Universidade de Brasília

Instituto de Ciências Biológicas

Programa de Pós-Graduação em Ecologia

ECOLOGIA COMPARADA DE TIRANÍDEOS (AVES)

RESIDENTES E MIGRATÓRIOS

ANDRÉ DE CAMARGO GUARALDO

BRASÍLIA – DF

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Tese apresentada ao Programa de Pós-graduação em Ecologia, do Instituto de Ciências Biológicas da Universidade de Brasília, como requisito parcial para a obtenção do título de Doutor em Ecologia.

Orientador: Miguel Ângelo Marini, Ph.D.

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CAPA: Fotomontagem das espécies utilizadas como modelo ao longo deste estudo. À esquerda, um indivíduo adulto da espécie residente, guaracava-de-topete-uniforme (*Elaenia cristata*), marcado com anilhas coloridas. À direita, um indivíduo adulto da espécie migratória, chibum (*Elaenia chiriquensis*).

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SUMÁRIO

APRESENTAÇÃO

Este documento é o produto de quatro anos de estudos e discussões com especialistas de diversas áreas do conhecimento, incluindo a ecologia de aves, ecologia da migração, biologia reprodutiva e comportamento. Os resultados deste trabalho encontram-se divididos em três capítulos, estruturados visando a publicação de artigos científicos independentes. Apesar disso, cada capítulo é complementar aos demais, de modo que sua análise conjunta convença o leitor da tese central do trabalho: o processo de migração impõe custos tanto ao indivíduos migratórios, quanto àqueles residentes com os quais interage. Especificamente, há um enfoque nas consequências do comportamento migratório e da interação entre migrantes e residentes sobre a dieta e aspectos reprodutivos dos indivíduos.

Os capítulos são precedidos por uma introdução geral, cujo objetivo é fornecer ao leitor o arcabouço teórico mínimo necessário à compreensão do restante do trabalho, bem como o estado da arte dos estudos de migração de aves na região Neotropical. Cada capítulo será publicado como um artigo científico em revistas especializadas internacionais e, por esse motivo, encontram-se versados em inglês. Para manter uma uniformidade visual, todos os capítulos foram formatados de acordo com as exigências de uma destas revistas (*The Auk: Ornithological Advances*). Por fim, a última seção deste documento apresenta uma visão crítica sobre os principais resultados e conclusões obtidos ao longo de cada capítulo, além de diretivas que possibilitem outros avanços no estudo deste processo ecológico que há milênios vem cativando o público em geral, filósofos e pesquisadores.

RESUMO

O fenômeno da migração das aves atrai a atenção de pesquisadores e leigos há milênios. Embora esse interesse histórico sobre o tema tenha propiciado o desenvolvimento de um amplo arcabouço teórico, características culturais e da história da própria ciência direcionaram o estado da arte da ecologia de aves migratórias. Quase a totalidade dos esforços dos pesquisadores permaneceram por séculos focados nos sistemas de migração envolvendo as espécies que se reproduzem na Europa (sistema Paleártico) e América do Norte (sistema Neártico-Neotropical) e que realizam migrações de longa distância. Nesse contexto, os objetivos gerais deste trabalho consistiram da avaliação (1) do sucesso reprodutivo dos migrantes como um produto indireto dos eventos vivenciados por eles durante o período não-reprodutivo e (2) da influência direta (competição) e/ou indireta (competição aparente) da chegada e permanência de uma grande população de migrantes sobre a dieta e reprodução dos residentes. Para tanto, duas espécies de Tyrannidae congêneres foram selecionadas como modelos, *Elaenia cristata* (guaracava-de-topete-uniforme) – residente na área de estudo – e *E. chiriquensis* (chibum), migratória. O estudo foi realizado em uma área de Cerrado *sensu stricto* em uma unidade de preservação na região central do Brasil (Brasília, Distrito Federal). Inicialmente, foi realizada a descrição isotópica dos micro-hábitats utilizados e dieta apresentada por residentes e migrantes ao longo de três etapas de seu ciclo anual (i.e. períodos de reprodução, invernada ou repouso reprodutivo e muda; Capítulo 1). Os resultados mostraram que, enquanto os residentes utilizaram diferentes micro-hábitats ao longo do ano, os migrantes buscaram ambientes semelhantes ao longo de sua jornada migratória. Adicionalmente, tanto residentes quanto migrantes

ocuparam nichos tróficos isotópicos variáveis em cada período. Para explicar os resultados encontrados, foram discutidas hipóteses sobre a demanda nutricional distinta entre espécies e as estratégias utilizadas pelos migrantes durante sua jornada. No capítulo 2, foi verificado se as hipóteses existentes sobre efeitos em cascata (EC) também são válidas para o sistema de migração intratropical sulamericano. O primeiro objetivo do capítulo foi verificar as influências das características dos sítios de invernagem sobre o sucesso reprodutivo dos migrantes. Considerando que alguns indivíduos podem atrasar sua chegada e/ou o início de seu período reprodutivo devido às condições vivenciadas no período não reprodutivo, o segundo objetivo específico foi avaliar as consequências da nidificação tardia dos indivíduos sobre as taxas de crescimento dos ninhegos. Para tanto, foram coletados os dados de sucesso reprodutivo dos casais pelo acompanhamento regular de seus ninhos, os valores das razões isotópicas de garras e penas dos parentais e a curva de crescimento dos ninhegos. Os resultados obtidos refutaram a ocorrência de EC sobre ambos os aspectos avaliados. Para explicar o padrão observado, foram discutidas hipóteses alternativas, como a compensação dos EC pelos indivíduos e as consequências da permanência dos indivíduos no sítio de reprodução durante o período não reprodutivo. Por fim, o capítulo 3 enfocou a ocorrência e possíveis consequências da competição por recursos entre residentes e migrantes durante o período reprodutivo. Para tanto, foram avaliados os nichos isotópicos alimentares de adultos e ninhegos, além das estratégias de forrageamento e reprodução adotadas por ambas as espécies. Embora os dados evidenciem a ausência de competição por alimento entre as espécies, os resultados mostraram padrões menos claros em relação às suas estratégias reprodutivas e destacaram aspectos biológicos e ecológicos que ainda carecem de elucidação. Por esse motivo, foram discutidas

explicações alternativas à competição para o sistema estudado, destacando questões e estratégias para um maior avanço na compreensão das relações entre residentes e migrantes intratropicais sulamericanos. Em síntese, o processo de migração influenciou de modo direto ou indireto aspectos reprodutivos e de uso de micro-hábitats tanto de migrantes quanto de residentes. No entanto, os dados demonstram que o comportamento migratório não deve ser utilizado como única explicação para as estratégias adotadas por essas espécies.

Palavras chave: Cerrado; *Elaenia chiriquensis*; *Elaenia cristata*; isótopos estáveis; migração; ninhos; reprodução; forrageamento; competição interespecífica.

ABSTRACT

Bird migration is a phenomenon that has been attracting the attention of researchers and ordinary people for millennia. Although the historical interest on the subject stimulated the development of a broad theoretical knowledge, cultural aspects and historical traits of the scientific process itself directed the state of the art of bird migration ecology. For centuries, researchers focused almost all of their efforts on the migratory systems involving long-distance migrants from Europe (Palearctic system) and North America (Nearctic-Neotropical system). In this context, this study had as general goals the evaluation (1) of whether the breeding success of migrants is an indirect by-product of the events they experienced during the non-breeding season; and (2) of how the arrival of a large population of migrants directly (competition) and indirectly (apparent competition) affects the diet and breeding of residents. To do so, two species were selected as models, the Plain-crested Elaenia *Elaenia cristata* – resident at the study site – and the migratory Lesser Elaenia *E. chiriquensis*. We conducted fieldworks in an area of preserved *sensu stricto* Cerrado in central Brazil (Brasília, Federal District). First, we developed an isotopic description of the microhabitats used by residents and migrants and their diets in each of three periods of their annual cycle (i.e., breeding, wintering, and molting; Chapter 1). Results showed that while residents used different microhabitats along the year, migrants searched for similar environments along their migratory journey. Moreover, both residents and migrants occupied variable isotopic trophic niches in each period. Then, we discussed the results found based on hypotheses that species may have different nutritional demands and on the strategies migrants had along their journey. In Chapter 2, we verified whether the existing hypotheses relative to carry-over effects (COEs)

are also valid for the South American Intratropical migratory system. The first goal of this chapter was to verify whether the breeding success of individuals was affected by traits of the non-breeding grounds. Considering that some individuals might delay their arrival and/or nesting period due to conditions faced at their non-breeding grounds, the second goal of this chapter was to evaluate the consequences of late nesting on nestlings' growth rate. To do so, we recorded the breeding success of pairs by periodically monitoring their nests, used stable isotope ratios of claws and feathers from parents, and nestling growth curves. Results did not support the occurrence of COEs for both evaluated aspects. To explain the patterns found, we discussed alternative hypotheses, such as the compensation of COEs by individuals, and the consequences of overwintering at the breeding grounds. Finally, Chapter 3 focused on checking the occurrence and possible consequences of competition for resources between residents and migrants during their breeding period. Thus, we evaluated the feeding isotopic niche of adults and nestlings, besides the foraging and breeding strategies adopted by both species. Despite the data showing an absence of interspecific competition for food, results showed less clear patterns regarding their breeding strategies and highlighted some biological and ecological aspects that still need to be clarified. For this reason, we discuss explanations alternative to competition, and propose questions and strategies for further advances on the relationships between residents and South American Intratropical migrants. In summary, the migratory process directly or indirectly affected the breeding aspects and types of microhabitat used by both migrants and residents. Nevertheless, data show that migratory behavior should not be considered as a unique driver of the strategies adopted by these species.

Key words: Cerrado; *Elaenia chiriquensis*; *Elaenia cristata*; stable isotopes; migration; nest; breeding; foraging; interspecific competition.

INTRODUÇÃO GERAL

Definições

A migração é um fenômeno que vem atraindo o interesse de leigos, filósofos e pesquisadores há dezenas de séculos (Lincoln 1979). No entanto, o termo migração tem sido equivocadamente utilizado para se referir a diferentes tipos de movimentos de organismos (Newton 2008b), dentre os quais podem ser destacados os movimentos diários, a dispersão e o nomadismo. Os movimentos diários se resumem a deslocamentos de curta distância, geralmente restritos a poucas centenas de metros e à área de vida do indivíduo (Newton 2008b). A dispersão envolve o deslocamento dos indivíduos em direções aleatórias pelo hábitat em determinada etapa da vida do indivíduo: dois exemplos de dispersão são os deslocamentos realizados pelos jovens após se tornarem independentes dos pais (dispersão natal) e a movimentação dos adultos pelo hábitat após o término de seu período reprodutivo (dispersão não-reprodutiva; Newton 2008b). No caso do nomadismo, o deslocamento se caracteriza pela ocupação temporária de uma série não ordenada de sítios, de acordo com a disponibilidade de recursos dos quais a espécie necessita (Newton 2008b). No sentido terminológico mais correto, a migração das aves é o único tipo de movimento que apresenta regularidade e sazonalidade, envolvendo um deslocamento “entre duas áreas distintas, geralmente um sítio de reprodução e outro de invernada ou repouso reprodutivo” (Schüz *et al.* 1971; Webster *et al.* 2002).

A conspicuidade e ocorrência global da migração entre as aves (Berthold 2001c; Newton 2008b) têm levado à produção de incontáveis trabalhos sobre o tema. Dentre as principais linhas de abordagem, se destacam desde a busca por respostas a questões básicas como “quais espécies apresentam comportamento migratório?”

(e.g.: Hayes *et al.* 1994; Capllonch e Lobo 2005) ou “de onde vêm e para onde vão os migrantes?” (e.g.: Sick 1983; Antas 1994; Kelly *et al.* 2005), até a proposição e verificação de hipóteses mais específicas envolvendo a ecologia (e.g.: Rappole e Warner 1976; Martin e Finch 1995; Joseph 1996) e a fisiologia das espécies migrantes (e.g.: Bairlein 2002; McWilliams e Karasov 2004) e estudos sobre a evolução deste fenômeno na classe Aves (e.g.: Baker 1978; Cox 1985; Alerstam e Hedenstrom 1998; Alerstam *et al.* 2003).

Padrões e sistemas de migração

Em sua maioria, as espécies de aves migratórias realizam deslocamentos latitudinais rumo a locais com condições climáticas favoráveis à sua reprodução ou repouso reprodutivo. Ainda, os migrantes podem se deslocar pelo continente seguindo determinadas condições climáticas como, por exemplo, regiões com amplitude térmica semelhante (Joseph e Stockwell 2000). No entanto, algumas espécies podem compensar as variações climáticas locais por meio de migrações altitudinais e, portanto, sem a necessidade de deslocamentos de grande distância. Por exemplo, a variação climática provocada pela variação na altitude ocasiona diferenças na fenologia de flores e frutos, acarretando em uma oferta sequencial de recursos às aves frugívoras e nectarívoras ao longo do gradiente altitudinal. Neste contexto, pode ser citado o comportamento de jacutingas (*Pipile jacutinga*) e de tucanos-de-bico-verde (*Ramphastos dicolorus*) acompanhando a frutificação sequencial do palmito-Jussara (*Euterpe edulis*) na Serra do Mar (Castro *et al.* 2007; Castro *et al.* 2012).

Em geral, após adquirir conhecimentos básicos de migração local e regional de muitas espécies, os pesquisadores avançam para um processo de análise comparativa dos resultados obtidos com aqueles existentes para outros sistemas de migração. Dada a pressão existente para a produção de resultados cada vez mais avançados na ciência, este comportamento dos pesquisadores promoveu uma concentração dos esforços no avanço do conhecimento daqueles sistemas que já vinham sendo estudados e, consequentemente, fez com que ainda hoje apenas alguns sistemas de migração sejam bem conhecidos. Dentre estes últimos, dois se destacam: (1) o sistema Paleártico (e.g.: Berthold 2001a; Newton 2008c), que engloba as espécies que migram longas distâncias entre a Europa e a África/Ásia; e (2) o sistema Neotropical (e.g.: Lincoln 1979; Greenberg e Marra 2004), que compreende os migrantes que se deslocam do norte da América do Norte rumo ao sul, alcançando a América Central e o norte e centro da América do Sul.

Somente no final do século XX dois estudos evidenciaram a grande diversidade de movimentos migratórios que ocorriam na região Neotropical, demonstrando a necessidade de maior enfoque na migração das espécies na América do Sul (Levey 1994) e sugerindo uma nova classificação para os sistemas de migração existentes (Hayes 1995). Segundo este último trabalho, as regiões biogeográficas por onde as espécies migratórias se deslocam devem ser consideradas ao se definir cada sistema, de modo que três sistemas distintos podem ser identificados no continente americano. O primeiro sistema, denominado Neártico-Neotropical, é formado pelas espécies migratórias que se reproduzem na América do Norte e invernam na zona tropical do continente. Consequentemente, todas as espécies migratórias que se reproduzem na América do Sul passam a compor dois novos sistemas de migração: (1) o sistema Neotropical-Austral, que compreende as espécies que se reproduzem na porção sul da América do Sul e migram para o norte durante o repouso reprodutivo; e (2) o sistema Intratropical, que inclui as espécies que também realizam migrações no sentido norte sul, mas de modo restrito à região tropical da América do Sul e, portanto, deslocamentos de curta distância em relação aos demais sistemas.

Efeitos em cascata

Há uma demanda muito grande por conhecimentos que vão além da identidade dos protagonistas do fenômeno da migração. Isto se confirma ao destacar a situação de declínio populacional em que se encontram inúmeras espécies de aves migratórias (e.g: Robbins *et al.* 1989; Sanderson *et al.* 2006). Reconhecidamente, o processo de migração envolve grandes riscos de morte aos migrantes, seja pela distância percorrida, pela ação de fenômenos naturais, como chuvas e ventos, ou devido a interferências antrópicas como a destruição de ambientes naturais, a caça e a construção de estruturas ao longo da rota das aves (Newton 2008a). Adicionalmente, a natureza cíclica do processo de migração faz com que algumas situações vivenciadas pelos indivíduos em uma dada etapa do seu ciclo anual influenciem indiretamente os eventos das etapas subsequentes (Sherry e Holmes 1996; Newton 2006).

Hipóteses para avaliar estes efeitos denominados efeitos em cascata, ou *carry-over effects*, foram propostas e testadas utilizando essencialmente espécies de aves migratórias nos sistemas Paleártico e Neártico-Neotropical. Dentre elas, a hipótese que tem sido abordada com maior frequência correlaciona positiva e significativamente o sucesso reprodutivo dos indivíduos migrantes de algumas espécies com a qualidade de seus sítios de repouso reprodutivo e/ou dos sítios que utilizaram como pontos de parada e de forrageamento durante a migração (Norris *et al.* 2004; Reudink *et al.* 2009). Por exemplo, esta linha de raciocínio foi base para estudos que demonstram a importância da qualidade dos sítios de invernada para a regulação das populações de espécies migratórias (Kaminski e Gluesing 1987; Gill *et al.* 2001). Outras duas hipóteses foram propostas e corroboradas também em relação à qualidade do sítio de repouso reprodutivo e de parada ao longo da migração. De acordo com estas hipóteses, indivíduos que utilizam sítios não-reprodutivos de melhor qualidade chegam mais cedo ao sítio de reprodução (Marra *et al.* 1998; Gill *et al.* 2001) e com melhor condição física (Marra *et al.* 1998; Ydenberg *et al.* 2002).

Avanços metodológicos

O recente e marcante progresso nos estudos sobre a migração de aves se deve principalmente aos avanços da tecnologia associada aos métodos de marcação e acompanhamento do deslocamento dos indivíduos. Se inicialmente os estudos se baseavam em observações naturalísticas (e.g.: Lincoln 1979) e registros de locais e datas de ocorrência (e.g.: Marini e Cavalcanti 1990), no início do século XX houve uma revolução nas possibilidades de rastreamento da movimentação dos migrantes à longa distância com a invenção da técnica de marcação com anilhas metálicas pelo ornitólogo alemão Johannes Thienemann (Fiedler 2009). Desde então, novas tecnologias foram desenvolvidas e novos métodos introduzidos aos estudos da migração de aves: modelagem de nicho (e.g.: Marini *et al.* 2010; Marini *et al.* 2013), radiotransmissores, radares meteorológicos, rastreadores via satélite (e.g.: Berthold 2001b; Hobson e Norris 2008) e, mais recentemente, os geolocalizadores (e.g.: Shaffer *et al.* 2006; Hobson e Norris 2008; Stutchbury *et al.* 2009; Egevang *et al.* 2010; Jahn *et al.* 2013). Em linhas gerais, estes métodos permitem identificar os locais de origem e as rotas utilizadas pelas espécies monitoradas (e.g.: Gschweng *et al.* 2008; Klaassen *et al.* 2010), além de fornecer dados precisos sobre os horários dos deslocamentos das aves, suas reações às condições climáticas adversas e correntes de vento (e.g.: Gill *et al.* 2005), o grau de conectividade de suas populações (Haig *et al.* 2002) e sua altitude, direção e velocidade de voo (e.g.: Gill *et al.* 2009; Klaassen *et al.* 2010).

Outra categoria de ferramentas utilizadas para o rastreamento dos indivíduos são os marcadores intrínsecos. Além dos bastante popularizados métodos moleculares (Kimura *et al.* 2002; Wink 2006), uma grande evolução metodológica foi introduzida aos estudos de migração na década de 1990 com a aplicação dos métodos de análise de isótopos estáveis (Alisauskas e Hobson 1993; Chamberlain *et al.* 1997). Até então, os métodos de rastreamento existentes restringiam o universo amostral àquelas espécies de aves de médio e grande porte, devido ao peso significativo dos equipamentos que necessitavam ser acoplados às aves e às restrições de detecção dos radares meteorológicos para aves de pequeno porte e bandos pequenos de espécies de médio porte. Atualmente, a tecnologia já possibilita a fabricação de geolocalizadores com até 0,5g, permitindo estudos de migração de espécies com peso corporal mínimo de cerca de 12g. No entanto, a utilização deste marcador extrínseco é por vezes impraticável por demandar a recaptura dos indivíduos para o acesso às informações coletadas pelo dispositivo. Neste contexto, o advento das técnicas que utilizam marcadores intrínsecos abre um novo e amplo horizonte às pesquisas sobre migração de aves de pequeno porte.

Recentemente, o aprimoramento dos métodos de análise de isótopos estáveis tornou esta técnica bastante promissora para os estudos de migração, especialmente por envolver análises laboratoriais simples, rápidas e de baixo custo (Hobson e Norris 2008). Além disso, esta técnica produz resultados adequados à compreensão do padrão de deslocamento em nível de indivíduo (Yerkes *et al.* 2008) e que também permitem inferir sobre aspectos ecológicos dos indivíduos amostrados (Inger e Bearhop 2008), tais como sua dieta (Tieszen *et al.* 1983; Hobson e Clark 1992a, b; Forero e Hobson 2003), seu nível trófico (Forero e Hobson 2003; Bugoni *et al.* 2010) e as características fisionômicas dos diferentes sítios utilizados por eles ao longo de seu ciclo anual (Yerkes *et al.* 2008; Larson e Hobson 2009; Rocque *et al.* 2009).

Utilizada amplamente em estudos de geologia, as análises de isótopos estáveis se baseiam na variação da proporção de dois isótopos de um dado elemento em relação a um valor padrão de referência (Allègre 2008). Por convenção, esta variação é expressa pela razão entre a proporção existente do isótopo mais pesado e o mais leve como, por exemplo, $^{13}C/^{12}C$ e $^{15}N/^{14}N$. Alternativamente, esta proporção é representada por delta (δ) procedida pelo símbolo do isótopo mais pesado, por exemplo $\delta^{13}C$ (lê-se proporção isotópica do carbono 13). Independentemente da simbologia, os valores são expressos em partes por mil (‰), de modo que valores maiores indicam uma maior proporção do isótopo mais pesado. No caso de $\delta^{13}C$ e $\delta^{15}N$, as referências são, respectivamente, a razão encontrada no rostro de um cefalópode do Jurássico denominado Peedee Belemnite (VPDB) e do ar atmosférico (Air; Fry 2006).

Embora os isótopos de determinado elemento apresentem as mesmas propriedades químicas, os isótopos mais leves são mais reativos do que os mais pesados. Deste modo, à medida que os diferentes elementos químicos formados por eles (p.ex.: água, nitrogênio atmosférico, carbonatos) passam por reações químicas e/ou mudanças de estado físico, seu valor δ pode se tornar mais positivo ou negativo, processo denominado por discriminação isotópica. Dois eventos biológicos exemplificam os processos de fracionamento do carbono e do nitrogênio (Fry 2006): a fotossíntese e a transferência de matéria ao longo da cadeia trófica. As plantas podem fixar o carbono atmosférico por diferentes vias metabólicas. Resumidamente, enquanto as plantas lenhosas (metabolismo C_3) realizam a absorção do carbono por um processo denominado Ciclo de Calvin, gramíneas que possuem metabolismo do tipo C_4 processam o CO_2 em uma cadeia de reações químicas mais extensa (Ciclo de Hatch-Slack). Como consequência, estes metabolismos provocam distintos fracionamentos isotópicos do carbono, sendo que plantas C_3 apresentam $\delta^{13}C$ mais negativos (na ordem de -29‰) e plantas C_4 têm $\delta^{13}C$ em torno de -13‰ (White 2009). No caso do nitrogênio, sua incorporação na cadeia trófica ocorre em larga escala através da fixação realizada por bactérias simbiontes, resultando em um valor de $\delta^{15}N$ do solo mais positivo em relação ao N_2 atmosférico (0‰). Assim, os valores de $\delta^{15}N$ tornam-se maiores à medida que os compostos nitrogenados passam para os níveis tróficos superiores da cadeia alimentar (Post 2002).

As primeiras interpretações ecológicas das análises de isótopos estáveis em ornitologia tinham como objetivo compreender a composição da dieta e posição trófica dos organismos a partir de $\delta^{13}C$ e $\delta^{15}N$ (e.g.: Hobson 1990; Mizutani *et al.* 1990; Hobson e Clark 1992a, b; Herrera *et al.* 2001). Dentro da temática da migração, estes valores também foram utilizados, por exemplo, para determinar os hábitats de origem do ganso-das-neves *Chen c. caerulescens* (Alisauskas e Hobson 1993).

Alguns cuidados são necessários na interpretação dos resultados fornecidos pelas análises de isótopos estáveis (Gannes *et al.* 1997; Phillips e Gregg 2001; Bearhop *et al.* 2002; Farmer *et al.* 2008; Paritte e Kelly 2009; Rocque *et al.* 2009; Smith *et al.* 2009a, b). Dentre eles, é importante conhecer previamente a taxa de renovação (ou *turnover*) específica do tecido estudado, isto é, o tempo que os isótopos levam desde a sua ingestão pelo organismo até a sua incorporação em cada tecido e subsequente excreção (Hobson e Clark 1992a). Uma vez conhecidas as taxas de renovação, o pesquisador pode referenciar temporal e espacialmente os valores isotópicos medidos em cada tecido. Por exemplo, uma vez desenvolvidas, as penas são tecidos metabolicamente inativos e, portanto, a medida de seu valor isotópico em qualquer período do ano reflete inevitavelmente o sítio onde a pena foi desenvolvida (Mizutani *et al.* 1990). No entanto, certa cautela deve ser tomada ao interpretar estes resultados, uma vez que diferentes espécies e indivíduos podem apresentar períodos, sequências e duração de muda distintos entre si (Silveira e Marini 2012). Além disso, deve-se ponderar o fato de que, enquanto algumas espécies realizam todo o processo de muda das penas em um único sítio, há aquelas que realizam a muda concomitantemente com o deslocamento migratório (e.g.: figura 2.3 em Hobson e Pérez et al. 2008). De modo semelhante, as garras das aves também são um tecido metabolicamente inativo após a sua formação. Entretanto, a base deste tecido apresenta crescimento lento e contínuo, a uma taxa estimada de cerca de 0,04 ± 0,01 mm por dia para Passeriformes (Bearhop *et al.* 2003). Deste modo, se um indivíduo possui uma garra com 5,00 mm de comprimento, o valor isotópico do milímetro terminal desta garra se refere às proporções isotópicas do local onde o indivíduo se alimentou há cerca de quatro meses. Por fim, o sangue como um todo é um dos tecidos com taxa de renovação mais rápida, com meia vida variando entre 4,5 a 20 dias nas espécies já estudadas de Passeriformes (Hahn et al. 2012). Assim, o valores isotópicos medidos no sangue total de um indivíduo representam indiretamente as proporções isotópicas encontradas no sítio onde este indivíduo se alimentou a menos de um mês.

Conforme explicitado, os isótopos estáveis têm grande potencial para ampliar os conhecimentos existentes a respeito da ecologia dos migrantes e do fenômeno da migração propriamente dito, além de fornecer informações importantes para embasar as medidas de conservação das aves migratórias (e.g.: Newsome *et al.* 2007; Inger e Bearhop 2008; Poesel *et al.* 2008; Hobson *et al.* 2009). Além de ser uma técnica aplicável às inúmeras espécies de aves migratórias de pequeno porte, inclusive aquelas que migram curtas distâncias como as espécies do sistema Intratropical (Mazerolle e Hobson 2005), a análise de isótopos estáveis apresenta como grande vantagem a rapidez e baixo custo analítico em relação a outras técnicas existentes (e.g.: marcadores moleculares), além de dispensar a recaptura dos indivíduos para o acesso aos dados. Por fim, a multitude de aspectos possíveis de serem interpretados por esta técnica a torna extremamente útil em estudos de migração que dispõem de pouco tempo e de recursos limitados para serem concretizados.

O desenvolvimento tecnológico e científico associados ao estudo da migração de aves oferece um horizonte de possibilidades para a realização de pesquisas aprofundadas sobre a migração de aves na América do Sul. Muito mais do que descrever como ocorrem os eventos de migração nos sistemas dessa região, estes métodos possibilitam o teste de hipóteses pré-existentes sobre o tema e a proposição de novas, visando uma compreensão mais holística deste fenômeno.

Estado da arte na região Neotropical

Embora a migração de espécies sul americanas já fosse foco de estudos desde o início do século XX (e.g.: Zimmer 1938; Sick 1968; McNeil 1982; Negret *et al.* 1984; Marini e Cavalcanti 1990; Antas 1994; Chesser 1994; Hayes *et al.* 1994), as publicações de Levey (1994) e Hayes (1995) certamente despertaram a atenção da comunidade científica e promoveram um maior enfoque sobre o tema no continente. Por exemplo, a busca pelos padrões básicos até então desconhecidos sobre os sistemas de migração locais (i.e.: identificação das espécies migratórias e seus padrões de deslocamento pela região) passaram a ser foco de diversos estudos (e.g.: Sanaiotti e Cintra 2001; Rumboll *et al.* 2005; Ortiz e Capllonch 2007; Capllonch *et al.* 2008; Cueto *et al.* 2008; Nunes e Tomas 2008; Marini *et al.* 2010; Ruiz-Esparza *et al.* 2011; Marini *et al.* 2013; Paiva e Marini 2013) e de uma extensa revisão para as espécies terrestres brasileiras (Alves 2007). Estes estudos estimularam a formação recente de uma rede de colaboração internacional de pesquisa sobre a migração na América do Sul (Red Aves Internacionales). Como consequência, os conhecimentos produzidos por estes estudos tornaram viáveis pesquisas abordando questões ecológicas e evolutivas sobre as aves migratórias sul americanas (e.g.: Jahn *et al.* 2010a,b), focando intencionalmente espécies da família Tyrannidae. Além de ser uma das famílias mais representativas no Novo Mundo com um total de 358 espécies (Remsen Jr. *et al.* 2011), os Tyrannidae representam pouco mais de um terço (n=74) das 229 espécies de aves identificadas com comportamento migratório na América do Sul (Chesser 1994, revisto por Chesser 2004).

A releitura cuidadosa das hipóteses mencionadas anteriormente (e.g.: efeitos em cascata), evidencia a necessidade de cautela em generalizar sua validade para o fenômeno da migração das aves como um todo. Tal cautela se dá por estas hipóteses terem sido corroboradas nos mesmos sistemas a partir dos quais foram propostas (e.g.: Marra et al. 1998; Norris et al. 2004; Ydenberg et al. 2002; Reudink et al. 2009), isto é, nos sistemas Paleártico e Neártico-Neotropical, ambos restritos ao Hemisfério Norte e compostos essencialmente por espécies que realizam migrações de longa distância. Assim, para que estas hipóteses sejam efetivamente válidas para o fenômeno de migração de aves como um todo, é evidente a necessidade de testá-las também em cenários distintos daqueles em que foram propostas, ou seja, sistemas de migração que contemplem padrões de migração inexistentes nos sistemas do

Hemisfério Norte. Neste contexto, os sistemas ocorrentes na África e na América do Sul são de grande interesse por apresentarem grande número de espécies que realizam migrações intratropicais – portanto de curta distância –, um padrão bastante distinto daquele que ocorre nos sistemas Paleártico e Neártico-Neotropical.

As espécies que compõem os sistemas Intratropical e Neotropical-Austral realizam migrações mais curtas em relação às espécies dos sistemas do Hemisfério Norte. Assim, espécies sulamericanas são modelos interessantes para validar, ampliar ou restringir a validade das hipóteses existentes sobre a migração que foram produzidas tendo como base as aves migratórias de longa distância.

OBJETIVOS

As teorias existentes sugerem que o processo de migração deve influenciar diretamente os parâmetros da história de vida tanto das espécies migratórias quanto das residentes com as quais interage. Estas teorias foram desenvolvidas utilizando como única base os sistemas de migração do Hemisfério Norte. Além disso, estudos para sua validação jamais foram realizados dentro do sistema de migração Intratropical sulamericano. Considerando a provável origem comum das espécies que compõem estes sistemas, espera-se que estas teorias também sejam válidas no sistema sulamericano.

A hipótese central deste trabalho é de que o processo de migração impõe custos tanto aos indivíduos migratórios quanto àqueles residentes com os quais interage. Para testar esta hipótese, o trabalho objetivou quantificar a influência do processo de migração sobre a escolha dos hábitats utilizados e dietas apresentadas pelo migrante ao longo de seu ciclo anual, bem como as alterações provocadas pela presença desta espécie no sítio reprodutivo sobre a dieta e a reprodução de um congênere residente. Este objetivo geral foi dividido em três específicos: (1) comparar as estratégias de uso de hábitat, reprodutivas e alimentares adotadas por migrantes e residentes ao longo de seu ciclo anual; (2) avaliar o sucesso reprodutivo dos migrantes como um produto indireto dos eventos vivenciados por eles durante o período não-reprodutivo; e (3) quantificar a influência direta (competição) e/ou indireta (competição aparente) da chegada e permanência de uma grande população de migrantes, durante o período reprodutivo, sobre a dieta e reprodução dos residentes.

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CAPÍTULO 1

CONTRASTING ANNUAL CYCLES OF AN INTRATROPICAL MIGRANT AND A TROPICAL RESIDENT BIRD

LRH: GUARALDO, KELLY, MARINI

RRH: COMPARATIVE ECOLOGY OF RESIDENTS AND MIGRANTS

CONTRASTING ANNUAL CYCLES OF AN INTRATROPICAL MIGRANT AND A TROPICAL RESIDENT BIRD

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ABSTRACT.–Throughout their annual cycle, migrants often adopt different foraging and microhabitat usage strategies. Previous studies treat migrants as niche-trackers or niche-followers, i.e. they track similar niches along their annual cycle, almost exclusively based on the food resource availability, inferred by the climate on either their wintering or breeding grounds. New techniques such as stable isotope analyses allow researchers to more directly infer a migrants' niche across seasons. In this study, we perform comparative analyses of stable carbon and nitrogen isotope ratios in tissues of the resident Plain-crested Elaenia and the intratropical migrant Lesser Elaenia to evaluate their year-round ecological niche. Our data suggest that both residents and migrants were consistent in their use of distinct microhabitats throughout the year, which would indicate niche-tracking behavior on the part of migratory individuals. On the other hand, migrants feed at higher trophic levels than residents at every season, but both species exhibit similar trophic level shifts along the year, feeding on higher trophic levels during breeding, and on the lowest while wintering. Hypotheses that could explain these trophic level shifts include the differential energetic demand by the migratory journey, distinct nutritional needs species have during each stage of the year, and the use of multiple wintering grounds by migrants. To test these hypotheses and elucidate the full life cycle ecology of short-distance intratropical South-American migrants will require wintering ecology studies as well as multidimensional and multi-temporal scale assessments of their niche.

Key words: Brazil; Cerrado; *Elaenia chiriquensis*; *Elaenia cristata*; microhabitat; stable isotopes; wintering ecology.

"Sedentariness will likely doom much tropical avian diversity, but increased vagility is a two-edged sword: beneficial in promoting immigration, but detrimental in that more than one habitat may be required." (Winker et al. 1997).

THROUGHOUT THEIR JOURNEYS, migrants must cope with unpredictable resource availability, especially food (Jenni and Schaub 2003; Chernetsov 2012 and references therein; but see Saino & Ambrosini 2007), and thus often use an array of different diets and habitats. Migrants may feed primarily on fruit during fall migration and on insects during spring migration (Stoate and Moreby 1995; Parrish 1997; Morrison et al. 2013). Migrants can use several different habitats while *en route* ("niche switchers"), which demands behavioral plasticity to deal with unpredictable habitats and resources (e.g., Martin and Karr 1990; Rappole 1995a). Alternatively, they might avoid drastic and costly behavioral and foraging strategy shifts (e.g., Renfrew et al. 2013; Trierweiler et al. 2013), thus behaving as "niche-follower" migrants (i.e., a "niche follower migrant"; Nakazawa et al. 2004).

Although these strategies have been well documented at temperate latitudes, almost nothing is known about the annual cycle of birds that migrate wholly within tropical latitudes of the New World (Faaborg et al. 2010). Ecological niche modeling (ENM) is the only method used so far to evaluate whether birds that migrate within South America behave as niche followers or switchers (e.g.: Joseph and Stockwell 2000; Marini et al. 2010; Marini et al. 2013; but see Hahn et al. 2013), and has provided groundbreaking insights on the climatic variables migrants may use as cues and drivers for their migratory movement. In spite of advances through ENM, predictions made through this method often provide only temporally and geographically coarse location of migrants' wintering grounds, thus offering few specific predictions to aid *in* *situ* wintering ecology studies. Empirical studies of intratropical migrants annual cycle are paramount both for advancing our understanding of their ecology, as well as on how to conserve them (Faaborg et al. 2010).

Stable isotope analyses allow ecological inferences across multiple migratory stages (Mazerolle and Hobson 2005). Once an individual ingests a given food item at a given microhabitat, the stable isotopes ratios of the prey are incorporated with a predictable offset in the bird's tissues growing at that moment. Thus, by sampling tissues with different turnover rates, i.e. grown at different times, one can make indirect ecological inferences about distinct stages of a bird's life (e.g. Hahn et al. 2013). Analysis of feathers' isotopes ratios allows inferences about the molting period. The tip of claws sampled at the start of the breeding season allows inferences about the wintering season. At last, blood plasma ratios reflect to a few days before the sampling date (Mazerolle and Hobson 2005). Moreover, stable isotopes of each element provide evaluations of distinct dimensions of the ecological niche. While nitrogen isotopes ratios are positively correlated with trophic level, carbon isotopes are more strongly influenced by the microhabitat used by birds: more mesic sites have more C_3 plants, which have tissues with more depleted $\delta^{13}C$ values, whereas xeric sites typically have more C_4 species, which have tissues with less depleted $\delta^{13}C$ values (Fry 2006).

Constraints on tracking and observing migrants throughout their annual cycle pose a challenge to our ability to evaluate birds' strategies regarding microhabitats used and diet. Although banding and tagging birds with radio and satellite devices are advantageous for tracking migrants (see Bridge et al. 2011 for an extensive review on the subject), these methods demand a large network of study sites and researchers, are expensive, or are restricted to studies of medium- and large-bodied species. These methods have limited application for studying South American intratropical system migrants (*sensu* Hayes 1995), as most of them are small Passerines (Stotz et al. 1996).

Here, we provide the first assessment of the annual cycle of an intratropical migrant in South America, focusing specifically on microhabitat use and diet. We used a comparative approach, by contrasting an intratropical migrant species with a closely related tropical resident. Unlike residents, which must adjust their behavior to local weather conditions and seasonality, we expect that intratropical migrants adopt a niche-follower strategy to reduce the already high costs associated with migration (Newton 2008, pp. 95-103 and 442). Moreover, we expect that such use of similar microhabitats allows migrants to maintain a less variable trophic level throughout the year compared to residents (i.e. while molting, wintering, and breeding). We also propose several hypotheses for future studies on wintering ecology to enhance our understanding of this important and yet understudied stage of a migrant bird's annual cycle (Rappole 1995b; Faaborg et al. 2010). Apart from the fact that intratropical migration is the most understudied system of bird migration (Faaborg et al. 2010), studies evaluating the hypotheses we highlighted in the context of avian migration as a whole are generally rare (e.g., Joseph and Stockwell 2000; Marini et al. 2010; Marini et al. 2013). Thus, our study seeks to both improve the empirical understanding of the ecology of intratropical migratory birds, as well as the theory on year-round ecology of migratory birds in general.

METHODS

Study area.–Estação Ecológica de Águas Emendadas (ESECAE) is a reserve of 10,500 ha composed of typical Cerrado vegetation (tropical savanna) in central Brazil

(15°42’ to 15°38’ S and 47°33’ to 47°37’ W). The area has a seasonal climate, the dry season lasting from May to September and the rainy season from October to April (Gottsberger and Silberbauer-Gottsberger 2006a). All data were collected at areas of Cerrado *sensu stricto* vegetation within a 100 ha plot, at least 1.5 km from other habitat types.

Model-species.–To achieve our goals, we carried out a comparative species analysis using phylogenetically closely-related flycatchers (Tyrannidae). We selected two species that are abundant at our study site, have similar body size, sexes are monomorphic, and are believed to be mainly frugivorous (Marini and Cavalcanti 1998), but differ in their migratory status. The Lesser Elaenia (*Elaenia chiriquensis albivertex*) is a small flycatcher weighing about 15 g at ESECAE (M. Â. Marini et al. unpubl. data). It is a migratory species at our study site, arriving in thousands for breeding between September and December (Medeiros and Marini 2007). This species is believed to winter in forested habitats somewhere in the Brazilian Amazon Basin (Marini and Cavalcanti 1990), but data on their wintering sites are lacking. The Plain-crested Elaenia (*E. c. cristata*) is a resident species, which weighs about 18 g and defends territories year-round (A. C. Guaraldo, unpubl. data). Previous research showed that this species breeds in the area from September to December (Marini et al. 2009), but further field observations revealed that their breeding season may start in early to mid-August in some years (A. C. Guaraldo, unpubl. data).

Residents molt their primaries at our study site from late October to late February (Silveira and Marini 2012) and 95% of the individuals start molting only after nesting. Migrants were previously recorded molting in our study area from late November to early March, with no sign of overlap with nesting (Silveira 2011). However, this information is based on a few individuals that overwintered in the area and, as highlighted by other research, may not accurately represent the molting schedule of migrants (Silveira and Marini 2012). In fact, about 65% of Lesser Elaenia individuals inadvertently captured in a coastal migration stopover site in southeastern Brazil (20°36’S 40°24’W) were molting flight and contour feathers by February (C.G. Duca, pers. comm.).

Tissue sampling.–During two consecutive breeding seasons (2011-2012), we captured and banded nesting females of the resident and migratory species by placing a small 3 m-long mist-net near (0.5-1.5 m) their active nests (i.e. containing eggs or nestlings). Subcutaneous fat content was estimated on a scale of 0 to 8 (Kaiser 1993). For every female with a fully developed brood patch, we plucked the left wing’s first primary, clipped 4 mm off of the tip of the left second claw, and collected whole blood samples through brachial or tibio-tarsal vein puncture. We used capillary tubes to collect and drop ca. 70 µL of whole blood on a glass slide. These samples were air dried in the field and then oven dried in the lab at 45 °C for 48 h. An additional ca. 25 µL of whole blood was stored on filter paper for molecular sexing analyses in a commercial laboratory (Santé Laboratório de Análises Clínicas).

Stable isotope analyses.–We only included in the samples females with active nests (i.e. containing eggs or nestlings), identified by the presence of a brood patch (Davis 1945; Jones 1971) and double-checked by molecular sexing to avoid any biases in isotope values (Bearhop et al. 2002). We cleaned dust particles from feathers and claws, as well as any oleaginous residues, following Paritte and Kelly (2009). Samples (350 ± 10 µg for feathers and whole blood, and 248 ± 7 µg for claws, weighed to the nearest µg) were then packed in tin capsules. Carbon and nitrogen stable isotope ratio measurements were performed on these samples at the University of Oklahoma using a ThermoFinnigan Delta V isotope ratio mass spectrometer connected to an elemental analyzer (CosTech). Isotope ratios are reported in per-thousand (‰), using *δ* notation based on international standards (Pee Dee Belemnite for carbon and air for nitrogen; Fry 2006). We corrected tissue values according to different isotope fractionation factors following Hobson and Bairlein (2003), thus allowing between tissues comparison. Hence, we respectively subtracted 1.7 ‰ and 2.4 ‰ from blood δ^{15}N and δ^{13}C values and 2.7 ‰ and 4.0 ‰ from claw and feather values. Measurement precision for δ^{13}C and δ^{15}N were respectively ±0.1 ‰ and ±0.2 ‰.

Isotope values of tissues sampled are indirect assessments of the environment and ecology of the individual at the time each tissue was formed. As whole blood has a half-life turnover rate varying from 4.5 to 20 d (higher values referring only to blood cells rather than whole blood; Hahn et al. 2012), samples reflect to the isotope ratios of the local breeding grounds. This is supported since (i) we only sampled females of each species with active nests and at least 15 d into the breeding season; and (ii) as the breeding condition of a bird begins much prior to initiation of nest building (e.g.: nest territory establishment and defense, pairing, copulation, and production of the egg), and at time of sampling females were nesting for at least 10 d (including nest building period), we are confident that females had enough time to a breeding diet for about two half-lives (22 d) of whole blood turnover rate. Moreover, the study species were not storing fat at the time of blood sampling, as no birds with more than level 1 of subcutaneous fat were sampled, which could otherwise be a source of bias (Auerswald et al. 2010). Blood sample δ^{13}C and δ^{15}N values from Plain-crested Elaenia (hereafter, “residents”) refer to late August to September (i.e., their nesting period, during which they were sampled) and October and November for Lesser Elaenia (hereafter, “migrants”), which breed later (Fig. 1). Feather samples refer to the molting grounds, since isotopes are incorporated in this tissue during molting (Fig. 1). On the other hand, despite being a metabolically inert tissue like feather, claws have a constant growth rate of about 0.04 ± 0.01 mm.day^{-1} in small Passerines (Bearhop et al. 2003). Since our model-species have claws of 5.1 ± 0.4 mm, claw-tips sampled at the breeding grounds represent the site each individual was at about four months before sampling, hereafter referred to as the wintering period of each species and corresponding to approximately April-May for residents and June-July for migrants (Fig. 1).

Statistical analyses.–We developed a set of eight models to test our hypotheses (Table 1) using the Information-Theoretic approach (Anderson 2010) and following model selection procedures recommended elsewhere (Anderson et al. 2001; Anderson and Burnham 2002; Burnham et al. 2011). As our dataset had no overdispersion, model selection and estimation procedures required no adjustment factor (c-hat). Specifically, we used the second-order Akaike's Information Criteria (AICc) because sample size was <40, considered the best models to be those with ΔAICc<4, and used Akaike weights (w_i) for assessing the relative importance of explanatory variables across multiple models. All analyses were run using packages lme4 (Bates et al. 2012), and AICcmodavg (Mazerolle 2013) in R environment version 2.15.3 (R Development Core Team 2013).

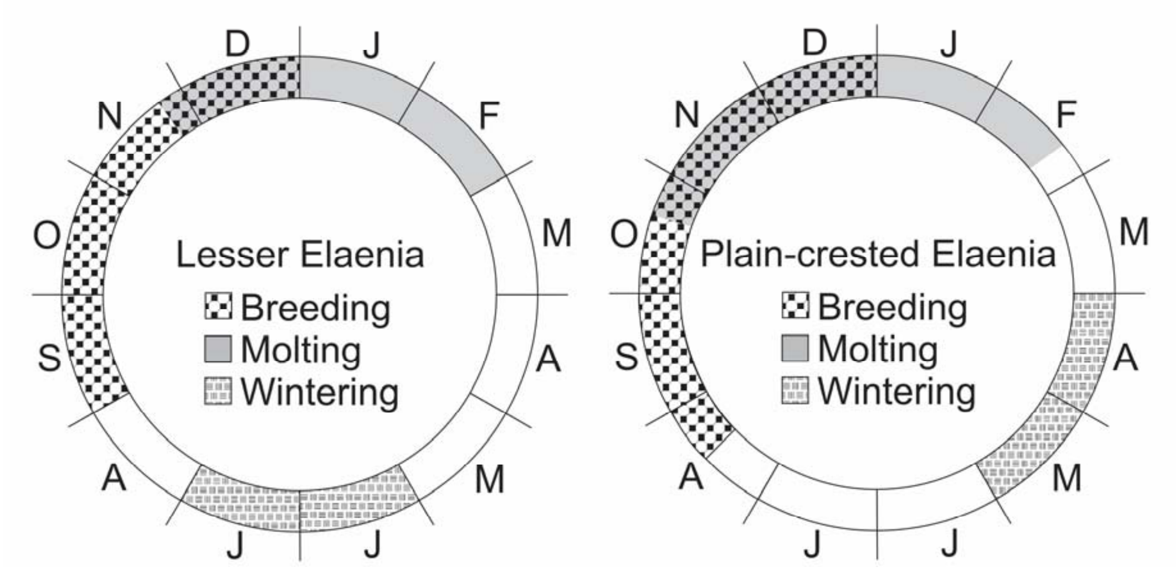

FIG. 1. Annual cycle of the migratory Lesser Elaenia (*Elaenia chiriquensis*) and the resident Plain-crested Elaenia (*E. cristata*) based on existing literature and field observations. See Silveira and Marini (2012) for uncertainties on migrant's molting period and on the overlap on resident's molting and breeding periods. Wintering periods are restricted to the time-window considered in this study.

RESULTS

We analyzed tissue samples from 19 migratory Lesser Elaenia individuals (breeding: n=8 samples; molting: n=14; wintering: n=12), and from eight resident Plain-crested Elaenia individuals (n=8; n=6; and n=5, respectively). The best models (i.e., those with less information loss) supported species and periods of the annual cycle (breeding, molting, and wintering) as the two most important explanatory variables of tissue δ^{13}C and δ^{15}N values (Table 1), including their interaction, i.e. isotope ratios differed between tissues within species.

TABLE 1. Results from a Generalized Linear Mixed Model (GLMM) analysis on the importance of factors affecting $\delta^{13}C$ and $\delta^{15}N$ values of feather, claw, and whole blood samples of resident Plain-crested Elaenia (*Elaenia cristata*) and migratory Lesser Elaenia (*E. chiriquensis*) females in Central Brazil. Individuals were considered as random effects in all cases. $\delta^{13}C$ and $\delta^{15}N$: carbon and nitrogen stable isotopes ratios of tissues; Period: breeding (blood), molting (feather), and wintering (claw); k: number of parameters; AICc: Akaike Information Criterion corrected for small sample sizes; AICc.w_i: Akaike weight; LL: model log-likelihood.

Model	k	AICc	ΔAICc	AICc.w_i	LL
Carbon:					
$\delta^{13}C$~sp+Period+sp*Period	8	138.2791	0.000	0.4650	-59.5395
$\delta^{13}C$~sp+Period	6	138.9445	0.665	0.3334	-62.5787
$\delta^{13}C$~Period	5	139.9515	1.672	0.2015	-64.3507
$\delta^{13}C$~sp	4	156.1372	17.858	0.0001	-73.6604
Nitrogen:					
$\delta^{15}N$~sp+Period	6	114.7759	0.000	0.6493	-50.4944
$\delta^{15}N$~sp+Period+sp*Period	8	116.0791	1.303	0.3384	-48.4395
$\delta^{15}N$~Period	5	122.7167	7.941	0.0123	-55.7334
$\delta^{15}N$~sp	4	175.1590	60.383	5.02E-14	-83.1714

Residents and migrants used isotopically similar habitats for molting and wintering, but migrants used microhabitats with slightly higher $\delta^{13}C$ on the breeding grounds (see $\delta^{13}C$ values in Fig. 2). Residents exhibited lower $\delta^{13}C$ values during breeding compared to the molting and wintering periods, indicating a temporal shift towards less mesic microhabitats. In contrast, migrants had comparatively less variable δ^{13}C values year-round, signaling that individuals used habitats that were more isotopically similar during each stage of the annual cycle.

Based on the variability of δ^{15}N values (Fig. 2), it is apparent that migrants and residents exhibited dietary shifts throughout the year. The two species have similar trophic levels during molt, but contrasting differences in the other two stages. Both species occupy the highest trophic level while on the breeding grounds, and the lowest while wintering. Migrants have considerably higher trophic level diets than residents in both seasons (Fig. 2).

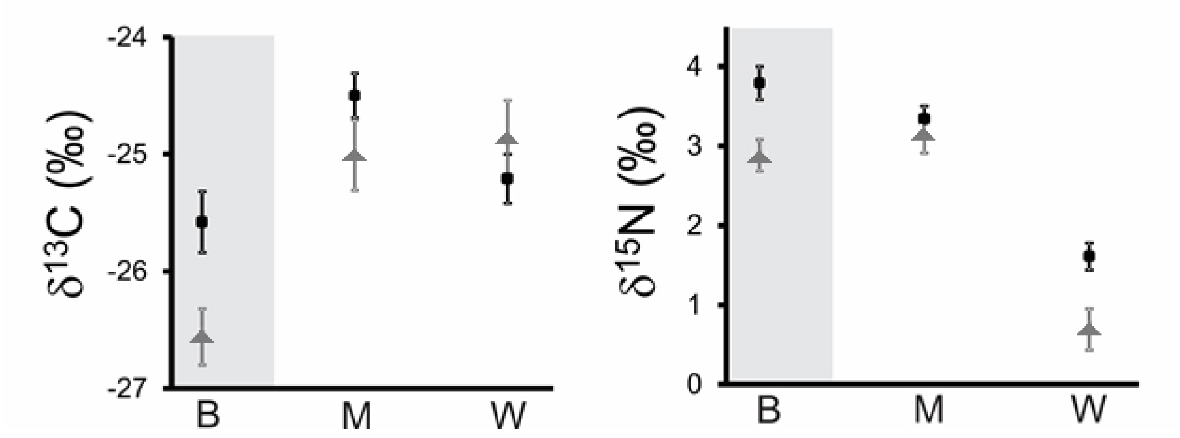

FIG. 2. Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope ratios referring to breeding (B), molting (M) and wintering (W) periods of the migrant Lesser Elaenia (*Elaenia chiriquensis*; black circles) and the resident Plain-crested Elaenia (*E. cristata*; grey triangles) sampled during the breeding season at Estação Ecológica Águas Emendadas, central Brazil. The shaded areas refer to the rainy season at the study site. Values represent marginal mean ± SD.

DISCUSSION

Overall, our results show that the annual cycle of an intratropical migrant and a closely related resident are similar in some respects but different in others. Migrants, as expected, pursued similar microhabitats along the year (similar $\delta^{13}C$ values between seasons), therefore behaving as niche-followers. Residents also showed such behavior despite they had used slightly more mesic microhabitats while breeding. Opposing to that, both species occupied variable trophic levels in each stage, shifting from a highly insectivorous diet during breeding and molting to a mostly frugivorous diet while wintering. Migrants always had more enriched $\delta^{15}N$ than residents, except while molting, when both species had similar $\delta^{15}N$ feather values. By examining each stage of the year, we infer that the high energetic demand of migration is the most plausible explanation for the interspecific trophic level differences we found.

Migrants and residents differ in their isotopic ecology during some periods of the year. It is clear that the migratory Lesser Elaenia pursue similar microhabitats year-round; in contrast, resident Plain-crested Elaenia slightly switch the microhabitats in which they forage during different stages of the year. While breeding (i.e., mainly during the last two months of the dry season), residents feed on prey from more depleted $\delta^{13}C$ microhabitats than during winter. It is known that some Cerrado plants develop deep root systems to access underground water (Sarmiento et al. 1985; Oliveira et al. 2005). By doing so, they not only end up being evergreen through the dry season, but also avoid hydric stress; ultimately leading to the development of more depleted $\delta^{13}C$ tissues (Farquhar et al. 1989; Marshall et al. 2007). Consequently, insects that feed on such plants, and the insectivorous birds that feed on these insects also synthetize depleted $\delta^{13}C$ tissues.

The diversity of the Cerrado plants' strategies to deal with drought ensures food resources for birds even during the dry season (Batalha and Mantovani 2000; Gottsberger and Silberbauer-Gottsberger 2006b). Indeed, many species bear fruit at this time of the year at our study site (A. C. Guaraldo, unpubl. data), and several arthropod orders are abundant year-round in a nearby Cerrado reserve about 60 Km from our study site (Pinheiro et al. 2002). Therefore, other variables, rather than food constraints are more likely to be driving the trophic differences between migrants and residents throughout the year as we discuss further below.

As is typical in flycatchers (Johnson et al. 2012), our study species rarely overlap the costly activities of molting and nesting. However, overlap should not be an issue if it occurs when enough food is available and/or if birds are able to adjust their life-history strategies, such as molting at a slow rate (Johnson et al. 2012; Echeverry-Galvis and Hau 2013). At our study site, residents are molting while still feeding their young by mid-late November (A. C. Guaraldo, unpubl. data), which may be related to the fact that residents shift to higher trophic level sources from the breeding to the molting period. If migrants were on this same time schedule, they would be molting while en route to the wintering grounds. Considering that young Lesser Elaenia are already foraging independently by the time they depart from the breeding grounds (A. C. Guaraldo, pers. obs.), migrants do not overlap molting with young attendance. Hence, in contrast to the life-history of residents, energetic intake needs of migrants while molting is expected to be lower than while nesting, as confirmed by their $\delta^{15}N$ values (Fig. 2).

Our data also reveal a contrasting scenario for the $\delta^{15}N$ values residents and migrants showed for the wintering period. Both species show a steep decline in their trophic levels during winter, in comparison to the molting period, with migrants showing about a two-fold higher level of δ^{15}N values than residents during winter. Although resource availability on the migrants' wintering grounds is unknown, resource limitation is not an issue for residents (A. C. Guaraldo, unpubl. data; Pinheiro et al. 2002; Gottsberger and Silberbauer-Gottsberger 2006b). Moreover, environments may have different basal δ^{15}N levels, which would lead to differences δ^{15}N values in tissues not necessarily related to the ingestion of different food items. During the winter, the low δ^{15}N value suggests residents ingest low trophic level food items; mostly or exclusively fruits (A. C. Guaraldo, unpubl. data). In contrast, our data show that migrants have a two-fold higher trophic level at this stage than residents. The most parsimonious explanation for this pattern relies on previous findings that suggest small-bodied migrants should have higher basal metabolic rates than residents (Jetz et al. 2008). However, a multitude of additional or alternative causal factors exists. First, our migrant model-species might be another interesting case of a migrant that keeps moving constantly between different wintering sites (e.g., loop migration), therefore demanding higher energy intake. This is a wintering strategy that has just been recently revealed within South America by the use of light-level loggers and that deserves further investigation in our study species (e.g., Heckscher et al. 2011; Jahn et al. 2013). This pattern might arise, for instance, if migratory Lesser Elaenia track variable fruit production associated with flooding pulses (Haugaasen and Peres 2007) within the putative Amazonian wintering grounds of this species (Marini and Cavalcanti 1990). Moreover, migrants might also face competition with residents for food on the wintering grounds, consistent with the "winter food-limitation hypothesis" (Sherry et al. 2004). In this scenario, birds would need to increase their energy intake as a way to compensate for greater energy expenses owing to interspecific competition (e.g., Rappole 1995c, and references therein). Lastly, migration is known for being an energetically costly activity due to the amount of physiological and morphological adjustments birds need to undergo long-distance flights (e.g.: Winkler and Leisler 2004; Newton 2008, pp. 95-103 and 442; Bauchinger and McWilliams 2010; Altizer et al. 2011; Arizmendi-Mejía et al. 2013). However, the extent to which migration affects the energetics of short-distance migrants is still an unexplored field. Based on our results, we expect future research using short-distance migrants as models to shed light on whether the higher $\delta^{15}N$ values by birds had during winter is related to a recovery from or preparation for migration or to differences in $\delta^{15}N$ values in the local food web.

Wintering ecology and physiology of South American intratropical migratory Passerines remains understudied (e.g., Vickery and Herkert 2001); thus, we still lack most of the basic data needed for a thorough evaluation of the hypotheses we present here. However, the emergence of new methods such as light-level loggers, stable isotope analysis, and DNA markers, combined with traditional field observations and banding are slowly but consistently improving our knowledge of the wintering ecology of migrants within South America (Jahn et al. 2013), and the mechanisms that might be driving intratropical migration (Jahn et al. 2006).

Migrants usually show phenotypic plasticity, being able to constantly adjust their physiology and regulate their behaviors according to the variable environmental traits they use as cues (Calvert et al. 2012; Ramenofsky et al. 2012). The findings from our comparative approach add to the perspective that “migrants are opportunists (…) wandering between two worlds” (Winkler and Leisler 2004). We show that the physiological plasticity typical of migrants should not be interpreted relative to microhabitats as they track similar microhabitats for molting and wintering. Migrants also had a plastic foraging behavior throughout the year, but given that the resident model-species showed similar shifts, such plasticity is unlikely to be caused by migration and or interspecific competition (Rappole 1995d). A recent study revealed an Old World long-distance migrant Passerine also undergoes seasonal trophic level shifts, but it might be associated with the distinct environments used during the breeding and non-breeding periods in this case (Hahn et al. 2013).

In conclusion, our study stresses the importance of evaluations of migration in multidimensional and temporal scales, searching for connections that go beyond two-worlds, i.e. breeding and wintering grounds. Further comparative studies should evaluate the annual cycles of temperate-tropical and intratropical migrants, and whether other intratropical migrant species show the same scenario described here. Knowledge of wintering ecology, as reinforced by this study, is central to understanding migration itself (Rappole 1995b). The widespread use of new tracking methods should soon improve our understanding of where intratropical migratory birds molt and winter in South America, which will be crucial in allowing refined, *in situ* studies and, ultimately, in assessing the validity of the hypotheses developed in this study for other intratropical migratory species.

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CAPÍTULO 2

DO CARRY-OVER EFFECTS APPLY TO A SHORT-DISTANCE, INTRATROPICAL MIGRANT BIRD?

LRH: GUARALDO, KELLY, MARINI

RRH: CARRY-OVER EFFECTS IN AN INTRATROPICAL MIGRANT

DO CARRY-OVER EFFECTS APPLY TO A SHORT-DISTANCE, INTRATROPICAL MIGRANT BIRD?

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ABSTRACT.–The Northern Hemisphere's bird migratory systems have been the main models to develop bird migration hypotheses and theories, demanding careful from researchers before assuming their worldwide validity. For this reason, we checked two hypotheses related to carry-over effects (COEs) using a South American intratropical migrant species as model, the Lesser Elaenia *Elaenia chiriquensis*. First, we predicted that harsher environmental conditions faced by individuals during the non-breeding season would lower their breeding success. Second, we propose that individuals that overwintered in harsher environments should also arrive in their breeding grounds with poorer body-conditions and/or delay their arrival. Consequently, their nesting period would be postponed and their nestlings should have increased growth rate to be fully grown in time for their departure to the wintering grounds with the remaining population. To check these hypotheses, we monitored nests and ran stable isotope analyses on parents' tissues. The results found are the first to refute the validity of these COEs hypotheses for the intratropical migratory system. Breeding success of individuals, measured through nests' daily survival rates, was unaffected by the conditions faced during their non-breeding season. Moreover, nestlings had a constant growth rate irrespective of the time they hatched along the breeding season. We base our discussion on alternative hypotheses that could explain the patterns found, highlighting the compensation of COEs by birds and the low risks imposed by climate to parents' survival if they need an extended stay or to overwinter at the breeding grounds to ensure the full development of late-hatched nestlings.

Key words: daily survival rates, nestling growth rate, stable isotope analysis, Brazil, Cerrado.

“Like searching for a lost object under a street-lamp because the light is brightest there, trying to untangle the complexities of migration by focusing on the most convenient or obvious migration system is at best restrictive and at worst misguided.” (Jahn et al. 2004).

Historically, most bird migration theories and hypotheses have been developed and proposed using Northern hemisphere migratory systems as models, mainly based on Nearctic-Neotropical and Palearctic-Paleotropical long-distance migrants (e.g.: Berthold 2001a; Newton 2008). Although a number of studies have been developed to test and corroborate these hypotheses, caution is needed in assuming they are valid in migratory systems worldwide (Levey 1994; Hayes 1995; Jahn et al. 2004). In spite of sharing common origins with the Nearctic-Neotropical system (Jahn et al. 2004), the South American Intratropical System (SAIS) is by definition composed exclusively of short-distance migrants (Hayes 1995). Moreover, Northern and Southern Hemispheres have contrasting landscapes and migratory barriers (Jahn et al. 2012), opening avenues for the evolution of different migratory strategies (Chesser 1994; Jahn et al. 2004).

Descriptive research can largely increase knowledge on SAIS dynamics, but testing whether hypotheses developed and evaluated only in the Northern Hemisphere can be generalized to the SAIS is also paramount. One of the emerging paradigms in migratory bird ecology is that the effects of non-lethal events and processes faced by migratory individuals in a given season, such as weather and habitat conditions, may influence the breeding or survival of the individual in the following seasons (Harrison et al. 2011), therefore playing an important role in population dynamics (Norris and Taylor 2006). Such carry-over effects (hereafter, COEs) are so influential in populations of long-distance migrants that recent studies recommend considering their effects in population dynamic models to evaluate population trends (Norris and Taylor 2006; Betini et al. 2013). Despite this, all theory surrounding COEs has been based on long-distance migrants, and the validity of only one of these models has been tested and corroborated with an experimental study (Legagneux et al. 2012). COEs have been increasingly recorded and described, but researchers should be careful in assuming their applicability to migratory bird species as a whole as some assumptions remain untested, such as the influence of macro and micronutrients on individual life histories (Harrison et al. 2011). In addition, hypotheses based on COEs were only supported for a fraction of existing migratory species and systems, namely the Nearctic-Neotropical and Palearctic-Paleotropical systems. Also, only a handful of the countless components that could be associated with COEs have been evaluated so far, such as habitat quality (e.g.: Marra et al. 1998; Gunnarsson et al. 2005), intrinsic individual traits (e.g.: Schmidt-Wellenburg et al. 2008; Faaborg et al. 2010 and references therein; Ramenofsky et al. 2012), and climate (e.g.: González-Prieto and Hobson 2013).

Temperature and day length are largely and seasonally variable at higher latitudes. For this reason, they were some of the first variables considered to explain why and how birds migrate and have been repeatedly found to be important drivers of migration in the Nearctic-Neotropical (Marra et al. 2005) and Palearctic-Paleotropical systems (e.g.: Gwinner 1977 and references therein; Both et al. 2006; Tøttrup et al. 2010; Singh et al. 2011), and for South American Temperate-Tropical migrants (e.g: Joseph 1996). Less is known about the relationship between resource seasonality and intratropical bird migration (but see Paiva and Marini 2013). Traditionally, the tropics have been viewed as being largely aseasonal (e.g.: Stutchbury and Morton 2001), often leading to the mistaken conclusion that breeding tropical birds largely face favorable weather conditions and unlimited resource availability (Stutchbury and Morton 2001; Jahn and Cueto 2012). This has been shown not to be the case for various tropical ecosystems. For example, central South American ecoregions such as the Chaco and the Brazilian Cerrado are characterized by distinct wet and dry seasons. Precipitation profoundly affects arthropod availability (e.g.: Pinheiro et al. 2002), and is considered the main driver of the Tropical Kingbird *Tyrannus melancholicus* migration towards the Amazon Basin, likely due to an increase in arthropod abundance at the start of the rainy season in that region (Jahn et al. 2010b).

If resource fluctuation at a tropical breeding site is strong enough, it could limit the breeding window for birds, such that intratropical migrants would still have to adjust their arrival and departure schedules to avoid harsh conditions similarly to that carried out by north-temperate breeding migrants at their higher latitude breeding sites. Consequently, we expect that late-hatched nestlings at such tropical sites speed up their development rate to allow their departure at the end of the breeding season to the non-breeding grounds in synchrony with adults and with nestlings that hatched earlier in the breeding season. They could potentially do so by using local environmental cues that have slight temporal variation (day length: Helm and Gwinner 1999; temperature: Tøttrup et al. 2010), besides by increasing the feeding rate to their nestlings. This could even occur through endogenous controls of growth rate based on pre-laying hormone deposition in the egg by the female (corticosterone: Hayward and Wingfield 2004; androgen: Groothuis et al. 2005). Moreover, some ontogenetic processes might be under a fairly rigid endogenous (i.e. genetic) control, such as in the faster juvenile molt of the Intratropical migrant Yellow-Green Vireo *Vireo flavoviridis* (Styrsky et al. 2004).

Here we verified two existing hypotheses related to COEs using the short-distance Intratropical migrant Lesser Elaenia *Elaenia chiriquensis albivertex* (Tyrannidae) as a model. We first evaluate whether the diet and habitat use on the molting and wintering grounds influence breeding success. We hypothesize that the ecology of Lesser Elaenias outside of the breeding season will have little or no effect on their reproductive success. In contrast to long-distance, north-temperate breeding migrants, short-distance migrants usually store little or no fat for their journey (Newton 2008, p. 100), either because they perform a single non-stop short-distance flight between breeding and wintering grounds or use multiple stopover sites where they can refuel (Newton 2008, p. 133). Such a strategy could dilute the effects of conditions faced by individuals at each stopover, reducing or eliminating any effects that could be carried-over to the breeding season (e.g.: Marra et al. 1998; Inger et al. 2010). We therefore predict that the breeding success of Lesser Elaenia females, as measured by nest survival rate, will not be related to the diet they had and microhabitat they used during the molting and wintering periods.

Harsh situations faced by migrants during the non-breeding period may delay their arrival at the breeding grounds and, consequently, the onset of their breeding period. Thus, we tested a second COE hypothesis, that growth rate (hereafter, GR) of nestlings varies as a function of hatch date. Rainfall is variable along the year within the Brazilian Cerrado (i.e.: Pinheiro et al. 2002; Gottsberger and Silberbauer-Gottsberger 2006b) and suggested as the main cue Southern Hemisphere migrants, partial migrants included (Jahn et al. 2010a), use to adjust their circannual rhythms (Gwinner 1996b; Gwinner 1996a; Dingle 2008). Nevertheless, a previous study found that the Lesser Elaenia had a fixed departure schedule unrelated to any weather variable (Paiva 2008). Such invariability led us to predict that the developmental rate of nestlings should be higher in late than early-born nestlings to ensure their full development prior to the departure of adults to the wintering grounds.

METHODS

Study site.–We conducted this study at the Estação Ecológica Águas Emendadas (ESECAE) located in the Cerrado ecoregion (a tropical savanna) of central Brazil (15°42’ to 15°38’ S and 47°33’ to 47°37’ W). This reserve is composed of 10,500 ha and is subjected to a seasonal climate, with the dry season lasting from May to September and the rainy season from October to April (Gottsberger and Silberbauer-Gottsberger 2006a). We only collected samples in areas of cerrado *sensu stricto* vegetation within a 100 ha plot.

Study species.–The Lesser Elaenia *E. c. albivertex* is a *ca.* 15 g intratropical migrant bird that arrives at ESECAE in mid-August to breed between September and December (Medeiros and Marini 2007; Paiva and Marini 2013). We selected this model-species for its high abundance of nests at ESECAE. In addition, there is detailed information about its breeding biology at the study site (Medeiros and Marini 2007; Paiva and Marini 2013). The species lay on average two eggs, which take around 13 d from laying until hatch and 16 d until fledge (Medeiros and Marini 2007). As usual for flycatchers, only females incubate the eggs (pers. obs.), but further details on the roles played by males and females regarding nest and nestling attendance and territory defense remains unknown. The species is particularly tolerant to constant nest monitoring (Lobo & Marini 2012), thus allowing females to be mist-netted close to the nest (pers. obs.). By sampling only females, we avoided biases in isotope ratios due to sex-related fractionation (Bearhop et al. 2002).

Data sampling.–We searched for and monitored Lesser Elaenia nests every other day during two consecutive breeding seasons (2011 and 2012). We set mist nets within 0.5-2 m of active nests (i.e. containing eggs or nestlings) to capture parents of each brood. Upon capturing a Lesser Elaenia, we color-banded and sexed each individual, using the presence of a well-developed brood patch to identify females (see Davis 1945; Jones 1971). We visually checked for newly grown or growing feathers to ensure none of the birds were molting at time of sampling. We also sampled tissues of the females captured at each nest by plucking primary #8 from their right wing, by clipping 3-4 mm off of the tip of their left second claw, and collecting approximately 30 µL of whole blood on filter paper. We analyzed the stable isotope ratios of feathers and claws (details below). We used blood samples to double-check each individual's sex through molecular sexing analysis in a commercial laboratory (Santé Laboratório de Análises Clínicas), and the results confirmed in females show developed brood patches. We video-recorded and made focal observations with binoculars to confirm we had captured and sampled the social parents at each nest. We recorded each nestling's hatch day and used a caliper to perform a time-series measurement of their tarsus length until they fledged or were predated. Nest predation (including partial predation) and logistical constraints prevented us from taking the same number of tarsus measurements across all nestlings, at standardized age intervals.

Stable isotope analyses.–We prepared samples of feathers, claws, and whole blood for stable isotope analyses following Paritte and Kelly (2009). We ran all analyses at the University of Oklahoma facilities using ThermoFinnigan Delta V isotope ratio mass spectrometer connected to an elemental analyzer (CosTech) and corrected values according to the fractionation factor of each tissue according to Hobson and Bairlein (2003). Isotope ratio values provide indirect ecological assessments regarding the time of formation of a given tissue. Our analyses reflect two periods of the previous year of life of each individual, one corresponding to feather and the other to claw growth. Because feathers are grown over a specific time of year and are metabolically inert, the isotopic ratios of this tissue ($\delta^{15}N_f$ and $\delta^{13}C_f$) refer to the molting period, which was outside of the breeding period (see Results). Despite the fact that claws are also metabolically inert, in Passerines they have a GR of about 0.04 ± 0.01 $mm.day^{-1}$ (Bearhop et al. 2003). Thus, since Lesser Elaenia has claws of 5.1 ± 0.4 mm long ($n = 9$), and because we sampled claws from September to December, the isotopic ratios found in samples of this tissue ($\delta^{15}N_c$ and $\delta^{13}C_c$) refer to the wintering period of the individual (approximately June-July).

Statistical analyses.–We considered the daily survival rate (DSR) of each monitored nest as a measure of breeding success. The estimated DSR of the nests considered in this study was of 28.2%, which is similar to previous findings for the species at the study site (Medeiros and Marini 2007). We compiled a matrix of the survival history and fate of each monitored nest to perform a nest survival analysis using the standardized (z-transformed) values of each tissues' $\delta^{13}C$ and $\delta^{15}N$ as covariates. We ran eight GLM models (Table 1) using the nest survival models in program MARK (White and Burnham 1999). In addition to a null model, we evaluated the fit of models considering the effect of each covariate alone ($\delta^{13}C_f$, $\delta^{13}C_c$, $\delta^{15}N_f$, $\delta^{15}N_c$), the effect of only wintering covariates ($\delta^{13}C_c$ and $\delta^{15}N_c$), of only molting ($\delta^{13}C_f$ and $\delta^{15}N_f$), of microhabitat ($\delta^{13}C_c$ and $\delta^{13}C_f$), trophic level ($\delta^{15}N_c$ and $\delta^{15}N_f$), and the additive effect of all covariates together.

To evaluate the second hypothesis (i.e. nesting GR as a function of hatch date), the tarsus growth curve of each nestling was fitted using model-based and model-free spline fits (grofit package; Kahm et al. 2010) in R environment version 2.15.3 (R

Development Core Team 2013). We considered the maximum slope (μ) derived from each of these curves as representative of the GR of each nestling. We restricted samples to nests with two nestlings, thus controlling for the effect of clutch size on nestling GR, and only estimated GR for nestlings with ≥ 5 tarsus measurements. We used a Generalized Linear Mixed Model (GLMM) to check how hatch date within the breeding season affects GR, under a Poisson distribution, and using nests as a random effect. For all analyses, we pooled data from 2011 and 2012 breeding seasons, as preliminary analyses using year as a covariate showed similar results.

To evaluate both hypotheses, we proposed model sets and interpreted the results considering the Information-Theoretic approach (Anderson 2010) and model selection procedures recommended elsewhere. We considered the best models to be those with ΔAICc<4, included model averaging for assessing beta estimates and model probabilities (w_i), used models evidence ratio (ER) to assess the importance of hatch date on GR, and considered the relative importance of each covariate on DSR (Anderson et al. 2001; Anderson and Burnham 2002; Burnham et al. 2011). We used packages lme4 (Bates et al. 2012) to run GLMM models and AICcmodavg (Mazerolle 2013) for model selection.

RESULTS

We found that diet ($\delta^{15}N$ values) and microhabitat used ($\delta^{13}C$) while molting and wintering (isotope ratios in feathers and claws, respectively) had no influence on breeding success of females (n = 36). This is shown by a number of parameters (Table 1), specifically the small deviance variation among models, increasing AIC_c values when adding covariates relative to the null-model (lowest AIC_c), and low beta estimates of covariates (Table 2) and their low relative importance ($\delta^{15}N_f$: 0.228; $\delta^{13}C_f$: 0.272; $\delta^{15}N_c$: 0.248; $\delta^{13}C_c$: 0.225).

TABLE 1**.** Results of Generalized Linear Model (GLM) analysis evaluating carry-over effects of individual diet and microhabitat usage at molting and wintering grounds on Lesser Elaenia *Elaenia chiriquensis* breeding success in central Brazil. DSR: Nest daily survival rate; $\delta^{13}C$ and $\delta^{15}N$: stable isotopes ratios of carbon and nitrogen in feathers (i.e. molting grounds; $\delta^{13}C_f$ and $\delta^{15}N_f$) and claws (i.e. wintering grounds; $\delta^{13}C_c$ and $\delta^{15}N_c$). k: number of parameters; AICc: Akaike Information Criterion corrected for small sample sizes; w_i: Akaike weight.

Model	k	AICc	∆AICc	w_i	Deviance
Null model: DSR ~ intercept	1	86.299	0.000	0.283	84.292
~ $\delta^{13}C_f$	2	87.685	1.386	0.142	83.662
~ $\delta^{15}N_c$	2	87.770	1.471	0.136	83.748
~ $\delta^{13}C_c$	2	88.251	1.952	0.107	84.228
~ $\delta^{15}N_f$	2	88.312	2.013	0.103	84.289
~ $\delta^{15}N_f + \delta^{13}C_f$	3	89.336	3.037	0.062	83.291
~ $\delta^{13}C_f + \delta^{13}C_c$	3	89.559	3.260	0.055	83.514
~ $\delta^{15}N_c + \delta^{13}C_c$	3	89.772	3.473	0.050	83.727
~ $\delta^{15}N_f + \delta^{15}N_c$	3	89.774	3.475	0.050	83.729
~ $\delta^{15}N_f + \delta^{13}C_f + \delta^{15}N_c + \delta^{13}C_c$	5	92.481	6.181	0.013	82.367

To evaluate our second hypothesis, we calculated the GR of 24 nestlings from 14 different nests. Three main results of our model selection procedure supported the conclusion that hatch date had a weak influence on nestlings GR (Table 3). First, model probabilities (w_i) and their ER show that the model including hatch date had about 3.7 times less support in explaining GR than the null model. Second, the model-averaged beta estimate for hatch date was virtually null (0.00 ± 0.02, unconditional SE = 0.02, approximate 95% lower and upper 95% CI values = -0.03 and +0.04). Lastly, hatch date provided no improvement in model fit as evidenced by similar AIC_c values and by deviance values differing only to the fourth decimal place among models (Table 3).

TABLE 2. Beta estimates of covariates considered to explain daily survival rate of female Lesser Elaenia *Elaenia chiriquensis* nests in central Brazil based on the GLMs model set (Table 1).

Covariates	Beta estimates ± SD	Lower 95% CI	Upper 95% CI
$\delta^{15}N_f$	0.023 ± 0.147	-0.264	+0.311
$\delta^{13}C_f$	-0.080 ± 0.167	-0.401	+0.248
$\delta^{15}N_c$	0.072 ± 0.165	-0.253	+0.396
$\delta^{13}C_c$	-0.022 ± 0.142	-0.299	+0.256

TABLE 3. Generalized Linear Mixed Model (GLMM) analysis results on the relationship between hatch date and growth rate (GR) of Lesser Elaenia *Elaenia chiriquensis* nestlings in central Brazil. Nests were considered as the random effect term in both models. k: number of parameters; AICc: Akaike Information Criterion corrected for small sample sizes; w_i: Akaike weight.

Model	k	AICc	∆AICc	w_i	Deviance
Null model: GR ~ intercept	2	5.607	0	0.788	1.0351
~ hatch date	3	8.235	2.628	0.212	1.0346

DISCUSSION

Our evaluation of COEs for a short-distance South American migrant is the first to demonstrate that current hypotheses are not appropriate for intratropical migratory birds. We present individual-level evidence that female breeding success in a short-distance migrant species was independent of $\delta^{15}N$ birds had and microhabitats they used during the non-breeding season. We also found that the GR of nestlings is invariable along the breeding season irrespective of their hatch date.

Despite these clear results, “the apparent absence of COEs in an animal system does not preclude the possibility that they are operating” (Harrison et al. 2011). Thus, we build our discussion based on a number of alternative hypotheses, possible additional variables, and directions future studies should pursue to explain, confirm, and broaden the patterns we found to other intratropical and short-distance migrants.

There are several possible explanations for the results found in this study. For instance, the lack of influence of environmental variables upon breeding success could happen in two contexts. First, if individuals were able to compensate COEs (Drake et al. 2013); alternatively, if the variables considered (i.e., $\delta^{15}N$ values and type of microhabitat used) interact with other variables not considered in our sampling design (Harrison et al. 2011). We intentionally avoided biases in isotope ratios due to. Nevertheless, we were unable to control other variables such as female age, which has been found to influence recruitment in the Greater Snow Goose *Chen caerulescens* (Juillet et al. 2012; Drake et al. 2013), and position of the individual in the social hierarchy during the non-breeding season, the effects of which may also carry-over to the next breeding season and affect individual fitness (Marra 2000). Although the wintering ecology of the Lesser Elaenia and any other South American intratropical migrant is virtually unknown, individuals of this species can live for at least 12 years (Marini et al., *unpublished data*), with unknown consequences of age on an individual's breeding success. Thus, future studies on COEs in the SAIS should consider these and other explanations, but specifically focus on the wintering ecology.

External factors can also affect the fitness of an individual, either within or between seasons. For instance, if nest predators respond to nest densities, a clumped distribution of nests could increase nest predation rate and lower nest success rates (Schmidt and Whelan 1999; but see Ackerman et al. 2004). Do conditions in the non-breeding grounds, such as temperature and precipitation (e.g.: Mazerolle et al. 2011), affect the reproductive output of migrants? Such inter-seasonal climate interactions are largely considered in studies evaluating COEs and population dynamics models (Norris and Marra 2007; Betini et al. 2013), but to our knowledge have never been investigated within the SAIS. Moreover, we need studies on whether and how the events faced by migrants during their annual cycle can enhance or buffer COEs (Gill et al. 2001; Legagneux et al. 2012).

Another confounding factor on breeding success of the Lesser Elaenia is associated with the migratory movement itself. It is unknown whether this species uses one or multiple stopover sites along its migration route or if it performs a single non-stop flight between molting, wintering, and breeding grounds. Each of these strategies may interact with the quality of stopover sites used and lead to different outputs of COEs on breeding success (Sheehy et al. 2011). For instance, by using multiple sites, migrants could compensate for the effects of poor-quality areas by varying their stopover time (Stutchbury et al. 2011), i.e. staying longer at better sites, especially if in need of recovering from a previous poor-quality stopover site. Thus, besides considering the variables listed previously, we reinforce the importance of studies on the migratory routes and strategies of South American intratropical migrants for a deeper knowledge of the mechanisms underlying the SAIS (Jahn et al. 2006).

We found little variation of nestlings' GR throughout the breeding season, which refutes our prediction and is inconsistent with the findings of previous studies for Nearctic-Neotropical migrants (Gwinner 1996b; Berthold 2001b; Styrsky et al. 2004). Hence, is resource availability in the Cerrado region enough limited seasonally to stimulate bird migration? Is nestling GR in our model-species under rigid endogenous control? A previous study reports the capture of some Lesser Elaenia individuals during the non-breeding season at our study site (Silveira and Marini 2012; Paiva and Marini 2013), and seems to be a recurring situation along the 12 year of fieldwork carried on by our lab (ACG and MÂM, unpublished data). Although these might be overwintering adults, an alternative and non-exclusive hypothesis is that such birds are young which hatched late in the previous season and overwintered at their natal sites because they were unable to conclude their development in time to migrate. Nestlings of tropical species have been shown to leave the nest with a smaller body size than temperate birds, and higher rates of nest predation might contribute to premature fledging (Robinson et al. 2010). Thus, GR may result from a combination of variables, including ecological and historical (biogeographical) processes.

Given the complexities associated with controls and accounting for all the variables acting on the GR of nestlings of our model-species, we propose several questions as starting points for future studies: (1) Which environmental and endogenous factors control GR in the Lesser Elaenia and other intratropical migrants? (2) Are overwintering Lesser Elaenia individuals in central Brazil indeed hatch-year birds? As expected, individuals captured in Jan-Feb were young hatched in the previous breeding season (Paiva and Marini 2013), but information is lacking for the rest of the non-breeding season. Are these all nestlings from the previous breeding season? (3) Do young birds follow adults on their first migratory journey, i.e. do young and adults have the same migratory routes? (4) Do young and adults have a similar and/or rigid migratory schedule? Answering these questions may demand an experimental approach (e.g.: Killpack and Karasov 2012), refined individual tracking methods such as light-level loggers (Bridge et al. 2013), and joint efforts of research groups within the continent (e.g.: *Red Aves Internacionales*).

In summary, a better understanding of COEs in the SAIS depends upon further studies on a number of aspects and variables related to intratropical migration and the particular location of the SAIS. Southern Hemisphere bird migrants have long been neglected in research (Dingle 2008), and most current research efforts and funding applied toward testing hypotheses on Northern Hemisphere migratory systems. Consequently, we still lack basic knowledge on the natural history of the species that make up SAIS (but see Jahn et al. 2013 for knowledge gaps that still exist even for the Nearctic-Neotropical migratory system).

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CAPÍTULO 3

MIGRANT AND RESIDENT BIRDS SHARE MEALS AT A TROPICAL SEASONAL HABITAT: BUT WHAT ABOUT BREEDING?

LRH: GUARALDO, KELLY, MARINI

RRH: COMPETITION BETWEEN RESIDENTS AND MIGRANTS

MIGRANTS AND RESIDENTS BIRDS SHARE MEALS AT A TROPICAL SEASONAL HABITAT: BUT WHAT ABOUT BREEDING?

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ABSTRACT.–Species' interactions are one of the greatest processes underlying community structure. Yet, there are no studies on interspecific interactions involving resident and migrant bird species in South America. Biases towards the study of Palearctic and Nearctic systems limit the development of unified theories on bird migration ecology and stimulated this work. Specifically, we evaluated whether two species, a resident and a congeneric migrant, compete for resources during their breeding season in a savanna-like biome, the Cerrado of Central Brazil. Using both traditional and novel approaches, such as behavioral observations and stable isotope analysis, we evaluated dietary niches of adults and nestlings, besides species' foraging and breeding strategies. As residents and migrants had highly overlapping diets and shared even the less abundant food items, our results deny the occurrence of competition for food between them. Moreover, residents made multiple nesting attempts in a long nesting period that started before the arrival of migrants to the breeding grounds but still overlapped with the nesting period of the latter. As predation rate of residents' nests was time-constant, we discuss the occurrence of density-independent nest predation. Moreover, nestlings of both species had similar isotopic diets, but only slightly overlapping isotopic niches. Thus, a paradox emerges. Is this pattern a result of past competition, or of different nutritional needs of each species' nestlings? We conclude proposing a set of new questions, expecting to stimulate further studies and fruitful advances in our knowledge of the South American intratropical system and bird migration ecology as a whole.

Key words: breeding ecology; foraging behavior; interspecific competition; intratropical migration; *Elaenia chiriquensis*; *Elaenia cristata*; nestlings.

“New discoveries are continually refining our understanding of the domain of competition, and we are well on the way to developing a multifaceted theory to match what is clearly a highly diverse natural world.” (Schoener 1982)

HUNDREDS OF THOUSANDS of birds undergo yearly movements between their wintering and breeding grounds. Along such journeys, these “birds of two-worlds” (Greenberg and Marra 2004) must not only adjust themselves to new environments and food sources, but also show eco-behavioral strategies to fit in different communities at each period of their annual cycle. The processes underlying the origin and evolution of bird migration are still obscure, but interspecific interactions, especially competition, are considered by some researchers as one of the main drivers of this behavior (Cox 1968, 1985; Salewski and Bruderer 2007). However, the use of competition theory to support this hypothesis has proven to be a hard task as it demands deep knowledge about (i) past availability of resources to resident species, and (ii) the consequences of possible agonistic interactions for each species (Greenberg 1986). In fact, verifying current or past competition is a challenging ongoing quest that has given rise to endless discussions (e.g.: Connell 1980; Bleken 1983; Davic 1985; Morris 1999; Zong-Ling Wang et al. 2002; Miller et al. 2009).

Studies on the interspecific interactions between migrants and residents are a stepping-stone to deepen our knowledge not only on bird ecology as a whole but also on the origins of the bird migration process itself. Few studies have evaluated the effects of migrants in the communities they join along their migration (Dhondt 2012b, p.115), and most of such studies focused on only two migratory systems (*sensu* Hayes 1995): the Palearctic-African and the Nearctic-Neotropical, both respectively reviewed by Leisler (1990) and Rappole (1995b). So far, it seems that migrants have a more plastic foraging behavior than residents, often ingesting the most abundant food items and especially those unexploited by residents (Leisler 1990; Leisler 1992). However, another study shows that residents had a more diverse diet than migrants, probably due to environmental constraints that limited local prey availability (Lack 1986). Moreover, residents and migrants may have different diets not because of mutual exclusion (e.g.: Willis 1966). For instance, residents may be more adapted to a local set of resources nonexistent at other sites used by migrants along their annual cycle (e.g.: Jedlicka et al. 2006), and this should be even more patent in those cases of highly neophobic migrants (Rappole 1995a, p. 66). These various behaviors highlight how far we are from describing a general pattern for the interactions involving residents and migrants. This is of even greater concern when we notice the absence of studies of other migratory systems (e.g.: Austral-Neotropical, and South American Intratropical) and that all information presented above refers exclusively to wintering grounds. Moreover, considering that one outcome of competition is an effect on individuals or species fitness (e.g.: Greenberg 1986), evaluation of the effects of co-occurrence of residents and migrants on nest survival becomes even more critical.

To unravel new aspects within this scenario of limited knowledge, we assessed the occurrence of direct and indirect competition between a resident and a migrant species in the South American Intratropical migration system. Four hypotheses guided our research. The first two hypotheses relate to the birds' diets. As found in other migratory systems, (i) intratropical migrants should adjust their diet and niches to the current community and habitat; thus, they are expected to have more plastic behavior than residents. Alternatively, (ii) residents could change their feeding behavior upon the arrival of migrants to avoid competition (e.g. realized niche shift; Hutchinson 1957). Thus, three main questions should be answered to test these hypotheses for the studied system: Is there a limitation in local prey abundance? Do migrants and residents have overlapping diets and niches? Do residents change their diet upon migrants' arrival to avoid competition? Two contrasting predicted scenarios arise from this. If food is abundant, closely related migrants and residents should have similar diets and niches. Alternatively, if food is a limiting resource, such birds could only co-occur at present due to long-term selection of non-competitive behavior, i.e. non-overlapping niches and diets.

The third and fourth hypotheses refer to the effects of migrants on breeding patterns of residents. Since nest predation is mostly a density-dependent phenomenon (Martin 1988), (iii) breeding success of residents should be negatively affected by an increased nest density during migrants' nesting period (i.e. indirect or apparent competition; Holt 1977; Hoi and Winkler 1994). Besides, (iv) if closely related and ecologically similar species overlap their nesting periods, and if food resources are limited, parents would compete for food items to provision their nestlings. To test these latter two hypotheses, we need a thorough evaluation of both species' breeding ecology. Do they indeed overlap their nesting periods? If so, does apparent competition play a role in their breeding success? What is the diet of each species' nestlings? We expected residents and migrants to avoid overlapping their nesting periods to decrease (direct of apparent) competition (Rappole 1995a, p. 69). We also expected nestlings of ecologically alike resident and migratory species to have overlapping diets, thus temporal displacement of nesting period would also avoid competition between parents of both species in provisioning their nestlings.

METHODS

Study site.–We collected our data in central Brazil at Estação Ecológica Águas Emendadas (ESECAE), in Planaltina-DF (between 15°42’ to 15°38’ S and 47°33’ to 47°37’ W). The area has a seasonal climate, with a rainy season lasting from October to April (Gottsberger and Silberbauer-Gottsberger 2006a), and a seasonal production of food resources to birds, e.g. flowers, fruits, seeds, and arthropods (Pinheiro et al. 2002; Gottsberger and Silberbauer-Gottsberger 2006b). The sampling site was a 100 ha plot within ESECAE where our study group has been developing a long-term bird breeding ecology research project since 2002. The plot has a well-connected trail system and is covered mostly with a savanna-like vegetation known as *sensu stricto* cerrado (further study site details in Paiva and Marini 2013 and references therein).

Model species.–We selected two Flycatcher (Tyrannidae) species as models, the Plain-crested Elaenia *Elaenia cristata* and the Lesser Elaenia *E. chiriquensis*. Both are morphologically similar, but the first has smaller body size compared with the latter (15 g *vs.* 18 g, respectively; ACG, unpublished data) and a (sometimes absent) white crest, while the second has a conspicuous crest (Fitzpatrick et al. 2004, Marini et al. unpublished data). As is usual for flycatchers, both species eat arthropods (Fitzpatrick et al. 2004), but stomach content analyses revealed they ingest a larger amount of fruits (Marini and Cavalcanti 1998; Fitzpatrick et al. 2004). Plain-crested Elaenia is resident at ESECAE, breeds from mid-September to mid-December (Negret et al. 1984; Marini et al. 2009), and molts between late-October and late-February (Silveira and Marini 2012). On the other hand, the Lesser Elaenia is migratory and arrives in large numbers at ESECAE in mid-August, breeds from September to December, and usually departs to unknown molting and wintering grounds by December-January

(Medeiros and Marini 2007). Both species build similar-sized low cup nests in *sensu stricto* Cerrado vegetation (Medeiros and Marini 2007; Marini et al. 2009), but only residents line the egg chamber with a white or pinkish layer of vegetal fibers (Marini et al. 2009). Mean clutch size is two for both species, incubation period lasts about 13 d for the migrants and 15 d for the residents, and nestling period is respectively of 14-15 and 16 d (Medeiros and Marini 2007; Marini et al. 2009). Previous studies show nest predation rate at the study site is high, with residents showing, on average, 27% of nest success (breeding seasons of 2002-2007; Marini et al. 2009) and migrants 33% (2002-2003; Medeiros and Marini 2007).

The two species are especially suitable models for this study, since they are closely related, with similar morphology and diet, but contrasting migratory status. Moreover, both have conspicuous foraging and territorial behavior, are abundant at our study site, are easily captured in mist-nets, and have a history of good sample size of nests found and monitored yearly at the study site since 2002.

Food phenology.–We sampled arthropods and fleshy fruits during six days split along the three main periods of the annual cycle of residents in 2011/2012: molting (mid-December 2011 and mid-February 2012 samplings), wintering (late-March), and breeding (mid-August, September, and October). We established five 100 x 4 m plots separated from each other by at least 50 m for fruit samplings, and used half of each (100 x 2 m) for arthropod sampling. We collected arthropods by sweep netting the herbaceous and shrubby vegetation. We covered the whole area of every plot at constant speed of 2-3 Km/h between 0900 h and 1100 h in sunny days. As this method may bias samplings towards certain groups or species (e.g. Lutinski et al. 2013), in each sampling day we vigorously beat 25 randomly assigned shrubs three times to sample insects that fell in an entomological umbrella (0.8 m^2). We then froze all arthropods, and assigned them to one of five groups, according to their average nutritional contents (*sensu* Bell 1990; Gäde and Auerswald 2002): (i) ants, which are a source of carbohydrates, but also have a high content of indigestible chitin; (ii) beetles, which are lipid-rich, but have variable trophic levels; (iii) spiders, which are lipid-rich and exclusively predators (e.g.: Collatz & Mommsen 1974); (iv) other non-alate arthropods, mostly nymphs and larvae, both lipid-rich and mostly low trophic level prey; and (v) other alate arthropods, mostly Diptera and Hymenoptera, which are carbohydrate-rich prey, with a lower amount of indigestible chitin content than ants. To estimate biomass for each group of arthropods by plot, we oven-dried all samples at 75 °C for 48 h before weighing to the nearest mg.

We recorded the number of unripe and ripe fruit produced by each identified tree species in each plot and collected 10 unripe and 10 ripe fruits of each to weigh their fresh biomass in a precision scale. We excluded seeds from fruits prior to weighing, as seeds are not a resource for flycatchers, and only considered those fruit species which fruits have a size suitable for ingestion by the Elaenia species (A.C.G., unpublished data) Finally, we used these values to estimate total biomass of fruit produced in each plot.

Foraging niche.–We recorded the foraging behavior of residents during molting, wintering, and breeding periods, and of migrants during the breeding period. We made observations from a safe distance (15-30 m) with binoculars to quantify the maneuvers made by each spotted bird to capture food items (adapted from Fitzpatrick 1980). To ensure data independence, only the first maneuver of each individual was recorded, usually within the first minute after we spotted the bird. As most individuals lack any marks, after each observation we walked at least 200 m before start looking for another foraging individual. Sex of individuals was not take into account as species lack sexual dimorphisms that could be noticed with binoculars. We classified the maneuvers according to targeted food item: a) prey in flight (in our case, aerial hawk maneuver only; Fitzpatrick 1980); b) landed or non-flying prey (e.g.: gleaning, striking, and picking maneuvers); and c) fruit.

Tissue sampling of adults.–Joint analysis of the isotopic ratios of tissues and of plausible food resources of a given organism provide indirect estimates of its isotopic diet. As each tissue has a specific turnover rate, the analyses of a proper set of tissues allow inferences on the isotopic diet of an individual at different periods of its annual cycle. Since sex is an individual variable that could bias isotope ratio analyses (Bearhop et al. 2002), we only sampled females, identified in flycatchers by the presence of a brood patch during the breeding season (Davis 1945; Jones 1971) and double-checked by molecular sexing analyses (details bellow).

We mist-netted females (residents: late August; migrants: late October), plucked primary #8 from the right wing, clipped the tip (3-4 mm) off of left claw #2 (resident species only), and collected 100 µL of whole blood (both species). We kept each feather and claw sample in paper envelopes. About 70 µL of the blood was air dried on a glass slide, transferred to a plastic container in the lab and then oven-dried at 35 °C for 48 h. We stored the remaining ~30 µL of blood on filter paper and used it for double-checking individuals' sex through molecular sexing analysis in a commercial laboratory (Santé Laboratório de Análises Clínicas).

As feathers are metabolically inert tissues, analysis of their isotopic ratios allow inferences about the isotopic diet of the individual while molting (i.e. late October to mid-February for the resident species; Silveira and Marini 2012). For Passerines similar in size to our models, whole blood has a half-life varying from 4.5 to 20 d (higher values referring only to blood cells rather than whole blood; Hahn et al. 2012), and claws grow at a constant rate of 0.04 ± 0.01 mm.day^{-1} (Bearhop et al. 2003). Thus, sampled whole blood allows inferences on the isotopic diet of each species while nesting. Moreover, as residents' claws are 5.25 ± 0.42 mm long (n = 6), isotopic analysis of sampled claw-tips allows diet inferences relative to the fourth month before the sampling period (i.e.: April to June), hereafter referred to as wintering period.

Nest search and nestlings' tissue sampling.–We conducted nest searches from mid-July to early-December and monitored each nest found every 2-4 d until egg hatching, then at 1-2 d intervals until nestlings fledged or the nest was predated. When nestlings achieved ~11 d, we collected and stored their right primary #1 in a paper envelope. High predation rates (see estimates in Results) limited our sample size and did not allow us to control for nestling sex, although it is unlikely isotopic ratio is also sex-biased in nestlings.

Isotopic analyses.–We followed the methodology described in Paritte and Kelly (2009) to clean feathers and claws prior to stable isotopes analyses. We oven dried the arthropods, fruits (pulp only), and blood samples for an additional 48 h at 35 °C. Then, we ground all samples of each food source until they became a homogenous fine powder. We ran the stable isotope analyses in a ThermoFinnigan Delta V isotope ratio mass spectrometer and an elemental analyzer (CosTech) at the University of Oklahoma facilities. Isotope ratios were reported in per-thousand (‰), using δ notation (e.g.: $\delta^{13}C$ and $\delta^{15}N$) based on international standards (Pee Dee Belemnite for carbon and air for nitrogen; Fry 2006).

We selected food samples of two 2012 periods for the isotopic analyses. The first period included late-March samples, thus allowing inferences about the wintering period diet of residents; and the second period included mid-October samples, used as a reference for the breeding periods of residents and migrants, and for diet of both species' nestlings. Moreover, we also used this second batch of samples to infer diet of residents while molting, as this period is well within the rainy season (October to April) and mostly overlaps the migrants' breeding season.

Data analyses.–We followed the Information-Theoretic approach (Anderson 2010) and model selection procedures recommended elsewhere (Anderson et al. 2001; Anderson and Burnham 2002; Burnham et al. 2011). The only exceptions were the stable isotopic diet and niche analyses, for which we used a Bayesian approach (details below).

To check for resource seasonality, we considered period (molting, wintering, and breeding) as predictors of total available biomass of each food item (i.e. an approach equivalent to One-Way ANOVA, with period as predictor and prey biomass as response variable). We used Morisita's index to quantify the foraging niche overlap between residents and migrants based on the matrix of observed foraging behaviors of each species. We chose this index over others as it is less biased by sample size (Wolda 1981). We ran three analyses to evaluate different scenarios. The first checked whether residents changed foraging niche along the year and was based on a matrix including only residents' records by period. The other two checked if residents and migrants overlapped foraging niches when co-occurring, i.e. molting and breeding period records of residents versus migrants.

We ran multiple Markov Chain Monte Carlo (MCMC) models with one million iterations each to estimate the isotopic diet and isotopic niche of (i) residents in each period of their annual cycle, (ii) migrants while breeding, and (iii) nestlings. In the latter, we only included nestlings hatched during the non-overlapping nesting period of both species (residents: late August to late October; migrants: November only). We ran four

MCMC models based on the following datasets: residents while molting; residents while wintering; migrants and residents while breeding; and nestlings by species.

Due to different reaction rates of light and heavy isotopes, each tissue may have different isotopic ratios due to the metabolic routes needed for their development. This so-called isotopic discrimination must be considered for an accurate estimate of isotopic diet of an organism (Gannes et al. 1997). Since each species has a unique metabolism, there are criticisms on estimating isotopic diet of an organism using discrimination factors experimentally calculated for other species (Caut et al. 2009). However, this is the only current alternative to carry out stable isotopic diet analyses in most cases (Bond and Diamond 2010), and especially for South American bird species where stable isotope analysis is still a novelty. Thus, to maintain a conservative approach, we averaged discrimination factor values found in the literature for Passerine species (Hobson and Bairlein 2003; Pearson et al. 2003) and considered a SD of 1.5‰ to account for additional uncertainty (e.g Frick et al. 2014). Specifically, for δ^{13}C and δ^{15}N in whole blood samples we used the values of 1.2‰ and 2.2‰, respectively and of 3.2‰ and 3.5‰ for keratin-based tissues (claws and feathers), respectively.

To infer species diet, we used Bayesian stable isotope mixing models. Using the isotopic ratios of the six sampled food sources and the above-described discrimination values, we calculated the median proportional contribution of each food source for a given species (i.e. isotopic diet). For additional descriptions of isotopic niche, we used Layman's metrics (Layman et al. 2007) based on δ^{13}C-δ^{15}N bi-plots of samples from each of the above-mentioned datasets: (i) δ^{15}N range, which correlates with the number of trophic levels in the targeted-species' isotopic diet; (ii) δ^{13}C range, which correlates with the number of basal resources in the target-species' food web;

(iii) total area of the convex polygon encompassing all samples in the bi-plot, which informs the total trophic diversity within the species' food web; and (iv) measures of species' isotopic niche redundancy (the mean nearest neighbor distance; MNND), and (v) individuals packing within the isotopic niche and (SD of MNND). To evaluate the species' isotopic niche overlap in each dataset, we used the overlapping area between Bayesian ellipses corrected for small samples that represent individuals' ratios in the bi-plot. We used this over Convex Hull methods, as it is insensitive to bias caused by sample size (Jackson et al. 2011).

We described each species' breeding season as the period between the day we found the first active nest (laying date of first egg) and the last nesting activity day (i.e. the fledging day of the last nestling or predation day of the last active nest) in 2012. To check if residents and migrants overlapped their breeding season, we ran a model set including a null model and a model with species as a predictor variable of nesting activity (i.e. an equivalent approach to unpaired t-test). For this model, the response variable was the average date of activity of each monitored nest, i.e. date between laying of the first egg in the nest and of fledging of last nestling or nest predation. We also ran a nest survival model considering constant survival to estimate daily survival rates (DSR) of each species' nests (pooled incubation and nestling periods). We then proposed a second model with overlap as covariate to evaluate the influence of nesting overlap with migrants on residents' nest survival.

As sample sizes were always <40, we used AICc values instead of AIC to select the best models of each model set, considering best models all those with ΔAICc<4. In addition, we used Akaike weights (w_i) to assess the importance of each predictor variable in the model set. We ran nest survival estimates in the Program MARK (White and Burnham 1999) and all other analyses in R environment version 2.15.3 (R

Development Core Team 2013) using multiple packages: spaa (Zhang 2013), nlme (Pinheiro et al. 2013), AICcmodavg (Mazerolle 2013), siar (Parnell and Jackson 2011). Whenever needed, we transformed the raw data to fulfill assumptions of each analysis.

RESULTS

Resource seasonality.–Data analyses show three patterns of food items biomass availability along the considered periods. Beetles and fruits were seasonal resources, as shown by high ΔAICc and w_i values of models considering period of the year as predictor of biomass (Table 1). While beetle biomass decreased from molting to wintering, to breeding seasons, fruit production was similar during molting and breeding periods, but lowest at wintering (estimates and 95% CI values in Table 2, and Fig. 1). Contrastingly, availability of ants was aseasonal (Table 1), as shown by low ΔAICc values and similar estimates between periods. Other alate prey also constituted an aseasonal resource, as the null model had best fit (ΔAICc~4) and ~88% w_i (Table 2, Fig. 1). Estimates for spiders and other non-alates show only a slight tendency of seasonality (Table 1), with highest biomass availability at molting and wintering periods and lowest at breeding (Table 2, Fig. 1).

Niches and diets.–We recorded 503 foraging maneuvers split unevenly in each period (molting period: 42 maneuvers, 27 h of observations; wintering: 8 maneuvers in 8 h; breeding: 218 maneuvers for residents and 235 for migrants in 318 h). Residents had high foraging niche overlap in molting *vs.* breeding and wintering *vs.* breeding but not in molting *vs.* wintering (Table 3). This pattern reveals that residents had a marked foraging behavior shift from molting to wintering periods. Residents and

TABLE 1. Results of model selection of multiple linear models sets to evaluate prey biomass seasonality in Central Brazil (Brasília, Federal District). k: number of parameters, AICc: Akaike Information Criterion corrected for small (<40) sample sizes, ∆AICc: difference of AICc values between models, and w_i: Akaike weight of the model. * indicates food source categories which biomass values were squared-rooted transformed to comply with the test assumptions of normality and homoscedasticity.

Models	k	AICc	∆AICc	w_i
Fruits*				
Period	4	-19.4091	0	0.934
Null model	2	-14.1084	5.3008	0.066
Beetles				
Period	4	-55.583	0	0.9793
Null model	2	-47.8653	7.7176	0.0207
Ants				
Period	4	-128.776	0	0.654
Null model	2	-127.502	1.2734	0.346
Other alate*				
Null model	2	41.1063	0	0.8779
Period	4	45.0508	3.9445	0.1221
Spiders				
Period	4	-57.5255	0	0.7536
Null model	2	-55.2901	2.2355	0.2464
Other non-alate*				
Null model	2	36.1054	0	0.6948
Period	4	37.7508	1.6454	0.3052

migrants had very similar foraging niches when they were co-occurring (i.e. residents' breeding and molting periods *vs.* migrants' breeding period; Table 3). Yet, the foraging niches of residents and migrants differs largely from their isotopic niches described below.

TABLE 2. Beta estimates and 95% CI of prey biomass availability in each period of the annual cycle of the resident Plain-crested Elaenia *Elaenia cristata* in Central Brazil. *: Normalized data through square-root transformation.

	Period	Estimates [a]	95% CI
Fruits*	Wintering	-0.2233	-0.3561 , -0.0904
	Breeding	0.0159	-0.1169 , 0.1488
Beetles	Wintering	-0.1097	-0.1860, -0.0334
	Breeding	-0.1388	-0.2151, -0.0626
Ants	Wintering	-0.0027	-0.0293, 0.0239
	Breeding	-0.03	-0.0551, -0.0049
Other alate*	Wintering	0.0743	-0.3233 , 0.4719
	Breeding	-0.1397	-0.5119 , 0.2325
Spiders	Wintering	0.0445	-0.0289, 0.1178
	Breeding	-0.0583	-0.1214, 0.0049
Other non-alate*	Wintering	-0.0939	-0.4531 , 0.2653
	Breeding	-0.3198	-0.6690 , 0.0290

a. Molting period as reference.

Analogous to findings connected to foraging strategies, residents also shifted isotopic niches and diets along the year. Layman's metrics (Table 4) show that molting residents based their diet on more food items of variable trophic levels and on a larger number of basal resources (respectively, δ^{15}N and δ^{13}C range values in Table 4), thus having the widest niche in this period of their annual cycle (Bayesian ellipse area in Table 4) than in other periods. During the other two periods, residents had isotopic niches with similar width. However, birds included a less diverse set of basal resources and trophic level of preys while wintering than breeding (Table 4). The more clumped distribution of individuals in the wintering than in the breeding period (lower MNND ± SD values; Table 4, Fig. 2) explains this apparently contradictory pattern. In other words, breeding individuals were more sparsely distributed along the species' isotopic niche, as noticed by the more elongated ellipse in Fig. 2. While wintering, the niche of residents differed totally from that at molting and at breeding (lack of overlap in Fig. 2), but their breeding isotopic niche overlapped 71.6% with the molting one (Fig. 2).

At the isotopic diet level, residents preferentially ingested prey types irrespective of abundance of food items estimated through biomass (Fig. 1; Table 5). For instance, fruits, other alate arthropods, and other non-alate arthropods were the most abundant food items during the molting period, yet residents ingested mainly beetles and spiders at that time. Then, during the wintering period residents switched to a more diverse diet: ants, fruits, and other alate and non-alate arthropods. However, ants were comparatively the least abundant prey and fleshy fruit production was at its lowest level at this time. Finally, in the breeding season residents returned to a diet similar to the one they had while molting, i.e. based on beetles and spiders, although these food items, together with ants, were once more the rarest resources in terms of biomass.

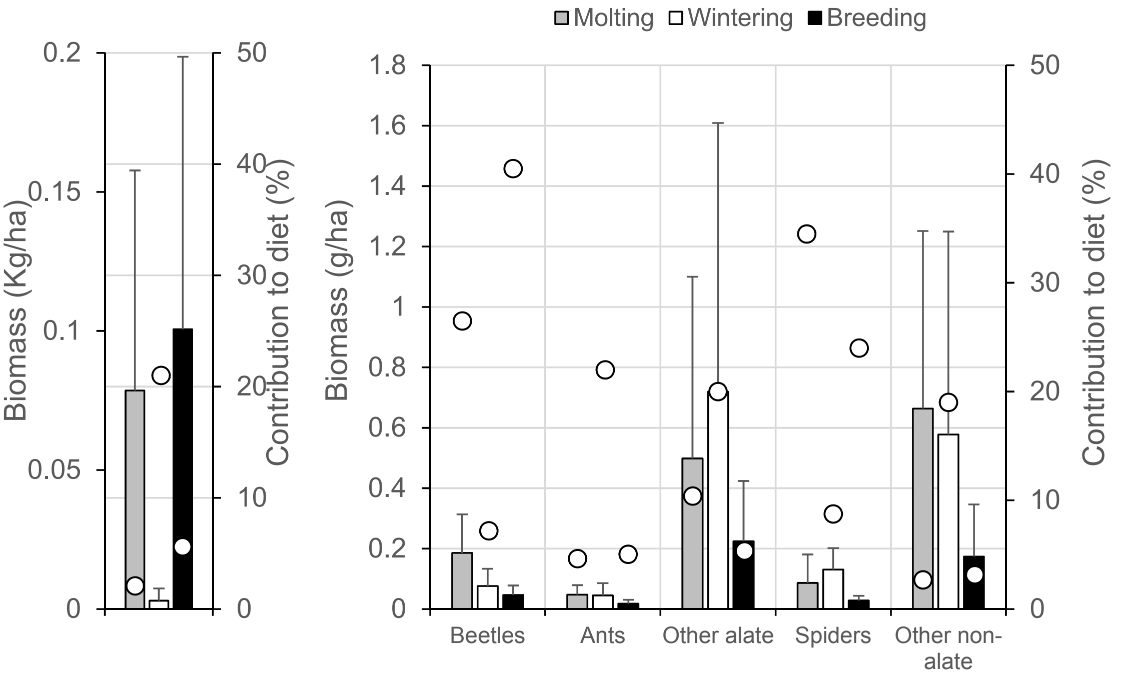

FIG. 1. Available biomasses of potential food items (bars) along each annual cycle period of the resident Plain-crested Elaenia *Elaenia cristata* in a *sensu stricto* Cerrado area in Central Brazil. White dots represent the median Bayesian estimated isotopic contribution of each prey type (siar output) to the diet of the resident species in the corresponding period.

Residents had a diet similar to that of migrants during the breeding period. Quantitatively, beetles and spiders were the main contributors to the migrants' diet, well over the estimated contribution of other food items (Table 5). The isotopic niche diversity ($\delta^{15}N$ range in Table 4 and Fig. 2) and number of basal resources ($\delta^{13}C$ range in Table 4 and Fig. 2) included by migrants in their food web were only slightly higher than that of residents (Table 4). Nevertheless, during their breeding period migrants had a markedly broader niche width, similar to the one residents had while molting. Altogether, these scenarios explain the more dissimilar isotopic niches and diets between residents and migrants when breeding (49.1% of isotopic niche overlap) and the almost totally overlapping niches (83.2%) between molting residents and breeding migrants (FIG. 2).

TABLE 3. Measures of foraging niches overlap (Morisita's index, in %) in multiple scenarios involving adults and nestlings of the resident Plain-crested Elaenia *Elaenia cristata* and the migratory Lesser Elaenia *E. chiriquensis* in Central Brazil.

Comparison	Foraging niche overlap (95% CI)
Resident:	
molting x breeding	97.0 (88.1 - 1.0)
wintering x breeding	63.5 (61.6 - 1.0)
molting x wintering	45.1 (29.4 - 1.0)
Resident x Migrant:	
breeding x breeding	93.1 (89.1 – 1.0)
molting x breeding	88.7 (84.2 – 1.0)

As found for adults, nestlings of both species had similar diets, mainly based on spiders and other alate arthropods (Table 6), and on a food web with a similar number of basal resources (Table 4). However, they differ in two aspects: residents' nestlings had a more diverse diet, as they also included ants as main food item; and migrants had a more trophic diverse diet (Table 4; Fig. 2 inset). Consequently, nestlings of both species had only slightly overlapping diets, 14.7%.

TABLE 4. Metrics of the isotopic niche of the resident Plain-crested Elaenia *Elaenia cristata* and the migratory Lesser Elaenia *E. chiriquensis* in Central Brazil. Values derive from $\delta^{15}N$ and $\delta^{13}C$ analyses of blood (breeding period), feather (molting), and claw (wintering) samples for adults, and new-grown feather samples for nestlings. SEA_c: Standard Ellipse Area corrected for small sample size; MNND: mean nearest neighbor distance; n: sample size. See Methods for details on each index.

Species	Period	$\delta^{15}N$ range (‰)	$\delta^{13}C$ range (‰)	SEA_c	MNND ± SD	n
Resident						
	Adults					
	Molting	2.6	2.9	4.05	0.93 ± 0.92	11
	Wintering	1.6	1.6	1.43	0.35 ± 0.43	11
	Breeding	2.0	2.8	1.12	0.88 ± 0.45	12
	Nestlings	1.7	1.1	1.49	0.63 ± 0.57	6
Migrant						
	Adults					
	Breeding	2.7	2.9	3.77	0.58 ± 0.71	12
	Nestlings	2.3	1.1	1.55	0.36 ± 0.42	8

Breeding season and nest survival.–We found and monitored 35 nests of each species. Residents nested for a period almost 50% longer than migrants, respectively 112 d (July 27th until November 16th) and 70 d (October 1st until December 10th, respectively; Fig. 3). The model considering species as predictor of average nesting date had a better support (AICc = 644.1; w_i = 1) than the null model (AICc = 696.5; w_I = 0), confirming that, despite the 46 d of overlap, residents and migrants had distinct nesting periods along the 2012 breeding season (Fig. 3). Indeed, DSR of residents' nests was similar irrespective of nesting overlap with migrants (null model AICc = 141.1 and w_i = 0.72; model considering overlap as DSR predictor: AICc = 142.9 and w_i = 0.28). Moreover, DSR of migrants' nests remained constant along their entire nesting period (Null model: AICc = 143.0, w_i = 1; time-variable DSR model: AICc = 224.8, w_i = 0), i.e. irrespective of overlapping with nesting migrants. Residents had slightly lower DSR estimate than migrants (respectively, 0.94 and 0.96), and higher predation rates (72.3% against 62.8% of migrants). Since residents' nestlings take ~4 d longer from egg laying to fledge than migrants' (32.4 d *vs.* 28.5; ACG unpublished data), estimated nest success of residents was 13.6% ($0.94^{32.4}$.100), ~58% lower than migrants ($0.96^{28.5}$.100 = 33.0%).

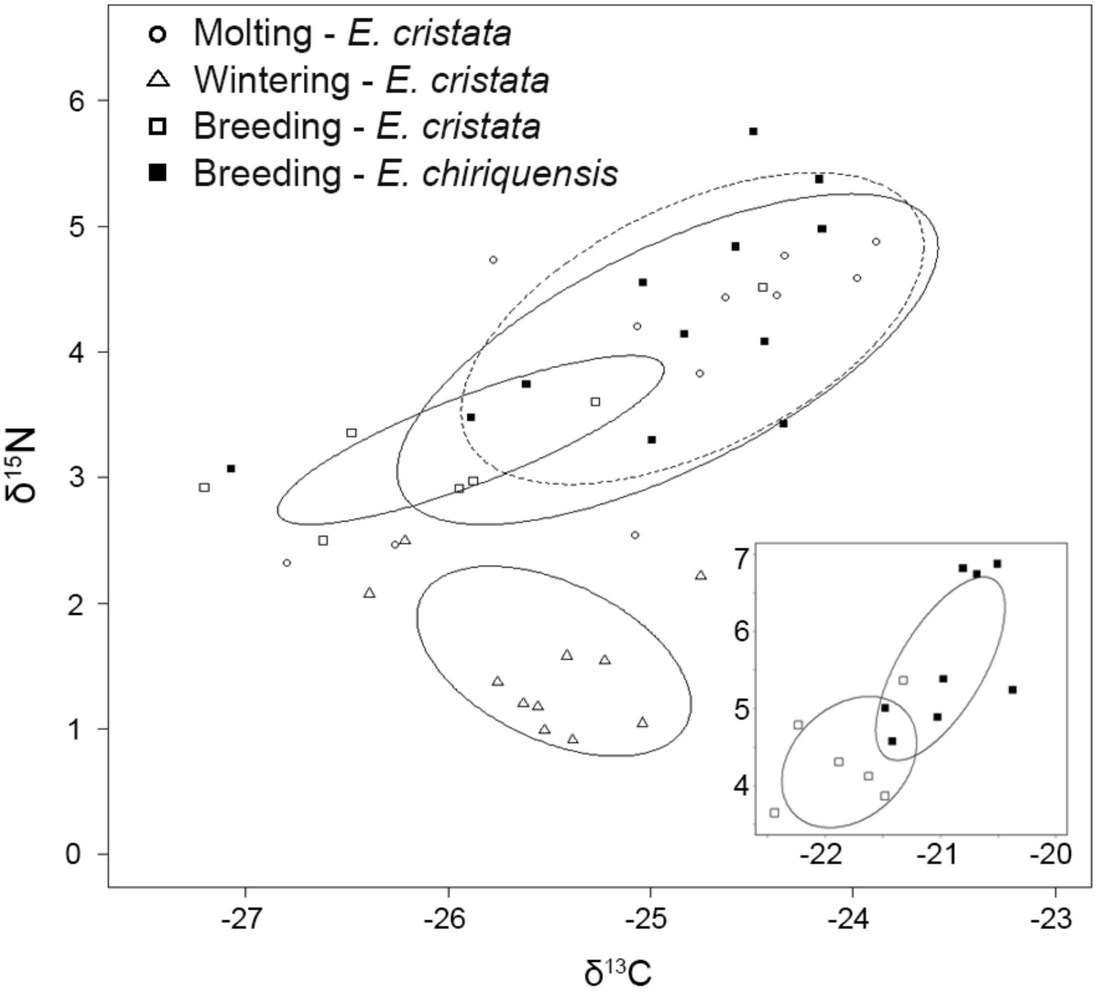

FIG. 2. Bi-plot of isotopic ratios of the resident Plain-crested Elaenia *Elaenia cristata* individuals highlighting the overlaps between the isotopic niches (Bayesian ellipses) of molting (dots), wintering (triangles), and breeding (white squares) periods. The isotopic niche of the migrant Lesser Elaenia *Elaenia chiriquensis* is overlaid here (black squares, dashed line ellipse) to show its overlap status with the residents' niches. Inset shows nestlings' data (residents: white squares; migrants: black squares).

TABLE 5. Bayesian maximum proportion estimations (%) of food sources consumed by adults of the resident Plain-crested Elaenia *Elaenia cristata* and the migrant Lesser Elaenia *E. chiriquensis* in Central Brazil. Values in parenthesis refer to 95% CI.

Source	Plain-Crested Elaenia			Lesser Elaenia
	Molting	Wintering	Breeding	Breeding
Fruits	2.1 (0-14.0)	21.0 (8.4-32.0)	5.6 (0-19.0)	1.3 (0-8.6)
Beetles	26.5 (5.4-43.0)	7.2 (0-23.0)	40.5 (20.0-59.0)	20.5 (3.9-36.0)
Ants	4.6 (0-28.0)	22.0 (6.0-36.0)	5.0 (0-26.0)	5.0 (0-27.0)
Other alate	10.4 (0-36.0)	20.0 (2.1-34.0)	5.3 (0-27.0)	5.9 (0-29.0)
Spiders	34.5 (13.0-60.0)	8.8 (0-21.0)	24.0 (5.2-40.0)	51.0 (26.0-69.0)
Other non-alate	2.7 (0-20.0)	19.0 (1.0-33.0)	3.2 (0-18.0)	2.0 (0-14.0)

TABLE 6. Bayesian maximum proportion estimations (%) of food sources consumed by nestlings of the resident Plain-crested Elaenia *Elaenia cristata* and the migrant Lesser Elaenia *E. chiriquensis* in Central Brazil. Values in parenthesis refer to 95% CI.

Source	Plain-Crested Elaenia	Lesser Elaenia
Fruits	1.6	1.0
	(0-9.8)	(0-6.9)
Beetles	3.71	2.0
	(0-21.0)	(0-14.0)
Ants	19	5.2
	(0.3-38.0)	(0-29.0)
Other alate	23.5	8.1
	(1.0-42.0)	(0-36.0)
Spiders	35.0	63.5
	(17.0-54.0)	(37.0-82.0)
Other non-alate	5.6	2.3
	(0-24.0)	(0-15.0)

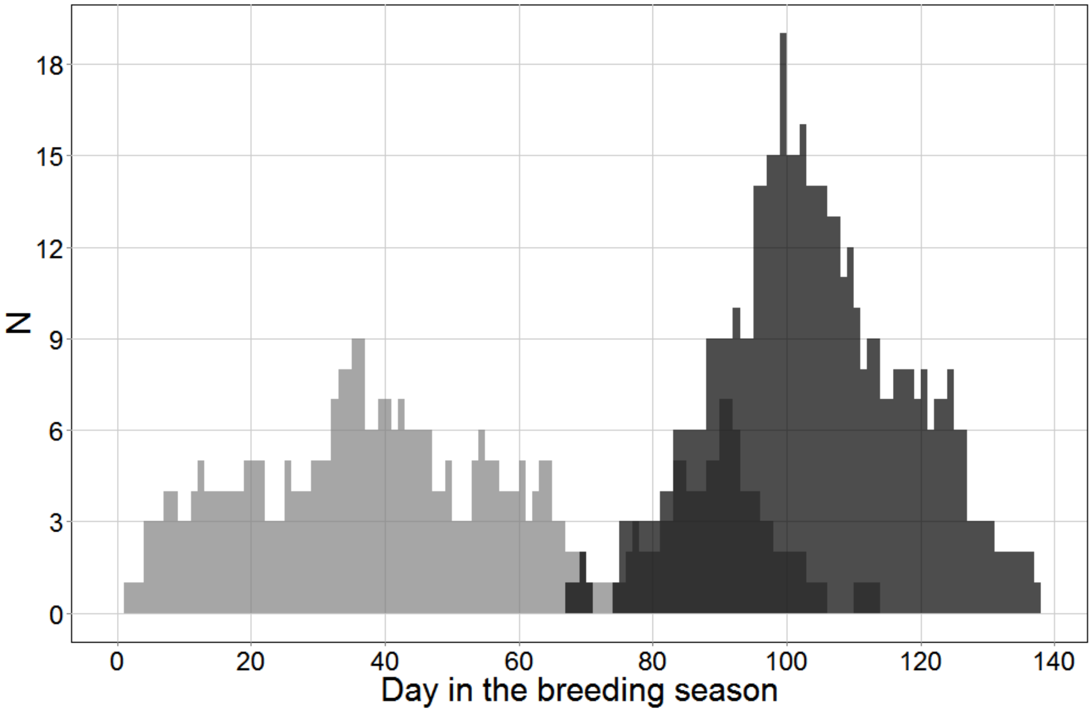

FIG. 3. Daily number of active nests of residents (light-gray bars) and migrants (dark-gray bars) along the 2012 breeding season in Central Brazil, highlighting the number of active residents' nests (black bars) within migrants nesting period. Season started in July 27th (day 0) and ended in December 10th (day 137).

DISCUSSION

The evaluation of species competition and its community-effects has been one of the greatest challenges in ecology studies (e.g.: May 1975; Connell 1980; Schoener 1982; Davic 1985). This is especially true where species coevolution shaped current stable communities, and species competition can only be inferred through the current consequences in species ecology and behavior (e.g.: Zong-Ling Wang et al. 2002; Miller et al. 2009), i.e. by the ecological and behavioral memory of past competition (Schoener 1982). The assessment of the occurrence of competition between residents and migrants seems an unreachable goal. Nevertheless, our data show unambiguous evidence that residents and migrants share even the less abundant food resources (e.g. beetles and spiders during the breeding period; Fig. 1). This finding is sufficient condition (Wiens 1977; Dhondt 2012a) to state that there is no competition for food between both species at our study site. Yet, nesting aspects of both species added a level of complexity in trying to answer the central question of this study. Thus, we present a detailed discussion on alternative hypotheses and propose a set of additional questions, so future approaches can deepen our understanding of the interspecific interactions in the South American intratropical migration system.

Foraging observations and diet assessments of residents provided interesting conclusions and insights on their strategies to survive in a seasonal tropical environment and to co-occur with migrants during the breeding season. The resident Plain-crested Elaenia had a plastic feeding behavior along the year and shifted their foraging and, especially, isotopic niche and diet between seasons. Contrary to expectations, such plasticity was not an effect of the presence of a large population of the congeneric intratropical migrant, the Lesser Elaenia. This could arguably be due to birds adopting a “better than nothing” foraging strategy when food items became scarce. Two facts confirm these previous two statements: (i) residents and migrants had high niche and diet overlap at the study site; and (ii) residents’ diet was based on the least abundant food items despite the high isotopic diet overlap with migrants. Thus, instead of interspecific competition, variable nutritional needs of residents in each period of their annual cycle (e.g.: Bairlein and Gwinner 1994, and references therein) seems to explain our results more parsimoniously.

Birds undergo a number of energy-demanding changes for breeding, either behaviorally (e.g. increased territoriality, mate pairing and guarding, nest building, and parental care) or morphologically (e.g. gonadal recrudescence, and egg development). Molting is also a costly activity and a period marked by a paradox for birds: to forage for lipid- and protein-rich food such as beetles and spiders (Bell 1990; Gäde and Auerswald 2002) while having reduced flight capability to escape predators.

In contrast to other periods, residents have the lowest energetic demand while wintering. Besides, since weather at our study site is warm even during winter (average ± SD for the period of 1962-2013: 19.6 ± 1.3 °C; INMET 2014), the Plain-crested Elaenia uses less energy for thermoregulation than resident species living in colder temperate latitudes. For this reason, a carbohydrate-rich diet based mainly on fruits (Fig. 1) fulfills the birds' energetic demands for body maintenance activities. Moreover, this low protein diet is more profitable for fat synthesis and storage (McWilliams et al. 2004), an important process to provide energy and ensure survival of resident individuals during unpredictable lean times. Fruits may also be consumed due to their high water content, as residents' wintering period coincides with dry season at our study site. Indeed, stomach content analysis suggested *Elaenia* spp. are highly frugivorous (Marini and Cavalcanti 1998). Nevertheless, we are cautious in interpreting these data, as (i) seeds are difficult to digest, thus could bias diet estimates based solely on stomach content analysis, and (ii) our data reveal birds may undergo extreme diet shifts along the year, so generalizations are only possible when considering year-round samples.

Residents clearly shared food resources with migrants instead of competing for them. Despite that, competition and its consequences could still underlie the current nestlings' diets (discussed further below) and species' nesting periods. Despite residents starting their nesting season earlier than migrants, they still overlapped about 40% with the latter. If our initial prediction (density dependent nest predation) holds true, coevolution between residents and migrants could have selected for an anticipated nesting period for residents, which would have increased their breeding success through avoidance of direct and apparent competition. However, two aspects of our results refute this hypothesis. First, DSR of residents' nests was unaffected by the presence of nesting migrants, suggesting nest predation was density-independent in that case. Second, the anticipated nesting period of residents could hypothetically be an adaptation to past competition with migrants. This way, residents should have had breeding success values similar to that of migrants. However, our result contradict this hypothesis.

We refer to an alternative hypothesis to explain the first aspect stated above (i.e. residents' DSR being unaffected by nesting migrants). Similar to our findings for the Plain-crested Elaenia, previous experiments found predation of artificial nests was density-independent (Schmidt and Whelan 1999; Ackerman et al. 2004; Vigallon and Marzluff 2005). Different factors may explain this pattern, among which is the availability of alternative food sources such as other species' nests, insects, and fruits. For instance, nests are often inconspicuous, thus demanding higher searching effort of nest predators. Contrastingly, fleshy fruits are often conspicuous and designed to attract seed dispersers, thus demanding little searching effort (Valido et al. 2011). Therefore, fruits may become a more profitable resource for generalist nest predators than nests' contents (e.g.: Schmidt and Whelan 1999). Since peak production of fleshy fruits at our study site matches birds' breeding period, Schmidt and Whelan's conclusions seems to adjust well to our results, especially because Passerines are listed as important nest predators at ESECAE (França et al. 2009), and all of them also include fruits and insects in their diet.

We should also take into account that predators may delay their response to nest density increases, as found previously at our study site (França 2008; Paiva 2008). In this case, residents would only escape the effects of increased nest density by ceasing nesting activities before predators functional response. Another obvious conclusion is that migrants, and other resident species nesting in synchrony with them, would still suffer the effects of increased activity of nest predators as their nesting period was only beginning when the Plain-crested Elaenia ceased their nesting activities. Contrary to expectations, DSR of residents nest remained constant along their entire nesting period, irrespective of overlap with the migrant, thus providing extra support for the density independent nest predation hypothesis during the 2012 breeding season. Since, by design, our dataset precludes further analysis in that sense, the hypothesis remains an important open question for this system.

The anticipation of nesting period by residents is yet harder to explain as demand evoking Connell's (1980) "ghost of competition past". Three facts are contrary to the hypothesis of occurrence of competition between residents and migrants. First, residents had high nest predation rates (73%) and low estimated breeding success (13.6%), but these values are similar to those previously recorded for this (Marini et al. 2009) and other resident species (Lopes and Marini 2005a; França and Marini 2009), including the migrant Lesser Elaenia (Medeiros and Marini 2007) at ESECAE community. In addition, many other residents nested at the same period as migrants (Table 7) but the occurrence of apparent competition with the migrant was discussed only once (e.g.: signs of apparent competition between the Chapada Flycatcher *Suiriri islerorum* and the Lesser Elaenia; França and Marini 2009). Second, the Plain-crested Elaenia had a nesting period of similar length to other local residents (average ± SD: 108 ± 22 d; Table 7), long enough to allow pairs to renest in the same breeding season

TABLE 7. Summary of breeding period records for resident bird species at Estação Ecológica Águas Emendadas (Brasília).

Species	Nesting onset	Nesting end	Length (days)	Reference
Plain-crested Elaenia *E. cristata*	early September	mid-December	~100	Marini et al. (2009)
	late July	mid-November	112	this study
Campo Suiriri *Suiriri affinis*	early July	late November	~150	Lopes and Marini (2005)
Chapada Flycatcher *S. islerorum*	mid-September	early December	~83	Lopes and Marini (2005a)
White-rumped Tanager *Cypsnagra hyrundinacea*	mid-August	mid-December	~95	Santos and Marini (2010)
Shrike-like Tanager *Neothraupis fasciata*	late August	early December	~100	Duca and Marini (2011)
Chalk-browed Mockingbird *Mimus saturninus*	late August	late December	~118	Rodrigues (2009)

and consequently increase their chances of nest success. Additional field observations (ACG, unpublished data) support this hypothesis, as we recorded pairs of Plain-crested Elaenia (n = 9; 28.1% of the breeding pairs monitored) renesting after an unsuccessful breeding attempt for up to five times (global average ± SD: 1.4 ± 0.8 attempts). Third, the anticipated nesting period could be a residents' strategy to avoid competition with migrants for nestling food. However, this hypothesis was also refuted. A temporal shift in nestling period of residents would release parents from competing with migrants if nestlings had overlapping diets. Despite both species feeding their nestlings with similar items (spiders and alate arthropods), there is little overlap of their isotopic niches. Whether this is a consequence of past competition remains unclear.

Taken together, our results reveal that the effects of any past competition between migrants and residents are less evident nowadays. Are competition and its proximal effects restricted to the community's past, and are other aspects now shaping the ecology of these ecologically similar species? Our study opens a wide horizon for future research on the ecology of intratropical migrants and their interactions with residents. We suggest such an ambitious goal can only be reached by merging the results of well-coordinated studies on multiple basic and complex ecological aspects involving the lives of migrants and residents. For instance, what triggers nesting activity of these birds? Although environmental variables (e.g.: precipitation, day-length) may well answer this question (e.g.: Duca and Marini 2011), what is the role of interspecific interactions? What is the identity and the eco-behavioral traits of nest predators in this system? What are the strategies of migrants and residents that have resulted in population viable sizes through time? In general, migrants have higher breeding success, i.e. they are r-strategists (O'Connor 1990), to compensate for the expected higher mortality rates of adults due to efforts connected to the migratory journey. On the other hand, residents often are k-strategists (O'Connor 1990). Thus, the Plain-crested Elaenia seems to ensure their fitness by compensating nest losses with increased survival rates of adults and the few young successfully reared in each breeding season. Only detailed population analysis of survival estimates of young and adults of both species will allow better conclusions on this hypothesis.

Our study shows that residents and migrants coexist during their breeding season by sharing food resources. Despite the interesting data obtained for both species, our discussion highlighted the difficulties of applying the plausible hypothesis of past competition in shaping current species' breeding ecology. Nevertheless, well-planned studies intending to evaluate interspecific competition and its effects (e.g. Miller et al. 2009) should provide new facts and evidence that will shed light on the subject. Thus, we reinforce that only through allying well-designed *in situ* experiments (Dhondt 2012c) and good observational data will we be able to vanquish the "ghost of competition". "[T]he serious study of the ecology of migrant birds in tropical areas has barely begun." (Greenberg 1986).

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CONSIDERAÇÕES FINAIS

Os resultados obtidos neste estudo fornecem informações inéditas sobre a ecologia de aves migratórias na América do Sul. As análises demonstram que a espécie residente (*Elaenia cristata*), portanto sujeita à sazonalidade climática da área de estudo, utilizou micro-hábitats distintos ao longo do ano. Em oposição, a migrante *E. chiriquensis* possuiu uma estratégia do tipo seguidora de nicho, buscando micro-hábitats semelhantes para utilizar em cada período de sua jornada migratória. Além disso, ambas as espécies alteraram de forma semelhante seu nicho alimentar em cada período, passando de uma dieta com altos valores de $\delta^{15}N$ durante o período reprodutivo para valores mais baixos durante o período de invernada. De fato, a espécie residente possuiu padrões distintos de dieta e de estratégias de captura de presas durante os períodos reprodutivo e não-reprodutivo. A confirmação dos padrões para a espécie migratória permanecerá pendente até que estudos em andamento utilizando geolocalizadores (Guaraldo et al., in prep.) revelem mais detalhes sobre os locais que os indivíduos da população estudada utilizam durante o período não reprodutivo e permitam, assim, observações diretas de sua ecologia. Ainda em relação à dieta, os dados evidenciam o compartilhamento de recursos entre residentes e migrantes.

Os resultados apresentados no segundo capítulo são um exemplo de uma generalização teórica equivocada de que todos os migrantes estão sujeitos aos efeitos em cascata, i.e. de que os eventos vivenciados em uma etapa de seu ciclo anual influenciam indiretamente os padrões, p. ex. reprodutivos, observados em etapas subsequentes. Tal generalização deve ser feita somente após a validação da teoria e/ou hipótese em uma ampla gama de sistemas distintos daqueles utilizados para o seu desenvolvimento. No caso deste estudo, a hipótese dos efeitos em cascata foi refutada, mas deve-se considerar a possibilidade de que o sistema utilizado como modelo no presente trabalho possa se tratar de uma exceção à regra. Até que novos estudos validem ou corroborem essa hipótese para outras espécies-modelo, é inadequado considerar que as situações vivenciadas pelos migrantes no período não-reprodutivo influenciam de alguma forma seu comportamento no sítio de reprodução. O crescente avanço dos estudos sobre a ecologia de aves migratórias na América do Sul deverá em breve esclarecer melhor esse tema.

Historicamente, estudos abordando um tema complexo como a competição interespecífica sempre geraram discussões acaloradas e, por vezes, interpretações e visões contraditórias dos resultados obtidos. Neste sentido, especial cuidado foi tomado ao longo das discussões relacionadas às interações entre residentes e migrantes para evitar interpretações equivocadas dos dados obtidos. Um exemplo disso é a extensa discussão apresentada para explicar os resultados das análises de sucesso reprodutivo e dieta dos ninhegos à luz da teoria da competição. Neste caso, as espécies estudadas apresentaram períodos de nidificação distintos e seus ninhegos possuíram dietas isotópicas pouco sobrepostas. Considerando as taxas de sucesso reprodutivo encontradas, este pode ser interpretado equivocadamente como um cenário em que não há competição entre as espécies. No entanto, deve-se ter em mente que este pode ser o resultado final de um processo de coevolução das espécies moldado pela competição. Em outras palavras, o atual período de nidificação e dieta dos ninhegos pode ser resultante de um passado competitivo. Aparentemente, a solução deste impasse pode parecer impossível, mas estudos bem planejados, especialmente aqueles envolvendo experimentação, serão capazes de prover evidências e dar sequência aos esforços visando corroborar ou refutar essa hipótese.

As estratégias adotadas pelas espécies ao longo de seu ciclo anual sofreram reflexos diretos e indiretos do processo de migração, de modo que o movimento migratório garantiu aos migrantes o uso de micro-hábitats semelhantes ao longo do ano. Além disso, residentes e migrantes diferiram em relação às datas e duração de seus períodos de nidificação (mais precoce e longo nos residentes). O sucesso reprodutivo da espécie residente foi reduzido em relação à migrante, mas a influência dos migrantes sobre esse resultado ainda é um campo que demanda investigações. Por outro lado, migrantes e residentes apresentaram padrões semelhantes de variação de dieta ao longo do ano, sugerindo a atuação de processos regulatórios de base fisiológica comum a ambas as espécies e independentes de seu comportamento migratório. Deste modo, embora o processo de migração influencie aspectos reprodutivos e de uso de micro-hábitats, tanto de migrantes quanto de residentes, o status migratório não deve ser utilizado como única explicação para as diferentes estratégias reprodutivas e alimentares apresentadas por essas espécies.