays of males are much reduced and the molting males stay out of their court for nearly 80 days.

Study areas

Study was conducted at six leks in the *restinga* ecosystem in lowland Atlantic forest, southeastern Brazil. LEK 0 with six resident males (24°31'59.83" S, 47°12'12.00" W), LEK 2 (four resident males; 24°31'40.65" S, 47°11'40.85" W), and LEK 3 (11 resident males; 24°28'7.62" S, 47° 7'13.20" W) are located at Juréia Itatins Ecological Station (JIES) in Iguape municipality. LEK 4 with nine active resident males is located at Itanhaém municipality (24°10'11.9" S, 46°55'32.81" W), while LEK 5 (two resident males; 24°15'13.87" S, 46°55'10.26" W) and LEK 6 (six resident males; 24°22'30.87" S, 47° 2'2.08" W) are located at Peruibe municipality. Distances between leks range from 9 to 49 km. Climate is subtropical and humid. Mean annual rainfall is 2278 mm with the rainy season occurring from October to April, and the dry season from May to September. Mean annual temperature is 21.4°C, with maximum and minimum temperatures averaging 25.8°C and 19.0°C, respectively (Tarifa 2004).

Field data

We conducted observations of nine color-banded *M. manacus* from LEKS 2, 3 and 4 (three individuals from each lek) from November 2009 to October 2010. In each month we observed the lek(s) from one study area (Itanhaém or JIES) for three days. Thus, each study area was visited six times over the course of the 12-month study. Only one male was observed at a time from concealed positions amidst the understory vegetation distant at least 5 m from the focal court. Lekking birds did not seem to notice the presence of the observer sitting on the same place after some hours of observation, as also reported by Darnton (1958). Observations were conducted according to the presence of resident males on leks, starting at dawn (between 05:11 and 07:13) and finishing at afternoon and late-afternoon (between 14:31 and 17:42).

The following parameters were recorded for each male observed: (1) the frequency and duration of display bouts (displaying time), (2) the frequency of court cleaning bouts, and

(3) the frequency of females' visits to court. A male display bout was defined as one uninterrupted sequence of leaps on court saplings. A court cleaning bout was recorded when a male picked up a fallen leaf, twig or other detritus from the ground and dropped it beyond the court edge or when a male perched on the ground uses short hovers pulling pieces of live leaves or rootlets that surrounded the court (Darnton 1958; Snow 1962; see appendix 4).

Seven randomly distributed seed traps with size similar to the size of courts (0.22 m^2) were used to sample fallen debris (leaves, twigs, and detritus) at the LEK 3 from November 2009 to October 2010. The collected material was dried and weighted in the lab and mean dry biomass of fallen debris was correlated with the monthly mean frequency of court cleaning bouts.

To verify if the court cleaning behavior may augment the natural luminosity of the court in relation to its border, we measured the intensity of light in the central point of the courts, and at four bordering points (nearly 50 cm from the central point) when the nine males firstly displayed in the mornings. For control purposes, we also measured light intensity in spots without courts located nearly 10 m from the courts. We used a digital luximeter Icel LD-510 on the soil surface to measure light intensity.

To verify if the court cleaning behavior may act as an antipredation mechanism, we recorded the reaction of males when presented to a resin replica of a pit viper (*Bothrops jararaca*), which is a potential predator of small birds in the region (Marques and Sazima 2004). To the human eye, it is highly camouflaged on the leaf litter but can be detected easily in the bare soil of the court (Fig. 1). The pit viper was placed in the leaf litter 10 - 20 cm from the court and in sequence in the central cleared area of the court. To begin each experimental trial, we profited from the brief periods of a male absence from its court (usually for foraging) to silently put the pit viper replica in one of the areas. Then, for 10 min upon the return of the male to its court, we recorded its reaction (reacted or not) to the replica through the emission (including the frequency) of its alarm "peerr" calls (Snow 1962) associated with small escape flights when it overly approached (less than 10 cm) the replica. We used frequency of alarm calls and small escape flights as factors of males' perception because resident males may utter alarm calls to any previous "unknown" object placed on the court that may negatively affect its displays (Cestari and Pizo 2012; Coccon et al. 2012). Thus, before the snake experiment, we placed a twisted twig with a shape similar to a snake in the central cleared area of the court to verify if five different males distinguished it as a potential

predator in five trials of 10 min. All of them uttered alarm calls, but in lower frequency than during the snake experiment (*t* test= 2.82; *df* = 4; *P* = 0.05). Furthermore, their close approaches to the twig (less than 10 cm; three of them perched on it) with no escape flights allowed us to conclude that the males did not react to a snake-shaped object as a potential predator. Calls of males were recorded with a directional microphone (Sennheiser ME-66) hidden in the vegetation. Experimental trials were made during periods of peak activity in the lek (from 6:10 to 8:10 and from 12:40 to 15:15). We performed the pit viper experiment with four males in LEK 0, two males in LEK 2, four males in LEK 3, six males in LEK 4, one male in LEK 5, and four males in LEK 6 from August to October 2011.

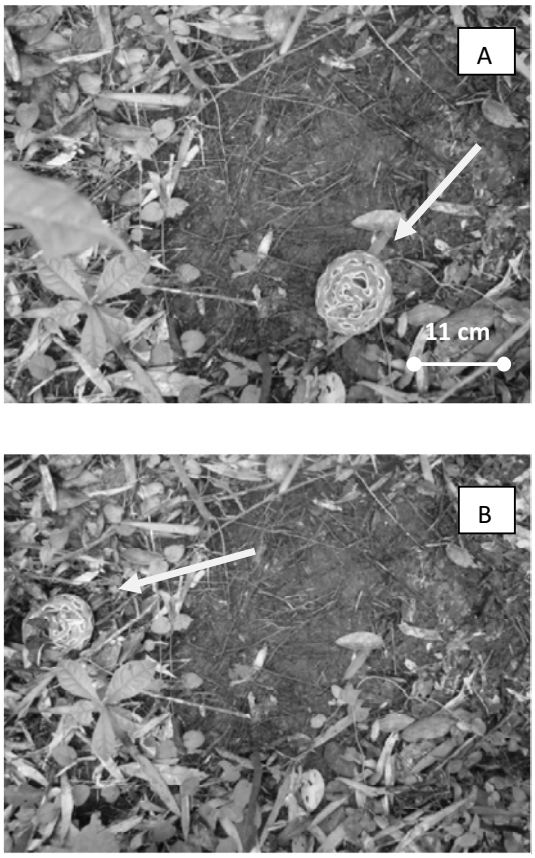


Fig. 1. Experimental predation trials during periods of peak activity in the lek of *Manacus manacus*. A pit viper (*Bothrops jararaca*) replica was placed on the cleared court area (A), and on leaf litter adjacent to the court area (B).

Statistical analysis

Data on cleaning behavior of *M. manacus* were grouped and analyzed bimonthly to obtain an overall view of this behavior once we analyzed three distinct leks each two months. Spearman correlation tests were used to verify the relationships between the following averaged variables: frequency of court cleaning, duration of display bouts by males, frequency of females' visits, and biomass of fallen debris on courts. Considering that court cleaning did not occur from May to June 2010 when males were absent from leks (see results), for statistical analysis we added the mean biomass of debris of this period to the following July - August 2010 period.

We used a Wilcoxon test to assess the differences in light intensity between the central points of the courts and the averaged light intensity of their bordering points. This analysis was also used to assess whether there are differences in light intensity between the control spots and their bordering points.

We used the G test with Yates correction to check for differences in reaction of males (reacted or not) to the pit viper replica when it was positioned in the leaf litter area adjacent to the court and in the central cleared area of the court. The paired Student´s t test was used to test for differences in the frequency of calls of males in the snake experiment on court and its adjacent area. We employed the Bioestat software 5.0 (Ayres et al. 2004) for all analysis. Significance was accepted at $P \leq 0.05$.

Results

Males did not display from May-June 2010 (non-lekking period). Duration and frequency of displays abruptly increased in July-August and November-December, decreasing in March-April (Fig. 2).

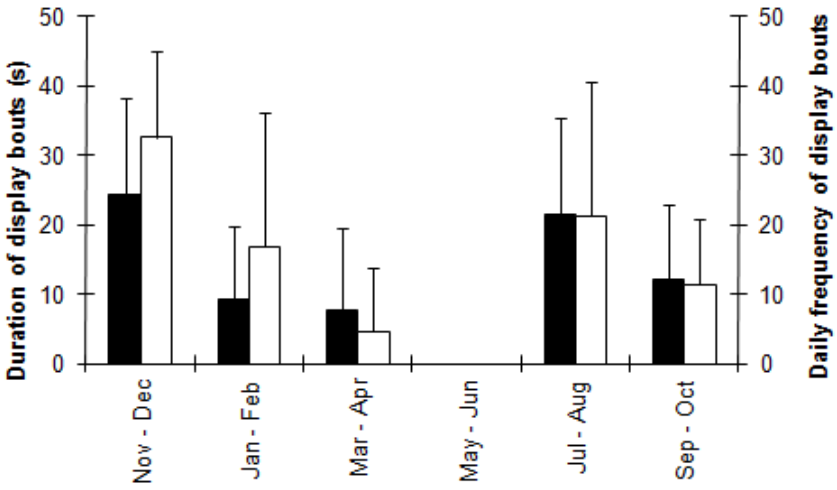
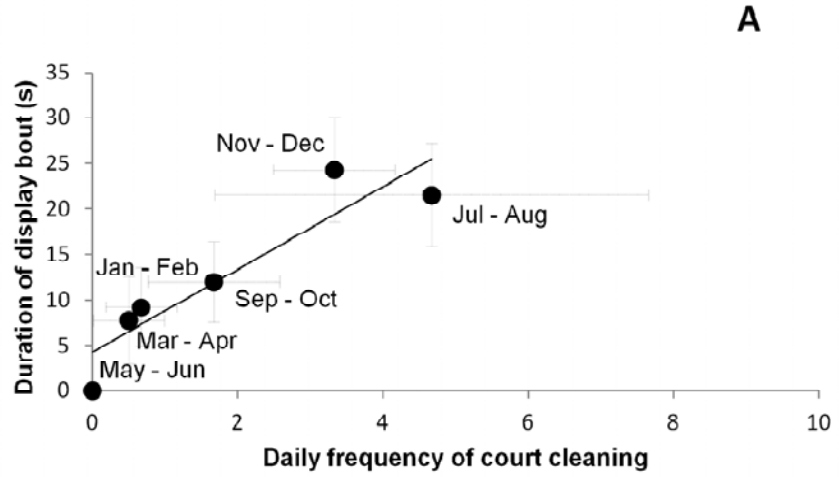
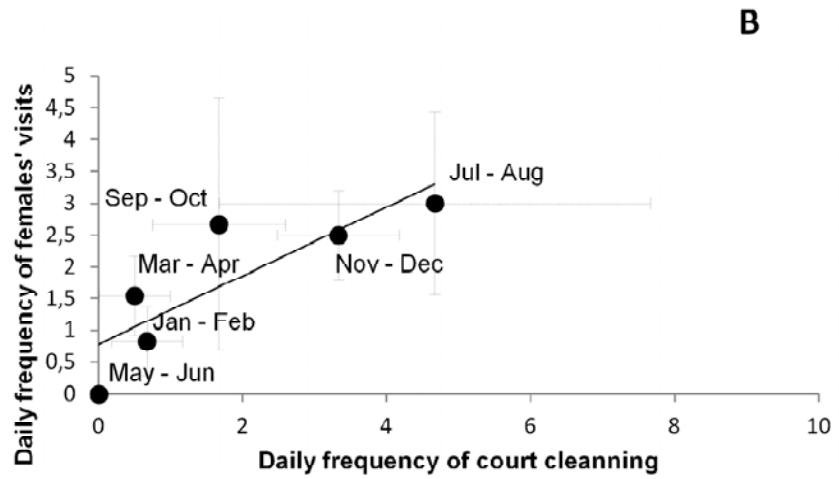


Fig. 2. Annual variation in the duration (black bars) and frequency of display bouts performed by nine lekking males of *Manacus manacus*. Vertical lines represent standard deviation.

The daily frequency of court cleaning behavior was 1.80 ± 3.50 (range: 0 - 19, N = 36) with peaks between 06:30 - 07:00 and 14:30 - 15:00. The frequency of court cleaning by males was positively correlated with duration of their display bouts (r_s = 0.90; P = 0.02). Even when we removed non-lekking period (May-June) from the analysis, we detected significant correlation between these two variables (r_s = 0.87; P = 0.05). Therefore, the probability of a male cleans its court increased when male displayed for longer periods, mainly during July-August and November-December (Fig. 3A). Similarly, the frequency of court cleaning and displaying time of males were positively correlated with the frequency of females' visits to courts (r_s = 0.94; P = 0.005 and r_s = 0.82; P = 0.04, respectively). These three parameters reached a peak in July-August and November-December periods (Fig. 3B and 3C). Additionally, the positive correlation between frequency of court cleaning and biomass of fallen debris (r_s = 0.92; P = 0.007) indicated that males increased the court cleaning behavior with the biomass of debris that fell on the courts along the year (Fig. 3D). Debris fallen during the non-lekking period (May-June) accumulated in the following early-lekking period (July-August) when the majority of males returned to lek activity, and females initiated visits to courts.


A
Duration of display bout (s)
35
30
25
20
15
10
5
0
Nov - Dec
Jul - Aug
Jan - Feb
Sep - Oct
Mar - Apr
May - Jun
0
2
4
6
8
10
Daily frequency of court cleaning


B
Daily frequency of females' visits
5
4,5
4
3,5
3
2,5
2
1,5
1
0,5
0
Jul - Aug
Sep - Oct
Mar - Apr
Nov - Dec
Jan - Feb
May - Jun
0
2
4
6
8
10
Daily frequency of court cleanning

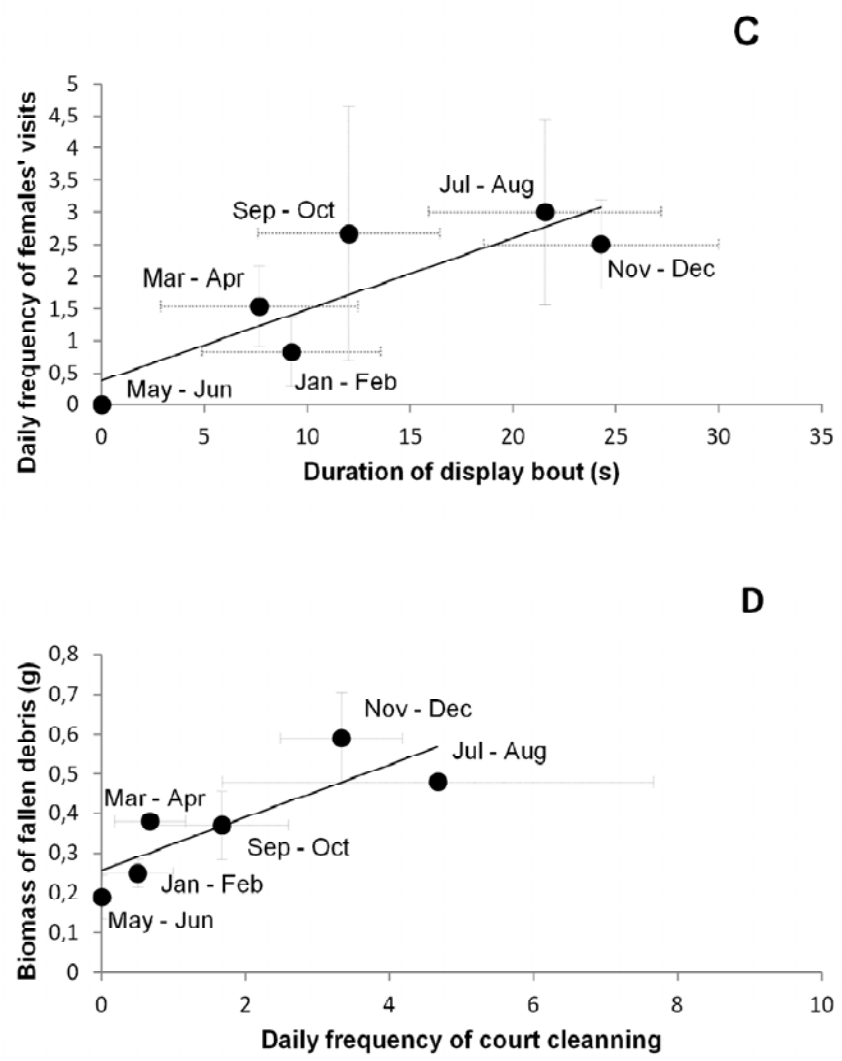


Fig. 3. Correlations between the mean frequency of court cleaning and mean duration of display bouts of males of *M. manacus* (A), mean frequency of court cleaning and mean frequency of females' visits to courts (B), mean duration of display bouts of males and mean frequency of females' visits to courts (C), and mean frequency of court cleaning and mean biomass of fallen debris (D). Vertical and horizontal lines represent standard errors. Nine resident males were observed each two months period.

The light intensity on the central point of the courts was higher (194.12 ± 298 lux) than on their bordering points (146.1 ± 214.3 lux) ($Z = 2.52$; $df = 8$; $P = 0.01$). In the control spots, no difference was detected between the central (151.5 ± 207.75 lux) and bordering

points (121.5 ± 171.13 lux) (z = 1.47; df = 8; P = 0.14) indicating that court cleaning behavior by males probably has a positive effect on incidence of light in their courts.

Seventeen out of 21 males reacted to the pit viper replica in the area with leaf litter adjacent to courts (average time until initial emission of call: 24 ± 73.9 s, range 0 – 295 s), whereas all the males promptly reacted to it in the central cleared area of courts rendering no difference in the reaction of males between these two experimental situations (G = 2.8; df = 1; P = 0.10). They usually performed small escape flights when overly approached the replica to investigate soon after the beginning of the alarm calls. Two males used other places inside their territories (probably auxiliary courts) to display when females visited them while the replica was still in their main courts. There was no difference in the frequency of alarm calls by males when the replica was placed in the leaf litter (6.7 ± 6.5 calls per min) or in the court cleared area (5.7 ± 6.5 calls per min) (t test= 0.8; df = 20; P = 0.45). Ten juveniles in six (14%) of the experimental trials, and ten neighboring adult males in nine (20%) of the experimental trials uttered alarm calls together with the experimental adult males. All the juveniles and three neighboring males also entered in the territory of experimental males to investigate.

Discussion

The frequency of court cleaning behavior by resident males of *M. manacus* was positively correlated with the displaying time, frequency of females' visits, and the biomass of fallen debris. These variables reached maximum values in the July-August and November-December periods. In the former period, males are returning from the molt period (Snow 1962) and their courts are filled with debris. Females also initiated the recognition of potential mates with more frequent visits to courts (Lill 1974a; Snow 1962). According to Lill (1974a), extensive male pre-copulatory displays are necessary to induce female sexual receptivity before females have selected their mates. In agreement with Snow (1962), our results indicated that males displayed hard with longer duration of display bouts as soon as the breeding season begins. Furthermore, during this early-lekking period, males employed greater efforts to clean their courts probably to attract a greater number of visiting females. In the subsequent months, males similarly displayed in longer bout sessions but they did not clean the courts as often as in the early-lekking period (July-August) probably due to the

small amount of litter to be cleaned resultant from their cleaning efforts in the previous months.

Studies frequently pointed to the importance of light levels in manakin leks as one of the environmental parameters that influence the mating success of lekking males (Snow 1962; Théry 1990; Théry and Vehrencamp 1995). The cleaning of surrounding leaves up to 1 m above the courts of *M. manacus* likely increased the amount of light in the central area of the court. This fact combined with the removal of soil debris, dead leaves, and rootlets from courts probably optimized the visual contrast of displaying males against background, as pointed by Uy and Endler (2004). Thus, more than adjusting the display movements to optimize the light conditions and plumage conspicuousness (Endler and Théry 1996; Heindl and Winkler 2003), the behavior of some lekking species modifying the physical structure of courts probably contributes to improve their display performance to conspecifics. We do not discard, however, that males have previously chosen brighter locations on the forest floor to establish their courts, a possibility deserving further investigation.

The reaction by the majority of males to the snake replica in the leaf litter and in the cleared court areas led us to refute the predator defense hypothesis suggested by Gilliard (1959). In the unique study with predation of a neotropical lekking bird, Trail (1987) found that the Cock-of-the-Rock (*R. rupicola*) exhibited alarm calls as defensive behavior against mammals and hawks but it had no defensive mechanism against snakes, and may rely for protection on the infrequency on which these terrestrial predators locate leks in Suriname. In contrast, males of *M. manacus* showed defensive behavior against the pit viper equally uttering alarm calls when the snake was placed in the cleared court or in adjacent areas with leaf litter. When they overly approached the snake, they promptly escaped with small flights. Neighboring adult and juvenile males also responded to alarm calls and entered in the territory of experimental males to investigate, suggesting that the combined attention of males in leks can make them less vulnerable to predation (Oring and Lank 1982; Trail 1987).

In conclusion, our results combined with other studies that highlighted the optimization of light incidence and the contrast of lekking males against the background of courts reinforce that sexual exhibition and not predation drives the court cleaning behavior in *M. manacus*. Given that male plumage brightness is correlated with mating success, and that court cleaning behavior may increases plumage conspicuousness in *Manacus* (Stein and Uy 2006; Uy and Endler 2004), we encourage further investigations to assess if the frequency of

court cleaning behavior affects mating success in an individual level, thus suggesting sexual selection acting upon males based on their court cleaning behavior.

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CAPÍTULO 4

Anting behavior by the White-bearded Manakin (*Manacus manacus*, Pipridae): an example of functional interaction in a frugivorous lekking bird

Cestari, C. 2010. Anting behavior by the White-bearded Manakin (*Manacus manacus*, Pipridae): an example of functional interaction in a frugivorous lekking bird. Biota Neotropica 10(4): 339-342.

Abstract

Behavioral studies of birds have reported several functions for active anting. Maintenance of plumage and prevention from ectoparasites are some examples. In this context, anting by males may be of particular importance in a classical lek mating system, where male-male competition is common and individuals with higher fitness may be more successful at attracting of females. In the present note, I describe the anting behavior of White-bearded Manakin (*Manacus manacus*) and I relate it to lek breeding and feeding (frugivory) habits of the species. Males used up to seven *Solenopsis* sp. ants. They rubbed each small ant from 4 to 31 times on undertail feathers until the ants were degraded; ants were not eaten. Males then searched for a new ant in the court. Seeds discarded by males on their individual display courts attract herbivorous ants that are used for anting as a way to maintain feathers and fitness. I hypothesize that anting in White-bearded Manakin may increase the probability of males to attract females to their display courts.

Keywords: ants, lek, male-male competition, maintenance of plumage, *restinga* forest, seeds.

Introduction

Active anting is defined as a bird holding an ant and rubbing it in parts of the body, discharging toxic and distasteful substances before ingesting or discarding it (Groskin 1950). Formic acid is one of the substances found in some groups of ants. It acts smoothing skin irritation and as an insecticide, bactericidal, and fungicide on bird feathers (Clayton 1999; Groskin 1950; Hart 1997; Simmons 1957; Simmons 1959). Thus, plumage maintenance and prevention of ectoparasites are some of the functions attributed to anting behavior (Groskin 1950; Judson and Bennett 1992; Simmons 1959; Simmons 1966). For birds that also eat the ant, removal of toxic or distasteful substances during rubbing and before the ingestion is also considered a protective behavior (Judson and Bennett 1992; Potter 1970). Several passerine birds are recorded anting in the Neotropical region (Sazima 2009; Sick 1997; Willis 1972).

Manakins (Pipridae) have the lek behavior and frugivory as predominant studied features (Snow 2004). The term lek refers to a variety of courtship behaviors that concentrate more than one male in a display area with the main purpose to attract and stimulate the

females to mate (Höglund and Alatalo 1995; Sick 1967). In the manakins, sexual competition by single or grouped males are well evident, as they spend great part of the day in fixed courtship places to attract females. In these occasions, brief intervals are dedicated to maintenance of plumage and feeding activities on fruits, or occasionally on insects (Sick 1967; Snow 2004). As a consequence, males frequently maintain a showy appearance in display sessions and regurgitate or defecate a lot of seeds in and around their fixed display courts (Snow 2004; Cestari and Pizo, unpubl. data, see chapter 7). In the present note, I describe the anting behavior of the White-bearded Manakin (*Manacus manacus*, Linnaeus 1766) and link it with the cycle of biotic and functional interactions of this species, including frugivory, self-care and lek behavior following this presumable sequence of events: (1) the accumulation of seeds defecated or regurgitated by competing males in and around display courts may (2) attracts herbivore ants that (3) *M. manacus* males use anting as a way to (4) maintain their feathers and individual fitness during intra-specific competition on lek areas.

Material and methods

Manacus manacus is a small forest bird with range of weight from 15 to 18 g. Males are black and white whereas females are dull green (Snow 2004). Observations of anting behavior of *M. manacus* were conducted in the lowland *restinga* forests at Itanhaém municipality (24°10'11.9"S; 46°55´32.81"W), and Juréia Itatins Ecological Station (Iguape municipality, 24°28´07.4"S; 47°07´13.17"W), São Paulo state in southeastern Brazil. These observations were part of a year-long study of this species' behavior in a lek system. Both areas are still covered with great part of *restinga* vegetation, an Atlantic forest ecosystem threatened by urban expansion (Sampaio 2005). Typical plants of the region are Myrtaceae, Leguminosae, Rubiaceae, Melastomataceae, Lauraceae and Annonaceae (Mamede et al. 2004). Climate is subtropical and humid. Mean annual rainfall is 2278 mm with the rainy season occurring from October to April, and the dry season from May to September. Mean annual temperature is 21.4ºC, with maximum mean temperature of 25.8°C and minimum mean temperature of 19.0ºC (Tarifa 2004).

The studied areas of nearly 400 m^2 concentrate 8 to 10 display courts where resident males peak their exhibitions between July to January (Cestari and Pizo, in press, see chapter 1). The display court is characterized as an oval arena delimited by two or more saplings on the ground and varies from 0.15 to 0.9 m diameter. It is actively cleared from litter by a

lekking resident male (Darnton 1958; Lill 1974a; Olson and McDowell 1983; Shorey 2002; Snow 1962). During the breeding season, males may spend 90% of their time on display grounds (Snow 1962). They use this amount of time in displays maneuvers, territory defense against co-specific male's invaders, foraging on fruits or occasionally insects, preening and anting.

"Ad libitum" observations were conducted in the present study (Martin and Baterson 1986). A distance of nearly five meters from a male's courts was kept and appropriated camouflaged clothes were adopted to minimize interference on the bird's behavior. Digital photographs were used to record the anting behavior and as parameter for descriptive analyses.

Results

On 17 and 19 December 2009, and 13 January 2010, I recorded anting behavior by lekking *Manacus manacus* males. Alternated observations of display courts of six different lekking males were conducted three days per month between 6:00 to 17:00hrs. From these, three males displayed anting behavior in periods of 16min, 21min, and 44min, respectively. As the anting events were similar for the three males, I chose the longest one (13 January 2010) to describe here.

The anting activity lasted 44 min. It started at 7:45hrs and ended at 8:29hrs including the period of searching for ants. My first impression was that the male was preening, but detailed observation revealed that the male was actively rubbing ants on its body and searching for more ants within its court. This male used a total of seven *Solenopsis* sp. ants during its anting activity. For a few seconds, the male rubbed each ant from 4 to 31 times on its undertail feathers until the ants were degraded. After this, the male searched for a new ant within the display court (Figure 1 a-c). Both the ground and the saplings of the display court were used for anting.

Fig.1. Anting behavior of a White-bearded Manakin (*Manacus manacus*) male on the ground. a: searching for ants; b: capturing an ant; c: rubbing the ant on its undertail coverts.

Discussion

Anting behavior was probably used for maintenance of plumage by males of *M. manacus* as it is suggested for several passerines species (Simmons 1959). Intra-specific competition between males becomes evident in a lek system and anting probably contributed to a male's fitness influencing the attraction of females to individual courts. Other not exclusive biological features may influence the mating system in *M. manacus*, such as larger male size, higher frequency of aggressive displays and territory defense, larger territory size, and low distance of the court from the lek centre (Lill 1974a; Olson and McDowell 1983; Shorey 2002; Snow 1962).

Courtship displays in lekking birds may be energetically costly for males (Höglund and Alatalo 1995; Vehrencamp et al. 1989). Regarding all factors that may drive the attractiveness of males, individuals that have better external and physical conditions will compete more efficiently for females (Kirkpatrick and Ryan 1991). Ectoparasites signalize the current health condition of birds, and affect negatively the fitness of males by increasing the cost of anti-parasite effects in their immune system, causing loss of blood, infections, and diseases (Delope et al. 1993; Doucet and Montgomerie 2003; Price 1980). Additionally, females are able to enhance the viability of their offspring by choosing males with better

physical conditions as an indicator of relative resistance to parasites (Hamilton and Zuk 1982).

Studies on parasite loads in lekking birds seem to indicate that parasites do have adverse effects on mating success (Höglund and Alatalo 1995). Thus, prevention of ectoparasites and other harmful organisms such as fungi and bacteria on feathers are advantageous for males by influencing their showy appearance and improving lek performance. Although the anting behavior has not been previously reported to manakins, it may be advantageous for individual males even if it may be a rare situation as appears to be in the present study.

Regurgitated and defecated seeds by manakin males in and around the display courts may retain part of fruit-nutrients that attract herbivorous insects, thus becoming important for anting behavior in *M. manacus*. Seven ornitochoric seeds and 18 *Solenopsis* sp. were found in the male court during the observation. According to Passos and Oliveira (2003), small Myrmicinae ants such as *Solenopsis* sp. are common in the lowland forest of *restinga*, and many nestmates are recruited to diaspores, consuming the pulp and aril locally.

Behavioral studies of *M. manacus* were available for at least since 50 years (see Darnton 1958; Lill 1974a; Lill 1974b; Olson and McDowell 1983; Shorey 2002; Snow 1962) and revealed a complexity of biological features that may influence the species' mating system. The cycle of functional interactions in which anting behavior of *M. manacus* occurs is another fascinating feature of this species' natural history. In spite the rarity of anting, experimental studies might demonstrate that males that use anting do in fact enhance their long-term fitness relative to males that do not use anting.

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I´m indebted to Ílson L. Prado, Rubens R. do Prado, Sr. Plínio and all the staff of Juréia Ecological Station that facilitate my logistics and share knowledge about natural history of the region. I thank two anonymous reviewers for considerably improving this manuscript, Marco A. Pizo for guidance in my thesis, and especially Cristina S. Gonçalves for help in field observations and love support. I also acknowledge the finantial support from FAPESP, and a research grant from the Brazilian Research Council (CNPq).

CAPÍTULO 5

Diet and frugivory by the White-bearded Manakin (*Manacus manacus*) in the *restinga* Atlantic forest ecosystem

Submetido em formato de *short* communication para Biota Neotropica

Abstract

Manakins are one of the most abundant fruit-eaters and seed dispersers in the understory of Neotropical forests. We describe the fruit diet of *Manacus manacus* based on a two-year study of its foraging behavior on fruiting plants, collecting seeds from feces and regurgitations of trapped individuals, and from lekking males' courts in *restinga*, a threatened Atlantic forest ecosystem. *Manacus manacus* consumed 58 species of fruits from 30 different plant families. Fruits were taken at 3.5 ± 1.9 m height and 1.5 ± 1.6 m below the forest canopy using mainly sally-strike and glean maneuvers. Most of the fruits were berries ranging from 3.1 to 17 mm in diameter and containing from 1 to 86 seeds. Fruits up to 12 mm in diameter were swallowed whole. Ripe and unripe fruits were equally consumed. Our results corroborate with the great variety of small fruits consumed by manakin species in the understory of Neotropical forests and indicate that *M. manacus* should be an important seed disperser in *restinga*.

Introduction

In tropical forests, most woody plants rely on frugivores to disperse their seeds (Gentry 1982). The number of fruit species consumed, the patterns of fruit removal, and the seed treatment given by a frugivore may influence seed dispersal effectiveness, and, ultimately, plant recruitment (Schupp 1993; Schupp et al. 2010). Manakins (Pipridae) are small frugivorous passerines abundant in the understory of primary and secondary Neotropical forests (Blake and Loiselle 2002; Loiselle et al. 2007). Manakins have broad diets, eating whole a great variety of small fruits, thus potentially exerting an important role as seed dispersers (Blake and Loiselle 2002; Snow 2004; Worthington 1982).

In *restinga* forests from southeastern Brazil, an Atlantic forest ecosystem heavily impacted by urbanization (Sampaio 2005), the White-bearded Manakin *Manacus manacus* (Linnaeus 1766) is one of the most common passerines. In the present study, we investigated the fruit diet of *M. manacus* in well-preserved patches of *restinga* forests in the southern portion of São Paulo state. More specifically, we assessed: (1) how many plant species have fruits eaten by *M. manacus*, (2) the ripeness and biometrics of these fruits, and (3) the fruit removal maneuvers and fruit handling techniques used by *M. manacus*.

Methods

Study area

This study was conducted in the lowland forests of Itanhaém (24°10'11.9"S; 46°55´32.81"W), Peruíbe (24°15'10.81"S; 46°55´16.94"W), and Juréia Itatins Ecological Station (Iguape, 24°28´07.4"S; 47°07´13.17"W), in the state of São Paulo, southeastern Brazil. Climate is subtropical and humid. Mean annual rainfall is 2,278 mm with the rainy season occurring from October to April, and the dry season from May to September. Mean annual temperature is 21.4ºC, with maximum temperatures averaging 25.8ºC and minimum temperatures averaging 19.0ºC (Tarifa 2004). Study areas are still covered in great part with *restinga*, a structurally simple vegetation composed by halophytic herbs and shrubs close to the sea, and more complex vegetation in lowland and lower mountain forests as one moved further into the continent (Sampaio 2005). The most speciose plant families in the region are Myrtaceae, Leguminosae, Rubiaceae, Melastomataceae, Lauraceae, and Annonaceae (Mamede et al. 2004). The bird community of the region includes 314 species. Tanagers (Thraupidae) and flycatchers (Tyrannidae) are the most speciose bird families (Develey 2004).

Bird species

Manacus manacus is a small frugivorous (15 – 18 g weight; 8 cm wide gape size) and lekking passerine from lowland forests in the Neotropics. It has a widespread geographic distribution from Colombia to NE Argentina, inhabiting continuous and fragmented forests of the Amazon basin and the Atlantic forest of South America (Sick 1997; Snow 2004). In *restinga*, *M. manacus* is one of the most common manakin species (other common species is the Swallow-tailed Manakin *Chiroxiphia caudata*). It is sympatric with nearly 76 frugivore bird species (C. C., pers. obs.). According to Snow (1962), secondary forests with high abundance of fruits are the preferred habitat of *M. manacus*. Resident males of this species concentrate their territories in lek areas composed by 2 to 70 oval courts of 0.15–0.9 m in diameter set on the ground of the forest wherein they display individually to attract potential mates (Snow 1962).

Data collection

To describe the diet of *M. manacus,* we conducted observations of its foraging behavior on plant species, collected seeds from feces and regurgitations of mist-netted individuals from April 2009 to March 2011, and collected seeds in 21 courts used by resident males in five lek areas from March 2010 to February 2011 in Itanhaém, Peruíbe, and Iguape municipalities. The foraging behavior of *M. manacus* was characterized considering the height of the fruits eaten, the foraging maneuvers according to (Remsen Jr. and Robinson 1990), and the fruit handling behavior (fruits swallowed whole or peacemeal). Considering that manakins may take several fruits during a feeding bout, we recorded only the first feeding event of individuals to quantify the species' foraging behavior. Characteristics of the fruit species such as fruit type, ripeness, length and width (measured with a digital caliper), and number of seeds were accessed in the field. Mist-netted individuals were kept in cages with foam-lined walls for 30 min before released, and all regurgitated or defecated seeds collected within this period were considered a sample. Seeds collected on courts and its immediate vicinity (0.70 m^2 of total sampled area per court) were accumulated monthly to a final number of species per court. All the seeds were identified to the lowest taxonomic level possible by comparison with a reference collection assembled during the study, and also consulting the literature and specialists. We followed the botanical nomenclature from (Garden 2011) and (Lorenzi 1998; Lorenzi 2009a; Lorenzi 2009b).

Data Analyses

We evaluated the degree of completeness of the fruit sampling in the diet of *M. manacus* by plotting accumulation curves of plant species consumed according to each of the methods employed to sample diet.

The frequency of feeding of *M. manacus* to ripe and unripe fruits were compared using 2 x 2 contingency tables applied to Chi-square tests (with Yates correction). The null hypothesis indicates equal proportion of ripe and unripe fruits ingested by *M. manacus*. We employed Bioestat 5.0 (Ayres et al. 2004) for all analyses. Significance was accepted at $P \leq 0.05$.

Results

Manakin foraging

Manacus manacus consumed fruits of 49 plant species which were taken at 3.5 ± 1.9 m height (range: 0.2 – 9 m) and 1.5 ± 1.6 m below the forest canopy (range: 0 – 6.5 m; N = 194). Birds frequently used sally-strike (59% of foraging maneuvers, N = 194) and glean (35%) maneuvers to take fruits, followed by reach (4%) and sally-hover (2%). Fruits were preferentially swallowed whole (89%). They do not have a preference to ripe (54% of feeding bouts) or unripe fruits (46%) (χ^2_1 = 1.32; P = 0.28). Seeds from 21 plant species were recorded from birds held in cages, while 45 species were collected below courts of male manakins. Overall, *M. manacus* consumed fruits (mainly of the berry type) of 58 plants species and 30 plant families that contained from 0 to 86 seeds, and varied from 3.1 to 12 mm in diameter (table 1; see also Appendix 5). Species accumulation curves revealed that new species might be added to our sampling (Fig. 1). Myrtaceae (10 spp.), Melastomataceae (5 spp.), and Rubiaceae (4 spp.) were the most consumed plant families.

Table 1. Plant species with fruits consumed by *M. manacus* in *restinga* forests in southeastern Brazil. Recording methods: foraging observations in the field (FO), seeds collected in the court (C), seeds defecated (D) or regurgitated (R) by mist-netted individuals. Fruit types: drupe (Dr), aril (Ar), berry (Be), catkin (Ca), endocarp (En), syconium (Sy). Fruit maturation: ripe (Ri), unripe (Un). Ingestion mode: whole (W), pieces (P). Fiften fruits of each plant species were measured. "--" indicates not collected and "SD" indicates standard deviation. We followed the botanical nomenclature from Garden (2011) and Lorenzi (1998, 2009a, b).

Family	Species	Registration method	Fruit type	Maturation	Length (±SD)	Width (± SD)	Number of seeds	Ingestion mode
Anacardiaceae	*Schinnus* sp.	C	--	--	--	--	--	--
Annonaceae	*Guatteria nigrescens* Mart.	FO, C	Dr	Ri/Un	10.70 ± 0.36	6.36 ± 0.36	1.00	W
	Xylopia sp.	C	Ar	--	8.87 ± 0.65	6.35 ± 0.54	--	W
Aquifoliaceae	*Ilex theezans* Mart. Ex Reissek	FO, C, D	Be	Ri	5.35 ± 0.47	5.36 ± 0.53	2.26	W
	I. brevicups Reissek	FO	Be	Ri	4.08 ± 0.25	5.16 ± 0.25	4.06	W
	I. paraguaiensis St. Hil.	FO, C	Be	Ri	3.99 ± 0.29	4.99 ± 0.32	3.93	W
Araliaceae	*Schefflera angustissima* (Marchal) Frodin	FO, C, R	Be	Ri/Un	7.27 ± 0.69	9.28 ± 1.27	2.00	W
	S. morototoni (Aubl.) Maguirre, Steyerm & Frodin.	FO, C	Be	Un	--	--	--	W
Araceae	*Anthurium sellowianum* Kunth	FO	Dr	Un	--	--	--	W
Arecaceae	*Euterpe edulis* Mart.	C	Dr	--	--	--	1.00	--
	Geonoma schottiana Mart.	C	Dr	--	--	--	1.00	--

Family	Species	Registration method	Fruit type	Maturation	Length (±SD)	Width (± SD)	Number of seeds	Ingestion mode
Cecropiaceae	*Cecropia pachystachia* Trécul.	FO	Ca	Ri	--	--	--	P
Celastraceae	*Maytenus robusta* Reissek	FO, C, R	Ar	Ri	8.74 ± 0.78	5.31 ± 0.47	1.33	W
Clusiaceae	*Clusia criuva* Cambess.	C	Ar	Ri	--	--	--	W
Chlorantaceae	*Hedyosmium brasiliensis* Mart. Ex Miq.	FO, C	Be	Ri	6.28 ± 0.73	6.31 ± 0.70	3.27	W
Dilleniaceae	*Davilla rugosa* Poir.	FO, C, R	Ar	Ri	5.33 ± 0.47	5.57 ± 0.49	1.00	W
	Doliocarpus sp.	FO, C	Be	Un	15.35 ± 1.23	16.99 ± 1.52	1.53	P
Ericaceae	*Gaylussacia brasiliensis* (Spreng.) Meisn.	FO, R	Be	Ri	6.43 ± 0.67	7.58 ± 0.54	7.93	W
Erythroxilaceae	*Erythroxylum decidum* A. St. Hil.	FO, C, R	Dr	Ri	7.38 ± 0.99	4.46 ± 0.70	1.00	W
Euphorbiaceae	*Alchornea triplinervia* (Spreng.) Müll. Arg.	FO	--	--	--	--	--	W
	Pera glabrata (Schott) Poepp. Ex Baill.	FO, C	Ar	Ri	6.03 ± 0.3	4.25 ± 0.14	3.00	W
Lacistemaceae	*Lacistema pubescens* Mart.	FO	En	Ri	--	--	0.00	P
Lauraceae	*Ocotea pulchella* (Nees) Mez	FO, C, R	Dr	Ri/Un	9.49 ± 0.47	5.37 ± 0.28	1.00	W

Family	Species	Registration method	Fruit type	Maturation	Length (±SD)	Width (± SD)	Number of seeds	Ingestion mode
	Endlicheria paniculata (Spreng.) J. F. Macbr.	FO	Dr	Ri	--	--	1.00	W
Lorantaceae	*Struthanthus* sp.	FO	Be	Un	2.32 ± 0.33	4.32 ± 0.53	0.86	W
Malpighiaceae	*Byrsonima ligustrifolia* A. Juss.	FO	Dr	Un	5.65 ± 0.62	6.08 ± 0.72	1.00	W
Melastomataceae	*Miconia hymenonervia* (Raddi) Cogn.	FO, C	Be	Ri/Um	3.55 ± 0.21	4.0 ± 0.35	1.00	W
	M. ridigiuscula Cogn.	FO, C, D	Be	Ri/Un	3.20 ± 0.37	3.54 ± 0.29	2.46	W
	M. cubatanensis Hoehne	FO, C	Be	Ri/Un	3.66 ± 0.41	5.66 ± 0.87	3.53	W
	Miconia sp.	FO	Be	Un	7.48 ± 0.46	6.15 ± 0.47	38.00	W
	Ossaea sp.	FO, C, R	Be	Ri	3.49 ± 0.41	4.71 ± 0.92	1.67	W
Meliaceae	*Guarea macrophyla* Vahl	FO, C	Ar	Ri	12.59 ± 2.55	7.26 ± 0.89	--	W
Moraceae	*Fícus enormis* (Mart. ex. Miq.) Miq.	FO, D	Sy	Ri	12.53 ± 0.97	11.99 ± 0.95	86.20	W
Myrsinaceae	*Rapanea parviflora* (A. DC.) Mez	FO, C, R	Dr	Ri/Un	4.80 ± 0.25	4.48 ± 0.24	1.00	W
	R. ferruginea (Ruiz & Pav.)	FO, C, R	Dr	Ri/Un	3.25 ± 0.17	3.12 ± 0.19	1.00	W
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O. Berg	FO, C, R	Be	Ri	5.08 ± 0.68	5.49 ± 0.52	1.72	W

Family	Species	Registration method	Fruit type	Maturation	Length (±SD)	Width (± SD)	Number of seeds	Ingestion mode
	Calyptranthes concinna DC.	FO, C, R	Be	Ri	5.72 ± 0.49	6.49 ± 0.83	2.27	W
	Calyptranthes sp.	C	--	--	--	--	--	--
	Eugenia pluriflora DC.	FO, C	Be	Ri	7.23 ± 0.69	6.9 ± 0.75	3.56	W
	E. sulcata Spring	FO, C, R	Be	Ri	7.08 ± 1.08	8.92 ± 1.55	1.00	W
	E. umbelliflora O. Berg.	FO, C	Be	Ri/Un	13.15 ± 2.27	8.47 ± 1.21	1.00	W
	Myrcia bicarinata (O. Berg) D. Legrand	FO, C	Be	Un	5.66 ± 0.60	6.84 ± 0.85	1.81	W
	Myrcia sp.	C	Be	--	--	--	--	--
	Pimenta cf *pseudocaryophyllus* (Gomes) Landrum	FO, C, R	Be	Um	6.62 ± 0.68	5.28 ± 0.72	1.13	W
	Siphoneugena guilfoyleiana C. Proença	FO, C	Be	Ri	3.93 ± 0.47	4.31 ± 0.45	3.36	W
Nyctaginaceae	*Guapira opposite* (Vell.) Reitz	FO, C, R	Dr	Ri	7.36 ± 0.94	5.11 ± 0.56	1.00	W
Pentaphyllaceae	*Ternstroemia brasiliensis* Cambess.	FO, C, R	Ar	Ri	7.97 ± 0.28	3.84 ± 0.30	5.10	W
Rubiaceae	*Chiococa alba* (L.) Hitchc.	FO, C, R	Be	Ri	6.80 ± 0.60	6.28 ± 0.67	1.80	W
	Psychotria carthagenensis Jacq.	FO, C, R	Dr	Ri	5.61 ± 0.38	5.92 ± 0.6	1.00	W

Family	Species	Registration method	Fruit type	Maturation	Length (±SD)	Width (± SD)	Number of seeds	Ingestion mode
	Psychotria sp.	FO, C	Be	Ri	6.61 ± 0.49	6.07 ± 0.65	126	W
	Psychotria sp. 2	FO, C	Be	Ri	7.06 ± 1.19	7.04 ± 0.64	4.00	W
Santalacea (Viscaceae)	*Rudgea* sp.	FO, C, R	Be	Ri	8.86 ± 0.96	7.91 ± 0.59	2.00	W
Sapindaceae	*Phoradendron* sp	FO, C	Be	Ri	1.88 ± 0.11	2.78 ± 0.14	1.00	W
	Cupania oblongifolia Mart.	C, R	Ar	Ri	9.2 ± 0.79	6.69 ± 0.24	1.00	W
Smilaceae	*Smilax rufescens* Griseb.	FO, C	Be	Ri	7.51 ± 0.63	7.95 ± 1.26	1.93	W
Symplocaceae	*Paullinia* sp.	FO, C, R	Ar	Ri	6.02 ± 0.72	6.33 ± 0.69	1.00	W
	Symplocos variabilis Mart.	FO	Be	Ri	5.20 ± 0.35	3.87 ± 0.28	--	W
Unidentified	sp. 1	--	--	--	6.04 ± 0.40	5.50 ± 0.32	--	W

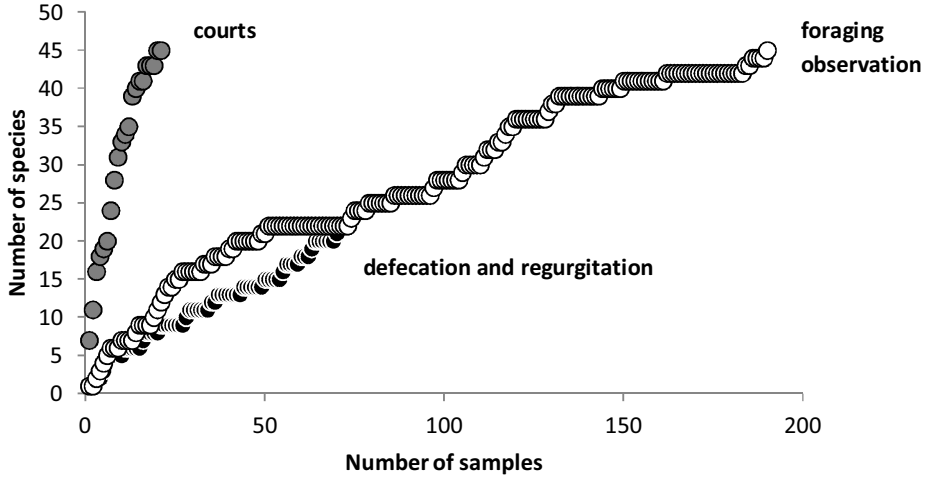

Figure 1. Accumulation curves of the number of plant species eaten by *Manacus manacus* in *restinga* forests in southeastern Brazil. Samples vary according to the method used (i.e., number of plants observed during bird foraging observations, number of defecations or regurgitations collected from caged birds, and number of courts inspected for seeds).

Discussion

Although forests may differ markedly in plant species diversity and researchers may use different sampling methods to collect data on bird diets, our results focused on the fruit diet of *M. manacus* in *restinga* forests corroborated data from other studies that showed a great variety of fruits consumed by manakin species in the understory of Neotropical forests. We recorded 58 species of plants consumed by *M. manacus* and more plant species will likely be added if we continued sampling. Snow (1962) recorded 105 species of fruits consumed by *M. manacus* in Trinidad Island. Worthington (1982) recorded at least 62 species of plants whose fruits were fed by Golden-collared Manakin *Manacus vitellinus* and Red-capped Manakin *Pipra mentalis* in Barro Colorado Island, while Loiselle et al. (2007) recorded 70 and 39 species of seeds in feces of *P. mentalis* and White-ruffed Manakin *Corapipo altera* in Costa Rica, plus 49 species of seeds in feces of Blue-crowned Manakin *Lepidothrix coronata*, 27 species for Golden-headed Manakin *Pipra erythrocephala*, 33 species for Wire-tailed Manakin *P. filicauda*, and 44 species for White-crowned Manakin *P. pipra* in Ecuador.

Manacus manacus and other manakins have a wide gape in relation to their body size, which allows them to swallow whole fruits that cannot be swallowed by larger birds such as

some tanagers (Snow 1962). In our study, *M. manacus* had no difficult to swallow fruits up to 12 mm width; fruits up to 16 mm width (e.g., *Coussarea paniculata* M. Vahl Standl.) were swallowed by this species in Trinidad (Snow 1962). *Manacus manacus* was also recorded consuming all types of available fruits, including unripe ones. According to Levey (1987b), the less rigorous fruit selection by manakins may be a consequence of their fruit-handling technique and foraging maneuvers that enable them to swallow fruits whole in such a way that does not permit the detection of fruit taste once birds rarely come into contact with any part of a fruit except skin surface. Also, manakins apparently do not suffer negative effects of toxic secondary compounds usually present in unripe fruits. Foster (1977) recorded a high frequency of unripe fruits eaten by the Long-tailed Manakin (*Chiroxiphia linearis*) during a period of fruit scarcity in Costa Rica but detected no difference in the weight of individuals between periods of normal availability and scarcity of fruits.

From the bird's perspective, the gulper condition of manakins may be disadvantageous because birds accumulate seeds in their guts (Levey 1987a). However, because their high metabolic rate (see Barske et al. 2011), studies indicated that some manakins (including *Manacus* spp.) evolved behavioral and physiological adaptations such as rapid passage of fruits (and seeds) in their guts, high assimilation of nonstructural carbohydrates, selective regurgitation, and rapid elimination of bulky seeds that allow them to ingest a high rate of fruits compared with larger birds see Worthington (1989). In another study, we estimated an average of four defecations (or regurgitations) containing 1.3 seeds per defecation (or regurgitation) at each 5 min (Cestari and Pizo, unpubl. data, see chapter 7). This defecation rate is relatively high even compared with other manakin species (Worthington 1989).

In conclusion, *M. manacus* ate a great number of small fruit species. Given the high abundance of this species, its rapid processing of fruits, and the fact that most of the fruits were swallowed whole, *M. manacus* should be an important seed disperser in *restinga*, an ecosystem constantly threatened by urban expansion.

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CAPÍTULO 6

Context-dependence in the quantity of seeds removed by a lekking and non-lekking frugivorous birds

Submetido em formato de *short communication* para Journal of Tropical Ecology

Abstract

Manakins are proeminent fruit-eaters and seed dispersers in the Neotropical region. Most manakin species establish lek areas where males devote long periods displaying to attract mates with brief absences to feed on fruits usually located near lek areas. We compare the frequency of visits to plants, the fruit handling behavior, and number of fruits ingested by the lek-forming *Manacus manacus* and species of non-lekking birds in two species of fruiting trees (*Miconia rigidiuscula* and *Ocotea pulchella*) in lek and non-lek areas during the lek and non-lek periods of *M. manacus* in a threatened Atlantic forest ecosystem. During the non-lek season, *M. manacus* and non-lekking birds did not differ in the frequency of visits to *Miconia* trees near lek and non-lek areas. However, *M. manacus* swallowed a higher number of fruits near leks than non-lekking birds while the opposite was true in non-lek areas. During the lek season, *M. manacus* had higher frequency of visits to *Ocotea* trees and swallowed a higher number of fruits than non-lekking birds in lek areas while no bird visits were recorded in non-lek areas. This work provides an example of context dependence in the quantity component of seed dispersal effectiveness in which the lek breeding system of a frugivorous species influence the identity of seed removers and the quantity of seeds removed in and around lek areas.

Introduction

Life story traits, reproductive status, and social organization of frugivorous animals may influence their movement behavior and foraging activities, thus affecting the seed dispersal service they provided (Schupp et al. 2010; Westcott et al. 2005). Lekking frugivores, for instance, have their activities concentrated in or around lek areas, which may constraint the spatial realm of their fruit-consuming and seed dispersal activities (Karubian and Durães 2009; Ryder et al. 2006).

Manakins are small lekking passerines that inhabit primary and secondary forests of the Neotropics (Blake and Loiselle 2002; Snow 2004; Worthington 1982). They eat a variety of small fruits (Levey 1987b; Snow 2004; Worthington 1982), and may process a great volume of fruits (and seeds) in a short period of time which provide usable energy for lekking activities (Höglund and Alatalo 1995; Snow 2004). During the lek season, which may last more than six months a year, males congregate in lek areas and perform displays for visiting

females (Höglund and Alatalo 1995; Snow 2004). In the rest of the year, manakins increase their home range due to the lack of commitment to reproductive activities. Thereby, the movement patterns of lekking manakins vary according to their lek breeding phenology with consequences for seed dispersal (Krijger et al. 1997; Théry 1992; Cestari and Pizo, unpubl. data, see chapter 7).

In present study we test if the foraging activity on fruiting plants by the *M. manacus*, a small lekking passerine widely distributed in the lowlands of Neotropical forests (Snow 2004), differs from non-lekking frugivorous birds according to the proximity to lek areas. We argue that manakins may be more active foragers near lek areas than non-lekking birds, thus outstanding in the quantitative aspect of the seed disperser effectiveness framework (Schupp et al. 2010), particularly in relation to the frequency of visits to fruiting plants and number of fruits consumed. Far from lek areas, we expect that manakins have similar or lesser frequency of visits to fruiting plants than non-lekking birds due to the intense engagement of the former on foraging activities mainly near lek areas.

Methods

Study area

The study was conducted in the lowland forests of Itanhaém (24°10'11.9"S; 46°55´32.81"W), Peruíbe (24°15'10.81"S; 46°55´16.94"W), and Juréia Itatins Ecological Station (Iguape, 24°28´07.4"S; 47°07´13.17"W), in the state of São Paulo, southeastern Brazil. Climate is subtropical and humid. Mean annual rainfall is 2,278 mm with the rainy season occurring from October to April, and the dry season from May to September. Mean annual temperature is 21.4ºC, with maximum temperatures averaging 25.8ºC and minimum temperatures averaging 19.0ºC (Tarifa 2004). Study areas are still covered in great part with *restinga*, an Atlantic forest ecosystem threatened by urban expansion. The *restinga* is structurally simple vegetation of halophytic herbs and shrubs close to the sea, and more complex vegetation in lowland and lower mountain forests as one moved into the continent (Sampaio 2005). In *restinga*, zoochorous plants usually have sharply peaked fruiting seasons, high annual fecundity, small seeds, and low rate of fruit removal (Argel-de-Oliveira 1999; Scherer et al. 2007). The most speciose plant families are Myrtaceae, Leguminosae, Rubiaceae, Melastomataceae, Lauraceae, and Annonaceae (Mamede et al. 2004). The bird

community of the region includes 314 species with 76 frugivorous species (24%) (Develey 2004; CC, pers. obs.).

Bird species

Manacus manacus is a small (15 – 18 g) lekking passerine from lowland Neotropical forests. It has a widespread geographic distribution from Colombia to NE Argentina, inhabiting continuous and fragmented forests of the Amazon basin and the Atlantic forest of South America (Sick 1997; Snow 2004). In *restinga*, *M. manacus* is one of the most common understory frugivores. Secondary forests with high abundance of fruits and small upright saplings are the preferred habitat of *M. manacus* (Snow 1962). Resident males concentrate their territories on a lek area with approximately 18 - 23 m long and 4 - 9 m wide (Darnton 1958; Snow 1962). Lek areas have from 2 to 70 main displaying courts, and neighboring males are often in visual and aural contact with each other. During the lek season from July to April, males may spend up to 82% of the day in lek areas (Cestari and Pizo, in press; see chapter 1), making brief excursions to forage at nearby fruit sources. Resident males are long-lived and are known to display at courts for up to 14 years (Lill 1974b; Snow 1962). Females visit several resident males during the breeding season before selecting a mate for copulation. Juveniles also practice display maneuvers in the courts mainly in periods of the day with reduced lek activity by resident males (Snow 1962).

Focal plant species

Based on the availability of fruiting trees and their distances from lek areas, we chose two plant species to conduct focal observations on frugivory by *M. manacus* and non-lekking birds. *Miconia rigidiuscula* Cogn. (Melastomataceae) is a tree with 2 – 15 m height commonly found in the border of non-flooded patches of *restinga* forests (Martins et al. 1996). It bears small berries (3.20 ± 0.37 mm length, 3.54 ± 0.29 mm width) with 1 - 4 seeds per fruit (N = 15). Seed size is 1.21 ± 0.37 mm in length, and 1.34 ± 0.22 in width (N = 15). Fruits are produced from April to August thus encompassing the end of the lek season and all the non-lek season of *M. manacus* in the region (May – June). *Ocotea pulchella* (Ness) Mez (Lauraceae) is a tree with 4 – 30 m height occurring in non-flooded patches of *restinga*. Its drupes have 9.49 ± 0.47 mm length and 5.37 ± 0.28 mm width (N = 15). Seed size is 8.19 ±

0.66 mm in length and 3.87 ± 0.24 in width (N = 15). The fruiting period of this species (July – January) overlapped with the lek season of *M. manacus* (Cestari and Pizo, in press; see chapter 1).

Data collection

To contrast the frugivory by *M. manacus* and non-lekking birds in lek and non-lek areas, we made focal observations on *M. rigidiuscula* and *O. pulchella* individuals and recorded the following parameters that affect the seed dispersal effectiveness (*sensu* Schupp 1993): (1) frequency of feeding visits to plants (i.e., visits with evidence of fruits consumption), (2) fruit handling behavior (swallowed whole or mandibulated), and (3) number of ingested fruits. The proportion of seeds consumed by a group of birds (either *M. manacus* or all other bird species) in relation to the total number of fruits consumed was taken as its dispersal service (Schupp et al. 2010). Bird nomenclature followed the American Ornithologists' Union (Remsen Jr. et al. 2012).

Observations were distributed all day long (0600 – 1800 h) from concealed places located at least 10 m from focal plants. Trees of similar height (*M. rigidiuscula*: 2.5 – 3.5 m, *O. pulchella*: 4 – 5 m) with full crop of mature fruits were chosen to minimize intrinsic differences that might interfere on the bird's choices. Each plant species was observed for 70 h. The observation effort was divided equally among plants located within 5 – 10 m from four lek areas (35 h) and plants located in non-lek areas (35 h) at least 50 m far from any lek. We observed seven fruiting individuals of *M. rigidiuscula* during the non-lek period (May-June 2011), three in lek areas and four in non-lek areas in Iguape. Eleven fruiting individuals of *O. pulchella*, four near lek areas and seven in non-lek areas, were observed during the lek period (August-September 2011) in Itanhaém and Peruíbe. In lek areas, the total number of plants observed was limited by the number fruiting individuals.

Data Analyses

Overall, few trees were visited by birds in lek (two trees of each of the focal species) and non-lek areas (one *Miconia*, and none *Ocotea*), what prevent us for using any statistical treatment for number of ingested fruit. The frequency of feeding visits by *M. manacus* and

non-lekking frugivorous birds to *M. rigidiuscula* and *O. pulchella* trees were compared between lek and non-lek areas using Chi-square tests (with Yates correction) or Fisher test (for small frequencies) applied to 2 x 2 contingency tables. The null hypothesis predicted equal frequencies of visits by *M. manacus* and other frugivores to trees at lek and non-lek areas. We employed the Bioestat software 5.0 (Ayres et al. 2004) for all analyses. Significance was accepted at $P \leq 0.05$.

Results

Four species of birds visited *Miconia* trees: *M. manacus* and the non-lekking Flame-crested Tanager *Tachyphonus cristatus*, Blue Dacnis *Dacnis cayana*, and Violaceous Euphonia *Euphonia violacea*. *Manacus manacus* and *T. cristatus* swallowed fruits whole, while *D. cayana* and *E. violacea* mandibulated fruits discarding part of their husks. The last two species were also considered potential dispersers of *Miconia* seeds because they swallowed the majority of the tiny seeds. *Manacus manacus* and the non-lekking birds did not differ in the frequency of visits to *Miconia* trees between lek and non-lek areas (Fisher test; $P = 0.16$; Fig. 1A), but the number of fruits they ingested differed: *M. manacus* ingested more fruits (27 fruits) than the other species (2) near lek areas, while the opposite was true in non-lek areas (*M. manacus* ingested 11 fruits; other species ingested 20 fruits). Thereby, the dispersal service provided by *M. manacus* to *Miconia* trees near lek areas was greater than other frugivores, whereas at non-lek areas other frugivores contributed more than *M. manacus* to the dispersal of *Miconia* seeds (Fig. 1B). Only juveniles and females of *M. manacus* ingested 27 fruits in lek areas. At non-lek areas, juveniles and females (2 visits; 3 fruits), and adults (4 visits; 8 fruits) of *M. manacus* ingested fruits.

Three species of birds visited *Ocotea* trees: *M. manacus* and the non-lekkings Brazilian Tanager *Ramphocelus bresilius* and Rufous-bellied Thrush *Turdus rufiventris*. They visited *Ocotea* trees near lek areas but no visits were recorded in non-lek areas. Compared with other species, *M. manacus* had greater frequency of visits near lek areas ($\chi^2_1 = 17.52$; $P < 0.001$; Fig. 1A). All the species swallowed fruits whole, but *R. bresilius* mandibulated the fruits and discarded 40% of all the seeds consumed by all non-lekking birds ($N = 15$). This seed handling behavior affected negatively the potential to disperse seeds by non-lekking birds when compared to seed treatment provided by *M. manacus*, which swallowed whole all ($N = 88$) the fruits. Thus, the dispersal service provided by *M. manacus* to *Ocotea* trees was

also greater than other frugivores near lek areas (Fig. 1B). Juveniles and females (18 visits, 38 ingested fruits) as well as adult manakins (21 visits, 50 ingested fruits) consumed fruits of *O. pulchella*. They presented a clear division in the time of visits: juveniles and females visited fruiting trees before the peak period of lek activityfrom 0630 h to 0800 h, and afterwards adult males predominate at fruiting plants.

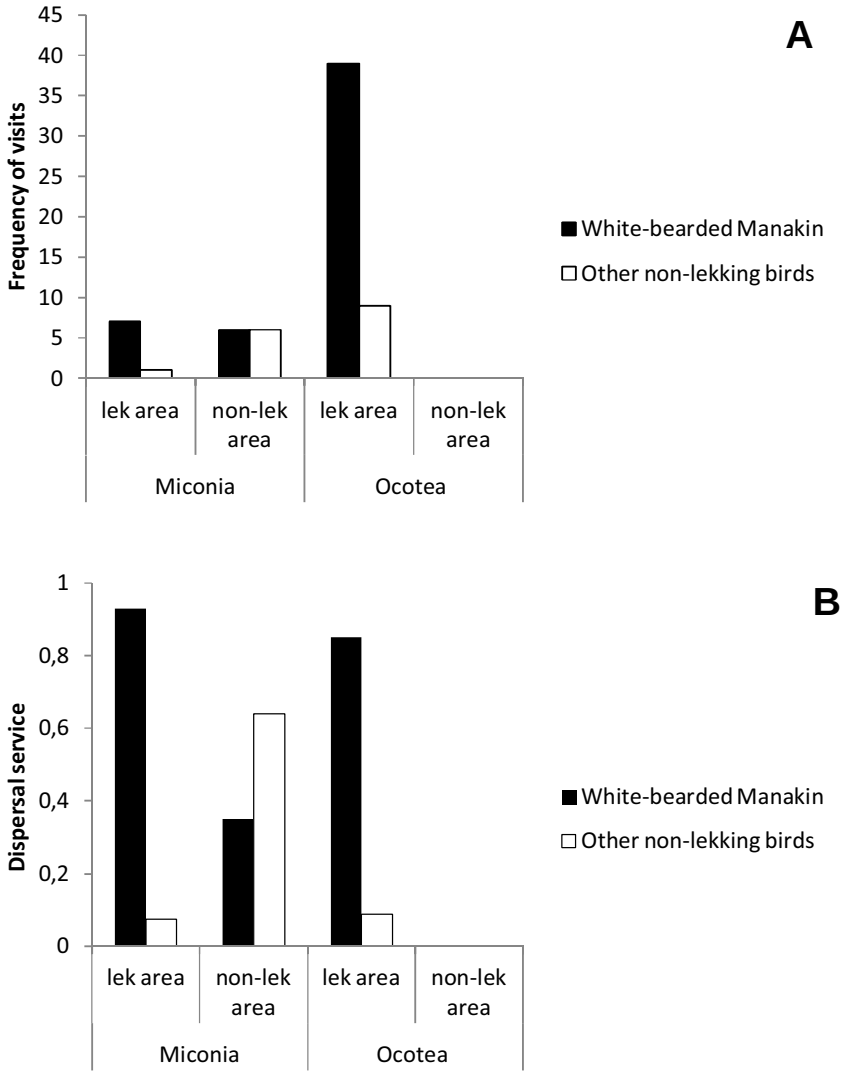

Figure 1. Frequency of visits to *Miconia rigidiuscula* and *Ocotea pulchella* fruiting trees and dispersal services (or total proportion of removed seeds) by White-bearded Manakin *Manacus manacus* and other non-lekking birds near lek areas and in non-lek areas.

Discussion

Manacus manacus swallowed more fruits of *Ocotea* and *Miconia* than other frugivores near lek areas. In addition, likely other manakins, *M. manacus* have a wide gape in relation to their body size, which allows them to swallow whole fruits that cannot be swallowed by birds such as some tanagers (Snow 1962). In our study, *M. manacus* had no difficult to swallow fruits of *Ocotea pulchella*, while the tanager *Ramphocellus bresilius* employed both fruit handling techniques, swallowing the smaller fruits of *O. pulchella* while mandibulating and dropping the seeds of larger fruits below mother-plants, thus wasting some fruits from the plant's perspective (Connell 1971; Janzen 1970; Schupp et al. 2010).

During the lek period, the staggered temporal pattern of visitation to fruiting plants of *O. pulchella* among lekking adult males, juveniles, and females, with the former visiting trees near lek areas more frequently after 0800 h when lek activities decrease (Cestari and Pizo in press, see chapter 1), and juveniles and females visiting fruiting trees before 0800 h, collaborate for the prominent role of manakins in fruit depletion near lek areas. During the non-lekking period *Manacus manacus* also feed on fruits of *M. rigidiuscula* more frequently in lek areas than non-lekking species. Even in the moulting period, when the majority of resident males were not lekking, individuals (mainly juveniles and females) may continue using the lek area to forage (Snow 1962; authors, pers. obs).

Lek areas of some manakins (e.g. *Pipra erythrocephala, P. filicauda, P. pipra*) have greater biomass of fruits compared with control areas (Ryder et al. 2006). This fact may lead manakin males to increase their reproductive success by using fruits near leks because they do not have to fly long distances to feed and abandon their courts for long periods. However, compared to non-lekking birds, seeds ingested by lekking males of *M. manacus* are likely to be dispersed to spatially restricted areas near leks (Cestari and Pizo, unpubl. data, see chapter 7). Studies in the Neotropics indicate that males of other lekking species (e.g., manakins and cotingids) clump a great variety of seeds below their display perches and may influence the spatial structure and dynamics of plant populations (Krijger et al. 1997; Théry and Larpin 1993; Wenny and Levey 1998).

Although we focused only in two species of plants, this work provides an example of context dependence in the quantity component of seed dispersal effectiveness in which the lek breeding system of a frugivorous species influence the identity of seed removers and the quantity of seeds removed in and around lek areas. We are aware, however, that information on the quality of seed deposition will complete the understanding of seed dispersal effectiveness promoted by *M. manacus* and other lekking birds because birds that feed on

large amounts of fruits do not necessarily deposit these seeds in sites viable to plant recruitment (Jordano and Herrera 1995; Loiselle and Blake 1999; Schupp et al. 2010). Future studies must be directed to fill this gap of knowledge.

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CAPÍTULO 7

Seed Rain in Lek and Non-lek areas: White-bearded Manakin (*Manacus manacus*, Pipridae) as Seed Disperser in the Atlantic Forest

Submetido para Biotropica

Abstract

Resident males of the frugivorous White-bearded Manakin (*Manacus manacus*) stay in lek areas for more than six months a year while females and juveniles only spend brief periods in leks. We tested whether manakins increased the abundance and species richness of seeds in lek areas in, a threatened *restinga* ecosystem of the Brazilian Atlantic forest. We evaluated the richness and abundance of seeds collected in traps placed in lek and non-lek areas. We further compared the richness, abundance, and composition of seeds in courts and non-court sites of lek areas. Using radio-telemetry, we investigated the potential seed distribution (dispersal kernel) generated by resident males and juvenile males plus females during the morning peak of lek activity, and when lek activity decreased in the afternoon during both lek and non-lek seasons. There were no significant differences in the richness and abundance of seeds between lek and non-lek areas, but both parameters increased significantly in courts compared with non-court sites. We argue that these results are a consequence of the longer time spent by resident males in preferred perches in or near display courts where they deposit seeds. Resident males move more extensively and potentially distributed seeds to greater distances during the afternoons of the lek and non-lek seasons while juveniles plus females moved more extensively and potentially distributed seeds to greater distances during the mornings thus indicating their daily complementarily contribution to seed dispersal regarding dispersal distance.

Key words: court; dispersal; frugivory; Neotropic, propagules; *restinga*.

Introduction

Lek behavior is a prominent feature of manakins (Passeriformes, Pipridae) whose colorful males display solitarily or in groups to attract potential mates (Höglund and Alatalo 1995; Prum 1990; Sick 1967). Lek attendance is supposed to be a primary factor affecting a males' mating success in many lekking animals (Fiske et al. 1998). Some manakins, for instance, stay in lek areas for more than six months a year and up to 90% of the day (Snow 2004; Cestari and Pizo, in press, see chapter 1).

Manakins are also common frugivorous birds in the understory of Neotropical forests where they act as important seed dispersers (Snow 1962, Worthington 1982, Krijger et al. 1997, Blake and Loiselle 2002). Manakins may deposit seeds in microhabitats suitable for

germination resulting in the recruitment of plants, thereby influencing the spatial structure and dynamics of plant populations and communities (Loiselle et al. 2007). Studies concerning seed dispersal of manakins (and their sister group, the cotingas) indicate that lekking males influence the high density and diversity of seeds deposited in lek areas (Théry and Larpin 1993, Krijger et al. 1997, Wenny and Levey 1998, Karubian et al. 2010). Leks of some manakins are usually located in areas where fruit resources (*i.e.*, plants with fleshy fruits) are abundant (Snow 1962, Ryder et al. 2006) and a clumped pattern of seed deposition in lek areas has been hypothesized to result from the long permanence of lekking males that defecate and regurgitate seeds consumed during frequent and brief feeding bouts (Théry 1992, Krijger et al. 1997, Snow 2004). In contrast, females and juveniles (both males and females), hereafter called "greens" due to their dull green body color contrasting with the colorful plumage of adult males, generally move longer distances than adult males to visit leks. Although little attention has been played to their role as seed dispersers, greens potentially reach greater distances from lek areas than lekking males (Krijger et al. 1997, Lill 1974b). Therefore, differential movements of resident lekking males and greens in a lek system may influence how far seeds are moved from lek areas.

In *Manacus* manakins species, males have peak periods of lek activity along the day with the highest frequency of displays occurring during early morning and afternoon. Outside of these periods, lek activity decreases and males may spend variable amount of time out of lek areas. Juvenile males and females stay out or in the vicinity of lek areas during much of the day, spending only brief periods in lek areas to practice display maneuvers and choose mates, respectively (Chapman 1935; Snow 1962; Cestari and Pizo, in press). Considering the temporal lek activity of manakins, a seed ingested by a male prior to their stationary period in the day, for instance during the peak of lek activity, is expected to be dispersed to smaller distances than if the same seed was ingested immediately prior to a bird's period of movement, ultimately influencing the spatial scale of seed dispersal (Westcott et al. 2005). In the present study, we investigated the seed rain in lek areas of White-bearded Manakin (*Manacus manacus*), and the seed dispersal activity by resident males and greens in the Atlantic forest in southeastern Brazil. More specifically, we asked the following questions considering seed rain in lek areas of *M. manacus* and paired non-lek areas: are there quantitative differences in the abundance and species richness of seeds falling in lek and non-lek (control) areas? In a finer-scale, are there differences in the abundance and species richness of seeds deposited in male courts and non-court sites within lek areas? Is there any

spatial structure in the composition of the seed pool deposited in male courts? Considering the movements of manakins, we asked: do resident males and greens differ in their capacity to distribute seeds during the period of peak activity in leks and when lek activity decreases?

We expected a greater abundance of seeds from bird-dispersed plants in lek areas than in non-lek areas due to the constant presence and dispersion of seeds by lekking males of *M. manacus*. Similarly, we expected a greater number of seeds concentrated immediately around courts than in non-court sites in lek areas due to the constant presence of lekking males in or in the immediate vicinity of their courts (see Cestari 2010). We also expected that greens (juveniles and females) generate a more extensive distribution of seeds than more sedentary lekking males.

Methods

Bird species.— The White-bearded Manakin (*Manacus manacus*, Pipridae) is a small (15-18 g) understory frugivorous bird that inhabits mainly lowland forests in the Neotropical region. It has a widespread geographic distribution in continuous and fragmented Amazonian and Atlantic forests (Sick 1997, Snow 2004). During the main breeding period that frequently overlaps with the rainy season, resident males concentrate their activities in lek areas (or display grounds) measuring 18-23 m long and 4-9 m wide (Darnton 1958, Snow 1962). Courts from 0.15-0.9 m diameter where males display to attract females are as little as a meter or less apart inside a display ground, which characterizes a classical lek (Snow 1962, Sick 1967, Théry 1992). Females and juvenile males frequently visit lek areas to mate and practice display maneuvers, respectively. Both categories have home ranges 5-10 times larger than the males' home ranges (Lill 1974b, Théry 1992). Each male court is an oval ground area cleaned from litter and delimited by two or more saplings wherein the male perform its snap-jump display (Darnton 1958, Snow 1962, Lill 1974a). Resident males may spend between 82–90 percent of the daylight hours at lek areas during the main breeding season, leaving only during brief intervals to forage at nearby fruiting trees (Snow 1962; Théry 1992). During the annual molt period, resident males are absent from their courts for two to three months, but lek areas may be used by juvenile males and adults without territories to display in the temporally vacant courts (Snow 1962; Lill 1974b; Cestari and Pizo, in press, see chapter 1).

Study areas.— Our study was conducted at two sites that included six lek areas in continuous lowland *restinga* forests in the state of São Paulo, southeastern Brazil. Four leks (LEK 0, LEK 1, LEK 2 and LEK 3) were located in a protected reserve (Juréia Itatins Ecological Station – JIES - 24°18' S, 47°00' W) while the other two leks (LEK 4 and LEK 5) were located in a non-protected area (NPA - 24°10' S, 46°55' W) separated by nearly 38 km from the northern reserve border. Distances between leks generally exceed 5 km; however, LEK 1 and LEK 2 were separated by 0.6 km at their closest border. Both sites (JIES and NPA) conserve areas of *restinga* vegetation, a coastal ecosystem included in the Atlantic forest domain that remains persistently threatened by urban expansion (Sampaio et al. 2005). Typical plant families in the region are Myrtaceae, Leguminosae, Rubiaceae, Melastomataceae, Lauraceae and Annonaceae (Mamede et al. 2004). The regional climate is subtropical and humid. Mean annual rainfall is 2,278 mm with the rainy season occurring from October to April, and the dry season from May to September. Mean annual temperature is 21.4ºC, with maximum and minimum temperatures averaging 25.8ºC and 19.0ºC, respectively (Tarifa 2004).

Seed rain sampling.— We used 0.36 m^2 seed traps suspended 0.25 m above the ground to assess the seed rain at three lek areas (LEK 0, LEK 2, LEK 3) and three non-lek areas (up to 2,500 m^2 each) arranged in a paired design. Paired lek and non-lek areas were located ~0.8 km from each other and had similar vegetation physiognomies. Seven seed traps were randomly distributed at each lek and non-lek area. We collected and counted the seeds in the traps monthly from July 2009 to June 2011. Seeds were identified to the lowest taxonomic level possible by comparison with a reference collection, and also consulting the literature and specialists. We followed the nomenclature from Royal Botanic Garden (2012), Lorenzi (1998) and Lorenzi (2009a, b).

Seeds in courts and non-court sites within lek areas were collected directly from the soil surface from March 2010 to February 2011. During this period, we alternated monthly seed samples in NPA and JIES (i.e. each site was sampled at bimonthly intervals), totaling six samples for each of these two areas. We defined a court site as a 0.22 m^2 area of bare soil where a male frequently performed its displays plus a 0.48 m^2 adjacent border area, generally covered with seedlings (Fig. 1). To enable comparison between courts and control sites, standardized non-court sites with a similar shape and dimension to that of courts (0.70 m^2) were delimited with a cord frame and set 5 m from courts in a randomly determined direction. Seeds from a total of 21 courts and their paired non-court control areas were collected, as

follows: three courts in LEK 1, two courts in LEK 2, seven courts in LEK 3, eight courts in LEK 4, and one court in LEK 5. Distances between courts were measured to analyze the spatial pattern of seed composition in courts within lek areas.

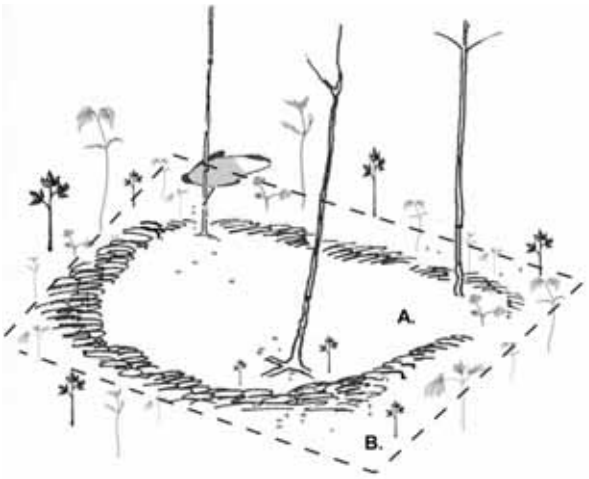


Figure 1. Court area of White bearded Manakin (*M. manacus*) showing: (A) the cleaned area of the court, and (B) the border area of the court with numerous seedlings. Seeds are commonly found in A and B.

Species movements.— We used radio-telemetry to assess the distances moved by resident males and greens from LEK 0, LEK 2, and LEK 3 during the main-lek period (September, October, and December 2010) and non-lek period (May and June 2011). One resident male and one green were monitored each month, except in June 2011 when two resident males and two greens were monitored. Individuals captured on mist-nests placed in lek areas were kept for 30 min in a cage with foam-lined walls to avoid injury (see Appendix 6). Then, we attached a 0.3 g transmitter (Advanced Telemetry Systems, model A2414) to the back plumage using glue (see Appendix 7). Birds were radio-tracked for 60 consecutive minutes during the peak period of males' lekking display (morning: 0615 h to 0900 h), and when the frequency of lek displays decreased or ceased (late-afternoon: 1515 h to 1800 h). Previous observations of free-living radio-tagged individuals indicated that they foraged and flew

without signs of annoyance after being released. Therefore, we used 1 h as a habituation interval prior to starting radio-tracking. We recorded 12 consecutive location fixes (*x* and *y* coordinates) per individual at 5 min intervals during one morning and one afternoon to obtain the straight-line distances between consecutive points. We used a high-sensitivity GPS receiver (Garmin eTrex Vista XCx, accuracy < 10 m) to record fixes and remained > 10 m from the radio-tagged individuals to avoid interfering with their behavior.

Seed dispersal.— We estimated the number of seeds dispersed at each 5 min by resident males and greens considering the time interval between consecutive defecations (or regurgitations) and the number of seeds per defecation or regurgitation. The time interval between defecations (or regurgitations) were obtained conducting *ad libitum* observations of resident males (187 samples) and greens (48 samples) in areas close to leks from July 2009 to June 2011 to record their mean rate of defecation and regurgitation at each 5 min.When a perched bird was detected, we started a stopwatch and followed it counting continuously the number of defecations and regurgitations before it flew away. Same resident males or greens might have been observed more than once because not all of them were color-banded. Estimates of the mean number of seeds per defecation or regurgitation were obtained by counting the number of seeds in defecation and regurgitation samples from 12 monitored individuals (see Species Movements above) and another 45 individuals (12 resident males and 33 greens) captured in leks from May 2009 to June 2011.

Dispersal kernel.— Here treated as the probability of seed deposition by adult males and greens at any distance from its origin. Dispersal kernels were estimated from the 60 min telemetry sample (12 fixes) by combining the straight-line distance moved by males and greens at each 5 min from a random initial point (see Species Movements above) with the mean number of seeds defecated and regurgitated at each 5 min interval (see Seed Dispersal above). For example, if we obtained an average regurgitation or defecation rate of four seeds at each 5 min, an individual that moved 15 m (straight distance from an initial point) in the first 10 min along its route is expected to regurgitate or defecate eight seeds. To apply this methodology, we assumed that foraging occurs randomly during the day (*sensu* Westcott et al. 2005).

Data analyses.— The number of seeds collected from traps in lek and non-lek areas, and the number of seeds in courts and non-court sites within lek areas were compared with repeated measures ANOVA. The monthly number of collected seeds was treated as a dependent variable. In a larger scale, lek and non-lek areas were used as factors, while in a smaller scale (within lek areas), courts and non-court sites were treated as factors.

Rarefaction analysis was used to compare the richness of seeds between lek and non-lek areas and between court and non-court sites using the Ecosim software 7.0 (Gotelli and Entsminger 2001). The number of seeds from control areas (either non-lek or non-court areas) was randomized for their respective lek or court areas through 1000 iterations to calculate the expected number of species. We reported the averaged rarified diversity values for lek and court areas plus their variance (σ), and 95% confidence intervals (CI).

Based on the abundances of seed morphospecies in the courts in leks with the greatest number of courts (LEK 3 and LEK 4) we calculated the similarity in seed composition using Morisita's index (C_λ). This index varies from 0 (no similarity) to 1 (complete similarity). To test whether seed composition showed any spatial relationship with the distance among courts within a lek, we correlated between-court seed similarity and metric distances using a Mantel test whose significance was determined by a permutation process with 1000 iteractions. A positive or negative correlation between seed similarity and court separation distances indicates a spatial structure in the composition of seeds deposited in lek areas. At a larger spatial scale, we also compared the seed composition between the group of courts from LEK 3 and LEK 4 using a non-parametric permutation procedure (ANOSIM) that considers a test statistic (R). *R* values range from -1 to +1, with dissimilarity between leks indicated by *R* values from 0 to +1. Past 2.0 software (Hammer et al. 2001) was employed in the above analyzes of correlation and similarity.

Differences in the rate of defecation (and regurgitation) and in the number of seeds per defecation or regurgitation between resident males and greens were analyzed using Mann-Whitney test. Differences in the straight-line distances moved between resident males and greens were compared in the morning and afternoon periods, and in the lek and non-lek periods using repeated measures ANOVA. Straight-line flight distances (dependent variable) were recorded at five minute intervals. Lek and non-lek areas, manakin status (resident males and greens), and daily periods (morning and afternoon) were treated as factors. Mann-

Whitney test and ANOVAs were performed using Statistica software 10.0 (StatSoft 2011). Significance of test results was accepted at $P \leq 0.05$.

Results

The abundance of seeds did not differ between lek and non-lek areas ($F_{2,36} = 2.44$; $P = 0.1$; Fig. 2). Seed species richness was similar between lek and non-lek areas (44 morphospecies; $\sigma = 0.37$; 95% *CI*: 42 – 44 expected morphospecies; Table S1).

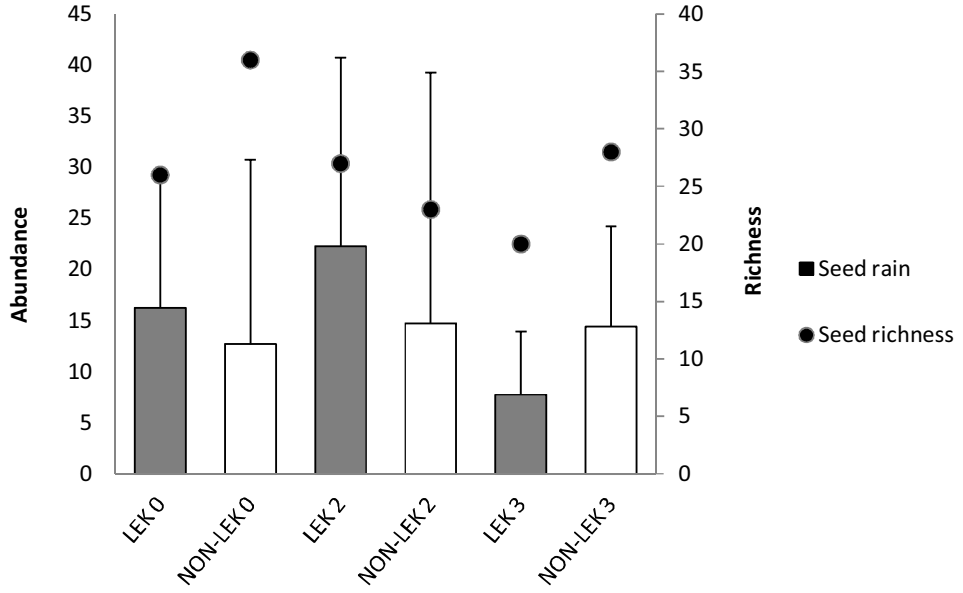


Figure 2. Mean number of seeds, and seed species richness in three lek and non-lek (control) areas. Vertical lines represent standard deviation. Seven seed traps of 0.36 m^2 were used in each lek and control area.

Courts had a greater abundance of seeds ($F_{1,30} = 23.85$; $P < 0.001$) than non-court sites indicating that seed deposition was concentrated in and around courts (Fig. 3). Similarly, seed richness was greater in courts than in non-court sites (45 morphospecies; $\sigma = 4.85$; 95% *CI*: 27 – 35 expected morphospecies; see morphospecies in Table S2; see Appendix 8).

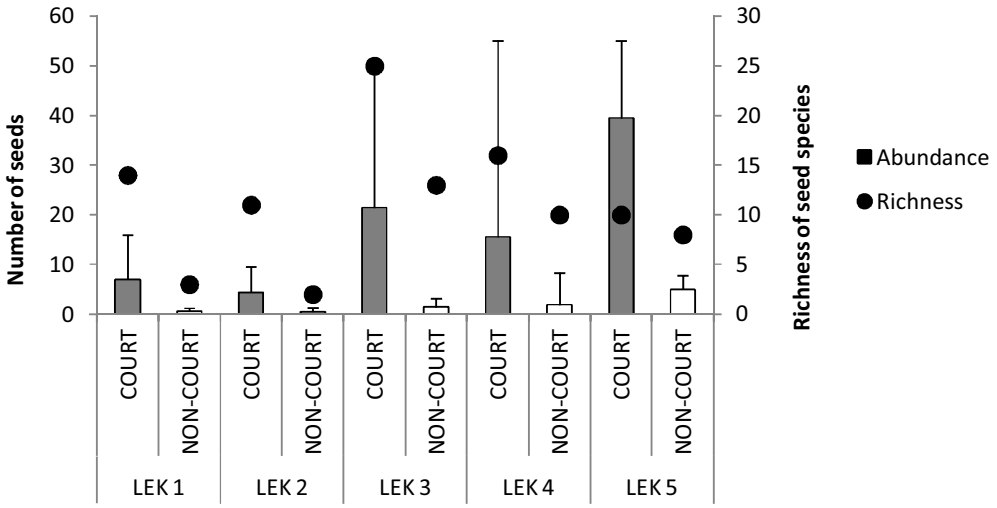


Figure 3. Mean number of seeds and seed species richness collected in 21 courts and their paired non-court sites. Vertical lines represent standard deviation.

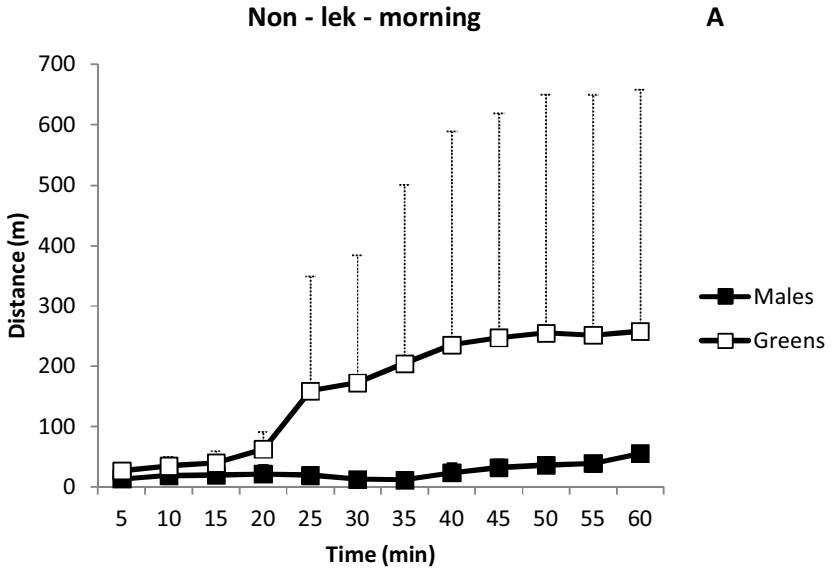
Seed similarity and distances among courts in LEK 3 ranged from 0.002-0.76 (median: 0.15; N = 21) and 9-82 m (median: 48 m), respectively. In LEK 4, seed similarity among courts ranged from 0.02-0.75 (median 0.46) and courts were more spatially concentrated (range 3-28.5 m; median: 14.25 m; N = 28). Examination of spatial autocorrelation with Mantel tests showed no correlation between seed similarity and distances among courts in either of the lek areas (LEK 3: R = 0.059; P = 0.34; LEK 4: R_p = - 0.02; P = 0.47) indicating no spatial structure in seed composition at the lek scale. However, ANOSIM analysis showed that LEK 3 and LEK 4 differed in the composition of seeds (R_p = 0.17; P = 0.04).

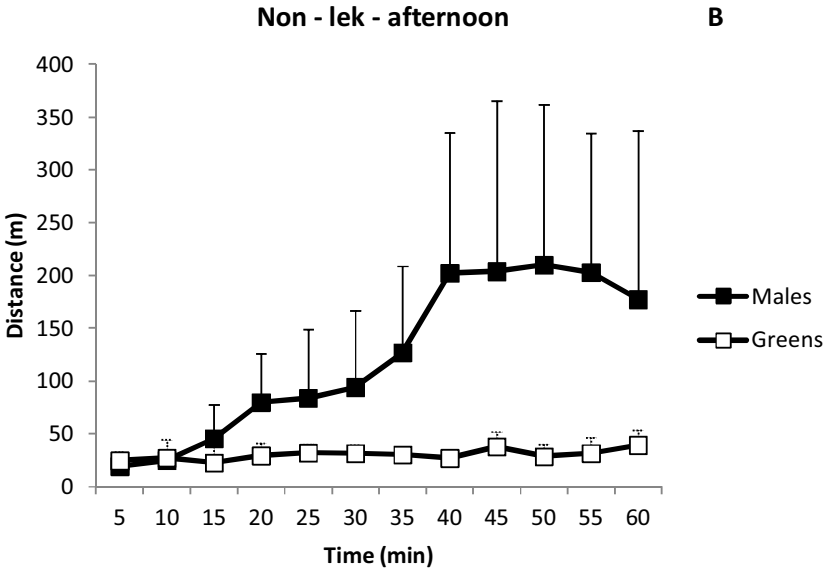
Resident males and greens did not differ in the rate of defecation (and regurgitation) per 5 min intervals (males: 4.4 ± 10.2 defecations, N = 187; greens: 3.6 ± 7 defecations, N = 48; U = 4151, P = 0.37) or in the number of seeds per defecation or regurgitation (males: 1.6 ± 3.3 seeds, N = 18; greens: 1.0 ± 1.8 seeds, N = 39; U = 308.5; P = 0.45). Although, the straight-line distances of resident and green males did not differ, our analysis showed a significant interaction involving manakin status and the daily periods (Table 1), which indicates that males and greens potentially generated different seed distributions during morning and afternoon periods. This analysis showed that greens moved longer straight-line distances than resident males in the mornings while resident males moved longer straight-line distances than greens in the afternoons (Fig. 4).

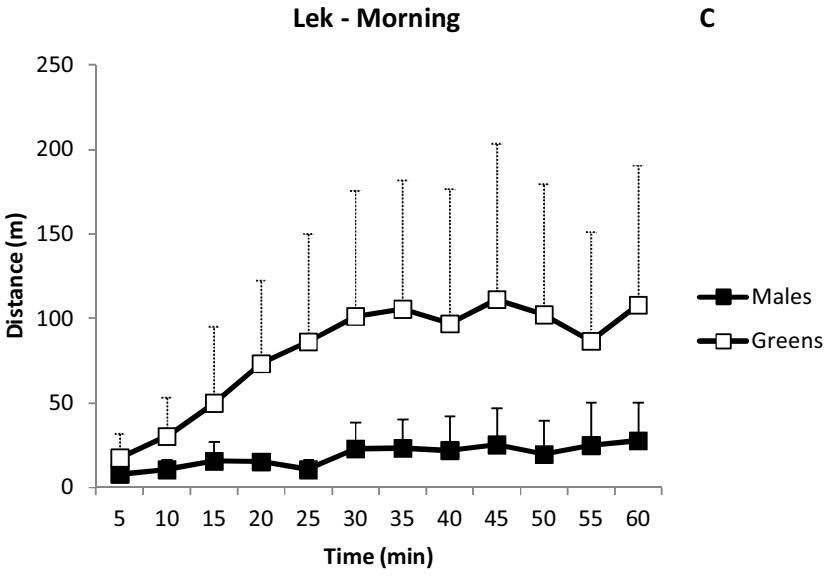
Table 1. Results of repeated measures ANOVA on straight-line distance moved by resident male and green manakins. Lek/non-lek seasons, morning/afternoon periods, and manakin status (resident males and greens) were used as factors.

Effect	Sum of Squares	Degrees of freedom	F	P
Season	67500	1	0.739	0.403
Period	1160	1	0.013	0.912
Manakin Status	28600	1	0.314	0.583
Season*Period	12800	1	0.140	0.713
Season*Status	387	1	0.004	0.949
Period*Status	455000	1	4.991	0.04*

*P < 0.05




Non - lek - afternoon
B
Distance (m)
400
350
300
250
200
150
100
50
0
5 10 15 20 25 30 35 40 45 50 55 60
Time (min)
Males
Greens


Lek - Morning
C
Distance (m)
250
200
150
100
50
0
5 10 15 20 25 30 35 40 45 50 55 60
Time (min)
Males
Greens

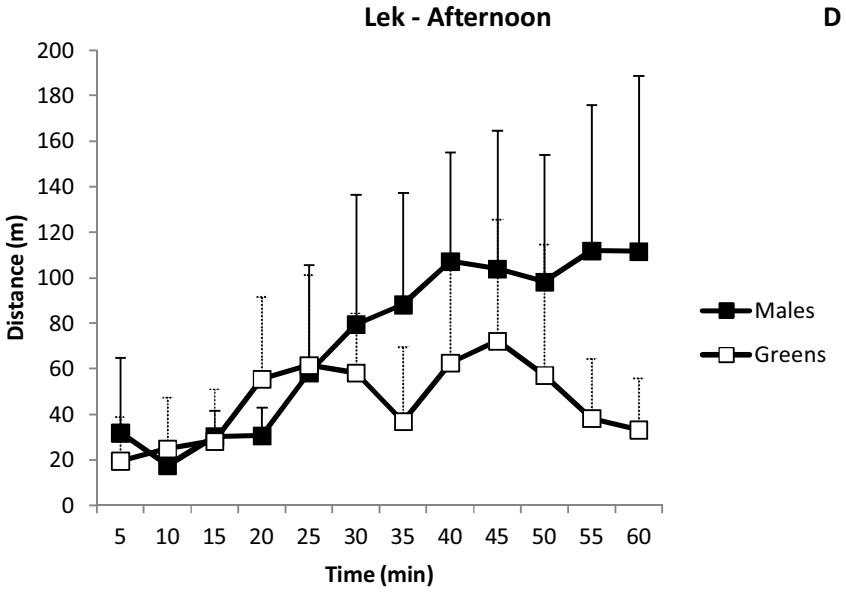


Figure 4. Straight-line distances moved by resident males (N = 3) and greens (N = 3) during 60 min periods in non-lek (A and B) and lek (C and D) periods during the mornings (A and C) and afternoons (B and D). Vertical lines represent standard deviation.

Discussion

Contrary to our expectations, the seed rain abundance in lek and non-lek areas of *M. manacus* was similar. However, the greater abundance of seeds in and near courts indicates that manakins (mainly resident males) disperse seeds to specific sites within lek areas. Manakin leks are usually located in or near areas where fruit resources (*i.e.*, plants with fleshy fruits) are abundant (Snow 1962, Ryder et al. 2006). When not displaying, resident males usually feed on fruits in these areas, defecating and regurgitating a large amount of seeds beneath preferred perches, which are usually located in or near their courts (Cestari 2010). Krijger et al. (1997) also demonstrated a greater density of viable seeds in the display sites ("mossy logs") of White-throated Manakin (*Corapipo gutturalis)* than in control areas in the evergreen forest of French Guiana. However, differences between these two manakin species emerge as a function of the spatial distribution of males within lek areas. In *M. manacus*, lekking males are often in visual contact each other and courts are much closer to each other

than in *C. gutturalis* whose males and display sites are dispersed over a relatively larger area (classical and exploded lek types, respectively; Snow 2004). Therefore, seeds in *M. manacus* leks are more spatially aggregated than in *C. gutturalis* leks.

As hypothesized for seed aggregation below parent trees (Janzen 1970, Connell 1971), seed clustering in courts may reduce seed survival due to competition, and the attraction of pathogens and seed predators. However, some of these density-dependent effects may be minimized because (1) pulps of deposited seeds are generally removed during the passage through the bird's gut, probably reducing fungal attacks, and (2) even seeds with small amounts of adhered pulp may be removed to distances of up to 13 m by common Atlantic forest secondary dispersers, such as myrmicinae and ponerine ant species (Pizo and Oliveira 2000). Future studies should test these hypotheses in lek areas of *M. manacus*.

Some studies suggested that the long term concentration and variety of seeds deposited by lekking birds may be important forest succession drivers in lek areas. For example, in French Guiana, Théry and Larpin (1993) found a mosaic of plant species typical of different vegetation communities in a lek of the Cock-of-the-Rock (*Rupicola rupicola*), showing that long-term seed dispersal by males promoted the succession from more open vegetation to high forest physiognomy. Employing the genetic technique of maternally inherited tissue in seeds of the tropical palm *Oenocarpus bataua*, Karubian et al. (2010) revealed that the seed pool in a lek area of the Long-wattled Umbrellabird *Cephalopterus penduliger* have five times more source trees than control areas and reinforced the contribution of lekking birds for increasing the local genetic diversity of vegetation. In our study, the high variability in the seed composition found in courts and the absence of spatial structure in the seed composition among courts also indicated the strong contribution of *M. manacus* in depositing a variety of seeds in lek areas. In addition, the difference in the seed composition between lek areas (distanced by nearly 38 km) suggests that males of different leks forage on different tree species. Between-lek differences in phenology and plant composition together with the opportunistic feeding habits of manakins that consume a wide variety of fruits according to their availability (Snow 1962, Worthington 1982, Loiselle & Blake 1991, Krijger *et al.* 1997, Haemig 2006) likely contributed to the observed differences.

Differences in the movement and foraging pattern of frugivores that affect seed dispersal depend on the reproductive status, life story, and social organization of species and individuals (Westcott *et al.* 2005). Our results revealed that straight-line distances moved by

lekking males and greens of *M. manacus* differed between morning and afternoon periods. The spatial extension of the seed distribution promoted by greens in the mornings of the lek period is expected to be four times larger than the seed distribution promoted by resident males, whereas in the afternoon resident males are expected to distribute seeds for distances 50% greater than greens (see fig. 4). During the mornings, males display in leks while greens visit leks only sporadically (Snow 1962; Cestari and Pizo, in press). During the non-lek season, the daily difference in patterns of straight-line distances moved by resident males and greens was maintained. These patterns suggest a daily complementarity in the seed dispersal roles of resident males and greens: resident males disperse more seeds closer to each other than greens during the morning while the opposite happens during the afternoon. Therefore, in what concerns seed dispersal distance, it matters both the period of seed ingestion and the lekking status of the seed disperser, if a resident male or a green manakin.

The scarcity of studies linking seed dispersal with the daily movements and spatial use of lekking species precludes the comparison of our results with other species. For the Southern cassowary *Casuarius casuarius*, a 50-76 kg non-lekking bird from humid forests of Australia, Westcott et al. (2005) found dispersal distances three times larger in the mornings than in the afternoons due to the longer time that individuals spent foraging and moving during the early period of the day. In the case of *M. manacus*, differences in the commitment to lekking activities led to the daily differences in distances moved by resident males and greens.

We have shown that the spatial aggregation of seeds in lek areas of *M. manacus* occurs at the court level, and the spatial distribution of deposited seeds likely varies with male lekking status and the daily period of foraging. Future studies should address the consequences for plant recruitment of seed aggregation in courts, and if resident males and greens of *M. manacus* use different microhabitats as shown for other manakins (Loiselle et al. 2007), which may add to the daily differences in movement patterns and determine their effectiveness as seed dispersers.

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Table S1. Abundances of species and morphospecies of seeds collected in *leks* of *Manacus manacus* and non-lek areas from July 2009 to June 2011 in a *restinga* forest, southeastern Brazil.

Plant family	Species/ Morphospecies	Lek Areas			Non-lek Areas		
		L1	L2	L3	NL1	NL2	NL3
Anacardiaceae	*Schinus* sp.	14	99	0	0	9	3
Annonaceae	*Guatteria australis*	2	2	5	0	6	1
	G. nigrescens	0	0	8	1	0	0
	Rollinia sericea	0	0	0	0	23	0
	Xylopia sp.	1	9	0	0	0	10
Aquifoliaceae	*Ilex theezans*	8	2	4	14	0	0
	I. brevicups	9	0	0	50	0	0
	I. paraguaiensis	0	0	0	1	1	0
Araliaceae	*Schefflera angustissima*	9	80	7	24	11	101
Arecaceae	*Euterpe edulis*	0	2	0	0	1	0
Celastraceae	*Maytenus robusta*	2	4	2	0	0	0
Chlorantaceae	*Hediosmium brasiliensis*	0	2	1	0	0	0
Dilleniaceae	*Davilla rugosa*	4	4	3	1	0	2
	Doliocarpus sp.	0	0	0	0	0	1
Ericaceae	*Gaylussacia brasiliensis*	0	0	0	2	2	0
	Pera glabrata	25	23	7	2	0	15
Lauraceae	*Ocotea pulchella*	25	66	5	12	4	11
	Endlicheria paniculata	0	0	0	0	1	0

Plant family	Species/ Morphospecies	Lek Areas			Non-lek Areas		
		L1	L2	L3	NL1	NL2	NL3
	Nectandra mollis	0	2	0	0	0	0
Melastomataceae	*Miconia ridigiuscula*	79	19	5	0	36	2
	M. cubatanensis	19	70	18	24	4	47
	Ossaea sp.	0	10	1	0	0	1
Moraceae	*Ficus enormis*	0	27	0	0	3	0
Myrsinaceae	*Rapanea parviflora*	86	9	37	41	9	30
	R. ferruginea	22	11	0	1	219	0
Myrtaceae	*Blepharocalyx salicifolius*	5	1	0	0	0	2
	Calyptranthes concinna	0	2	0	0	0	1
	Eugenia pluriflora	37	11	4	31	0	1
	E. sulcata	2	0	2	0	0	7
	E. umbelliflora	8	0	2	2	0	15
	Gomidesia sp.[a] *(Myrcia* sp.*)*	0	3	2	0	0	6
	Myrcia rostrata	0	9	0	0	0	0
	Neomitranthes sp.	0	3	1	0	2	3
	Pimenta pseudocaryophyllus	3	4	0	24	0	5
Pentaphyllaceae	*Ternstroemia brasiliensis*	3	0	0	54	0	0
Rubiaceae	*Psychotria carthagenensis*	0	6	1	0	1	0
	Psychotria sp.	0	0	0	2	0	0
Santalacea (Viscaceae)	*Rudgea* sp.	2	0	5	1	0	5

Plant family	Species/ Morphospecies	Lek Areas			Non-lek Areas		
		L1	L2	L3	NL1	NL2	NL3
Sapindaceae	*Phoradendron crassirostris*	0	16	5	1	7	6
	Cupania oblongifolia	0	9	1	1	4	26
Smilaceae	*Smilax rufescens*	0	1	1	1	0	2
Symplocaceae	*Paullinia* sp.	4	1	0	0	0	1
No identified	Sp. 1	2	1	9	3	0	0
	Sp. 2	4	3	0	9	0	4
	Sp. 3	0	0	1	0	0	0
	Sp. 4	0	1	0	0	0	0
	Sp. 5	0	2	0	0	1	0
	Sp. 6	0	0	0	0	1	0
	Sp. 7	0	1	0	0	0	1
	Sp. 8	0	0	1	0	0	0
	Sp. 9	0	0	1	0	0	1
	Sp. 10	1	3	0	0	0	0
	Sp. 11	1	0	0	0	0	0

[a] Synonym. Accepted names are in parenthesis.

Table S2. Abundances of species and morphospecies of seeds collected in court of *Manacus manacus* and non-court sites from LEK 1 - 5 from March 2010 to February 2011 in *restinga* forest, southeastern Brazil.

Plant Family	Morphospecies	Court	Non-court
Anacardiaceae	*Schinus* sp.	16	8
Annonaceae	*Guatteria nigrescens*	19	9
	Xylopia sp.	7	0
Aquifoliaceae	*Ilex theezans*	7	1
	I. paraguaiensis	7	0
Araliaceae	*Schefflera morototoni*	136	13
	S. angustissima	81	20
Arecaceae	*Euterpe edulis*	1	1
	Geonoma schottiana	16	0
Celastraceae	*Maytenus robusta*	7	0
Chlorantaceae	*Hediosmium brasiliensis*	5	0
Clusiaceae	*Clusia criuva*	20	1
Dilleniaceae	*Davilla rugosa*	23	1
	Doliocarpus sp.	3	0
Ericaceae	*Pera glabrata*	24	0
Erythroxylaceae	*Erythroxylum decidum*	88	0
Lauraceae	*Ocotea pulchella*	112	6
Melastomataceae	*Miconia cubatanensis*	102	0
	M. hymenonervia	14	0
	M. ridigiuscula	36	1

Plant Family	Morphospecies	Court	Non-court
	Ossaea sp.	3	0
Meliaceae	*Guarea macrophylla*	23	0
Myrsinaceae	*Rapanea parviflora*	492	68
	R. ferruginea	121	3
Myrtaceae	*Blepharocalyx salicifolius*	38	1
	Calyptranthes sp.	0	1
	C. concinna	42	2
	Eugenia pluriflora	30	1
	E. sulcata	17	0
	E. umbelliflora	126	14
	Gomidesia sp.[a] *(Myrcia* sp.*)*	0	1
	Myrcia bicarinata	62	0
	Pimenta pseudocaryophyllus	25	1
	Siphoneugena guilfoyleiana	1	0
Nyctaginaceae	*Guapira opposita*	17	0
Pentaphyllaceae	*Ternstroemia brasiliensis*	4	0
Rubiaceae	*Chioccoca alba*	12	0
	Psychotria carthagenensis	11	0
	Psychotria sp.	54	0
Santalacea (Viscaceae)	*Rudgea* sp.	4	0
Sapindaceae	*Phoradendron crassirostris*	0	15

Plant Family	Morphospecies	Court	Non-court
Smilaceae	*Smilax rufescens*	0	4
Symplocaceae	*Paullinia* sp.	39	3
No identified	Sp. 1	18	0
	Sp. 2	2	0
	Sp. 3	1	0
	Sp. 4	2	0
	Sp. 5	2	0
	Sp. 6	2	0

[a] Synonym. Accepted names are in parenthesis.

References

ANCIÃES, M.; PRUM, R. O. Manakin display and visiting behaviour: a comparative test of sensory drive. **Animal Behaviour,** v. 75, p. 783-790, Mar 2008. ISSN 0003-3472.

ANCIÃES, M. et al. Diversidade de piprídeos (Aves: Pipridae) amazônicos: seleção sexual, ecologia e evolução. **Oecologia Brasiliensis,** v. 13, n. 1, p. 165-182, 2009.

ARGEL-DE-OLIVEIRA, M. M. **Frugivory by birds in a restinga forest patch at espirito Santo State, Brazil**. 1999. 153 (PhD thesis). Instituto de Biologia, Unicamp, Campinas.

ASTOR, I. N. C. **Distribuição espacial e comportamento de corte de *Pipra rubrocapilla*, *P. pipra* e *Manacus manacus* em área de Mata Atlântica na reserva Biológica de Poço das Antas, RJ**. 1997. Universidade de Brasília, Brasília.

AYRES, M. M. et al. **BioEstat 5.0: Aplicações estatísticas nas áreas das ciências biológicas e médicas**. Belém: Sociedade Civil Mamirauá/MCT-CNPq/Conservation International 2004.

BARSKE, J. et al. Heart rate as an index of increased metabolic output in a bird with a complex courtship display. **Integrative and Comparative Biology,** v. 51, p. E6-E6, Mar 2011. ISSN 1540-7063.

BEEHLER, B. M.; FOSTER, M. S. Hotshots, hotspots, and female preference in the organization of lek mating systems. **American Naturalist,** v. 131, n. 2, p. 203-219, Feb 1988. ISSN 0003-0147.

BERRES, M. E. Long-term persistence of White-bearded Manakin (*Manacus manacus*) leks in the Arima Valley of Trinidad, West Indies. **Ocasional Papers,** v. 11, p. 131-138, 2002.

BLAKE, J. G.; LOISELLE, B. A. Manakins (Pipridae) in second-growth and old-growth forests: Patterns of habitat use, movement, and survival. **Auk,** v. 119, n. 1, p. 132-148, Jan 2002. ISSN 0004-8038.

BLENDINGER, P. G.; BLAKE, J. G.; LOISELLE, B. A. Connecting fruit production to seedling establishment in two co-occurring *Miconia* species: consequences of seed dispersal by birds in upper Amazonia. **Oecologia,** v. 167, n. 1, p. 61-73, Sep 2011. ISSN 0029-8549.

BUCHER, T. L.; WORTHINGTON, A. Nocturnal hypothermia and oxygen-consumption in manakins. **Condor,** v. 84, n. 3, p. 327-331, 1982. ISSN 0010-5422.

CESTARI, C. Anting behavior by the White-bearded Manakin (*Manacus manacus*, Pipridae): an example of functional interaction in a frugivorouslekking bird. **Biota Neotropica,** v. 10, n. 4, 2010.

CESTARI, C.; PIZO, M. A. The use of auxiliary courts by the lek-forming White-bearded Manakin *Manacus manacus* (Aves, Pipridae). **Acta Ethologica,** v. 15, n. 1, p. 73-79, 2012.

CESTARI, C.; PIZO, M. A. Lek phenology of the White-bearded Manakin (*Manacus manacus*, Pipridae) in a subtropical region. **Journal of Natural History,** in press.

CHAPMAN, F. M. The courtship of Goulds's manakin (*Manacus vitellinus vitellinus*) on Barro Colorado Island canal zone. **Bulletin of the American Museum of Natural History,** v. 68, p. 471-525, 1935. ISSN 0003-0090.

CHAZDON, R. L.; PEARCY, R. W. The importance of sunflecks for forest understory plants. **Bioscience,** v. 41, n. 11, p. 760-766, 1991.

CLAYTON, D. H. Feather-busting bacteria. **Auk,** v. 116, n. 2, p. 302-304, Apr 1999. ISSN 0004-8038.

COCCON, F.; SCHLINGER, B. A.; FUSANI, L. Male Golden-collared Manakins *Manacus vitellinus* do not adapt their courtship display to spatial alteration of their court. **Ibis,** v. 154, n. 1, p. 173-176, Jan 2012. ISSN 0019-1019.

CONNELL, J. H. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: DEN BOER, P. J. e GRADWELL, G. H. (Ed.).

Dynamics of populations: proceedings of the advanced study. Wageningen: for Agricultural Publishing and Documentation, 1971. p.298-313.

DARNTON, I. The display of the manakin *Manacus manacus*. **Ibis,** v. 100, n. 1, p. 52-58, 1958.

DELOPE, F. et al. Increased detrimental effects of ectoparasites on their bird hosts during adverse environmental-conditions. **Oecologia,** v. 95, n. 2, p. 234-240, Aug 1993. ISSN 0029-8549.

DEVELEY, P. As aves da Estação Ecológica Juréia-Itatins. In: MARQUES, O. A. V. e DULEBA, M. (Ed.). **Estação Ecológica Juréia-Itatins. Ambiente físico, flora e fauna.** Ribeirão Preto: Holos, 2004. p.278-295.

DOUCET, S. M.; MONTGOMERIE, R. Structural plumage colour and parasites in satin bowerbirds Ptilonorhynchus violaceus: implications for sexual selection. **Journal of Avian Biology,** v. 34, n. 3, p. 237-242, Sep 2003. ISSN 0908-8857.

EMLEN, S. T.; ORING, L. W. Ecology, sexual selection, and evolution of mating systems. **Science,** v. 197, n. 4300, p. 215-223, 1977. ISSN 0036-8075.

ENDLER, J. A. The color of light in forests and its implications. **Ecological Monographs,** v. 63, n. 1, p. 1-27, Feb 1993. ISSN 0012-9615.

ENDLER, J. A.; THÉRY, M. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. **American Naturalist,** v. 148, n. 3, p. 421-452, Sep 1996. ISSN 0003-0147.

FISKE, P.; RINTAMAKI, P. T.; KARVONEN, E. Mating success in lekking males: a meta-analysis. **Behavioral Ecology,** v. 9, n. 4, Jul-Aug 1998. ISSN 1045-2249.

FOSTER, M. S. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. **Ecology,** v. 58, n. 1, 1977. ISSN 0012-9658.

GALETTI, M. et al. Ecology and conservation of the Jacutinga *Pipile jacutinga* in the Atlantic forest of Brazil. **Biological Conservation,** v. 82, n. 1, p. 31-39, Oct 1997. ISSN 0006-3207.

GARDEN (ROYAL BOTANIC). **World Checklist of Selected Plant Families** 2011. Disponível em: http://apps.kew.org

GENTRY, A. H. Patterns of neotropical plant-species diversity. **Evolutionary Biology,** v. 15, p. 1-85, 1982. ISSN 0071-3260.

GILLIARD, T. Notes on the courtship behavior of the Blue-backed Manakin (*Chiroxiphia pareola*). **American Museum Novitates,** v. 1942, p. 1-19, 1959.

GOTELLI, N. J.; ENTSMINGER, G. L. **EcoSim: Null models software for ecology**: Acquired Intelligence Inc. & Kesey-Bear 2001.

GROSKIN, H. Observations on "anting" by birds. **Auk,** v. 67, n. 2, p. 201-209, 1950.

HAEMIG, P. D. **Dançarinos e as plantas da família Melastomataceae.** 2006. Dispon;ivel em: http://www.ecologia.info/pipridae-melastomataceae.htm

HAMILTON, W. D.; ZUK, M. HERITABLE TRUE FITNESS AND BRIGHT BIRDS - A ROLE FOR PARASITES. **Science,** v. 218, n. 4570, p. 384-387, 1982. ISSN 0036-8075.

HAMMER, O.; HARPER, D. A. T.; RYAN, P. D. **PAST: Paleontological Statistics Software Package for Education and Data Analysis.** 2001.

HART, B. L. Behavioral defense. In: CLAYTON, D. H. e MOORE, J. (Ed.). **Host-parasite evolution: general principles and avian models**. Oxford: Oxford University Press, 1997. p.59-77 (488 p.).

HEINDL, M.; WINKLER, H. Vertical lek placement of forest-dwelling manakin species (Aves, Pipridae) is associated with vertical gradients of ambient light. **Journal of the Linnean Society,** v. 80, p. 647-658, 2003.

HÖGLUND, J.; ALATALO, R. V. **Leks**. New Jersey: Princeton University Press, 1995. 224.

JANZEN, D. H. Herbivores and the number of tree species in tropical forests. **American Naturalist,** v. 104, n. 940, p. 501-528, 1970. ISSN 0003-0147.

JOHNSGARD, P. A. **Arena birds. Sexual selection and behavior**. Washington and London: Smithsonian Institution Press, 1994. 330.

JORDANO, P. et al. Ligando frugivoria e dispersão de sementes à biologia da conservação. In: DUARTE, C. F.;BERGALLO, H. G., *et al* (Ed.). **Biologia da conservação: essências**. São Paulo: Rima, 2006. p.411-436.

JORDANO, P.; HERRERA, C. M. Shuffling the offspring - uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. **Ecoscience,** v. 2, n. 3, p. 230-237, 1995. ISSN 1195-6860.

JUDSON, O. P.; BENNETT, A. T. D. Anting as food preparation - formic-acid is worse on an empty stomach. **Behavioral Ecology and Sociobiology,** v. 31, n. 6, p. 437-439, Dec 1992. ISSN 0340-5443.

KARUBIAN, J.; DURÃES, R. Effects of seed disperser social behavior on patterns of seed movement and deposition. **Oecologia Brasiliensis,** v. 13, n. 1, p. 45-57, 2009.

KARUBIAN, J. et al. Destination-based seed dispersal homogenizes genetic structure of a tropical palm. **Molecular Ecology,** v. 19, n. 8, p. 1745-1753, Apr 2010. ISSN 0962-1083.

KIRKPATRICK, M.; RYAN, M. J. The evolution of mating preferences and the paradox of the lek. **Nature,** v. 350, n. 6313, p. 33-38, Mar 7 1991. ISSN 0028-0836.

KRIJGER, C. L. et al. Courtship behaviour of manakins and seed bank composition in a French Guianan rain forest. **Journal of Tropical Ecology,** v. 13, p. 631-636, Jul 1997. ISSN 0266-4674.

LEVEY, D. J. Seed size and fruit-handling techniques of avian frugivores. **American Naturalist,** v. 129, n. 4, p. 471-485, Apr 1987a. ISSN 0003-0147.

_____. Sugar-tasting ability and fruit selection in tropical fruit-eating birds. **Auk,** v. 104, n. 2, p. 173-179, Apr 1987b. ISSN 0004-8038.

LILL, A. Sexual behavior of the lek-forming White-bearded Manakin (*Manacus manacus trinidatis* Hartert). **Zeitschrift für Tierpsychology,** v. 36, p. 513-530, 1974a.

_____. Social organization and space utilization in the lek-forming White-bearded Manakin (*Manacus manacus trinitatis* Hartert). **Zeitschrift für Tierpsychology** v. 36, p. 513-530, 1974b.

_____. Lek behavior in the Golden-headed Manakin, *Pipra erythrocephala*, in Trinidad, West Indies. **Forsch Verhalt,** v. 18, p. 1-84, 1976.

LOISELLE, B. et al. Ecological redundancy in seed dispersal system: a comparison between manakins (Aves:Pipridae) in two tropical forests. In: DENNIS, A. J.; SCHUPP, E. W., *et al* (Ed.). **Seed dispersal: theory and its application in a changing world**. Wallingford, UK: CABI Publishing, 2007. p.178-195.

LOISELLE, B. A.; BLAKE, J. G. Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. In: MORRISON, M. L.; RALPH, C. J., *et al* (Ed.). **Avian foraging: theory, methodology, and applications**, 1991. (Studies in Avian Biology).

_____. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. **Ecology,** v. 80, n. 1, p. 330-336, Jan 1999. ISSN 0012-9658.

LORENZI, H. **Árvores brasileiras. Manual de identificação e cultivo de plantas arbóreas do Brasil**. 2. São Paulo: Plantarum, 1998.

_____. **Árvores brasileiras. Manual de identificação e cultivo de plantas arbóreas do Brasil**. 3. São Paulo: Plantarum, 2009a.

_____. **Árvores brasileiras. Manual de identificação e cultivo de plantas arbóreas do Brasil**. 1. São Paulo: Plantarum, 2009b.

MAMEDE, M. C. H. et al. Mata Atlântica. In: MARQUES, O. A. V. e DULEBA, W. (Ed.). **Estação Ecológica Juréia-Itatins. Ambiente físico, flora e fauna**. Ribeirão Preto: Holos, 2004. p.115-132.

MARQUES, O. A. V.; SAZIMA, I. História natural dos répteis da Estação Ecológica Juréia-Itatins. In: MARQUES, O. A. V. e DUBELA, W. (Ed.). **Estação Ecológica Juréia-Itatins. Ambiente físico, flora e fauna**. Ribeirão Preto: Holos, 2004. p.157-177.

MARTIN, P.; BATERSON, P. **Measuring behaviour, an introductory guide**. Cambridge: Cambridge University Press, 1986.

MARTINS, A. B. et al. O gênero *Miconia* Ruiz & Pav. (Melastomataceae) no Estado de São Paulo. **Acta Botanica Brasilica,** v. 10, n. 2, p. 267-316, 1996.

OLSON, D. H.; MCDOWELL, M. K. A comparison of White-bearded Manakin (*Manacus manacus*) populations and lek systems in Suriname and Trinidad. **Auk,** v. 100, n. 3, p. 739-742, 1983. ISSN 0004-8038.

ORING, L. W.; LANK, D. B. Sexual selection, arrival times, philopatry and site fidelity in the polyandrous Spotted Sandpiper. **Behavioral Ecology and Sociobiology,** v. 10, n. 3, p. 185-191, 1982. ISSN 0340-5443.

PASSOS, L.; OLIVEIRA, P. S. Interactions between ants, fruits and seeds in a restinga forest in south-eastern Brazil. **Journal of Tropical Ecology,** v. 19, p. 261-270, May 2003. ISSN 0266-4674.

PIZO, M. A. Frugivory by birds in degraded areas of Brazil. In: DENNIS, A. J.; SCHUPP, E. W., *et al* (Ed.). **Seed dispersal: Theory and its application in a changing world**. Wallingford: CAB International, 2007. p.615-627.

PIZO, M. A.; OLIVEIRA, P. S. The use of fruits and seeds by ants in the Atlantic forest of southeast Brazil. **Biotropica,** v. 32, n. 4B, p. 851-861, 2000. ISSN 0006-3606.

POTTER, E. F. Anting in wild birds, its frequency and probable purpose. **Auk,** v. 87, n. 4, p. 692-&, 1970. ISSN 0004-8038.

PRICE, P. H. **Evolutionary biology of parasites**. Princeton: Princeton University Press, 1980.

PRUM, R. O. Observations of the White-fronted Manakin (*Pipra serena*) in Suriname. **Auk,** v. 112, p. 384-387, 1985.

_____. Phylogenetic analysis of the evolution of display behavior in the neotropical manakins (Aves, Pipridae). **Ethology,** v. 84, n. 3, p. 202-231, Mar 1990. ISSN 0179-1613.

REMSEN JR., J. V.; ROBINSON, S. K. A classification scheme for foraging behavior of birds in terrestrial habitats. **Studies in Avian Biology,** v. 13, p. 144-160, 1990.

RYDER, T. B.; BLAKE, J. G.; LOISELLE, B. R. A. A test of the environmental hotspot hypothesis for lek placement in three species of Manakins (Pipridae) in Ecuador. **Auk,** v. 123, n. 1, p. 247-258, Jan 2006. ISSN 0004-8038.

SAMPAIO, D. Restinga. In: SAMPAIO, D.;SOUZA, V. C., *et al* (Ed.). **Árvores da restinga: guia de identificação**. São Paulo: Neotrópica, 2005. p.25-30 (275).

SAZIMA, I. Anting behavior with millipedes by the dendrocolaptid bird *Xiphocolaptes albicollis* in Southeastern Brazil. **Biota Neotropica**. v. 9, n.1, 2009.

SCHERER, A.; MARASCHIN-SILVA, F.; BAPTISTA, L. R. M. Padrões de interações mutualísticas entre espécies arbóreas e aves frugívoras em uma comunidade de Restinga no Parque Estadual de Itapuã, RS, Brasil. **Acta Botânica Brasílica,** v. 21, n. 1, p. 203-212, 2007.

SCHUPP, E. W. Quantity, quality and the effectiveness of seed dispersal by animals. **Vegetatio,** v. 108, p. 15-29, Jun 1993. ISSN 0042-3106.

SCHUPP, E. W.; JORDANO, P.; MARIA GOMEZ, J. Seed dispersal effectiveness revisited: a conceptual review. **New Phytologist,** v. 188, n. 2, p. 333-353, 2010. ISSN 0028-646X.

SHOREY, L. Mating success on White-bearded Manakin (*Manacus manacus*) leks: male characteristics and relatedness. **Behavioral Ecology and Sociobiology,** v. 52, n. 6, p. 451-457, Nov 2002. ISSN 0340-5443.

SHOREY, L. et al. Fine-scale genetic structuring on *Manacus manacus* leks. **Nature,** v. 408, n. 6810, p. 352-353, Nov 16 2000. ISSN 0028-0836.

SICK, H. Courtship behavior in the manakins (Pipridae): a review. **Living Bird,** v. 6, p. 5-22, 1967.

_____. **Ornitologia Brasileira**. Rio de Janeiro: Nova Fronteira, 1997.

SIGRIST, T. **Aves do Brasil: uma visão artística**. São Paulo: Ministério da Cultura, 2006. 672.

SIMMONS, K. E. L. A review of the anting-behavior of passerine birds. **British Birds,** v. 50, p. 401-424, 1957.

_____. Anting movements and their relationship to certain other behavior patterns. **Ibis,** v. 101, n. 3, p. 368-373, 1959.

_____. Anting and problem of self-stimulation. **Journal of Zoology,** v. 149, p. 145-&, 1966. ISSN 0952-8369.

SNOW, D. A field study of the Black and White Manakin, *Manacus manacus*, in Trinidad. **Zoologica,** v. 47, n. 8, p. 65-104, 1962.

_____. Coevolution of birds and plants. In: GREENWOOD, P. H. e FOREY, P. L. (Ed.). **The evolving biosphere**. Cambridge: University Press, 1981. p.169-178 (264 pp).

_____. Family Pipridae (Manakins). In: DEL HOYO, J.; ELLIOT, A., *et al* (Ed.). **Handbook of the Birds of the World: Cotingas to Pipits and Wagtails**. Barcelona: Lynx Editions, v.9, 2004. p.110-169 (863 p.).

STEIN, A. C.; UY, J. A. C. Plumage brightness predicts male mating success in the lekking Golden-collared Manakin, *Manacus vitellinus*. **Behavioral Ecology,** v. 17, n. 1, p. 41-47, Jan-Feb 2006. ISSN 1045-2249.

TARIFA, J. R. Unidades climáticas dos maciços litorâneos da Juréia-Itatins. In: MARQUES, O. A. V. e DULEBA, W. (Ed.). **Estação Ecológica Juréia-Itatins. Ambiente físico, flora e fauna**. Ribeirão Preto: Holos, 2004. p.42-50.

THÉRY, M. **Ecologie et comportement des oiseaux Pipridae en Guyane: leks, frugivorie et dissemination des graines**. 1990. I´Université Paris

_____. The evolution of leks through female choice - differential clustering and space utilization in 6 sympatric manakins. **Behavioral Ecology and Sociobiology,** v. 30, n. 3-4, p. 227-237, Apr 1992. ISSN 0340-5443.

THÉRY, M.; LARPIN, D. Seed dispersal and vegetation dynamics at a Cock-of-the-Rock's lek in the tropical forest of French Guiana. **Journal of Tropical Ecology,** v. 9, p. 109-116, 1993.

THÉRY, M.; VEHRENCAMP, S. L. Light patterns as cues for mate choice in the lekking White-throated Manakin (*Corapipo gutturalis*). **Auk,** v. 112, n. 1, p. 133-145, Jan 1995. ISSN 0004-8038.

TRAIL, P. W. Predation and antipredator behavior at Guianan Cock-of-the-Rock leks. **Auk,** v. 104, n. 3, p. 496-507, Jul 1987. ISSN 0004-8038.

UY, J. A. C.; ENDLER, J. A. Modification of the visual background increases the conspicuosness on Golden-collared Manakin displays. **Behavioral Ecology,** v. 15, n. 6, p. 1003-1010, 2004.

VEHRENCAMP, S. L.; BRADBURY, J. W.; GIBSON, R. M. The energetic cost of display in male Sage Grouse. **Animal Behaviour,** v. 38, p. 885-896, Nov 1989. ISSN 0003-3472.

WENNY, D. G.; LEVEY, D. J. Directed seed dispersal by bellbirds in a tropical cloud forest. **Proceedings of the National Academy of Sciences of the United States of America,** v. 95, n. 11, p. 6204-6207, May 26 1998. ISSN 0027-8424.

WESTCOTT, D. A. Lek locations and patterns of female movement and distribution in a Neotropical frugivorous bird. **Animal Behaviour,** v. 53, p. 235-247, Feb 1997. ISSN 0003-3472.

WESTCOTT, D. A. et al. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. **Oecologia,** v. 146, n. 1, p. 57-67, Nov 2005. ISSN 0029-8549.

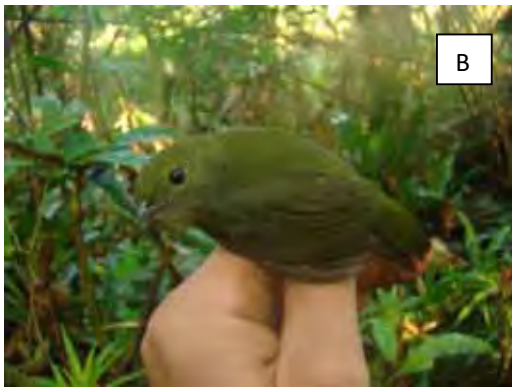
WILLIS, E. O. Behavior of Plain-brown Woodcreepers, *Dendrocincla fuliginosa*. **Wilson Bulletin,** v. 84, n. 4, p. 377-420, 1972. ISSN 0043-5643.

WORTHINGTON, A. Population size and breeding rhythms of two species of manakins in relation to food supply. In: LEIGH JR., E. G.; RAND, A. S., *et al* (Ed.). **The ecology of a tropical forest: reasonal rhythms and long-term changes**. Washington D. C,: Smithsonian Institution Press, 1982. p.213-225 (480 pp.).

WORTHINGTON, A. H. Adaptations for avian frugivory: assimilation efficiency and gut transit time of *Manacus vitellinus* and *Pipra mentalis*. **Oecologia,** v. 80, n. 3, p. 381-389, 1989. ISSN 0029-8549.

Appendices

APPENDIX 1. Adult male (A), adult female (B) and juvenile male (C) of White-bearded Manakin (*Manacus manacus*). Females and juveniles have similar green color pattern in their plumages. We distinguished them observing their behavior. Juvenile males snap their wings when visiting courts while adult females did not. Photos: César Cestari



APPENDIX 2. Lekking male of White-bearded Manakin (*Manacus manacus*). Photo: César Cestari.

APPENDIX 3. *Restinga* ecosystem in Juréia Itatins Ecological Station, Iguape, southeastern Brazil. Photo: César Cestari.

APPENDIX 4. Male of *Manacus manacus* carrying a leaf to outside the court. This is a common court-cleaning maneuver used by *Manacus* spp (see chapter 3). Photo taken by M. D. England and published in J. del Hoyo, A. Elliot, and D. A. Christie. Handbook of the Birds of the World: Cotingas to Pipits and Wagtails. Barcelona, Lynx Editions.

APPENDIX 5. Some species of plants consumed by *Manacus manacus* in *restinga* forests from southeastern Brazil (see chapter 5). (A) *Anthurium* sp., (B) *Byrsonima ligustrifolia*, (C) *Blepharocalyx salicifolius*, (D) *Chiococca alba*, (E) *Calyptranthes concinna*, (F) *Cecropia pachystachia*, (G) *Davilla rugosa*, (H) *Doliocarpus* sp., (I) *Erythroxylum decidum*, (J) *Eugenia pluriflora*, (K) *E. sulcata*, (L) *E. umbelliflora*, (M) *Ficus enormis*, (N) *Gaylussacia brasiliensis*, (O) *Guarea macrophyla*, (P) *Guatteria nigrescens*, (Q) *Guapira opposita*, (R) *Hedyosmium brasiliensis*, (S) *Ilex brevicups*, (T) *I. paraguaiensis*, (U) *I. theezans*, (V) *Lacistema pubescens*, (W) *Myrcia bicarinata*, (X) *Miconia cubatanensis*, (Y) *M. hymenonervia*, (Z) *M. ridigiuscula*, (A1) *Maytenus robusta*, (B1) *Ocotea pulchella*, (C1) *Ossaea* sp., (D1) *Psychotria carthagenensis*, (E1) *Pera glabrata*, (F1) *Pimenta* cf. *pseudocaryophilus*, (G1) *Paullinia* sp., (H1) *Phoradendron* sp., (I1) *Rapanea ferruginea*, (J1) *R. parviflora*, (L1) *Rudgea* sp., (M1) *Schefflera angustissima*, (N1) *Siphoneugena guilfoyleiana*, (O1) *Symplocos variabilis*, and (P1) *Ternstroemia brasiliensis*. Photos: César Cestari.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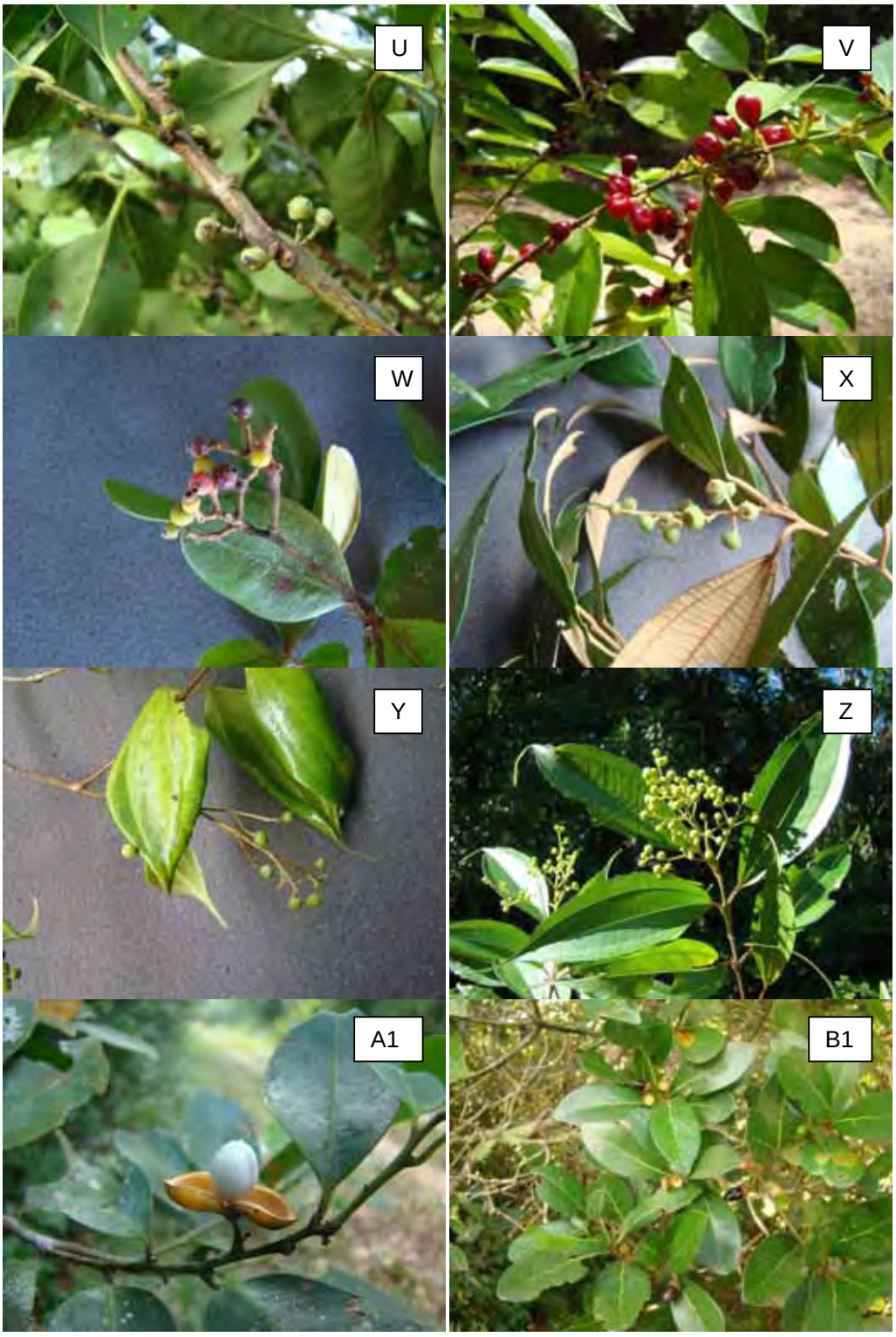
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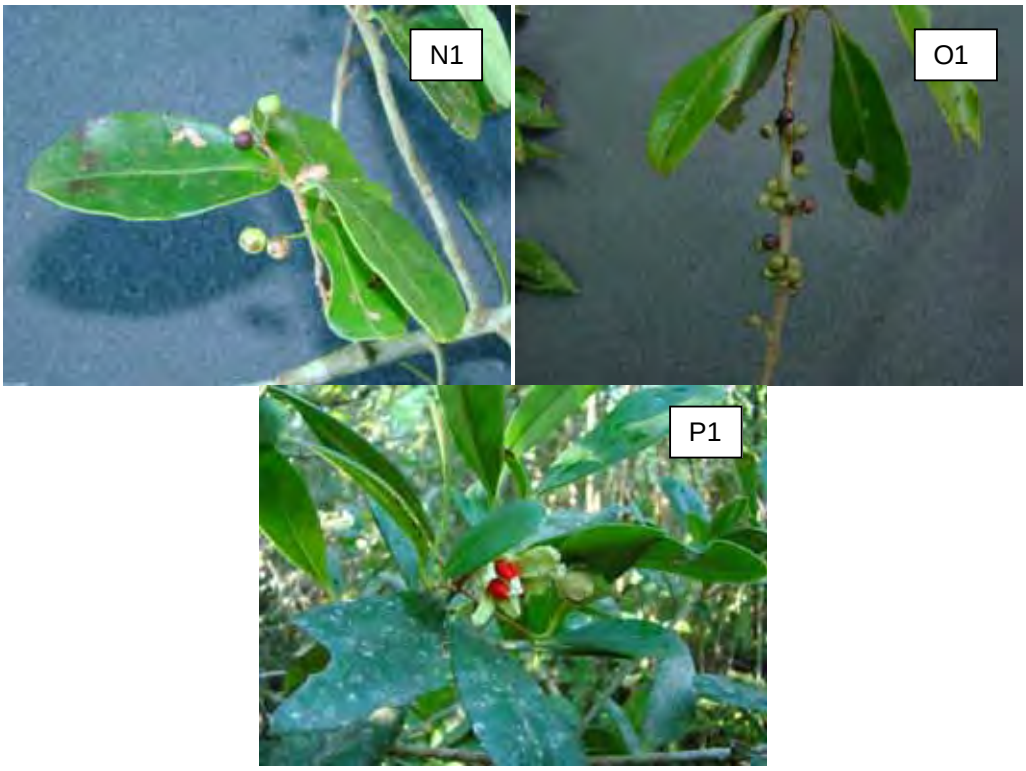
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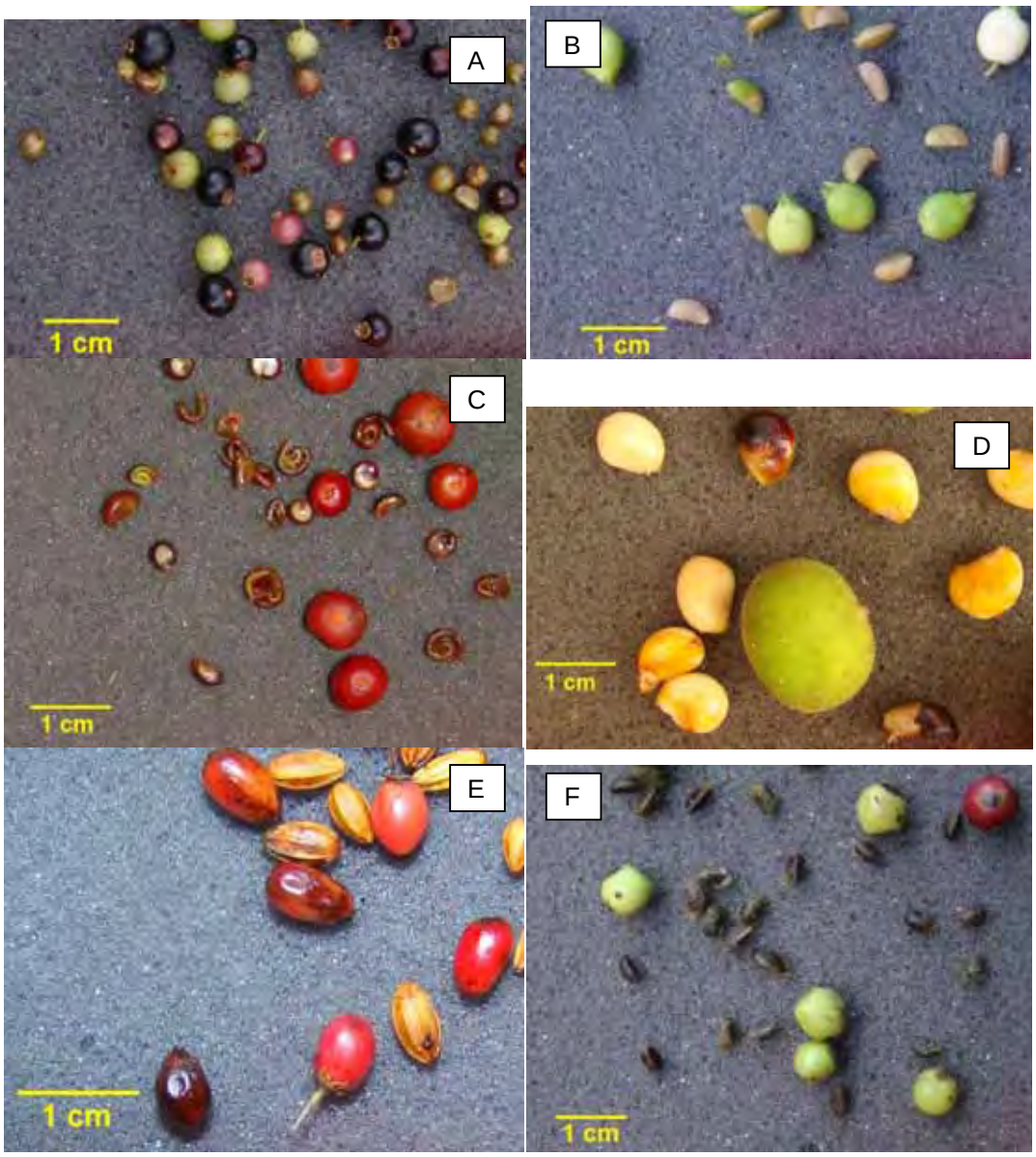
APPENDIX 6. A cage with foam-lined walls wherein manakins were kept for 30 minutes (see chapter 7). Photo: César Cestari

APPENDIX 7. Adult male of *Manacus manacus* with transmissor on the back (see chapter 7). Photo: César Cestari

APPENDIX 8. Some fruits and seeds consumed by *Manacus manacus* in *restinga* forests from southeastern Brazil (see chapter 7). (A) *Blepharocalyx salicifolius*, (B) *Chiococca alba*, (C) *Calyptranthes concinna*, (D) *Doliocarpus* sp., (E) *Erythroxylum decidum*, (F) *Eugenia pluriflora*, (G) *E. sulcata*, (H) *E. umbelliflora*, (I) *Guatteria nigrescens*, (J) *Guapira opposita*, (K) *Hedyosmium brasiliensis*, (L) *I. theezans*, (M) *Myrcia bicarinata*, (N) *Miconia cubatanensis*, (O) *M. hymenonervia*, (P) *M. ridigiuscula*, (Q) *Maytenus robusta*, (R) *Ocotea pulchella*, (S) *Ossaea* sp., (T) *Psychotria carthagenensis*, (U) *Phoradendron* sp. (V) *Pera glabrata*, (W) *Pimenta* cf. *pseudocaryophilus*, (X) *Paullinia* sp., (Y) *Rapanea ferruginea*, (Z) *R. parviflora*, (A1) *Rudgea* sp., (B1) *Schefflera angustissima*, (C1) *Siphoneugena guilfoyleiana*, and (D1) *Ternstroemia brasiliensis.* Photos: César Cestari.

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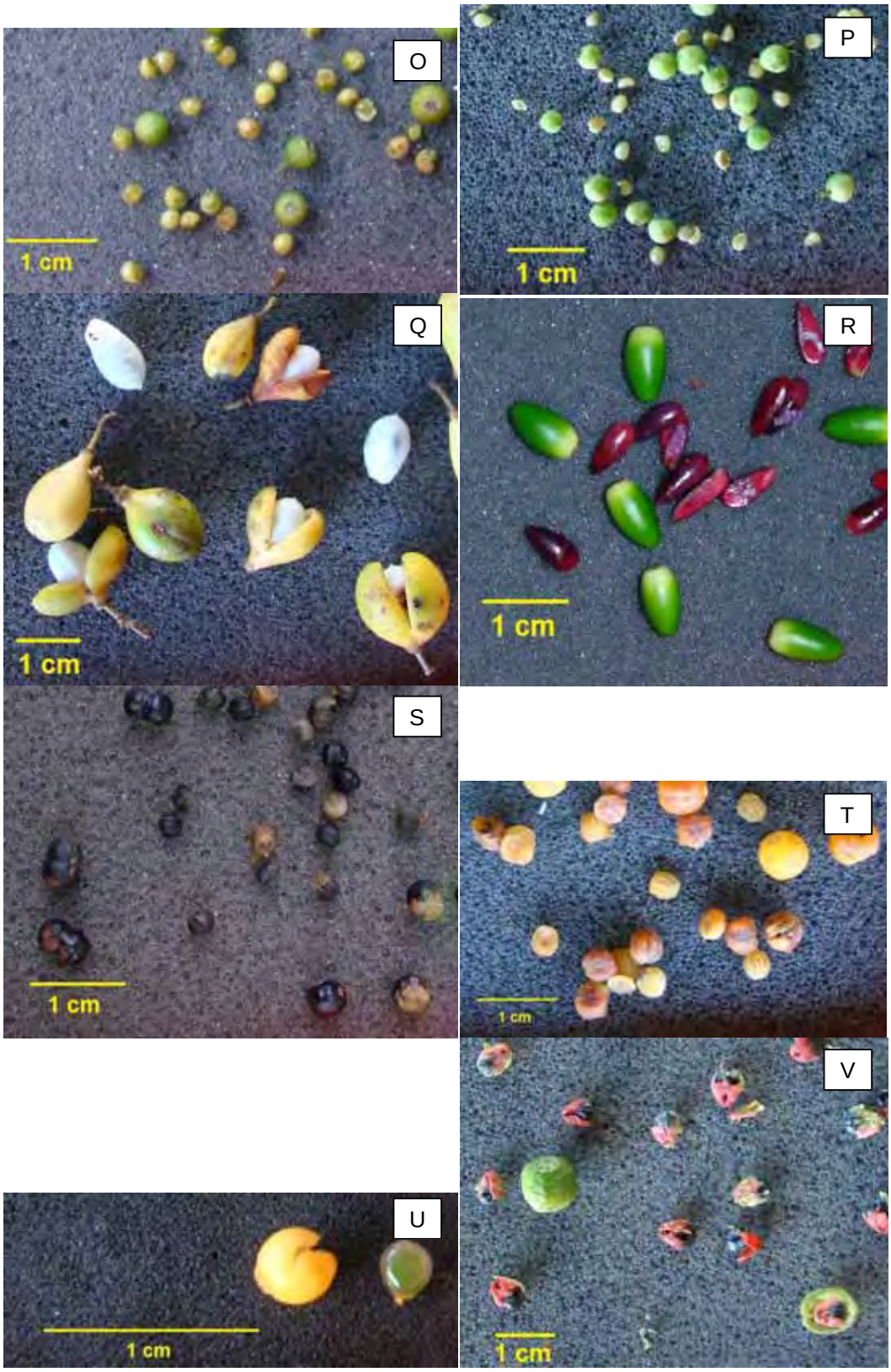
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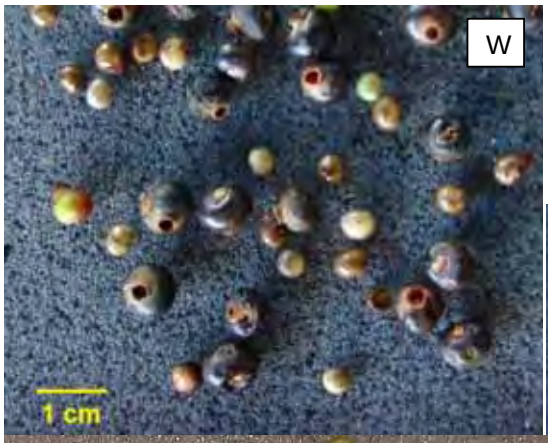
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