

PONTIFÍCIA UNIVERSIDADE CATÓLICA DO RIO GRANDE DO SUL
FACULDADE DE BIOCÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

**HISTÓRIA NATURAL DE *Sporophila hypoxantha* CABANIS, 1851
(AVES: EMBERIZIDAE) EM CAMPOS DE ALTITUDE
NO SUL DO BRASIL**

Ismael Franz
Orientador: Dra. Carla Suertegaray Fontana

DISSERTAÇÃO DE MESTRADO
PORTO ALEGRE - RS - BRASIL
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*Para meus pais Antonio e Ilani,
meus manos Fabiano e Marco Antonio,
minha afilhada Isabela
e meu amor Bárbara.*

Dedico.

*“The death-like stillness of the plain, the dogs keeping watch,
the gipsy-group of Gauchos making their beds round the fire,
have left in my mind a strongly-marked picture of this first
night, which will never be forgotten.*

(...)

This was the first night which I passed under the open sky...

(...)

*Their politeness is excessive; they never drink their spirits
without expecting you to taste it; but whilst making their
exceedingly graceful bow, they seem quite as ready, if
occasion offered, to cut your throat.”*

*“A quietude quase de morte da planície, os cães vigiando, o
grupo de gaúchos viajantes fazendo suas camas em volta do
fogo, deixaram na minha mente uma imagem fortemente
marcada dessa primeira noite, que nunca será esquecida.*

(...)

Essa foi a primeira noite que eu passei sob o céu aberto...

(...)

*Sua polidez é excessiva; eles nunca bebem seus aguardentes
sem esperar que você experimente; mas enquanto fazem sua
excessivamente educada reverência, eles parecem sempre
prontos, se a ocasião permitir, para cortar sua garganta.”*

Charles Darwin

11 de agosto de 1833

AGRADECIMENTOS

Seria injusto não abrir essa sessão agradecendo aos casais Joaca e Nair e Antônio e Ivonete, da Estância do Meio (São Joaquim) e às suas famílias. Sem seu apoio, um projeto em local tão ermo seria inconcebível. Muito obrigado pelo convívio no rancho, pelos ensinamentos, pela ajuda de várias formas e por serem meus pais emprestados. Desde os simples atos de ceder o cavalo e a canoa ou ajudar com o conserto do "fuque" até o episódio do "salvamento no rio Lava-Tudo", suas ações e hospitalidade foram essenciais e marcantes.

À minha dedicada orientadora, Dra. Carla S. Fontana, agradeço demais por me acolher tão bem no laboratório, quando migrei para a cidade grande. Obrigado pela confiança e por tudo que aprendi contigo. Que possas ainda orientar muitos e muitos alunos, desvendando a vida das nossas renegadas aves de campo. Aos demais professores do PPG em Zoologia da PUCRS, pelas ótimas aulas e pela ajuda nestes dois anos.

Devo boa parte desse trabalho aos colegas campeiros Cristiano E. Rovedder, Márcio Repenning e Mariana L. Gonçalves. Em primeiro lugar, agradeço pelo convite para participar do projeto, na ocasião do CBO de 2007! Obrigado pela companhia, amizade, pelas idéias e ajuda incansável em campo e fora, achando e revisando tantos ninhos e analisando dados. Gracias, xirús! Aos ajudantes de campo Natália, Cybele (também no laboratório), Gabriel, Emily, Úrsula e Jonas, pelo auxílio e pela disposição.

Meus sinceros agradecimentos aos avaliadores, doutores Juan C. Reboreda (Universidad de Buenos Aires), James J. Roper (UVV) e Leonardo F. França (UFERSA), por gentilmente aceitarem revisar esta dissertação.

Ao CNPq e à CAPES pela concessão de bolsa de estudos. À Fundação Grupo Boticário de Proteção à Natureza e Neotropical Grassland Conservancy pelo apoio financeiro ao projeto, e à IGRÉ - Associação Sócio Ambientalista pelo apoio logístico.

Ao casal Sérgio Cardoso e "Dona Nida" pelo acolhimento caloroso durante nossas passagens por Vacaria.

Ao Sr. Élvio, por rebocar a F100 com o trator no "mata-burro" (que não chegou a nos matar) e emprestar gasolina. Aos demais joaquinenses: Bastião, Joaquinção, Jorge,

Ambrósio, Aníbal, Tadeu, Chico e Anacleto, por facilitarem o acesso às áreas e serem presença única nos confins da “cuxía”.

Como milhares de espécies de plantas ocorrem naqueles campos, sem a ajuda da Dra. Ilsi I. Boldrini e de sua equipe (Departamento de Botânica, UFRGS) na determinação dos capins, arbustos e ervas, não teríamos alcançado os objetivos. Obrigado!

Ao Bret Whitney (Field Guides) pelo reconhecimento e apoio ao nosso projeto e por ir conhecer as áreas de estudo e aquelas aves sensacionais.

Ao Dr. Jay Rotella (Montana State University) pela enorme ajuda com as análises no programa MARK e script do R. Ao Dr. Adrian S. Di Giacomo (Universidad de Buenos Aires) pela ajuda com gráficos de DSR. Ao Dr. Leonardo E. Lopes (UFV) pelas dicas sobre territórios e pela planilha Mayfield.

Ao Glayson A. Bencke (FZBRS), pelos ensinamentos muito além da ornitologia.

Aos mestres do tempo da Feevale: Marcelo P. de Barros, Jairo L. Schmitt, Paulo H. Ott e Rage W. Maluf, devo grande parte da minha formação e do meu entusiasmo pela pesquisa. Obrigado sempre!

Meus queridos pais, Antonio e Ilani, respeitaram desde piá a minha ânsia por conhecer os bichos (deixar que eu fosse picado pelas saúvas e sair pra caçar girinos fazia parte dos "estudos"). Obrigado pelo estímulo constante, pela torcida, pelas horas do chimarrão, pelos almoços no sítio, pelos ovos e verduras, pelo uninho e pelo exemplo de valores e união em família. Enfim, por tudo! A vocês, agradecer é insuficiente. Aos meus irmãos Fabiano e Marco Antonio (Mano e Toko), por me alegrarem, pelo apoio “tecnológico”, e por mostrarem como ser um irmão do meio melhor. À Pri e Gabi, minhas cunhadas queridas. E à pequena afilhada Isabela, já despontando como futura grande zoóloga, por fazer a família e o "dido Ija" tão mais felizes.

Finalmente, agradeço a ela que tem sido minha luz em todos esses dias. Bá, com teu lindo sorriso, fostes a minha inspiração. Tua presença trouxe um novo sentido à vida. Obrigado por me apoiar e ajudar em tudo, pelo teu entusiasmo cativante, por entender a ausência, por ensinar sobre filogenia, sistemática, esqueletos, diafanização e coisas que eu pouco conhecia. Pelas pescarias e pelos queridos amigos que fiz na ictiologia. E por teres escolhido estar ao meu lado, fazendo com que eu nunca me esqueça do motivo precioso de tudo isso. Te amo! Para a tua família (Valdo, Roze Ane e João Pedro), que é tão especial, agradeço imensamente pelo acolhimento em seu lar. Muito obrigado!

RESUMO GERAL

Estudamos a história natural do caboclinho-de-barriga-vermelha (*Sporophila hypoxantha*), uma espécie importante nos habitats campestres sul-americanos e pobremente conhecida do ponto de vista da sua biologia e ecologia. Dados foram coletados durante três temporadas reprodutivas (entre novembro e março de 2007/2008, 2008/2009 e 2009/2010) em áreas de campos secos íngremes ao longo do rio Lava-Tudo, localidades de Coxilha Rica (Lages) e Estância do Meio (São Joaquim), sudeste de Santa Catarina (28° 18' S, 50° 17' W; 800-1000m de altitude). Monitoramos 69 ninhos, revisando o conteúdo a cada 2-6 dias, e avaliamos aspectos da cronologia, territorialidade, nidificação, atributos dos habitats selecionados, características dos ninhos, ovos e ninhegos, cuidado parental, destino dos ninhos (sucesso reprodutivo) e sobrevivência diária. Machos imigram na primeira semana de novembro e logo iniciam o estabelecimento e defesa de territórios. Com a chegada das fêmeas, alguns dias após, inicia a seleção dos machos e escolha dos sítios de nidificação. O pico de ninhos ativos se deu na segunda quinzena de novembro. Fêmeas constroem os ninhos sozinhas, mas assistidas de perto pelos machos, atividade que leva 3-6 dias. A espécie selecionou sítios planos marcados por um denso estrato médio, ricos em arbustos como *Vernonia chamaedrys*, *Eupatorium polystachyum*, *Baccharis caprariifolia* e touceiras de *Andropogon lateralis*, evitando habitats com maior adensamento do estrato superior, maior declividade e ocorrência de pequenas árvores como *Escallonia megalotamica*. Esses ambientes preferenciais ocorrem em áreas de intensidade moderada de pastoreio e pouca queima. Os pequenos ninhos têm formato de tigela, feitos com pendões finos de capins como *Eragrostis polytricha*, sobre arbustos (principalmente *V. chamaedrys* e *E. polystachyum*, 66%), a uma altura média de $41,9 \pm 0,8$ cm em relação ao solo. A ninhada é de dois (91%) ou três ovos. A incubação, realizada apenas pela fêmea, dura 12 dias. Em 60% do tempo a fêmea permanece incubando e cada visita dura entre 20 e 31 min. Os ninhegos são alimentados pelas fêmeas nos primeiros dias de vida e, a partir do quinto, o macho passa a ajudar. São realizadas $4,6 \pm 0,7$ e $8,95 \pm 1,8$ visitas para alimentar ninhegos de 1-4 e 6-9 dias de vida, respectivamente. Com 30 dias os filhotes tornam-se independentes. Os parâmetros básicos da biologia reprodutiva encontrados assemelham-se aos disponíveis na literatura para as populações residentes da Província

de Formosa, Argentina, salvo por apresentar temporada mais curta, construção de ninhos mais rápida e menor média de duração de visitas de cuidado aos ninhegos. De 55 ninhos que tiveram o status final confirmado, 40% tiveram sucesso. O sucesso Mayfield foi de 25%. Predação foi a principal causa de perda de ninhadas (55% dos ninhos insucesso), seguida de abandono, infestação por larvas subcutâneas de *Philornis seguyi*, pisoteio pelo gado e queima. A taxa de sobrevivência diária foi maior no período de incubação (0,945) do que de ninhego (0,927). Esse padrão também foi corroborado pela análise no programa MARK, que encontrou uma forte queda na sobrevivência diária ao longo dos 21 dias (12 de incubação e nove de ninhego) de ciclo de nidificação. Isso pode estar relacionado com a atividade no ninho (maior nas fases finais do ciclo), como prediz a hipótese de Alexander Skutch. Também ocorreu uma queda gradual na taxa de sobrevivência diária ao longo da temporada reprodutiva, que pode ser resultado de menor aptidão (*fitness*) nos reprodutores tardios, além da maior intensidade de infestação por *Philornis*, com aumento de temperatura. A produtividade média foi de 0,77 filhotes por casal, que produz apenas uma ninhada por estação (salvo dois casos de casais que perderam a ninhada e tentaram novamente). Por fim, analisamos um possível híbrido entre *S. hypoxantha* e *S. melanogaster* registrado por dois anos consecutivos na área de estudos e bem documentado. Esse apresentava vocalização completamente condizente com o padrão de *S. hypoxantha* e plumagem como em *S. melanogaster*, embora possa representar um típico caso de aprendizagem interespecífica de canto. Esse padrão nunca havia sido constatado.

ABSTRACT

We studied the natural history of the Tawny-bellied Seedeater (*Sporophila hypoxantha*), an important and poorly known species from South American grasslands, regarding its biology and ecology. Data were collected during three breeding seasons (from November to March in 2007/2008, 2008/2009 and 2009/2010) on steep dry fields along the Lava-Tudo River at *Coxilha Rica* (Lages) and *Estância do Meio* (São Joaquim) in southeastern Santa Catarina State, Brazil (28° 18' S, 50° 17' W; 800-1000 m a.s.l.). We monitored 69 nests, every 2-6 days, to evaluate aspects of the chronology; territoriality; nesting; habitat selection; features of the nest, eggs and nestlings; parental care; nest fate (reproductive success or failure) and daily nest survival. Males arrive in the first week of November and then initiate the establishment and defense of their territories. With the arrival of females some days later, the selection of mates and nesting sites begins. The number of active nests peaked in the second half of November. Females construct the nest by themselves, with the males watching close by, over a period of 3-6 days. Selected sites are located on flat terrain and are characterized by the presence of a rich middle vegetation stratum such as shrubs of *Vernonia chamaedrys*, *Eupatorium polystachyum*, and *Baccharis caprariifolia* and clumps of *Andropogon lateralis*. Habitats with a dense high stratum, steep slope and small trees such as *Escallonia megapotamica* were avoided. The preferred habitats occur in areas of moderate intensity of grazing and little burning. The small nests are in the shape of an open cup, made with thin stems of grasses such as *Eragrostis polytricha*, on bushes (mainly *V. chamaedrys* and *E. polystachyum*, 66%), at a mean height of 41.9 ± 0.8 cm from the ground. Clutch size is two (91%) to three eggs. Incubation, performed by the female, lasts for 12 days. During this period, the female incubates for 60% of the time, and each visit takes between 20 and 31 min. Nestlings are fed by the female during the first days of life, and from the fifth day, the male begins to assist with feeding. A mean of 4.6 ± 0.7 and 8.95 ± 1.8 visits were performed to feed nestlings 1-4 and 6-9 days old, respectively. Juveniles become independent after 30 days. The basic parameters of reproductive biology resemble those described for the resident population of the province of Formosa, Argentina, except for having a shorter season, building nests more rapidly, and shorter mean durations of visits and parental care. Forty percent of 55 nests were

successful. Mayfield success was 25%. Predation was the main cause of nest failure (55%), followed by abandonment, subcutaneous infestation by larvae of *Philornis seguyi*, cattle trampling, and grass burning. The daily survival rate (DSR) was higher in the incubation period (0.945) than in the nestling period (0.927). This pattern was corroborated by analysis using the MARK program, which found a sharp decrease in DRS during the 21 days of nesting (12 incubation days plus 9 nestling days). This may be related to the nesting activity (increased during the final stages of the cycle) as predicted by the hypothesis of the Alexander Skutch. There was a gradual decline in DSR during the breeding season, which may be a result of lower fitness of late breeders, as well as the effect of the intensity of *Philornis* infestation, with the temperature increase. The mean productivity was 0.77 young per pair, producing a single brood per breeding season (with the exception of two pairs that lost their brood and tried twice). Finally, we analyze the existence of hybrids between *S. hypoxantha* and *S. melanogaster* based on one individual monitored for two consecutive years at the study site. This individual had vocalizations completely consistent with the pattern of *S. hypoxantha* and plumage as in *S. melanogaster*, although it may represent a typical case of interspecific song learning. This pattern has never been observed previously.

APRESENTAÇÃO

“In fact, science began as the study of nature. (...) We need to know how the earth works so we can better manage the earth’s resources and conserve all life. (...) I suggest that natural history as a field of study again merits taking its place as a formal and recognized field of academic study.”

(Beehler, B. M. 2010. The forgotten science: a role for natural history in the twenty-first century? *Journal of Field Ornithology* 81[1]: 1-4)

Campos sulinos

Os campos sulinos ou campos do sul do Brasil são considerados um ecossistema negligenciado, especialmente do ponto de vista da conservação (Overbeck *et al.* 2007). Fazem parte, além do bioma Pampa (os chamados campos do Rio da Prata), os campos do bioma Mata Atlântica. Esses são conhecidos fisiograficamente por Campos de Cima da Serra (Bond-Buckup e Dreier 2008) ou campos do Planalto das Araucárias (também Meridional/Sul-Brasileiro), situam-se a norte do paralelo 30°S de latitude, que também divide as províncias do Paraná (norte) e Pampeana (sul), bem como os domínios biogeográficos Amazônico e Chaquenho, respectivamente (Cabrera e Willink 1980). Formam um mosaico campo-florestas com araucárias e são caracterizados predominantemente pela alta diversidade de plantas herbáceas (*e.g.* Poaceae, Cyperaceae, Asteraceae e Apiaceae; Klein 1979). Boldrini *et al.* (2009) contabilizaram 1161 táxons para a flora dos Campos de Cima da Serra, que ainda se destacam pelo alto grau de endemismo, possuindo 296 espécies exclusivas (Iganci *et al.* 2011). Mas os biomas campestres foram fortemente modificados pelas atividades humanas, restando poucos remanescentes de campos naturais (Behling 2002). Apesar da urgente necessidade de conservação desses ambientes, eles têm sido substituídos por culturas agrícolas e monoculturas de pinheiros exóticos, e impactados pela pecuária intensiva e proliferação de espécies invasoras, entre outros fatores. Adicionalmente, é notável sua baixa representatividade em unidades de conservação da natureza (Brandão *et al.* 2007).

Na região de Lages e São Joaquim, sudeste do estado de Santa Catarina, sul do Brasil, onde o presente estudo foi desenvolvido, as principais atividades econômicas desenvolvidas são a pecuária, mais antiga, a fruticultura na forma de extensas

plantações de maçãs (nas quais defensivos agrícolas são utilizados de forma expressiva) e, mais recentemente, a silvicultura de *Pinus eliotti*, mantida por proprietários não residentes ou em terras arrendadas. Ademais, a supressão de vegetação em decorrência de alagamentos por usinas hidrelétricas é uma ameaça crescente. Até fins da década de 1970, a extração do pinheiro-brasileiro (*Araucaria angustifolia*) foi realizada de forma intensiva. O manejo do campo com uso de fogo é utilizado há muitas gerações naquela região. Queimadas parciais (mas sem o total controle das dimensões e consequências) são realizadas anual ou bianualmente, entre agosto e outubro.

Do ponto de vista faunístico, a região se destaca pela grande riqueza de aves (337 espécies), mas especialmente pela composição característica, incluindo espécies raras, endêmicas, ameaçadas de extinção e pouco conhecidas, das quais se destacam os emberizídeos do gênero *Sporophila* (Fontana *et al.* 2008).

Espécie foco do estudo: *Sporophila hypoxantha*

Nos campos sul-americanos, especialmente na região subtropical, aves do gênero *Sporophila* Cabanis, 1844 (no passado, *Spermophila* Swainson, 1827) são elementos importantes e característicos devido a sua representatividade (Silva 1999). Das cerca de 35 espécies conhecidas como “papa-capins” (Ridgely e Tudor 1989, Ouellet 1992, CBRO 2009), apenas *Sporophila torqueola* (Bonaparte, 1950) ocorre além da região Neotropical (até os Estados Unidos). São pequenos pássaros de bicos coniformes que habitam quase que exclusivamente áreas abertas (Ridgely e Tudor 1989), onde se alimentam de sementes de dicotiledôneas. Trinta espécies ocorrem no Brasil (CBRO 2009), principalmente nos biomas Cerrado, Pantanal, Pampa e Mata Atlântica. Nos campos de altitude do Rio Grande do Sul e de Santa Catarina, previamente caracterizados, ocorrem sete espécies do gênero (Fontana *et al.* 2008). Uma delas, o caboclinho-de-barriga-vermelha (*Sporophila hypoxantha*), é um táxon particularmente interessante, por contemplar pelo menos cinco unidades evolutivas aparentemente distintas, alopátricas, chamadas de “regiolects” devido à diagnose fundamentada na vocalização, acompanhada de particularidades nos habitats reprodutivos preferenciais (Areta e Repenning 2011). A espécie faz parte, juntamente com outras 10, do grupo dos caboclinhos (nome cunhado originalmente em espanhol: “capuchinos”, o “G group” de Ridgely e Tudor 1989). Esse clado monofilético é considerado resultado de uma

irradiação evolutiva muito recente (~0,5 m.a.), de acordo com Lijtmaer *et al.* (2004) e Campagna *et al.* (2009, 2011). Descrita em 1851 por Jean Cabanis com base em um indivíduo proveniente de Montevideu, Uruguai (mas vide Hellmayr 1938), *S. hypoxantha* foi originalmente considerada subespécie de *S. minuta* Linnaeus, 1758, e assim tratada por mais de um século (*e.g.* Hellmayr 1938, Pinto 1944, Meyer de Schauensee 1970). Sibley e Monroe (1990) consideraram ambas as formas como uma superespécie, mas recentemente a filogenia do grupo revelou, como já havia sido sugerido por Short (1969), que essas não são espécies irmãs (clados de “northern” e “southern capuchinos”; Lijtmaer *et al.* 2004, Campagna *et al.* 2009). Desde o estudo de Lester L. Short Jr., o tratamento como espécies distintas é amplamente aceito, tendo como base claras diferenças morfológicas e biológicas, além da sua acentuada alopatria (Short 1969).

As fêmeas apresentam coloração pardacenta, seguindo o padrão conhecido de todos os papa-capins, com um pequeno "espelho" branco aparente nas asas. Para Benites *et al.* (2010), fêmeas indistinguíveis ao olho humano podem ser reconhecidas entre si pelas diferentes espécies de caboclinhos, resultado revelado por meio de uma análise de espectrofotometria. Os machos têm a parte anterior (ventre-peito, axilas e garganta), bochechas e uropígio de cor ferrugíneo-alaranjados, de diferentes tonalidades. A parte posterior é cinza, cauda e asas são escurecidas (com o mesmo “espelho”). O bico é negro. Os jovens assemelham-se às fêmeas, apresentando a cor parda que varia em tons ligeiramente distintos. Machos no período pós-reprodutivo realizam uma muda de penas que os cobre parcial ou totalmente com manchas pardas (o bico pode apresentar tons amarelados), sendo a chamada plumagem de eclipse, que pode lhes dar a aparência de fêmea ou jovem, com a qual passam o período de invernagem. Recentemente, Facchinetti *et al.* (2011) encontraram que a espécie (“Formosa regiolect”) realiza duas mudas anualmente, antes e após a estação reprodutiva. Segundo esses autores, machos apresentam um atraso na maturação da plumagem, pois indivíduos de primeiro ano diferem de machos mais velhos. Para eles, essa relação entre coloração da plumagem e idade dos machos pode ter um importante papel na seleção sexual. Nas populações do sul do Brasil, aparentemente machos de primeiro ano já ostentam a plumagem de adulto, apenas com diferenças discretas (I. Franz obs. pess.), mas esse assunto requer um melhor aprofundamento. Pesando 9 g e medindo 10 cm, esses pequenos papa-capins

parecem possuir dimorfismo sexual de tamanho, com machos apresentando asas e cauda sutilmente maiores (vide Tabela abaixo; valores obtidos no presente estudo).

Comparação (Teste *U* de Mann-Whitney) entre medidas corporais de machos ($n = 37$) e fêmeas ($n = 36$) de caboclinho-de-barriga-vermelha (*Sporophila hypoxantha*) capturados no sul do Brasil. Médias \pm DP.

Sexo	Peso	Bico				Tarso	Asa***	Cauda
		Cúlmen*	NP**	Altura	Largura			
Machos	8,8 \pm 0,6	8,1 \pm 0,7	6,2 \pm 0,3	6,3 \pm 0,4	6,7 \pm 0,2	13,6 \pm 0,3	55,3 \pm 1,5	41,6 \pm 4,3
Fêmeas	8,9 \pm 0,7	8,4 \pm 0,5	6,1 \pm 0,3	6,3 \pm 0,4	6,7 \pm 0,3	13,5 \pm 0,4	54,2 \pm 1,5	39,8 \pm 1,5
<i>P</i>	0,3	0,06	0,1	0,4	0,4	0,2	0,005	0,004

*Cúlmen exposto. **Narina-ponta. ****Flat wing*.

Dos cinco regiolects descritos, o “southern Brazil” é tido como o mais distinto e isolado (Areta e Repenning 2011). Esse ocorre desde o nordeste do Paraná (Campos Gerais) até o nordeste gaúcho e sudeste catarinense (Campos de Cima da Serra), passando pelo núcleo de campos de Água Doce e Palmas, na divisa entre Santa Catarina e Paraná. Provavelmente, os campos de altitude nesses três estados sul-brasileiros representam toda área de reprodução desse grupo dentro de *Sporophila hypoxantha*, que em fevereiro/março migra para invernar no Cerrado do Brasil central (Silva 1999). A espécie se distribui, ainda, da Bolívia, Argentina, Paraguai e Uruguai ao Brasil, onde ocorre desde o Rio Grande do Sul até Mato Grosso, Mato Grosso do Sul, Goiás, São Paulo e Minas Gerais (Ridgely e Tudor 1989, Willis e Oniki 1990, Sick 1997, Lopes *et al.* 2009). Recentemente, indivíduos foram registrados no sudeste do Pará (Somenzari *et al.* 2011) e compondo bandos mistos com dezenas de *Sporophila* spp., no estado do Tocantins (Olmos e Pacheco 2010).

De hábitos estritamente campestres, o caboclinho-de-barriga-vermelha habita capinzais altos e banhados de vegetação densa (Ridgely e Tudor 1989, Sick 1997, Di Giacomo 2005). Especialmente fora da estação reprodutiva, forma bandos com outras espécies de caboclinhos, com dezenas de indivíduos (às vezes mais de 100), para se alimentar em locais de concentração de gramíneas frutificando. A dieta consiste basicamente de sementes de capins nativos (Bencke *et al.* 2003, Di Giacomo 2005). Forrageia principalmente em capinzal alto, se agarrando nos pendões ou alcançando suas pontas do chão. O conhecimento de aspectos da reprodução da espécie está concentrado em estudos conduzidos na Província de Formosa, Argentina (Di Giacomo 2005, Facchinetti

et al. 2008), onde a espécie é residente. No sul do Brasil, onde as populações são migratórias, nenhum estudo foi realizado até hoje com a espécie.

Uma das ações recomendadas por Bencke *et al.* (2003) no Livro Vermelho da Fauna Ameaçada de Extinção no Rio Grande do Sul foi “investigar a biologia da espécie”, que está em declínio devido aos efeitos combinados da perda e modificação dos habitats campestres e da captura frequente de indivíduos na natureza para o comércio ilegal de pássaros canoros. Portanto, conhecer sua história de vida representa um passo importante para se avaliar quais são as suas necessidades ecológicas e como esse caboclinho pode ser beneficiado com ações conservacionistas ou afetado por medidas de manejo.

Organização e estrutura da dissertação

A dissertação de mestrado aqui apresentada é composta de um conjunto de quatro artigos científicos relacionados com a história natural de *Sporophila hypoxantha*, notadamente aos aspectos da sua reprodução no sul do Brasil. Os artigos não foram submetidos para publicação e estão redigidos em inglês americano (salvo o terceiro, que visa um periódico europeu), de modo a aprimorar a revisão posterior de um formato o mais próximo possível da versão final para publicação.

O primeiro artigo (**Capítulo 1**) versa sobre a biologia reprodutiva básica da espécie em questão, desde a imigração dos casais na área de estudos, incluindo aspectos da cronologia, territorialidade, dos ninhos, ovos, ninhegos e do comportamento parental. Contém uma comparação dos parâmetros avaliados com o conhecimento disponível proveniente de uma população residente da Argentina. Uma versão preliminar desse estudo foi apresentada na forma de pôster durante o 25th *International Ornithological Congress*, em agosto de 2010, em Campos do Jordão/SP. O artigo está no formato apropriado para ser submetido no periódico *The Wilson Journal of Ornithology*, que nos últimos anos tem sido referência na divulgação de estudos de biologia reprodutiva.

Na busca pelo entendimento da dinâmica populacional de aves, a estimativa de parâmetros populacionais como sucesso reprodutivo e sobrevivência de ninhos representa o primeiro passo, principalmente na região Neotropical, onde o conhecimento é inexistente para a maioria das espécies (Lima e Roper 2009). Foi pensando nisso que desenhamos e produzimos o segundo artigo (**Capítulo 2**), que

envolve o sucesso reprodutivo de *Sporophila hypoxantha*. Utilizamos ferramentas recentes de modelagem que permitem testar hipóteses e previsões e incorporar variáveis temporais e individuais nos cálculos de sobrevivência de ninhos, gerando estimativas biologicamente mais significativas e permitindo avaliar rigorosamente questões biológicas específicas envolvendo variações no sucesso reprodutivo (Dinsmore *et al.* 2002). O artigo está no formato apropriado para ser publicado no periódico *The Condor*.

O terceiro artigo (**Capítulo 3**) trata dos habitats selecionados para nidificação em meio à matriz campestre, utilizando variáveis de estrutura da vegetação e de composição e abundância florísticas. Por apresentar fortes implicações para a conservação da espécie nos campos sulinos, o artigo está no formato apropriado para ser publicado no periódico *Bird Conservation International*.

O quarto e último artigo (**Capítulo 4**) apresenta informações sobre um possível híbrido entre a espécie foco e o caboclinho-de-barriga-preta (*Sporophila melanogaster*), táxon endêmico do Brasil. Esse achado, que não fazia parte dos objetivos originais do projeto, foi incluído por estar diretamente relacionado com a reprodução das duas espécies, que ocorrem em simpatria na área de estudo. O artigo está no formato apropriado para ser publicado no periódico *The Wilson Journal of Ornithology*.

Ao longo dos textos, os Capítulos são citados como Franz and Fontana 2012 (e letras para distingui-los quando há mais de um). Como estão dispostos na ordem em que serão submetidos para publicação (1, 2, 3 e 4), um determinado Capítulo só pode citar os demais anteriores a ele. Por exemplo, o Capítulo 3 pode apenas citar os Capítulos 1 e 2. As Conclusões Gerais foram sintetizadas após o Capítulo 4, na página 123. Ao final, decidimos acrescentar uma seção que chamamos de Apêndice Fotográfico, com o intuito de facilitar ao leitor a visualização de aspectos apresentados nos capítulos e que em geral não são incluídos em artigos científicos, como a espécie foco, a área de estudos e os impactos regionais, algumas plantas importantes na vegetação campestre e parte dos métodos empregados.

O projeto foi aprovado pelo SISBIO/IBAMA (Licenças nº 13310-1 e 13310-2), prevendo captura e marcação de aves *in situ*, coleta de amostras biológicas e material botânico, manutenção temporária de indivíduos em cativeiro, além do devido transporte. O anilhamento foi autorizado pelo CEMAVE/ICMBio (Licença nº 2968/1).

Literatura citada

- Areta, J. I. and Repenning, M. 2011. Systematics of the Tawny-bellied Seedeater (*Sporophila hypoxantha*). I. Geographic variation, ecology, and evolution of vocalizations. *The Condor* 113(3):664-677.
- Behling, H. 2002. South and Southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177: 19-27.
- Bencke, G. A.; Fontana, C. S.; Dias, R. A.; Maurício, G. N. e Mähler Jr., J. K. F. 2003. Aves. Pp. 189-479. In.: Fontana, C. S.; Bencke, G. A. e Reis, R. E. (orgs.). *Livro vermelho da fauna ameaçada de extinção no Rio Grande do Sul*. Porto Alegre: Editora EDIPUCRS.
- Benites P.; Eaton, M. D.; Lijtmaer, D. A.; Loughheed, S. C. and Tubaro, P. L.. 2010. Analysis from avian visual perspective reveals plumage colour differences among females of capuchino seedeaters (*Sporophila*). *Journal of Avian Biology* 41:597–602.
- Boldrini, I. I.; Eggers, L.; Mentz, L. A.; Miotto, S. T. S.; Matzenbacker, N. I.; Longhi-Wagner, H. M.; Trevisan, R.; Schneider, A. A. e Setúbal, R. B. 2009. Flora. In.: Boldrini, I. I. (org.). *Biodiversidade dos campos do Planalto das Araucárias*. Brasília: Ministério do Meio Ambiente.
- Bond-Buckup, G. e Dreier, C. 2008. Paisagem natural. Pp. 10-19. In.: Bond-Buckup, G. (org.). *Biodiversidade dos Campos de Cima da Serra*. Porto Alegre: Editora Libretos.
- Brandão, T.; Trevisan, R. e Both, R. 2007. Unidades de conservação e os campos do Rio Grande do Sul. *Revista Brasileira de Biociências* 5(suppl. 1): 843-845.
- Cabrera, A. L e Willink, A. 1980. *Biogeografia da América Latina*. 2ed. Washington: OEA.
- Campagna, L.; Lijtmaer, D. A.; Kerr, K. C. R.; Barreira, A. S.; Hebert, P. D. N.; Loughheed, C. S. e Tubaro, P. L. 2009. DNA barcodes provide new evidence of a recent radiation in the genus *Sporophila* (Aves: Passeriformes). *Molecular Ecology Resources* 10(3): 449-458.
- Campagna, L.; Benites, P.; Loughheed, S. C.; Lijtmaer, D. A.; Di Giacomo, A. S.; Eaton, M. D. e Tubaro, P. L. 2011. Rapid phenotypic evolution during incipient speciation in a

continental avian radiation. *Proceedings of the Royal Society B (Biological Sciences)*. Available online before print.

CBRO. 2009. *Listas das aves do Brasil*. Disponível em <http://www.cbro.org.br> (acesso em 30/11/2011).

Di Giacomo, A. G. 2005. Aves de la Reserva El Bagual. Pp. 201-465. *In.*: Di Giacomo, A. G. e Krapovickas, S. F. (eds.). *Historia natural y paisaje de la Reserva El Bagual*. Temas de Naturaleza y Conservación 4.

Dinsmore, S. J.; White, G. C. e Knopf, F. L. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83(12): 3476-3488.

Facchinetti, C.; Di Giacomo, A. G. e Reboreda, J. C. 2008. Parental care in Tawny-bellied (*Sporophila hypoxantha*) and Rusty-collared (*S. collaris*) Seedeaters. *The Wilson Journal of Ornithology* 120(4): 879-883.

Facchinetti, C., Mahler, B., Di Giacomo, A. G. e Reboreda, J. C. 2011. Stages of plumage maturation of the Tawny-bellied Seedeater: evidence of delayed plumage maturation and cryptic differentiation between juveniles and females. *The Condor* 113(3):1-8.

Fontana, C. S.; Rovedder, C. E.; Repenning, M. e Gonçalves, M. L. 2008. Estado atual do conhecimento e conservação da avifauna dos Campos de Cima da Serra do sul do Brasil, Rio Grande do Sul e Santa Catarina. *Revista Brasileira de Ornitologia* 16(4): 281-307.

Hellmayr, C. E. 1938. *Catalogue of birds of the Americas*. Part XI. Field Museum of Natural History (Field Mus. Nat. Hist. Zool. Ser., 13).

Iganci, J. R. V.; Heiden, G.; Miotto, S. T. S. e Pennington, R. T. 2011. Campos de Cima da Serra: the Brazilian Subtropical Highland Grasslands show an unexpected level of plant endemism. *Botanical Journal of the Linnean Society* 167: 378-393.

Klein, R. M. 1979. Ecologia da flora e vegetação do Vale do Itajaí. *Sellowia* 12: 17-44.

Lijtmaer, D. A.; Sharpe, N. M. M.; Tubaro, P. L. e Loughheed, S. C. 2004. Molecular phylogenetics and diversification of the genus *Sporophila* (Aves: Passeriformes). *Molecular Phylogenetics and Evolution* 33(3):562-579.

- Lima, A. M. X. e Roper, J. J. 2009. Population dynamics of the black-cheeked gnateater (*Conopophaga melanops*, Conopophagidae) in southern Brazil. *Journal of Tropical Ecology* 25: 605-613.
- Lopes, L. E.; Malacco, G. B.; Franc, E.; Alteff, A.; Vasconcelos, M. F.; Hoffmann, D. e Silveira, L. F. 2009. Range extensions and conservation of some threatened or little known Brazilian grassland birds. *Bird Conservation International* 19: 1–11.
- Meyer de Schauensee, R. 1970. *A guide to the birds of South America*. Pennsylvania: Livingston Publishing Co.
- Olmos, F. e Pacheco, J. F. 2011. Marsh Seedeater *Sporophila palustris* and Tawny-bellied Seedeater *S. hypoxantha* recorded in Tocantins state, Brazil. *Cotinga* 33: 137-138.
- Ouellet, H. 1992. Speciation, zoogeography and taxonomic problems in the Neotropical genus *Sporophila* (Aves: Emberizidae). *Bulletin of the British Ornithological Club* 112a: 225-235.
- Overbeck, G. E.; Müller, S. C.; Fidelis, A.; Pfenhauer, J.; Pillar, V. D.; Blanco, C. C.; Boldrini, I. I.; Both, R. e Forneck, E. D. 2007. Brazil's neglected biome: The South Brazilian *Campos*. *Perspectives in Plant Ecology, Evolution and Systematics* 9: 101–116.
- Pinto, O. M. O. 1944. *Catálogo das aves do Brasil*. 2ª parte. São Paulo: Departamento de Zoologia, Secretaria da Agricultura, Indústria e Comércio.
- Ridgely, R. E. e Tudor, G. 1989. *The birds of South America*. Vol. 1 - The oscine passerines. Austin: University of Texas Press.
- Short, L. L. 1969. Relationships among some South American seedeaters (*Sporophila*), with a Record of *S. hypochroma* for Argentina. *Wilson Bulletin* 81: 216-219.
- Sibley, C. G. e Monroe, B. L. Jr. 1990. *Distribution and taxonomy of birds of the world*. New Haven, Connecticut: Yale University Press.
- Sick, H. 1997. *Ornitologia brasileira*. Rio de Janeiro: Ed. Nova Fronteira. 912p.
- Silva, J. M. C. 1999. Seasonal movements and conservation of seedeaters of the genus *Sporophila* in South America. Pp. 272-280. *In.*: Vickery, P. D. e Herkert, J. R. (eds.).

Ecology and conservation of grassland birds of the Western Hemisphere. Lawrence, Cooper Ornithological Society (Studies in Avian Biology, 19).

Somenzari, M.; Silveira, L. F.; Piacentini, V. Q.; Rego, M. A.; Schunck, F. e Cavarzere, V.. 2011. Birds of an Amazonia-Cerrado ecotone in southern Pará, Brazil, and the efficiency of associating multiple methods in avifaunal inventories. *Revista Brasileira de Ornitologia* 19(2): 260-275.

Willis, E. O. e Oniki, Y. 1990. Levantamento preliminar das aves de inverno em dez áreas do sudoeste de Mato Grosso, Brasil. *Ararajuba* 1: 19-38.

CAPÍTULO 1

Breeding biology of the Tawny-bellied Seedeater (*Sporophila hypoxantha*)
in southern Brazilian upland grasslands

Artigo a ser submetido para publicação no periódico *The Wilson Journal of Ornithology*

BREEDING BIOLOGY OF THE TAWNY-BELLIED SEEDEATER (*SPOROPHILA*
HYPOXANTHA) IN SOUTHERN BRAZILIAN UPLAND GRASSLANDS

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ABSTRACT.—The life history of most *Sporophila* seedeaters is virtually unknown. We present detailed information on the breeding biology of a migratory population of the Tawny-bellied Seedeater (*Sporophila hypoxantha*), a typical member of the “capuchinos” group. Data were collected for 69 nests found over three breeding seasons from 2007 to 2010 in areas of hilly dry grasslands in southern Brazil. Breeding begins in early November, a week after the seedeaters arrive from migration, peaks in late November, and lasts until late February, when individuals migrate north. In three to six days, females build small open-cup nests in small shrubs (mainly *Vernonia chamaedrys* and *Eupatorium polystachyum*), 41.9 ± 0.8 cm (range 27-60 cm, $n = 38$) above the ground. The clutch size is two (91%) or three eggs ($n = 43$), which measure 16.22 ± 0.51 mm by 11.93 ± 0.28 mm ($n = 10$), and incubation, which is performed by the female, lasts 12 days. Average nest attentiveness during incubation was $60 \pm 5\%$ ($n = 5$) with 20 to 31 min on-bouts. Males help feed the nestlings beginning on the fifth day after hatching (biparental care). Provisioning visits hr^{-1} averaged 4.6 ± 0.7 ($n = 6$) and females brooded after feeding the young in 48% of the visits when nestlings were one to four days old. When nestlings were six to nine days old, the average trips. hr^{-1} were statistically more frequent (8.95 ± 1.8 , $n = 11$; $z = -2.5$, $P = 0.012$), with brooding after feeding in 14% of the visits. Nestlings fledge after nine to ten days. The basic reproductive characteristics of the migratory population are very similar to those found in the resident population in the Formosa region, Argentina, but the breeding season, time spent building the nest, and length of visits to the nest during the nestling stage are shorter.

In the Neotropics, one of the best represented genera of the family Thraupidae is *Sporophila* Cabanis, 1844, with roughly 35 known species of small, finch-like birds with conical bills that almost exclusively inhabit open areas, where they feed on small seeds (Ouellet 1992, Ridgely and Tudor 1989). Reproduction in this group is so poorly studied that the nests of the White-bellied Seedeater *S. leucoptera* (Vieillot, 1817) and Black-bellied Seedeater *S. melanogaster* (Pelzeln 1870) were only recently described (Francisco 2009, Rovedder and Fontana 2012), even though these species are widespread in southern South America.

The genus *Sporophila* includes the “capuchinos group”, which presently is not considered to be a taxonomic unit. These 12 closely-related species have similar plumage patterns (Areta 2008, Areta et al. 2011, Machado and Silveira 2011, Ouellet 1992, Sick 1997) and little genetic divergence (Campagna et al. 2009, Kerr et al. 2009, Lijtmaer et al. 2004). The Tawny-billed Seedeater *Sporophila hypoxantha* Cabanis, 1851, which weighs 9 g and measures 10 cm in total length, occurs from Bolivia, Argentina, Paraguay and Uruguay to Brazil, where it ranges from Rio Grande do Sul to Mato Grosso do Sul, Mato Grosso, Goiás, São Paulo and Minas Gerais (Lopes et al. 2009, Ridgely and Tudor 1989, Sick 1997, Willis and Oniki 1990). Among the seedeaters, this species has the widest range in central and southern South America (Ridgely and Tudor 1989). *S. hypoxantha* migrates to its reproductive grounds in southern Brazil in November/December, and before the weather cools (February/March), it returns to its wintering grounds, which are still not completely understood but may be located in central Brazil (Sick 1997, Silva 1999). This species is a resident in a few areas in Argentina and Paraguay (Di Giacomo 2005, Hayes 1995).

Little is known about the natural history of *Sporophila hypoxantha* (Di Giacomo 2005), and most of the available information has been provided by a few studies that were

conducted in Formosa Province, Argentina. The long-term study by Di Giacomo (2005) in the Reserva El Bagual stands out for revealing information that was previously unknown. Facchinetti et al. (2008) then studied parental care for young at the same reserve. The lack of information on this species in Brazil has led to its being included in the Data Deficient category of the Brazilian list of threatened and endangered species of fauna (Machado et al. 2005). The southern Brazilian populations, which constitute a distinct evolutionary entity (“SE Brazil regiolect” *sensu* Areta and Repenning 2011), are considered regionally threatened (IGNIS 2010, Marques et al. 2002, Straube et al. 2004). The principal causes of population declines are the alteration and loss of grassland areas and intense pressure from the illegal pet trade (Bencke et al. 2003, Straube et al. 2004). Filloy and Bellocq (2006) related that this species has suffered significant declines with increasing intensive agricultural practices in grassland environments in Argentina.

Here, our main goal was to provide information about the reproductive biology of the Tawny-bellied Seedeater (“SE Brazil regiolect” *sensu* Areta and Repenning 2011). Specifically, we wished to understand the breeding phenology (timing of breeding), nest construction and characteristics of nests, eggs and nestlings, nesting habitat and parental care. We then place this information in context by comparison with the few other published records from Argentina.

METHODS

The study was conducted in the southern Brazilian grasslands, or *Campos*, in the extreme southeast of Santa Catarina State, southern Brazil (Fig. 1), in a physiographic region known as *Campos de Cima da Serra* (*Araucaria* plateau grasslands). We studied in two sites

divided by the Lava-Tudo river which are part of the same landscape matrix (the areas were separated to aid in their location, merely). The study sites were the *Coxilha Rica* grasslands (Site 1) in the municipality of Lages (28° 18' S, 50° 17' W), and the *Estância do Meio* grasslands (Site 2) in the municipality of São Joaquim (28° 19' S, 50° 15' W). The altitude varies from 800 to 1,000 m and the topography is characterized by a marked altitudinal gradient. The area is primarily composed of fields with a sparse lower stratum, dense middle stratum rich in shrubs (i.e., *Eupatorium* and *Vernonia* spp.) and grasses (i.e., *Piptochaetium*, *Sorghastrum*, *Andropogon*, *Paspalum* and *Setaria* spp.), and an upper stratum that is particularly characterized by “eryngos” (*Eryngium horridum*) and a few small trees (i.e., *Escallonia megapotamica*). The climate is “mesothermic superhumid” of temperate type, with cold winters and no distinct dry season. The average annual temperature and precipitation are 15.8°C and 1,384 mm, and August, September and October are the months with the greatest rainfall (Nimer 1971). Between 2007 and 2010, the highest amount of rainfall occurred in July 2007, September 2008, September 2009 and January 2010, when an unexpected amount of rainfall occurred. The average temperature gradually increased over the months of the study, from $15.13 \pm 0.77^\circ\text{C}$ in October to $18.28 \pm 0.45^\circ\text{C}$ in February.

We collected data during three consecutive years (2007 – 2010) from October to March, during the period of reproduction. We attempted to always arrive in the field before the arrival of the seedeaters, and then we followed pair activity after the arrival of the first individuals to the study area. Nest-searching was conducted by identifying active territories, then by localizing and following female behavioral cues such as carrying nesting material or food for young. Other forms of nest identification included identifying nestling begging calls, random searching for potential nest support plants and flushing incubating females. We marked each nest with a small biodegradable red flag placed 5-10 m from the nest and

recorded the location with a handheld GPS device. We visited the nests every three to six days in order to verify content and activity status and estimate the duration of events such as nest-building, egg incubation and nestling feeding. At times it was also necessary to inspect nests daily in order to improve event timing estimates.

We characterized nests by the type of substrate plant utilized (species, height and width) and the following measurements that were taken with 0.01 mm precision calipers and ruler: internal and external diameter, internal and external height, number and diameter of branches supporting the nest, distance to the center and edge of substrate plant (measured from the upper plane of the plant) and height above the ground. Some unused nests were collected in order to determine the materials used to build the nests, which were also identified by observing the adults during nest construction. The collected nests were weighed to the nearest 0.01 g with a digital scale and nest characterization followed the criteria proposed by Simon and Pacheco (2005).

Eggs were characterized and some were measured with calipers. In order to avoid disturbing parental behavior or cause abandonment, we did not measure eggs in active nests. Measurements were taken only of eggs from nests that had been recently abandoned during the incubation period.

During nestling growth, we visited each nest and described the nestlings. Descriptions included relative amount of feathers, eyes opening and skin and bill coloration. After a short period we were able to form precise age estimates. We collected blood samples from some nestlings for PCR sex determination in the laboratory and to estimate sex ratio. When possible, we verified and quantified the occurrence of subcutaneous parasites on all nestlings (*Philornis* fly larvae) and the principal parts of the body parasitized by careful inspection of the nestlings and posterior searching for pupae in the nest walls.

Adult individuals were captured with mist nets and cage traps. Birds were marked with unique combinations of two colored bands and one standard CEMAVE/ICMBio (Brazilian banding agency) aluminum band. Nestlings were banded shortly before fledging (after six days old) or soon after fledging while they remained nearby and could be caught by hand.

We documented parental behavior (nest-building, incubation and care of offspring) through focal observations with a Kowa TSN-821M spotting scope at a distance of 15 m and remote filming (a Sony DSC-H9 camera camouflaged by vegetation at 4-7 m from the nest). Video recordings were one to three hours in duration and the observations with the spotting scope were conducted for up to six consecutive hours during one of three periods of the day (after sunrise, mid-day and afternoon). We also documented activity at each bird's arrival and whether or not the individual was male or female during nest construction and incubation. During observations, we described the behavior of each couple and the duration of specific activities performed by males and females. To calculate nest attentiveness (% time on nest incubating), we divided the time in which the adult remained on the nest by the total time of observation or recording for each individual nest. We also noted the length of each visit and time spent away from nest (interval). We consider incubation to be the period between laying the first egg and hatching of the first nestling since this species begins incubation when the next to last egg (or first in clutches of two) is laid (Facchinetti et al. 2008). Video recordings were conducted during two nestling development periods: initial (one to four days old) and end (from six days old and on). We calculated the parental brooding attentiveness (%) based on the amount of time brooding divided by the total amount of recording time and by the number of nest visits per hour by each parent, and the average length of visits and time between visits (Martin et al. 2000). We also calculated the average rate of food delivery to young by each parent. We defined the nestling period as the period between hatching of the

first nestling to the last fledging (Robinson et al. 2000) because the events occur synchronously. Means were compared by non-parametric analyses for paired data (normality tested with Shapiro-Wilk) with a two-tailed P adjusted to a confidence level (α) of 0.05 in BioEstat 5.0 (Ayres et al. 2007). Values are presented as mean \pm SD.

We conducted a qualitative comparison of the reproductive characteristics of Tawny-bellied Seedeaters between the data obtained in the present study (migratory population) and those collected at the Reserva El Bagual, Argentina, where it is a resident, by Di Giacomo (2005) and Facchinetti et al. (2008). Voucher specimens (eggs, young and primarily nests) were collected for the ornithological collection of the Museu de Ciências e Tecnologia - MCT at Pontifícia Universidade Católica do Rio Grande do Sul - PUCRS.

RESULTS

We found a total of 69 *Sporophila hypoxantha* nests during the three reproductive seasons: 14 (20%) during the nest-building period, 31 (45%) during incubation, 18 (26%) during the nestling phase and six (9%) soon after the nestlings had fledged and were still close to the nest.

Chronology of the breeding cycle

Seedeaters arrived the first week of November with the earliest dates being 4 November 2007 and 1 November 2009 (the two seasons that we were able to accompany from October). During this time, the principal grasses available that the species consumes are *Sorghastrum setosum*, *Piptochaetium stipoides*, *P. montevidense* and *Briza calotheca*. First the males arrive, either alone or in small groups (< five individuals). The first females were

documented two to six days after the arrival of the first males. In the first three days of November 2009, we recorded (1) two distinct males, (2) four males and (3) six males and three females. On the ninth day, the first nest was found during the beginning of the nest-building phase and another female searched for potential nest sites and plants for construction (similar timing was documented during the other reproductive seasons). Therefore, in roughly a week after migration, the first nests were built. By mid-November, all of the main territories were occupied and most of the pairs had been observed, with many of them nesting.

The earliest nesting record occurred on 4 November (beginning of nest-building) and the latest on 5 March, when the last nestling was seen in the nest before being preyed upon. The first egg was found on 12 November and the last on 16 February. Each reproductive period lasted about 100 days (the 2009/2010 period was closely followed and lasted 101 days). Construction of the last nest to be documented began on 10 February. The nesting peak occurred in late November, with an apparent second peak in late December (Fig. 2). The second peak was primarily related to the establishment of territories by satellite males in areas that had previously been occupied by successful pairs, late arrivals and unsuccessful pairs that built a second nest. Pairs that are successful early on migrate early, during the reproductive season. No couple was observed beginning new reproductive activities after having been successful with the first brood in the same period (single-brooded). Between mid to late March, the seedeaters form flocks composed of families (adults and young from the current season) and some migrating individuals in order to migrate in groups. Most of the females and young migrate before the adult males. On 24 February 2010, we observed a monospecific flock of about 40 individuals (~60% adult males), which had less than ten individuals on the following day. On 26 February we searched for the seedeaters and did not find any individuals. It is important to highlight the available grasses during this period, which include

Andropogon selloanus, *Paspalum plicatulum* and *P. notatum*, which are heavily used by seedeaters.

Territoriality, copulation and nesting habitat

From the first moments after the arrival, males begin to aggressively defend territories. As they arrive in the area, females choose their mates (or territories) and remain within territorial boundaries. We observed copulation on five occasions. While perched in a visible location close to the male and the nest site, the female assumes a submissive posture, with her body lowered and head raised, and raises her tail, forming a “U” shape. The wings are held partially and loosely open, exposing the speculum, and the female emits soft appeal calls while moving her body sideways to follow the male. The male approaches in short, rapid flights and copulation takes 1 to 1.5 s. We observed one pair copulate on two occasions during the incubation period (the first days with eggs in the nest). A few males with female-like (brown) plumage (<3%, considering ~140 males observed) were seen defending territories during the three reproductive seasons, but none of these formed pairs (they remained as satellite males).

Territories are located in the middle of or at the base of hills (no nests were found on hilltops) and are generally close to small bodies of water in dry grasslands. The average altitude of nest sites was 900 ± 23 m (from 833 to 948 m). This species' areas of reproduction are used for extensive livestock grazing (low stocking density), and biannual prescribed burns are used to manage field plots from July to September (more than two months before the reproductive season begins). Nests were found mainly in areas with high shrub (<1.5 m in height) density that were characterized by dense groups of the shrubs *Eupatorium*

polystachyum and *Vernonia chamaedrys*. The seedeaters seem to avoid dense patches of small trees such as *Escallonia megapotamica*.

Nest construction and nests

Before they begin to construct the nests, females explore nesting microhabitats. They wander carefully through the middle vegetation stratum, sometimes adopting a brooding posture, as if they were “molding” the nest in potential plants. We watched one female test nine different plants, and in the end she “nested” for 7 sec in one shrub (*Eupatorium polystachyum*, in which the nest was later constructed). Only the females construct the nests. During this time, they remain virtually silent, move around in the lower part of the vegetation and are very difficult to observe. The nest is finished after about five days of construction (median 5, from 3 to 6, $n = 8$). One female that was closely observed from the first moment of nest-building and on constructed a nest in only three days. In some cases, the female only lays the first egg two to four days after the construction is finished. Although males do not participate in the nest-building, they remain nearby and defend the territory boundaries. The males appear to vocalize with lower frequency and intensity during this period as compared with the pre-nesting, incubation and nestling periods, and mainly emit short calls, in which they likely remain in contact with the females and warn of potential predators. When a female was observed, the male was found a few meters away (<5 m). We often observed males performing low fast flights to scare the females that had exposed themselves too much during their off-bouts back into the underbrush.

The low cup/fork format nests (height less than the external diameter and attached to branch forks, *sensu* Simon and Pacheco 2005) are built with dry grass stems, mainly thin *Eragrostis polytricha* interlaced with the panicles of digitate rames of *Eustachys ulignosa*

(Fig. 3). The upper border is reinforced with *Paspalum* spp. and *Digitaria corynotricha* panicles (heads) without spikelets. Spider webs are used to bind the material, especially in the upper border (Fig. 3). Mean height of nests above the ground was 41.9 ± 0.8 cm (from 27 to 60 cm, $n = 38$) and nest measurements were: external (nest) diameter 59.8 ± 4.47 mm ($n = 34$), internal (cup) diameter 44.7 ± 3.79 mm ($n = 34$), outside depth (height) 50.3 ± 5.11 mm ($n = 36$) and inside (cup) depth 32.9 ± 4.29 mm ($n = 36$). Nest mass was 2.1 ± 0.4 g ($n = 10$), which is 24% of that of the adults. Nests are supported by two to five branches (most had three) that measured 1.9 ± 1.31 mm (between 0.2 and 6.6 mm, $n = 109$) in diameter. The nest is held laterally by vertical or diagonal branches that stem off of the principal support plant, and the bottom of the nest rarely touches the base of the fork. Thus, the nest is only attached at the sides (mainly by spider web, rarely by projections from the nest's wall), which classifies these nests as "bottom multiple (vertical)", according to Hansell (2000).

The Tawny-bellied seedeater constructs nests in low shrubs and herbaceous plants, and we identified nine species of plants that supported 68 nests. Two of these species were responsible for 66% of the records: *Vernonia chamaedrys* ($n = 26$, 38%) and *Eupatorium polystachyum* ($n = 19$, 27%). The other species used included *Baccharis caprariifolia* ($n = 9$), *E. intermedium* ($n = 6$), *E. serratum* ($n = 3$), *E. multicrenulatum* ($n = 2$), *E. laevigatum* ($n = 1$), *B. aff. erioclada* ($n = 1$) and *Stevia* sp. ($n = 1$). The support plants measured 76.9 ± 12.04 cm in height, 42.8 ± 17.57 cm in greatest diameter and 30.9 ± 14.29 cm in least diameter ($n = 38$). The average distance from the nest to the center of the support plant was 26.7 ± 47.6 cm (from 0 to 230, $n = 37$) and the average distance from the nest to the edge of the plant was 77.16 ± 62.23 (from 10 to 275, $n = 37$). Oftentimes the nests were so camouflaged by shrubs and dense clumps of grass that it was difficult to see the nest, even at less than 2 m away. Even though they are small and appear fragile (isolated shrubs sway hard during gusts of

wind), the nests are structurally strong, resist storms and may remain intact for more than a year. Nests are not reused.

Clutch size, eggs and incubation period

Mean clutch size was 2.09 ± 0.29 ($n = 43$ nests) eggs. Two (91%, $n = 39$) was the modal clutch size, with some of up to three eggs. Eggs are laid during the morning on consecutive days, one egg per day. The eggs are ovoid and Pearl Gray (color 81 of Smithe 1975; RGB 211-208-189 measured by photo), with some cream-white or pale light green, speckled with small dark and pale brown spots that are more concentrated at the obtuse end, sometimes forming a ring (Fig. 3B). The eggs measured 16.22 ± 0.51 mm by 11.93 ± 0.28 mm ($n = 5$ nests).

Incubation begins the day that the last egg is laid (however, on the first day in most of the broods). The female performs the incubation, which lasts for 12 days ($n = 6$). Based on 11 h of observation, average nest attentiveness was $60 \pm 5\%$ ($n = 5$ nests), with on-bouts of 20 to 31 minutes (24 ± 6 min per visit, $n = 8$, approximately two visits per hour). Intervals between off-bouts last for 12 ± 2.4 min (from 9 to 15 min, $n = 6$). In one visit of 30 min, a female changed her position twice, each time turning 180° , remaining for 14.7, 5.3 and 10 min each time. In a 21 min visit, a female adjusted the position of the eggs six times. Three females were seen sleeping during incubation. We did not observe males feeding females on the nest.

Nestlings, fledglings and parental care

Eggs hatch up to seven hours apart from one another ($n = 2$), during which the female becomes agitated and makes quick visits (<7 s) to inspect the nest. Newly-hatched nestlings have rosy skin, closed eyes and light gray down in the principal feather tracts, principally on

the top of the head (capital tract). The beak is bright yellow with a light yellow commissure and an orange-red mouth (Fig. 3C). Nestlings' eyes open after four to five days, when they show protruding shafts of remiges and minute contour feathers in the dorsal, pelvic and ventral regions. The nestlings fledge when they are 9.2 ± 0.4 days old (9-10, $n = 12$). At this age, the remiges and coverts are partially complete (a dark brown center with a tawny edge), the retrices are just beginning to develop, contour feather coverage (tawny) is filling out in the ventral region (Fig. 3D and E) and the flight capacity is limited. Of the 20 nestlings that were sexed, 11 were females and nine were males, resulting in an approximate sex ratio of 1:1.

Sixty one percent of nests with nestlings were infested by larvae of the botfly *Philornis seguyi* Garcia (1925) (Diptera, Muscidae; identified by Márcia S. Couri based in adult specimens), a subcutaneous blood-feeding parasite. The effect of this interaction on nestling development was not directly analyzed. Two severe cases caused the host to die. In one of these cases, two nestlings with 24 and 26 larvae died in the nest on the eighth day of life. The larvae parasitized their head ($n = 9$ and 11), neck, wings, chest, dorsal area and thighs. After the subcutaneous larval phase, the pupae always became lodged in the walls of the nest.

Only females brooded and fed young until they were around 4 days of age, after which time males began to help. When nestlings were 1-4 days old ($n = 13$ h recorded time in six nests), provisioning visits hr^{-1} averaged 4.6 ± 0.7 ($n = 6$) and females brooded after feeding in 48% of the visits. Visits lasted 77.9 ± 58.6 sec ($n = 46$) and parental brooding attentiveness was 73%. From the fifth day of development and on ($n = 19$ hr recorded in seven nests), average trips/hr was statistically highest (8.95 ± 1.8 , $n = 11$, Wilcoxon signed-rank test: $z = -2.5$, $P = 0.012$; Fig. 4). Brooding after feeding (only by females) was observed in 14% of the provisioning visits, corresponding to 24% of parental brooding attentiveness. At this stage in

the nestlings' lives, the males make 3.8 ± 1.2 trips/hr ($n = 9$), lasting an average of 19.6 ± 9.4 sec ($n = 68$). Females make 4.9 ± 0.9 trips/hr ($n = 10$), lasting an average of 25.5 ± 8.0 sec ($n = 84$), with there being no difference between the means ($z = -0.63$, $P = 0.52$). The interval time between visits for the males and females was 10.48 ± 1.3 min ($n = 62$) and 12.38 ± 1.52 min ($n = 48$), respectively. The interval between visits when the nestlings were 1-4 days old (only females) was greater (10.43 ± 1.01 min, $n = 46$; $z = -3.39$, $P = 0.0007$) than when the nestlings were 6-9 days old (both parents; 6.86 ± 0.94 min) and equal when compared to the average time of only the female ($z = -1.05$, $P = 0.29$).

The rate of food delivery to nestlings during each visit was slightly higher in males (8.61 ± 2.79 seeds/visit, $n = 68$) than for females (7.29 ± 3.05 seeds/visit, $n = 74$; $z = -2.37$, $P = 0.017$). Although the diet fed to the nestlings is composed primarily of grains (e.g., *Piptochaetium* spp., *Panicum* spp., *Setaria* spp., *Paspalum* spp., *Andropogon* spp.), we observed females capturing and feeding termites to their young on three occasions. Additionally, a female that was captured while feeding small young had three spiders (Aranae) in her beak. These spiders are captured from the spiny leaves of *Eryngium horridum*, a characteristic plant of these grasslands. Fecal sacs were removed during 35% of the visits to the nest during the 1-4 day-old period and in 21% of the visits during the 6-9 day-old period (15% of the males' visits and 26% of the females' visits). When very hot (between 1200 and 1500 hrs BRST), the female perched on the nest rim, providing shade for the nestlings ($n = 4$ observations).

After fledging the nest, juveniles remained in the study areas for a few weeks until migration time and were always accompanied by the parents. A 36 day-old juvenile was seen feeding alone less than 20 m from the nest on three occasions. Although it begged for food from its parents, they did not feed it. One female fed *Paspalum* sp. to a 20 day-old juvenile

less than 10 m from a nest. A 29 day-old juvenile was seen being fed by both parents while it tried to feed alone. One 37 day-old juvenile that was able to fly as well as adults (well-developed tail) fed alone 70 m from the nest. We conclude that juveniles begin feeding themselves after about a month of age, generally remain less than 100 m from their nests during this time and receive assistance from their parents. When they are close to 40 days old, the juveniles have completely developed plumage, are able to fly as well as adults and are, therefore, able to migrate.

DISCUSSION

In southern Brazil, the Tawny-bellied Seedeater breeding season begins in early November and lasts until early March (or late February), and each season lasts for about 100 days. William Belton documented a nest in Rio Grande do Sul state, southern Brazil, on 24 November 1971, in addition to specimens that were collected during the reproductive period (Belton 1994). Recently, Rupp et al. (2008) commented on a juvenile being fed by two adults on 20 February 2009, in Santa Catarina and Repenning et al. (2010) described various reproductive sites of this species in southern Brazil, without presenting data. These brief accounts represent the previous knowledge about this species' reproductive status in Brazil. In the Reserva El Bagual, Formosa Province, Argentina, Di Giacomo (2005) intensively studied reproduction in Tawny-bellied Seedeaters in a study that was based on a sample of 390 nests. In this region, where the species is a resident, the reproductive period begins in late October and lasts until late March, lasting at least one month more than the reproductive period of the migratory populations in southern Brazil. In Argentina, the first breeding peak occurs in the second half of October (A. G. Di Giacomo et al. pers. comm.), at a time in which the

seed eaters are not yet present in Brazil. This difference may be explained by the migratory status of one population and the resident status of the other one. Migratory individuals begin reproduction late and have a shorter reproductive period than resident individuals (Bruderer and Salewski 2009, Reppening and Fontana 2011). Four main hypotheses (summarized by Tökölyi and Barta 2011) may explain the shorter breeding season: the “life history hypothesis”, the “spring predictability hypothesis”, the “migration time hypothesis” and the “time allocation hypothesis.” Since it is widely accepted that migration by seed eaters of the genus *Sporophila* is related to grass seed production (Remsen and Hunn 1979, Sick 1997, Silva 1999), we tentatively suggest that the last two hypotheses could fit these seed eaters, and the high cost of seasonal movements (Sillet and Holmes 2002) would be compensated by an increase in adult survival rates in wintering sites (“time allocation”; Greenberg 1980). The time spent on migration would also jeopardize the reproductive activities (“migration time”; Tökölyi and Barta 2011) and reduce the breeding season length. However, various factors combined may determine these differences in the reproductive phenology of migrants *vs.* non-migrants, related or unrelated to the different latitudinal patterns such as differential food supply, parental effort, adult and young survivorship and annual productivity (Greenberg 1980, Martin 1995, Wyndham 1986). More studies are necessary to test these hypotheses, particularly those involving reproductively isolated populations of the same species. Similar breeding season length and chronology (128 days, from early November to early March) were found in Black-bellied Seed eaters *Sporophila melanogaster* (Rovedder and Fontana 2012). A Dark-throated Seed eater *S. ruficollis* nest was found in October (Narosky and Martelli 1995) and two Marsh Seed eater *S. palustris* nests were found in December-January (F. Jacobs and J. Vizentin-Bugoni pers. comm.). Rusty-collared Seed eaters *S. collaris* nests have been documented from early November to early April (Di Giacomo 2005). Similarly, the breeding

season of Lined Seedeaters *S. lineola* lasts from mid November to early April (Oliveira et al. 2010) and of Double-collared Seedeaters *S. caerulescens* from early December to early May (Francisco 2006). Five White-bellied Seedeater *S. leucoptera* nests were found between late December and mid February (Francisco 2009). Therefore, southern South American *Sporophila* seedeaters seem to reproduce in spring-summer (October/November-March/April), which is later than most other passerines of the same regions (September; Oliveira et al. 2010, Sick 1997), and may be due to a delay in seed production after rain (Carvalho et al. 2007). On the other hand, no seedeaters from north of the Amazon appear to reproduce between October and February/March. In Panama, Alderton (1961) monitored *S. nigricollis* nests between June and October. In Venezuela, Ramo and Busto (1984) found nests of *S. minuta* and *S. intermedia* in June and June and September, respectively. *S. americana* nests were found between late May and October in Panama (Gross 1952). But *S. corvina*, in Costa Rica, has a bimodal breeding season, with nests between November-February and April-August (Wolfe et al. 2009).

The clutch size was the same (two eggs in most and a few with three) in the migratory and resident populations (Di Giacomo 2005). This is the most frequently encountered pattern in *Sporophila* spp. (Skutch 1985), and has been documented in *S. melanogaster*, *S. caerulescens*, *S. nigricollis*, *S. collaris*, *S. americana*, *S. intermedia*, *S. schistacea* and *S. leucoptera* (Alderton 1961, Di Giacomo 2005, Francisco 2006, 2009, Gross 1952, Ramo and Busto 1984, Rovedder and Fontana 2012, Stutchbury et al. 1996). A subject that should be further investigated is the frequency of occurrence of three-egg clutches (9% in the present study) among *Sporophila* species and populations with a two- to three-egg tendency and the implications of this strategy. In agreement with the classical hypothesis of the larger clutch size in the northern hemisphere (many authors since Lack 1947), the *Sporophila*

representative that occurs at the greatest latitudes (*S. torqueola*) has the greatest clutch size among the species of this genus (3-4 eggs; Eitnier 1997).

Tawny-bellied Seedeaters exclusively use plants of the Asteraceae family as support for their nests, including the genera *Eupatorium*, *Vernonia*, *Baccharis* and *Stevia*. Whether they actively choose these over other plants is uncertain, because these plants are also the dominant shrubs. But it's important to note that small trees and taller, more open shrubs were not utilized. Di Giacomo (2005) also discovered that most of the nests in Argentina were constructed in Asteraceae, and in particular *Eupatorium ivifolium* and *Vernonia chamaedrys*, with the latter being the most utilized plant in the present study. One factor that seems to be important in the selection of support plants, in addition to plant height, is plant density (consequently, good camouflage; IF unpubl. data).

Only females build nests (Di Giacomo 2005, Facchinetti et al. 2008), during which time males mate-guard, perhaps to protect the female against predation or to avoid extra-pair copulations (Gill 1989). The nest construction period of the resident population in Argentina lasted for 7-10 days (Di Giacomo 2005). However, construction clearly occurs more rapidly in the migratory population in southern Brazil (3-6 days). We speculate that this may be another attribute affected by the reduced amount of time for parental activities in the migratory population (Tökölyi and Barta 2010). *Sporophila hypoxantha* nests have the same average weight (2 g) as those of *S. lineola*, which are constructed in five days (Oliveira et al. 2010). *S. collaris* and *S. melanogaster* females also construct nests alone in 7-9 days (Di Giacomo 2005) and 3-8 days (Rovedder 2011), respectively. Although both *S. nigricollis* parents participate in nest construction, construction may still take up to 19 days (Alderton 1961).

While Tawny-bellied Seedeater nests in this study are similar to those in Argentina (Di Giacomo 2005), due to lack of information, we cannot compare our measurements. The average height above the ground was greater for nests in Formosa (70 vs. 42 cm in southern Brazil), which is likely related to the structure of the vegetation in these two areas. In our study areas, grassland management with prescribed fire is a common practice that keeps the vegetation low each year. All *Sporophila* species build a cup shaped nest that mainly varies in size, thickness of nest walls and materials used. Generally, seedeaters utilize grass stems and heads and spider web in the exterior part of the nest and for attachment, and the small nests with relatively thick walls are constructed close to the ground. All of the measurements of the Black-bellied Seedeater nests presented by Rovedder and Fontana (2012) resemble those of the Tawny-bellied Seedeater nests, with the exception that the former builds nests with slightly thicker walls.

The incubation behavior was very similar to what was encountered in the Argentinean resident population (Facchinetti et al. 2008): close to two bouts/hr, with the female spending 60% of her time on the nest, but with an apparently higher average of on-bouts (24 vs. 16 min). We did not document males feeding females, as was seen in *Sporophila melanogaster* (Rovedder 2011). Young hatch after 12 days (11-12 in Formosa; Di Giacomo 2005), as in *S. ruficollis* (11-12 days; De La Peña 2005), *S. melanogaster* (12-13 days; Rovedder 2011), *S. nigricollis* (Alderton 1961), *S. caerulescens* (11-12 days; Francisco 2006), *S. americana* (Gross 1952, Skutch 1945), *S. collaris* (12-13 days; Di Giacomo 2005) and *S. corvina* (Skutch 1945). The shortest incubation known is that of *S. lineola* (11 days, with a few records of 10; Oliveira et al. 2010). As was stated by Francisco (2006), the incubation duration reported for *Sporophila* seedeaters is among the shortest periods in open-cup nesting Neotropical passerines (Geffen and Yom-Tov 2000).

In the Tawny-bellied Seedeaters, most parental care is by females (Facchinetti et al. 2008, this study). Males help little when the nestlings are young, but their contribution increases over time (biparental care). *S. lineola* males contribute to the feeding of young at a lower rate than females (Oliveira et al. 2010). In Argentina, only females brood the nestlings after feeding in 86% of the visits (Facchinetti et al. 2008). In the present study, females brooded nestlings in 48% of the visits. Although these values may be related to the weather (Facchinetti et al. 2008 found a correlation between brooding time and air temperature), it seems that the difference is pronounced. Even more noticeable is the difference between the length of the visits: close to 700 sec in Argentina and 78 sec in southern Brazil, when nestlings were less than five days old. The same difference was found when nestlings were older: ~300 vs. 23 sec. The length of the visits largely includes brooding time. Therefore, the females in the resident population spend more time and energy on brooding than do those of the migratory population. This difference may be related to the climate of the two geographic regions. Gran Chaco, where Reserva El Bagual is located, is known as a hot region with extreme variations in temperature from -7 to 48°C. The average temperature in January is 26.7°C (Gorleri 2005). The average temperature during this month in our study area (south Brazilian grasslands) was 17.9°C. Therefore, it seems that the high temperature in Argentina would cause the need for females to spend more time brooding (to prevent overheating rather than to heat) during each visit to the nest. However, we don't reject that the differences found were due to differences on the technique used to collect data in both studies. The number of provisioning visits hr^{-1} was similar between the two populations. A similar pattern (considerably higher participation from females) was found in *S. collaris* in the same reserve, but the length of visit was slightly lower and males participate in brooding activities (Facchinetti et al. 2008).

Nestlings fledged quickly (9-10 days, mostly nine), as was seen in the resident population (Di Giacomo 2005). Rovedder (2011) documented 8-11 days for *Sporophila melanogaster*. *S. lineola* and *S. caerulescens* nestlings remained in the nest for 9-13 (Oliveira et al. 2010) and 12-15 days (Francisco 2006), respectively. *S. nigricollis* fledglings fledged after 8-9 days (Alderton 1961) and those of *S. collaris* after 9-12 days (Di Giacomo 2005). Skutch (1945) found the following nestling periods in Central America: 12 days for *S. corvina*, 11-13 for *S. americana*, 10-11 for *S. torqueola* and 10-12 for *S. [Oryzoborus] funereus*. Nestlings of the closely related Blue-black Grassquit *Volatinia jacarina* remained in the nest for 10 days (Carvalho et al. 2007). Contrary to the hypothesis that nestling (and incubation) periods are longer in the tropics (refuted by Geffen and Yom-Tov 2000), the rapid nestling development and short incubation period presented within the species of the Neotropical genus *Sporophila* is clear. Short nestling (and incubation) periods may compensate for the apparent high exposure to predators in open habitats (Santos and Marini 2010) and near ground breeders.

The most efficient nest localization method is to enter an active territory and search for the female, mainly near the male's song perches (sometimes even observation of the male may reveal the female's location since males closely accompany the females' activities). Then one should follow and observe behavioral cues: carrying dry grass or spider webs (nest-building), collecting or carrying food for nestlings (bill full of seeds or sticky seed husks is visible) or leaving the nest during incubation to preen on a nearby perch.

Knowledge about the natural history of the seedeaters may serve as a tool for developing more effective conservation measures for these seedeaters and other threatened grassland species. As with most other representatives of the genus, *Sporophila hypoxantha* presents strong territoriality, quick nest building, a single brood per season, short incubation

and nestling periods and biparental care (female biased). Compared with the resident population (Di Giacomo 2005, Facchinetti et al. 2008), the southern Brazilian migratory population had a shorter breeding season, fast nest building and less brooding attentiveness, which may be due to the reduced amount of time for reproductive activities. Nevertheless, we can't totally reject that distinct regiolects could present differences in life history traits related to their evolutionary history and taxonomic status, which is still undefined. The causes, costs and consequences of these variations and the attributes of the annual cycle of these seedeaters are unknown and the hypotheses presented here need to be tested. A comparative analysis of *S. hypoxantha* populations reproducing in distinct environments such as wetlands and dry grasslands is necessary. Finally, we suggest a greater research effort for this species and others of the genus that focuses on questions such as reproduction, annual productivity, seasonal movements, nest site selection and other life history characteristics that are still poorly known.

ACKNOWLEDGMENTS

We thank J. J. Roper, J. C. Reboreda and L. F. França for helpful comments and suggestions that improved a previous version of this manuscript. Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES for providing funding for IF. Fundação Grupo Boticário de Proteção à Natureza and Neotropical Grassland Conservancy for funding and support this project. CEMAVE/ICMBio for permission to band. C. E. Rovedder, M. Repenning and M. L. Gonçalves for the untiring assistance in the field and friendship. I. I. Boldrini for plant

identification. M. S. Couri for *Philornis* identification. Couples Joaquim and Nair, Antônio and Ivonete for support with logistics and permission to work in the study areas.

LITERATURE CITED

- Alderton, C. C. 1961. The breeding cycle of the Yellow-bellied Seedeater in Panama. *The Condor* 63:390-398.
- Areta, J. I. 2008. Entre Ríos Seedeater (*Sporophila zelichi*): a species that never was. *Journal of Field Ornithology* 79(4):352-363.
- Areta, J. I. and M. Repenning. 2011. Systematics of the Tawny-bellied Seedeater (*Sporophila hypoxantha*). I. Geographic variation, ecology, and evolution of vocalizations. *The Condor* 113(3):664-677.
- Areta, J. I., J. I. Noriega, L. Pagano, and I. Roesler. 2011. Unraveling the ecological radiation of the capuchinos: systematics of Dark-throated Seedeater *Sporophila ruficollis* and description of a new dark-collared form. *Bulletin of the British Ornithologists' Club* 131:4-23.
- Ayres, M., M. Ayres Jr., D. L. Ayres, and A. A. Santos. 2007. BioEstat. Version 5.0. USP, São Paulo, Brazil.
- Belton, W. 1994. Aves do Rio Grande do Sul: distribuição e biologia. Universidade do Vale do Rio dos Sinos, São Leopoldo, Brazil.
- Bencke, G. A., C. S. Fontana, R. A. Dias, G. N. Maurício, and J. K. F. Mähler Jr. 2003. Aves. Pages 189-479 in *Livro vermelho da fauna ameaçada de extinção no Rio Grande do Sul* (C. S. Fontana, G. A. Bencke, and R. E. Reis, Editors). Editora EDIPUCRS, Porto Alegre, Brazil.

- Bruderer, B. and V. Salewski. 2009. Lower annual fecundity in long-distance migrants than in less migratory birds of temperate Europe. *Journal of Ornithology* 150(1):281-286.
- Campagna, L., D. A. Lijtmaer, K. C. R. Kerr, A. S. Barreira, P. D. N. Hebert, C. S. Loughheed, and P. L. Tubaro. 2009. DNA barcodes provide new evidence of a recent radiation in the genus *Sporophila* (Aves: Passeriformes). *Molecular Ecology Resources* 10(3):449-458.
- Carvalho, C. B. V., R. H. F. Macedo, and J. A. Graves. 2007. Reproduction of Blue-black Grassquits in central Brazil. *Brazilian Journal of Biology* 67(2):275-281.
- De La Peña, M. R. 2005. Reproducción de las aves argentinas (con descripción de pichones). L.O.L.A., Buenos Aires, Argentina.
- Di Giacomo, A. G. 2005. Aves de la Reserva El Bagual. Pages 201-465 *in* Historia natural y paisaje de la Reserva El Bagual (A. G. Di Giacomo and S. F. Krapovickas, Editors). Temas de Naturaleza y Conservación 4. Asociación Ornitológica del Plata, Buenos Aires, Argentina.
- Eitnier, J. C. 1997. White-collared Seedeater (*Sporophila torqueola*). The birds of North America. Number 278.
- Facchinetti, C., A. G. Di Giacomo, and J. C. Reboreda. 2008. Parental care in Tawny-bellied (*Sporophila hypoxantha*) and Rusty-collared (*S. collaris*) Seedeaters. *The Wilson Journal of Ornithology* 120(4):879-883.
- Filloy, J. and I. Bellocq. 2006. Spatial variations in the abundance of *Sporophila* seedeaters in the southern Neotropics: contrasting the effects of agricultural development and geographical position. *Biodiversity and Conservation* 15:3329-3340.
- Francisco, M. R. 2006. Breeding biology of the Double-collared Seedeater (*Sporophila caerulescens*). *The Wilson Journal of Ornithology* 118:85-90.

- Francisco, M. R. 2009. First description of nests and eggs of the White-bellied Seedeater (*Sporophila leucoptera*). *The Wilson Journal of Ornithology* 121(3):628-630.
- Geffen, E. and Y. Yom-Tov. 2000. Are incubation and fledging periods longer in the tropics? *Journal of Animal Ecology* 69:59-73.
- Gill, F. B. 1989. *Ornithology*. W. H. Freeman and Company, New York, USA.
- Gorleri, M. C. 2005. Caracterización climática del Chaco Húmedo. Pages 13-25 *in* Historia natural y paisaje de la Reserva El Bagual (A. G. Di Giacomo and S. F. Krapovickas, Editors). *Temas de Naturaleza y Conservación* 4. Asociación Ornitológica del Plata, Buenos Aires, Argentina.
- Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493-504 *in* Migrant birds in the Neotropic: ecology, behavior, distribution and conservation (A. Keast and E. S. Morton, Editors). Smithsonian Institution Press, Washington D.C., USA.
- Gross, A. O. 1952. Nesting of Hick's Seedeater at Barro Colorado island, Canal Zone. *The Auk* 69:433-446.
- Hansell, M. 2000. *Bird nests and construction behaviour*. Cambridge University Press, Cambridge, UK.
- Hayes, F. E. 1995. *Status, distribution and biogeography of the birds of Paraguay*. American Birding Association, New York, USA.
- IGNIS. 2010. Lista das espécies da fauna ameaçadas de extinção em Santa Catarina. IGNIS, Itajaí, Brazil.
- Kerr, K. C. R., D. A. Lijtmaer, A. S. Barreira, P. D. N. Hebert, and P. L. Tubaro. 2009. Probing evolutionary patterns in Neotropical birds through DNA barcodes. *PLoS One* 4(2):1-6.

- Lack, D. 1947. The significance of clutch size. Parts I and II. *Ibis* 89:302-352.
- Lijtmaer, D. A., N. M. M. Sharpe, P. L. Tubaro, and S. C. Loughheed. 2004. Molecular phylogenetics and diversification of the genus *Sporophila* (Aves: Passeriformes). *Molecular Phylogenetics and Evolution* 33(3):562-579.
- Lopes, L. E., G. B. Malacco, E. Franc, A. Alteff, M. F. Vasconcelos, D. Hoffmann, and L. F. Silveira. 2009. Range extensions and conservation of some threatened or little known Brazilian grassland birds. *Bird Conservation International* 19:1-11.
- Machado, E. and L. F. Silveira. 2011. Plumage variability and taxonomy of the Capped Seedeater *Sporophila bouvreuil* (Aves: Passeriformes: Emberizidae). *Zootaxa* 2781:49-62.
- Machado, A. B. M., C. S. Martins, and G. M. Drummond. 2005. Lista da fauna brasileira ameaçada de extinção, incluindo as listas das espécies quase ameaçadas e deficientes em dados. Fundação Biodiversitas, Belo Horizonte, Brazil.
- Marques, A. A. B., M. Schneider, C. S. Fontana, G. A. Bencke, R. E. Reis, and E. V. Martin. 2002. Lista das espécies da fauna ameaçadas de extinção no Rio Grande do Sul. Secretaria do Meio Ambiente do Estado do Rio Grande do Sul, Porto Alegre, Brazil.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs* 65:101-127.
- Martin, T. E. 2002. A new view for avian life history evolution tested on an incubation paradox. *Proceedings of the Royal Society of London, Series B* 269-309-316.
- Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000. Parental care and clutch sizes in North and South American birds. *Science* 287:1482-1485.
- Narosky, T. and A. Martelli. 1995. Una nueva visita al este de Formosa. *Nuestras Aves* 31:28-29.

- Nimer, E. 1971. Climatologia da região sul do Brasil: Introdução à climatologia dinâmica. Subsídios à geografia regional do Brasil. *Revista Brasileira de Geografia* 33(4):3-65.
- Oliveira, L. S., L. M. S. Sousa, P. V. Davanço, and M. R. Francisco. 2010. Breeding behavior of the Lined Seedeater (*Sporophila lineola*) in southeastern Brazil. *Ornitología Neotropical* 21:251-261.
- Ouellet, H. 1992. Speciation, zoogeography and taxonomic problems in the Neotropical genus *Sporophila* (Aves: Emberizidae). *Bulletin of the British Ornithological Club* 112a:225-235.
- Ramo, C. and B. Busto. 1984. Nidificación de los Passeriformes en los Llanos de Apure (Venezuela). *Biotropica* 16(1):59-68.
- Remsen, J. V. Jr. and E. S. Hunn. 1979. First records of *Sporophila caerulescens* from Colombia; a probable long distance migrant from southern South America. *Bulletin of the British Ornithologists' Club* 99:24-26.
- Repenning, M., C. E. Rovedder, and C. S. Fontana. 2010. Distribuição e biologia de aves nos campos de altitude do sul do Planalto Meridional Brasileiro. *Revista Brasileira de Ornitologia* 18(4):283-306.
- Repenning, M. and C. S. Fontana. 2011. Seasonality of breeding, moult and fat deposition of birds in subtropical lowlands of southern Brazil. *Emu* 111:268-280.
- Ridgely, R. E. and G. Tudor. 1989. The birds of South America. Vol. 1 - The oscine passerines. University of Texas Press, Austin, USA.
- Robinson, W. D., T. R. Robinson, S. K. Robinson, and J. D. Brawn. 2000. Nesting success of understory forest birds in central Panama. *Journal of Avian Biology* 31:151-164.

- Rovedder, C. E. 2011. História natural de *Sporophila melanogaster* (Pelzeln, 1870) (Aves: Emberizidae) com ênfase em sua biologia reprodutiva. Dissertation. Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil.
- Rovedder, C. E. and C. S. Fontana. 2012. Nest, eggs, and nest placement of the Brazilian endemic Black-bellied Seedeater (*Sporophila melanogaster*). The Wilson Journal of Ornithology 124(1):173-176.
- Rupp, A. E., G. T. Silva, R. R. Laps, and C. E. Zimmermann. 2008. Registros relevantes de aves campestres e aquáticas no Planalto Norte de Santa Catarina, Brasil. Revista Brasileira de Ornitologia 16(4):369-372.
- Santos, L. R. and M. A. Marini. 2010. Breeding biology of White-rumped Tanagers in central Brazil. Journal of Field Ornithology 81(3):252-258.
- Sick, H. 1997. Ornitologia brasileira. Editora Nova Fronteira, Rio de Janeiro, Brazil.
- Sillet, T. S. and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296-308.
- Silva, J. M. C. 1999. Seasonal movements and conservation of seedeaters of the genus *Sporophila* in South America. Studies in Avian Biology 19:272-280.
- Simon, J. E. and S. Pacheco. 2005. On the standardization of nest descriptions of Neotropical birds. Revista Brasileira de Ornitologia 13(2):143-154.
- Skutch, A. F. 1945. Incubation and nestling periods of Central American birds. The Auk 62:8-37.
- Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Ornithological Monographs 36:575-594.
- Smithe, F. B. 1975. Naturalist's color guide. The American Museum of Natural History, New York, USA.

- Straube, F. C., A. Urben-Filho, and D. Kajiwara. 2004. Aves. Pages 145-496 in Livro vermelho da fauna ameaçada no estado do Paraná (S. B. Mikich and R. S. Bérnils, Editors). Instituto Ambiental do Paraná, Curitiba, Brazil.
- Stutchbury, B. J. M., P. R. Martin, and E. S. Morton. 1996. Nesting behavior of the Slate-colored Seedeater (*Sporophila schistacea*) in Panama. *Ornitología Neotropical* 7:63-65.
- Tökölyi, J. and Z. Barta. 2011. Breeding phenology determines evolutionary transitions in migratory behaviour in finches and allies. *Oikos* 120:184-193.
- Willis, E. O. and Y. Oniki. 1990. Levantamento preliminar das aves de inverno em dez áreas do sudoeste de Mato Grosso, Brasil. *Ararajuba* 1:19-38.
- Wolfe, J. D., P. Pyle, and C. J. Ralph. 2009. Breeding seasons, molt patterns, and gender and age criteria for selected northeastern Costa Rican resident landbirds. *The Wilson Journal of Ornithology* 121(3):556-567.
- Wyndham, E. 1986. Length of birds' breeding seasons. *The American Naturalist* 128(2):155-164.

FIGURE CAPTIONS

FIG. 1. Location of the study area (black dot) in the southern limit of the Brazilian plateau (brownish tones), state of Santa Catarina near Rio Pelotas, southern Brazil.

FIG. 2. Number of nests initiated (first day of construction, $n = 69$) during three breeding seasons (2007-2010) for Tawny-bellied Seedeaters (*Sporophila hypoxantha*) at biweekly (15 days) intervals in southern Brazil.

FIG. 3. Nest with eggs (A), eggs in detail (B), day-old nestlings (C), eight day-old nestlings (D) and 10 day-old young of the Tawny-bellied Seedeater (*Sporophila hypoxantha*) in southern Brazil.

FIG. 4. Frequency and duration of nest visits by females and males of the Tawny-bellied Seedeater (*Sporophila hypoxantha*) by nestling age groups in southern Brazil.

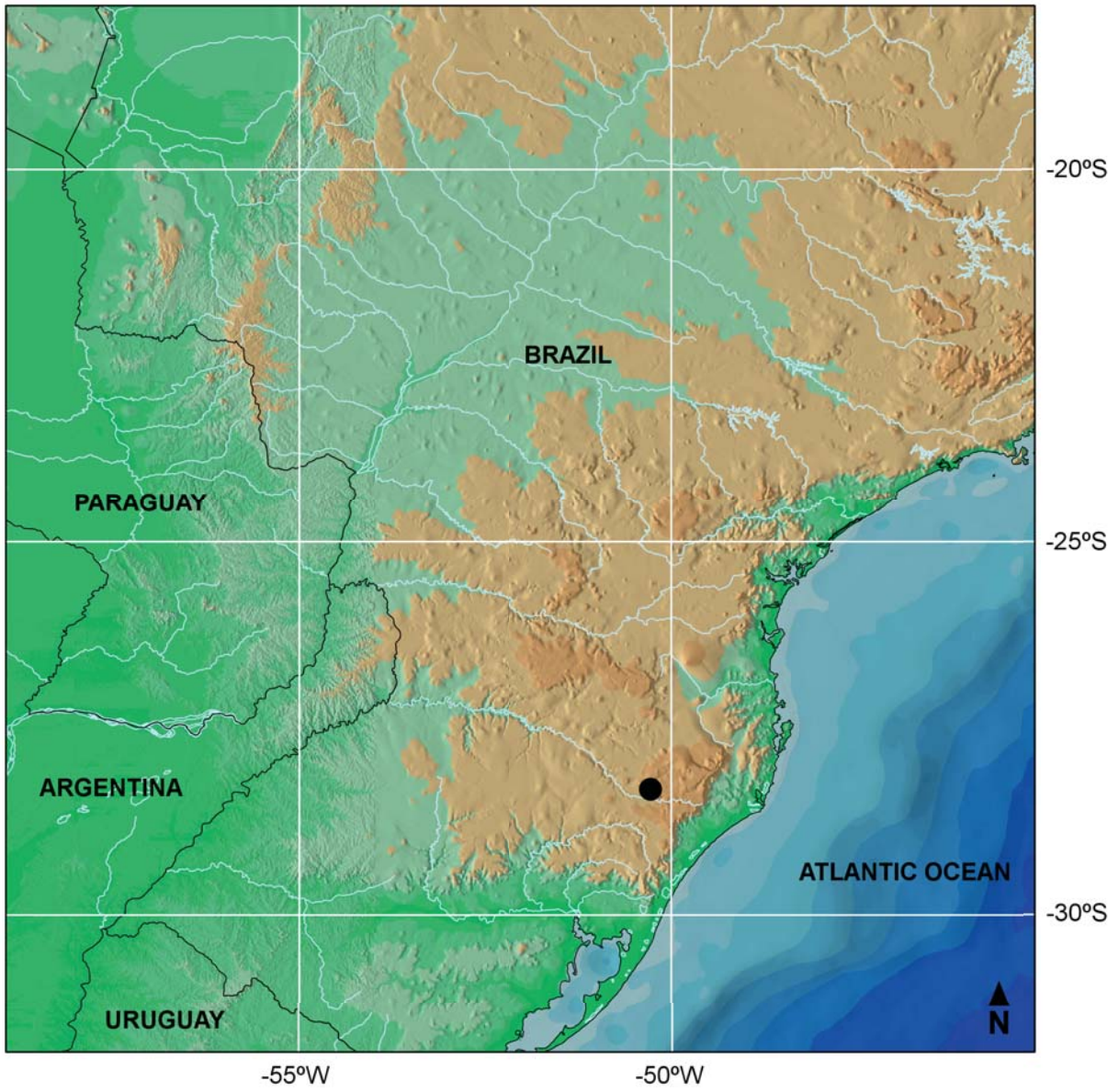


FIG. 1

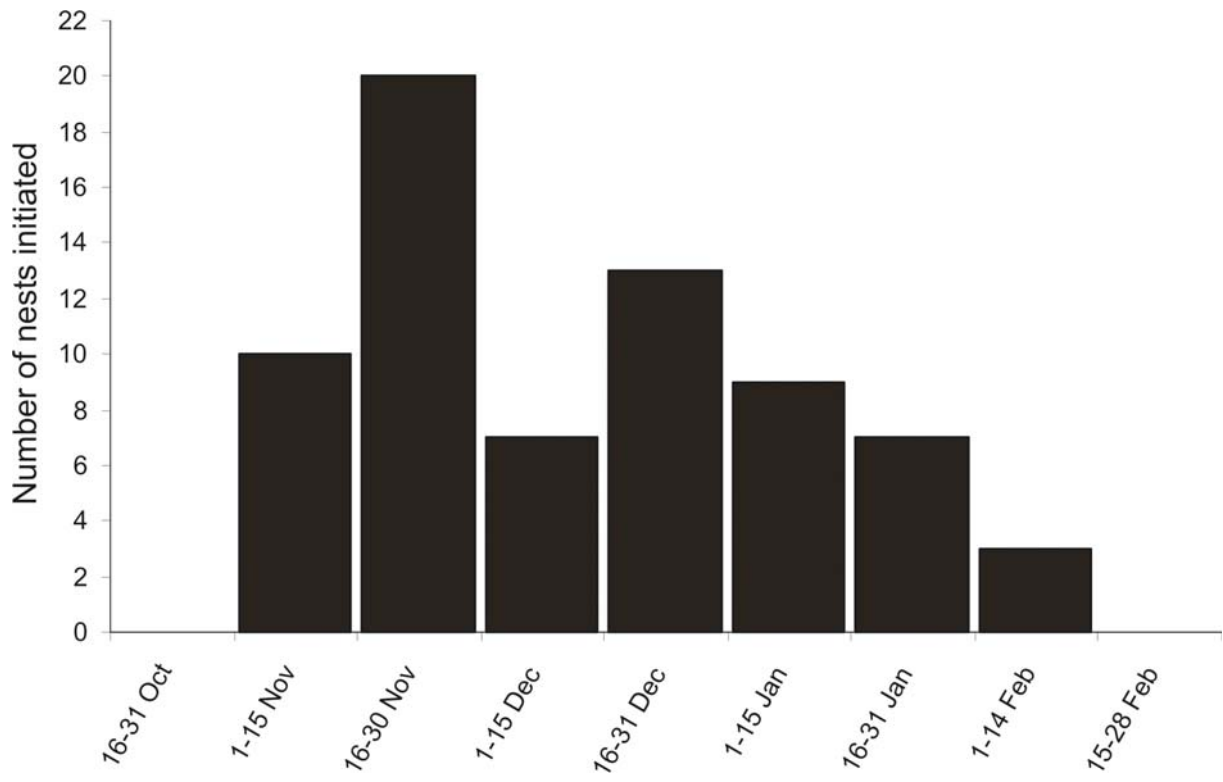


FIG. 2



FIG. 3

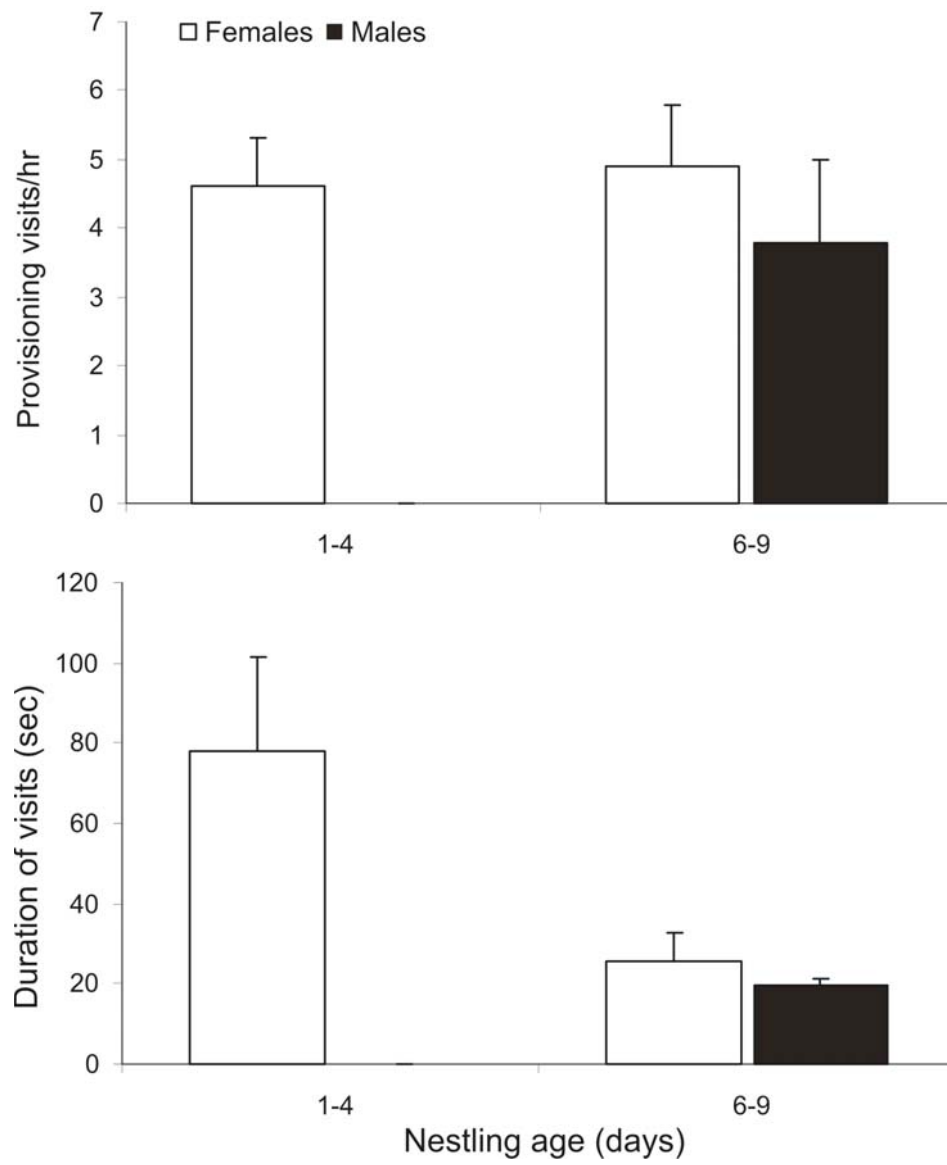


FIG. 4

CAPÍTULO 2

Reproductive success of Tawny-bellied Seed eaters (*Sporophila hypoxantha*) in Brazilian subtropical grasslands: strong influence of time-specific factors on nest survival

Artigo a ser submetido para publicação no periódico *The Condor*

REPRODUCTIVE SUCCESS OF TAWNY-BELLIED SEEDEATERS
(*SPOROPHILA HYPOXANTHA*) IN BRAZILIAN SUBTROPICAL
GRASSLANDS: STRONG INFLUENCE OF TIME-SPECIFIC
FACTORS ON NEST SURVIVAL

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Short title: REPRODUCTIVE SUCCESS OF THE TAWNY-BELLIED SEEDEATER

Abstract. We analyze the reproductive success, nest survival (logistic regression models with program MARK) and productivity of the Tawny-bellied Seedeater (*Sporophila hypoxantha*) in a migratory population over three breeding seasons (2007-2010). The study was conducted in the hilly dry grasslands near the Lava-Tudo river, Santa Catarina, southern Brazil (28° 18' S, 50° 17' W; 800-1,000m in altitude). The apparent success of 55 nests was 40%, with 25% Mayfield success. Predation was the main cause of failure (possibly by snakes and birds), affecting 55% of the unsuccessful nests, followed by desertion, infestation by *Philornis* fly larvae, cattle trampling and burning. Productivity was low (0.77 young per pair). Best models include time-specific factors (nest age and time of breeding season). Nest site characteristics did not influence nest survival. A gradual reduction in nest survival over the nesting cycle, accompanied by an increase in both temperature and subcutaneous larvae infestation along the nesting season, cause the greatest rate of predation on nests. These are more prevalent in the nestling rearing period than during incubation. This tendency may be caused by an increase in the activity in the nests, as is predicted by the Skutch hypothesis. The reduction in survival with the time of breeding may be related to pairs with lower fitness and experience. Clutch size seems to be higher in the beginning of the season.

Key words: breeding, nesting, predation, productivity, MARK

Éxito reproductivo de *Sporophila hypoxantha* en pastizales subtropicales de Brasil: fuerte influencia del tiempo en la supervivencia de los nidos.

Resumen. Se evaluó el éxito reproductivo, la supervivencia de los nidos (modelos de regresión logística con el programa MARK) y productividad de *Sporophila hypoxantha* en una población migratoria durante tres temporadas reproductivas (2007-2010). El estudio fue realizado en pastizales a lo largo del río Lava-Tudo, Santa Catarina, sur de Brasil (28° 18' S, 50° 17' W, 800-1000m de altitud). El éxito aparente de 55 nidos fue de 40% y éxito Mayfield 25%. La depredación fue la principal causa de fracaso (posiblemente por serpientes y aves), y afectó 55% de los nidos perdidos, seguida del abandono, de la infestación por larvas de *Philornis* (Diptera), pisoteo por ganado y la quema de campo. La productividad fue baja (0,77 pichones por pareja). Los mejores modelos incluyeron factores temporales (edad de los nidos y el tiempo de la época de cría). Características de los sitios de anidación no influyeran en la supervivencia de los nidos. La reducción gradual de la supervivencia en ciclo de anidación, que acompaña a un aumento de la temperatura y de la infestación por larvas subcutáneas, representa la mayor tasa de depredación en el período de cuidado de los pichones en comparación con la incubación. Esa tendencia puede ser causada por un aumento en la actividad en los nidos, como predice la hipótesis de Skutch. La reducción en la supervivencia a lo largo de la época de cría puede estar relacionada con la reproducción de parejas con menor aptitud y experiencia. El tamaño de puesta parece ser mayor en el inicio de la temporada.

INTRODUCTION

Nest predation is the most important single factor reducing nest success (Ricklefs 1969, Willis 1974, Roper 1992) and therefore may often be an important force in life history evolution (Martin 2004). The higher rate of predation shown by Neotropical birds in relation to patterns in the northern hemisphere has been debated (Ricklefs 1969, Oniki 1979, Skutch 1985, Martin 1995). The simple differences in clutch size, a widely discussed and tested attribute among North and South American birds, have been well-known since the study by Reginald Moreau (1944), although variations between latitudes are in need of a major revision (Martin et al. 2000a). However, reproductive success is not only related to predation and clutch size.

Nest success varies spatially and temporally due to differences in climate, predator community and human disturbance (Skutch 1985). Time-specific factors, such as nest age or time of breeding season, may be related to variation in the nest predation risk for many species (Grant et al. 2005). An increase in predation during the nestling phase (the age-specific effect) may be due to increased activity at the nest as a consequence of feeding nestlings (the Skutch hypothesis, Skutch 1949). The selection pressure exerted by predation would force pairs to visit the nest less often and would thus restrict the potential clutch size. Lack (1947) proposed an alternative to Skutch, stated that the latitudinal difference in clutch size would actually be related to food availability and the ability of the parents to obtain it. Longer day length would allow individuals to find more food each day and, therefore, feed more nestlings. Testing Skutch's predictions, Roper and Goldstein (1997) demonstrated that the activity at a nest does not increase its chance of predation, which elucidates the need to rethink the role of predation in the evolution of tropical and temperate life histories. Indirect factors

such as habitat features (i.e. whether or not variation in the height of a nest from the ground and support plant species favor nest concealment) influence the probability of predation and, therefore, reproductive success (Slagsvold 1982, Martin and Roper 1988).

Although 80% of all passerines occur in tropical latitudes, the disproportional majority of studies that serve as a theoretical base for the understanding of behavioral ecology in birds has been conducted with temperate zone species (Stutchbury and Morton 2008). These authors estimate the proportion of temperate *vs.* tropical bird studies to be >100:1. Martin (1996) called the state of knowledge about the life history traits of tropical/southern hemisphere birds as “extremely poor.” The majority of comparisons are drawn between the northern hemisphere and the tropics, and subtropical regions (south temperate) are even more poorly studied. In addition, grassland areas are poorly represented in comparative analyses (Robinson et al. 2010).

Although some studies have provided estimates of reproductive success for *Sporophila* seedeaters, typical representatives of open habitats in southern South America (Silva 1999), none have inquired into the factors that are related to nest survival for the representatives of this genus. The present study aims to estimate the reproductive success of Tawny-bellied Seedeaters (*Sporophila hypoxantha*) in Brazilian subtropical grasslands and evaluate the factors that apparently influence nest survival and productivity and discuss the dynamics of these factors.

METHODS

STUDY SITE AND SPECIES BACKGROUND

The study was conducted in the physiographical region Campos de Cima da Serra (the Brazilian Subtropical Highland Grasslands *sensu* Iganci et al. 2011), in dry grasslands that occur along the Lava-Tudo river, in the municipalities of São Joaquim and Lages (considered two subareas in the analyses), southeastern Santa Catarina State, southern Brazil (central point: 28° 18' S, 50° 17' W). Hills are an important element in the regional landscape and vary in altitude from 800 to 1,000 m. The vegetation is characterized as being rich in Asteraceae shrubs, grasses such as *Sorghastrum*, *Andropogon*, *Paspalum* and *Setaria* spp. and the “caraguatá” *Eryngium horridum*. See a detailed description of the study site in Franz and Fontana (2012).

Meteorological data such as maximum daily temperature was an average of daily values from each of three years of the accompanied reproductive seasons. These were collected at the meteorological station National Institute of Meteorology (INMET), located in São Joaquim, near the study area.

In southern Brazil, the breeding season of the Tawny-bellied Seedeater lasts about 100 days, from the first week of November until the end of February (Franz and Fontana 2012). Females arrive a few days after the males, which arrive in the study area the first week of November and quickly establish territories. The nest is constructed slightly above the ground (~40 cm) and is camouflaged by shrubs such as *Eupatorium*, *Vernonia*, *Baccharis* and *Stevia* spp. The clutch size is two but may be three in some cases, and incubation lasts for 12 days. Nestlings are fed by the pair (the males feed nestlings once they are older) and fledge the nest after 9-10 days (Franz and Fontana

2012), which is similar to the timing in resident populations in Argentina (Di Giacomo 2005, Facchinetti et al. 2008).

FIELD PROCEDURES

During three breeding seasons (2007-2010), we conducted intensive nest-searching since the first seedeaters arrived in the study area, from the first week of November until March, in which we principally observed the behavior of females in territories defended by males (Martin and Geupel 1993). Each nest was marked with small biodegradable colored tape 5-10 m from the nest and a point location with GPS. In order to verify the content and determine the activity status of nests, we visited each nest every 2-6 days until it became inactive (success or predated/deserted) and eggs or nestlings were quantified. We considered incubation to be the period between the laying of the first egg and the hatching of the first chick (Facchinetti et al. 2008, Franz and Fontana 2012). The nestling period was considered to be the period from the hatching of the first egg until the first nestling fledged the nest (synchronous events in this species). The nests and contents were not manipulated except for a few nestlings that were banded after reaching seven days in age. Given the short nestling period (9-10 days) and knowledge of the morphological characteristics of each day of development, we were able to rapidly and reliably estimate the age of nestlings in nests found during this period. For nests found during incubation, we estimated age by counting backwards from the hatching date. Nestlings found during the nestling period were aged directly. We considered a nest successful if at least one nestling fledged. When a nest was found empty before the expected fledging date (incubation or nestling phase not concluded) or with modified content or structure, we classified it as unsuccessful. Predated nests were

those in which eggs or nestlings disappeared before reaching the completion date for each phase of development, when a predation event was documented or when the nest was found deformed. Abandoned nests were those in which incubation exceeded the expected limit for egg eclosion or were no longer visited by the female during construction.

The nest site characteristics that were evaluated and measured included support plant species (herbarium specimens were prepared and sent to appropriate specialists for identification), support plant height, support plant cover area (greater diameter x lesser diameter in a vertical projection), nest height (from the border of the nest to the ground; these last three with a ruler) and an estimate of nest concealment (% nest cover from breast height of the same observer, with 0 = completely uncovered and 100% = completely covered by plants, in a vertical projection). Whenever possible in nests with young, we verified the occurrence of subcutaneous parasites (larvae of the dipteran *Philornis seguyi*) by quickly observing the nestlings and once a nest was inactive, searching for pupae in the nest walls.

DATA ANALYSIS

We employed logistic regression models to evaluate the effect of the measured variables on daily nest survival rates for the Tawny-bellied Seedeaters. For this, we used the nest survival model available on the program MARK (White and Burnham 1999). Initially, we continuously numbered each day of the reproductive period from day 1 on, which corresponds with the day in which the first nest was found during the three breeding seasons together, until the last day of the season, which is the latest hatching or failure date. Thus, we had a nesting season of 105 days, beginning on 16 November and

ending on 28 February. We considered a nesting cycle to be 21 days based on 12 days of incubation and nine days with nestlings, both of which have little variability (Franz and Fontana 2012). From the general sample of 69 nests encountered, we selected 47 nests in which we could reliably evaluate the information required for the method indicated by Dinsmore et al. (2002): that (1) the nests be correctly aged when found, (2) the nest fates be determined with confidence, (3) inspections did not influence survival, (4) the nest fates are independent and (5) there is homogeneity in the daily nest survival rates.

We divided the analysis into two sets of candidate models and each one of the covariates or sets was utilized to represent *a priori* hypothesis and predictions. In addition to the model that assumes a constant survival (null hypothesis model), the first set included a linear time trend model and a quadratic model (polynomial model that includes both a linear and squared value). We hypothesized that the DSR may vary temporally and if so, the time trend models should be favored. Survival may vary linearly, decreasing over the reproductive period in function of a tendency for there to be greater success in early breeders (Ainley and Schlatter 1972), or curvilinearly (quadratic model), in which it may present a better pattern for the intermediate phase of the nesting season. The second set of models includes the covariates in all possible combinations and is the set that formed the basis for choosing the models that best fit the data. Five nest-site variables were included as covariates (previously described in field procedures), which is nest height (no. of parameters [K] = 1), plant height ($K = 1$), plant species ($K = 2$), plant cover ($K = 1$) and nest concealment ($K = 1$). We tested whether nest height or support plant or plant cover influenced nesting success. One spatial variable (in which of two study sites the nest was found, $K = 1$) may reveal a

preference for a specific area on a greater scale. The covariate year represents each of three reproductive seasons ($K = 2$) and the search for variations in DSR during each season. The covariate nest age (*ageday1 sensu* Rotella 2011), which represents the day of the first egg for each nest in relation to day 1 of the reproductive period ($K = 1$), tests the well-known Skutch (1949) hypothesis that at the measure at which the age of a nest increases, the probability of predation, especially from greater activity by the parents, also increases.

We compared the values of the candidate models to the constant/null model. To run the null model, we utilized the sin link function, and for those that included the covariates, the logit link function (Dinsmore et al. 2002). Once the competing models were constructed, the support was evaluated among the set of candidate models by means of Akaike's Information Criterion, adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002). According to these authors, only models with $\Delta AIC_c \leq 2$ show substantial support. We tabulated all of the models that were better than the null model of each set of competing models and excluded the rest. We utilized the Delta method (Seber 1982) on the 'emdbook' package (Bolker 2011) of the software R version 2.14.0 (R Development Core Team 2011) to calculate and plot the product and variance from the β values of the best model adopted. We did not perform the goodness of fit because there is no reliable GOF test for MARK users on nest survival; moreover, the saturated model fit the data well in these cases (Rotella 2011).

Considering the wide use of the constant daily nest survival estimate and in order to compare with other studies conducted in the Neotropics, we calculated reproductive success and survival by the Mayfield method (Mayfield 1975) with modifications that allow for the estimation of variance of the DSR for each period of the

nesting cycle (Hensler and Nichols 1981, Mason 1985). We calculated productivity based on the number of fledglings in relation to the number of reproducing pairs followed and rate of eclosion, which is the number of eggs that hatch in relation to the number of eggs observed. In this way, we determined the frequency of occurrence of brood reduction (partial nest losses) during each phase of the nesting cycle. To determine the degree of association among the measured variables, we ran non-parametric tests for independent samples in the software BioEstat 5.0 (Ayres et al. 2007). We presented values as means \pm SD.

RESULTS

Of the 55 nests in which the final status was known (seven in 2007/2008, 26 in 2008/2009 and 22 in 2009/2010), 22 (40%) were successful, with 57%, 35% and 41% during the seasons 2007/2008, 2008/2009 and 2009/2010, respectively. Of these 22 nests, 39 young fledged, which represents an average productivity of 1.77 ± 0.52 young per pair per reproductive season (this species is one-brooded) in successful nests. Six pairs fledged one, 15 fledged two and one fledged three young. During the incubation period, partial nest loss occurred in 10 nests, five of these due to predation (four of one egg and one of two eggs) and five from not hatching. Of the 60 eggs studied during incubation, eight did not hatch, resulting in a hatch rate of 86% (or 14% of the eggs failed to hatch). During the nestling phase, partial losses occurred in six nests (18% of 33), always with the loss of one nestling. Overall, the average young fledged per nest (successful and unsuccessful nests) was 0.71 ± 0.93 .

Predation was the main cause of failure, affecting 55% of the unsuccessful nests, followed by abandonment (30%), infestation by fly larvae (6%), cattle trampling (6%)

and burning (3%). We documented a predation event *in situ*, when a 40 cm Brazilian Green Racer Snake (*Philodryas aestiva*, Dipsadidae) preyed on two three-day-old nestlings and left an opening of 1.5 cm diameter in the bottom of the nest. Predated nests were generally found in two forms: intact (most common pattern) or damaged (with holes, pulled apart or totally destroyed). The causes of nest desertion were not confirmed but were likely related to intense winds and rain that caused the females to leave the nests and eggs. Although we documented parasitism by *Philornis seguyi* in 27 nests, young only died ($n = 3$) in two nests.

Based on an effective sample size of 443 nest-days, we estimate Mayfield success to be 25.72%. The daily survival rate was 0.945 ± 0.01 during incubation and 0.927 ± 0.01 during the nestling phase. At the end of each period, survival was 0.509 ± 0.09 and 0.504 ± 0.08 (matched because of three days more during the incubation period, which had a greater DSR), respectively, which results in a 0.25 cumulative probability of survival during the nesting cycle.

The most parsimonious models found include time-specific factors such as the linear time trend and, particularly, nest age (Table 1). Only the temporal variables were related to daily nest survival rate. The five nest site variables did not affect the DSR, and their AIC_c values were higher than that of the null model when treated without the addition of the variable of nest age (Table 1, second set). We note that in the third candidate set, the weight “dilutes” itself in the models when the variable nest age is included in the calculation. Only two of the candidate models received substantial support, with Akaike weights summed at 1.0 (0.71 for the best model) for the second set and 0.48 for the third set (Table 1). Although the model with only the nest age variable is better than the linear + nest age model, it is necessary to consider the penalty caused

by the additional parameter of the latter, even though the better model has 1.78 AIC_c units less. The logistic regression equation for this best model was simply $\text{Logit}(\hat{S}) = 5.26 - 0.18 (\text{nest age})$. However, we found that DSR decreases over the reproductive season and that it decreases rapidly with the increasing age of the nests (Figure 1).

Daily nest survival values were negatively correlated with maximum daily temperature in the study area ($r_s = -3.346$; $P = 0.001$), which gradually increases between November (monthly average 19.9 ± 4.2 °C) and February (monthly average = 22.9 ± 2.54 °C).

DISCUSSION

The estimated reproductive success for Tawny-bellied Seedeaters in southern Brazil (40% apparent success and 0.25 Mayfield successes, $n = 55$ nests) is similar to that found in other species of *Sporophila* seedeaters, although only a few studies are available. In the only study of reproductive success in the capuchinos group, Rovedder (2011) obtained an estimated reproductive success of 42% and a Mayfield success of 21.4 ($n = 64$) for the Black-bellied Seedeater (*S. melanogaster*), which is also found in Brazilian subtropical grasslands. Francisco (2006) found an aparent success of 36% ($n = 41$) for the Double-collared Seedeater (*S. caerulescens*) in southeastern Brazil. In this same region, the apparent success of Lined Seedeaters (*S. lineola*) was higher (56%, $n = 41$; Oliveira et al. 2010). Blue-black Grassquits (*Volatinia jacarina*), a closely related species that nests in open areas, had a lower success (24%, $n = 81$) in central Brazil (Aguilar et al. 2008). Skutch (1985) found a success of 54.5% ($n = 44$) in nests of the Variable Seedeater (*S. ["aurita"] corvina*), in Costa Rica. Chestnut-throated Seedeaters (*S. telasco*) had a success of 37% ($n = 190$) in Equador (Marchant 1960). The 40%

success found for *S. hypoxantha* (between 36% and 56% for *Sporophila* seedeaters studied up to today) can be considered median, within the normal range and close to the average for tropical birds, even though the Mayfield success is low (25%). The apparent high susceptibility to predation (open nests close to the ground in open areas and with low nest defense capability), principally by terrestrial predators, could be compensated by the rapid development (21-day nesting cycle) and discrete parental behavior (Franz and Fontana 2012). Martin's (1995) compilation resulted in average nesting success of 40% for species that nest in shrubs in shrub/grassland habitats. In the Brazilian subtropical grasslands, there are almost no published studies involving the reproductive success of birds that can be used to make comparisons and establish general patterns.

As was expected, predation was the principal cause of nest failure and affected 55% of the unsuccessful nests (33% of the total). The rate of predation is more closely related to the pattern found in birds of temperate zones (40-60%, Martin 1993) than with the high predation pressure exerted on tropical (55-85%; Stutchbury and Morton 2001 but see Oniki 1979). This apparent reduced predation rate may be related to the efficient camouflage of the nests in general. In the same area, nests of other shrub-nesting species such as the Bearded Tachuri (*Polystictus pectoralis*) that are more visible in the vegetation have higher rates of predation (Fontana et al. unpubl. data). Characteristics of the vegetation near nests influence the probability of predation (Martin and Roper 1988, Martin 1993, Roper 2000, Fontaine et al. 2007). Additionally, behavioral adjustments due to the risk of predation (Fontaine and Martin 2006) seem to be efficient and cause nesting activities to be more inconspicuous. Roper et al. (2010) state that individuals that are under lower than average predation risks may be favored in the selection that leads to lower predation rates.

Most of the nests that were preyed upon remained intact (this type of predation includes some cases of partial nest loss). For these nests, we attribute brood loss to predation by snakes (such as the *Philodryas aestiva* that was documented in a predation event), birds or, less likely, mice. Potential avian predators of Tawny-bellied Seedeater nests that are common in the area include Swallow-tailed Kites (*Elanoides forficatus*), American Kestrels and Aplomado Falcons (*Falco sparverius* and *F. femoralis* [documented consuming *Sporophila hypoxantha* adults by Di Giacomo 2005]), Roadside Hawks (*Rupornis magnirostris*), Azure Jays (*Cyanocorax caeruleus*), but perhaps particularly passerines that can more easily access small, low and inconspicuous nests such as Great Kiskadees (*Pitangus sulphuratus*) and Boat-billed Flycatchers (*Megarynchus pitangua*). On the other hand, some nests were found damaged and completely predated. We attribute the predation of these nests to medium-sized mammals in the region which include Pampas Foxes (*Lycalopex gymnocercus*, frequently observed inspecting shrubs), Tayras (*Eira barbara*), South American Coatis (*Nasua nasua*), Crab-eating Racoons (*Procyon cancrivorus*), White-eared Opossums (*Didelphis albiventris*) and Molina's Hog-nosed Skunks (*Conepatus chinga*, which has been documented eating eggs of other ground-nesting birds in another area of southern Brazil [Kasper et al. 2009]) or Tegu Lizards (*Tupinambis meriana*). We also found a nest with nestlings being consumed by army ants. While monitoring nests of 13 North American grassland passerines with video cameras, Pietz and Granfors (2000) documented predation by squirrels (most frequent), foxes, deer, mice, weasels, badgers and birds (*Circus cyaneus*, *Buteo* sp. and *Molothrus ater*). In non-native pastures in Wisconsin, Renfrew and Ribic (2003) registered predation of nests of grassland birds ($n = 24$) by raccoons (most frequent), squirrels, snakes, badgers, cats, opossums, mice,

deer, weasels, skunks and birds. Thompson and Burhans (2003) found that snakes were more important predators than mammals and birds in old fields (also see the revision of Weatherhead and Blouin-Demers [2004] on predation by snakes). In the cerrado of central Brazil, França et al. (2009) demonstrated the importance of birds, and particularly passerines, in predation, and recorded species of the families Bucconidae, Tyrannidae, Thraupidae and Corvidae (more frequent) as consumers of eggs and nestlings. We stress that knowledge about the community of nest predators in subtropical regions is still lacking.

All cases of nest desertion occurred during the incubation period ($n = 7$) or nest construction ($n = 3$), and is the second most important cause of nest failure, affecting 30% of unsuccessful nests. Egg desertion seems to be principally related to the occurrence of hard rains, which forces the female to flee and leave the content exposed (we found recently abandoned nests with wet eggs). According to Ricklefs (1969), egg desertion may be related to the lack of food resources in extremely variable environments such as marshes. However, nest desertion may simply be a consequence of the parents' perceived risk of predation (Berger-Tal et al. 2010, Zanette et al. 2011 and also see the Martin 2011 comments). This risk and its variations may play a key role in the expression and selection of parental strategies (Martin 1992, Fontaine and Martin 2006).

Parasitism by *Philornis seguyi* (Diptera) was common in nests of Tawny-bellied Seedeaters (61% of nests with nestlings), but mortality occurred in only three nestlings of two nests (two of them had 24 and 26 larvae; Franz and Fontana 2012). In this species, infestations of more than 20 larvae per nestling is apparently lethal (we documented that nestlings with between five and 17 larvae fledged successfully),

although the age of the nestling at the time of infestation may influence the effect. Although botfly larvae infestation is not considered to be a form of effective predation, it may indirectly act on predation rates because infected nestlings move considerably more in the nest (possibly due to the bodily discomfort) and vocalize louder, which facilitates their being found by predators. Perhaps parasitized nestlings need more food (the demand for parental visits would consequently increase), which reduces the chances of survival. Gross (1952) documented the death of two *S.* (“aurita”) *americana* nestlings parasitized by *P. pici*. Forty-seven larvae emerged from one of the nestlings during inspection. Dodge and Aitken (1968) reported parasitism by *P. trinitensis* in *S. lineola* and *S.* (formerly in *Oryzoborus*) *angolensis* in Trinidad. In his revision, Löwenberg-Neto (2008) mentions parasitism by *Philornis* in *S. lineola*, *S. nigricollis*, *S. angolensis*, *S. bouvreuil*, *S. intermedia* and *S. caerulescens*. Lopes and Marini (2005) claim that parasitism by *Philornis* spp. affects various species in the Cerrado of central Brazil. The study by Rabuffetti and Reboreda (2007) in Argentina on parasitism by *P. seguyi* in Chalk-browed Mockingbird (*Mimus saturninus*) nests revealed infestation rates between 30 and 58% in each breeding season. The authors discovered negative effects of infestations on chick survival and nestling growth and an increase in parasitism with time of breeding. These same patterns were found by Segura and Reboreda (2011), also in Argentina, in Red-crested Cardinals (*Paroaria coronata*) nests parasitized (28%) by the same species of fly. In the present study, we found that 50% of the nestlings were parasitized in the beginning of the breeding season (November-December) and 81% at the end (January-February). We hypothesized that the frequency and intensity of parasitism increases with increasing temperatures in the study area. However, this is a subject that needs further study.

We included in the experimental design the hypothesis that the daily survival rates of Tawny-bellied Seedeater nests would be influenced by nest site characteristics such as height above ground, support plant species and nest concealment. However, none of these ecological variables tested influenced the DSR. We attribute this to the low amount of variation in the measured values of these variables. Nests are higher than 25 cm and lower than 60 cm (Franz and Fontana 2012), and perhaps this variation is not sufficient in providing an effect on the differential access capacity to nests by predators. The same theory could serve for the support plants, which are structurally similar (more than 80% of the nests were in the shrubs *Vernonia chamaedrys* e *Eupatorium polystachyum*; Franz and Fontana 2012), and thus vary little with respect to nest concealment. The third variable seems to be the most important (Table 1, third set). We believe that the inclusion of more nest concealment variables, which represent the real visibility of the nest at different distances, may reveal a distinct effect by this parameter. Additionally, it is important to note that the candidate models that included ecological factors received little support due to competition with strong temporal models.

We found that nest age was the most relevant factor to survival in *Sporophila hypoxantha* nests, with DSR sharply falling over the nesting cycle (Figure 1a). In this species, the frequency of visits to the nest are considerably higher during the nestling feeding period than during incubation (4-9 visits hr^{-1} and 2 visits hr^{-1} , respectively; Franz and Fontana 2012). Furthermore, provisioning visits per hour increase as nestlings develop and males care for the young particularly when they are more developed, after they reach four to five days of age (Facchinetti et al. 2008, Franz and Fontana 2012). Therefore, nest activities clearly increase along the nesting cycle, which could aid diurnal predators to find the nests. This pattern is in agreement with the amply

debated and partially tested Skutch hypothesis (see Introduction). Various studies have shown this tendency. Recently, Di Giacomo et al. (2011) found this condition in Strange-tailed Tyrants (*Alectrurus risora*) in open savannas of the eastern Chaco, Argentina. Both Brawn et al. (2011) and Auer et al. (2007), which studied various passerine species in Panama and Argentina, respectively, found lower rates of survival during the nestling period than during incubation for some of the studied representatives. França and Marini (2009), in the first study modeling survival of nests of Brazilian birds, reported the decrease in survival over the nesting cycle of Chapada Flycatchers (*Suiriri islerorum*). The DSR of another species of seedeater, the Black-bellied Seedeater, was also influenced by nest age, among other variables (nest concealment and plant species), in southern Brazil (Rovedder 2011). Similarly, Lined and Double-collared Seedeater nests have a higher probability of survival during the incubation period than during nestling rearing (Francisco 2006, Oliveira et al. 2010). Although some studies support Skutch's theory (Martin et al. 2000b, Muchai and Plessis 2005), others search for alternatives. Roper and Goldstein (1997) argued against the theory based on an experiment in which they demonstrated that predation does not increase with increased nest activity and the principal predators are nocturnal and not visually oriented. Among the other studies that have appeared after this study, we highlight the study by Fontaine et al. (2007) which showed that other aspects such as nesting guilds and nest sites seem to influence nest predation risk and that parental care activities need more investigation. For the species studied here, an increase in nest activity, and, as seen, an increase in nestling parasitism, seems to be the principal cause of the elevated predation rates at the end of the nesting cycle since most of the potential predators are diurnal and light and visibility are higher in natural grasslands.

The Linear time trend model was the temporal model that best explained our data and indicated that the DSR decreases over the breeding season (Figure 1b). This pattern, which would not be achieved with only Mayfield's estimator, can be seen in many species. Grant et al. (2005) monitored the nests of two passerine species in North Dakota and found a better model for both species that considers only nest age (but with a cubic effect) and a second best model that also included a linear time trend. In southeastern Brazil, Duca and Marini (2005) found a sharp decline in the probability of survival in Red-rumped Cacique (*Cacicus haemorrhous*) nests over the nesting season. *Sporophila melanogaster* (Rovedder 2011), Stripe-tailed Yellow-finches (*Sicalis citrina*; Gressler 2007) and *Alectrurus risora* (Di Giacomo et al. 2011) also reflected this linear effect on DSR. In the present study, we exclude the ideas that this pattern is due to the occurrence of renesting because this rarely occurs with this species in the study area (Franz and Fontana 2012) or a decrease in protective cover (Davis 2005), since the shrubs and surrounding vegetation do not change during the months of study. Alterations in the predator community (Grant et al. 2005) and food resource availability were not tested. As seen, temperature increases throughout the season and, consequently, so does intensity of nestling parasitism by subcutaneous *Philornis* larvae. This could reduce the DSR as the end of the breeding season approaches. Males immigrate first in the study areas, and soon after arriving they begin to establish and fight for the "best" territories. When they arrive, females, one by one, seem to select males by both phenotypic characteristics such as voice and plumage and territory quality (Franz and Fontana unpubl. data). In this sense, although this was not tested, we hypothesized that the pairs with best fitness would reproduce at the beginning of the breeding season. Since unoccupied territories (pairs with success in the beginning

emigrate early) are soon occupied by new individuals (late arrivals or satellite individuals), those reproducing at the end of the season would be less fit (and possibly younger) and more susceptible to failure. In a broader sense, producing fledglings soon before the moment of emigration, at the end of the season, could reduce the amount of time for parental care out of the nest (we documented nestlings when there were practically no more seedeaters in the region, in mid- to late February). Verhulst et al. (1995) discuss the relationship between the seasonal decline in reproductive success with the phenotypic quality of early and late breeders. These ideas are only hypotheses and require more investigation. We believe that sexual selection is an important subject that needs to be studied in this species.

We did not include the variable of clutch size in the models due to few observations of variation during the study. However, we emphasize that the four cases of a clutch size of three eggs (9.3% of the total; modal value is two) occurred in November, in the beginning of the reproductive period. Di Giacomo et al. (2011) found a reduction in the clutch size over the breeding season of Strange-tailed Tyrants in Argentina. This pattern is more frequent in species that have short breeding seasons, such as the Tawny-bellied Seedeater studied here (100 days), and may be related to decreasing reproduction conditions over the season (Slagsvold 1982). If the risk of predation is greater as the breeding season approaches the end, parents could reduce energy expenditure by producing fewer eggs since the chance of completely losing a clutch is higher (Slagsvold 1982, Martin 2011, Zanette et al. 2011).

In summary, Tawny-bellied Seedeaters present a medium reproductive success and low annual productivity, predation is the principal cause of nest failure followed by nest desertion during incubation, and more than half of the nestlings are infested by

Philornis. There is a noted influence of time-specific factors on nest survival and there is a drop in the probability of survival over the nesting cycle and date of breeding season, accompanied by an increase in temperature. We consider the study areas (“Coxilha Rica” and “Estância do Meio” grasslands) to be of utmost importance in the conservation of this species and others that reproduce in and/or utilize this region as a stopover during migration. We suggest comparative intraspecific studies with this typical representative of subtropical grasslands in distinct habitats such as wetlands and marshes with resident populations in areas such as Formosa Province, Argentina. Some interesting interspecific comparisons include southern capuchinos, a geographically intermediate species (Black-and-tawny Seedeater [*Sporophila nigrorufa*]) and, particularly, tropical capuchinos: Ruddy-breasted Seedeater (*S. minuta*) and Chestnut-bellied Seedeater (*S. castaneiventris*).

ACKNOWLEDGMENTS

We thank Jay J. Rotella (Montana State University) for the enormous amount of help with processing the data and interpreting the results in program MARK and R code. Cristiano E. Rovedder, Márcio Repenning and Mariana L. Gonçalves for their assistance with field work. Adrian S. Di Giacomo (Universidad de Buenos Aires) for help with nest survival calculations. Márcio Borges-Martins (Universidade Federal do Rio Grande do Sul) for snake identification. Joaquim and Nair, Antônio and Ivonete for logistic support and permission to work in the study areas. Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES for the scholarship for IF.

Funding was provided by Fundação Grupo Boticário de Proteção à Natureza (project no. 0795-20082) and Neotropical Grassland Conservancy.

LITERATURE CITED

Aguilar, T. M., R. I. Dias, A. C. Oliveira, and R. H. Macedo. 2008. Nest-site selection by Blue-black Grassquits in a Neotropical savanna: do choices influence nest success? *Journal of Field Ornithology* 79:24-31.

Ainley, D. G., and R. P. Schlatter. 1972. Chick raising ability in Adelie Penguins. *The Auk* 89:559-566.

Auer, S. K., R. D. Bassar, J. J. Fontaine, and T. E. Martin. 2007. Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. *The Condor* 109:321-333.

Ayres, M., M. Ayres Jr., D. L. Ayres, and A. A. Santos. 2007. *BioEstat*. Version 5.0. USP, São Paulo, Brazil.

Berger-Tal, R., O. Berger-Tal, and K. Munro. 2010. Nest desertion by Grey Fantails during nest building in response to perceived predation risk. *Journal of Field Ornithology* 81:151-154.

Bolker, B. M. 2011. *Ecological models and data in R*. Princeton University Press, New Jersey.

Brawn, J. D., G. Angehr, Nicole Davros, W. D. Robinson, J. N. Styrsky, and C. E. Tarwater. 2011. Sources of variation in the nesting success of understory tropical birds. *Journal of Avian Biology* 42:61-68.

- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2 ed. Springer-Verlag, New York.
- Davis, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *The Condor* 107:605-616.
- Di Giacomo, A. G. 2005. Aves de la Reserva El Bagual, p. 201-465. In A. G. Di Giacomo and S. F. Krapovickas [eds.], *Historia natural y paisaje de la Reserva El Bagual*. Temas de Naturaleza y Conservación 4.
- Di Giacomo, A. S., A. G. Di Giacomo, and Juan C. Reboreda. 2011. Male and female reproductive success in a threatened polygynous species: the Strange-tailed Tyrant, *Alectrurus risora*. *The Condor* 113:619-628.
- Dinsmore, S. J.; White, G. C. e Knopf, F. L. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83: 3476-3488.
- Dodge, H. R., and T. H. G. Aitken. 1968. *Philornis* flies from Trinidad (Diptera: Muscidae). *Journal of Kansas Entomological Society* 41:134-154.
- Duca, C., and M. A. Marini. 2005. Temporal variation in the reproductive success of *Cacicus haemorrhous* (Linnaeus) (Aves, Icterinae) in an Atlantic Forest reserve in Southeast Brazil. 22(2):484-489.
- Facchinetti, C., A. G. Di Giacomo, and J. C. Reboreda. 2008. Parental care in Tawny-bellied (*Sporophila hypoxantha*) and Rusty-collared (*S. collaris*) Seedeaters. *The Wilson Journal of Ornithology* 120:879-883.
- Fontaine, J. J., and T. E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* 9:428-434.

Fontaine, J. J., M. Martel, H. M. Markland, A. M. Niklison, K. L. Decker, and T. E. Martin. 2007. Testing ecological and behavioral correlates of nest predation. *Oikos* 116:1887-1894.

França, L. F., and M. A. Marini. 2009. Low and variable reproductive success of a neotropical tyrant-flycatcher, Chapada Flycatcher (*Suiriri islerorum*). *Emu* 109:265-269.

França, L. F., N. O. M. Sousa, L. R. dos Santos, C. Duca, D. T. Gressler, F. J. A. Borges, L. E. Lopes, L. T. Manica, L. V. Paiva, R. C. S. de Medeiros, and M. A. Marini. 2009. Passeriformes: nest predators and prey in a Neotropical Savannah in Central Brazil. *Zoologia* 26:799-802.

Francisco, M. R. 2006. Breeding biology of the Double-collared Seedeater (*Sporophila caerulescens*). *The Wilson Journal of Ornithology* 118:85-90.

Franz, I., and C. S. Fontana. 2012. Breeding biology of the Tawny-bellied Seedeater (*Sporophila hypoxantha*) in south Brazilian upland grasslands. Chapter 1 - this study.

Grant, T. A., T. L. Shaffer, E. M. Madden, and P. J. Pietz. 2005. Time-specific variation in passerine nest survival: new insights into old questions. *The Auk* 122:661-672.

Gressler, D. T. 2007. Biologia e sucesso reprodutivo de *Sicalis citrina* Pelzeln, 1870 (Aves: Emberizidae) no Distrito Federal. MSc. dissertation, Universidade de Brasília, Brasília, DF, Brazil.

Gross, A. O. 1952. Nesting of Hick's Seedeater at Barro Colorado island, Canal Zone. *The Auk* 69:433-446.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield Method of estimating nest success: a model, estimators and simulation results. *Wilson Bulletin* 93:42-53.

- Iganci, J. R. V., G. Heiden, S. T. S. Miotto, and R. T. Pennington. 2011. Campos de Cima da Serra: the Brazilian Subtropical Highland Grasslands show an unexpected level of plant endemism. *Botanical Journal of the Linnean Society* 167:378-393.
- Kasper, C. B., M. L. da Fontoura-Rodrigues, G. N. Cavalcanti, T. R. O. de Freitas, F. H. G. Rodrigues, T. G. de Oliveira, and E. Eizirik. 2009. Recent advances in the knowledge of Molina's Hog-nosed Skunk *Conepatus chinga* and Striped Hog-nosed Skunk *C. semistriatus* in South America. *Small Carnivore Conservation* 41:25-28.
- Lack, D. 1947. The significance of clutch size. Parts I and II. *Ibis* 89:302-352.
- Lopes, L. E., and M. A. Marini. 2005. Low reproductive success of Campo Suiriri (*Suiriri affinis*) and Chapada Flycatcher (*S. islerorum*) in the central Brazilian Cerrado. *Bird Conservation International* 15:337-346.
- Löwenberg-Neto, P. 2008. The structure of the parasite-host interactions between *Philornis* (Diptera: Muscidae) and neotropical birds. *Journal of Tropical Ecology* 24:575-580.
- Marchant, S. 1960. The breeding of some S.W. Ecuadorian birds. *Ibis* 102:584-599.
- Martin, T. E. 1992. Interaction of nest predation and food limitation in reproductive strategies. *Current Ornithology* 9:163-197.
- Martin, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141:897-913.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. *Ecological Monographs* 65:101-127.

- Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? *Journal of Avian Biology* 27:263-272.
- Martin, T. E. 2004. Avian life-history evolution has an eminent past: dos it have a bright future? *The Auk* 121:289-301.
- Martin, T. E. 2011. The cost of fear. *Science* 334:1353-1354.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507-519.
- Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *The Condor* 90:51-57.
- Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, and J. J. Fontaine. 2000a. Parental care and clutch sizes in North and South American birds. *Science* 287:1482-1485.
- Martin, T. E., J. Scott, and C. Menge. 2000b. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society B (Biological Sciences)*. 267:2287-2293.
- Mason, P. 1985. The nesting biology of some passerines of Buenos Aires, Argentina. *Ornithological Monographs* 36.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-467.
- Moreau, R. 1944. Clutch size: a comparative study, with reference to African birds. *Ibis* 86:286-347.

- Muchai, M., and M. A. du Plessis. 2005. Nest predation of grassland bird species increases with parental activity at the nest. *Journal of Avian Biology* 36:110-116.
- Oliveira, L. S., L. M. S. Sousa, P. V. Davanço, and M. R. Francisco. 2010. Breeding behavior of the Lined Seedeater (*Sporophila lineola*) in southeastern Brazil. *Ornitología Neotropical* 21:251-261.
- Oniki, Y. 1979. Is Nesting Success of Birds Low in the Tropics? *Biotropica* 11:60-69.
- Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64:71-87.
- R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org/>> (16 December 2011).
- Rabuffetti, F. L., and J. C. Reboresda. 2007. Early infestation by bot flies (*Philornis seguyi*) decreases chick survival and nesting success in Chalk-browed Mockingbirds (*Mimus saturninus*). *The Auk* 124:898-906.
- Renfrew, R. B., and C. A. Ribic. 2003. Grassland passerine nest predators near pasture edges identified on videotape. *The Auk* 120:371-383.
- Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9:1-47.
- Robinson, W. D., M. Hau, K. C. Klasing, M. Wikelski, J. D. Brawn, S. H. Austin, C. E. Tarwater, and R. E. Ricklefs. 2010. Diversification of life histories in New World birds. *The Auk* 127:253-262.

Roper, J. J. 1992. Nest predation experiments with quail eggs: too much to swallow? *Oikos* 65:528-530.

Roper, J. J. 2000. Experimental analysis of nest-sites and nest predation for a neotropical bird: stuck between a rock and a hard place. *Ararajuba* 8:85-91.

Roper, J. J., and R. R. 1997. A test of the Skutch Hypothesis: does activity at nests increase predation risk? *Journal of Avian Biology* 28:111-116.

Roper, J. J., K. A. Sullivan, and R. E. Ricklefs. 2010. Avoid nest predation when predation rates are low, and other lessons: testing the tropical-temperate nest predation paradigm. *Oikos* 119:719-729.

Rotella, J. 2011. Nest survival models (Chapter 17), p. 17/2-17/21. *In* E. Cooch and G. White [eds.], Program MARK: a gentle introduction. 11 ed. <<http://www.phidot.org/software/mark/index.html>> (25 January 2012).

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. 2 ed. Chapman, London and Macmillan, New York.

Segura, L. L., and J. C. Reboreda. 2011. Botfly parasitism effects on nestling growth and mortality of Red-crested Cardinals. *The Wilson Journal of Ornithology* 123:107-115.

Silva, J. M. C. 1999. Seasonal movements and conservation of seedeaters of the genus *Sporophila* in South America. *Studies in Avian Biology* 19.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91:430-455.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. *Ornithological Monographs* 36:575-594.

Slagsvold, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* 54:159-169.

Stutchbury, B. J. M., and E. S. Morton. 2001. Behavioral ecology of tropical birds. Academic Press, San Diego.

Stutchbury, B. J. M., and E. S. Morton. 2008. Recent advances in the behavioral ecology of tropical birds. *The Wilson Journal of Ornithology* 120:26-37.

Thompson III, F. R., and D. E. Burhans. 2003. Predation of Songbird Nests Differs by Predator and between Field and Forest Habitats. *The Journal of Wildlife Management* 67:408-416.

Verhulst, S., J. H. van Balen, and T. M. Tinbergen. 1995. Seasonal decline in reproductive success of the Great Tit: variation in time or quality? *Ecology* 76:2392-2403.

Weatherhead, P. J., and G. Blouin-Demers. 2004. Understanding avian nest predation: why ornithologists should study snakes. *Journal of Avian Biology* 35:185-190.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120-139.

Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panamá. *Ecological Monographs* 44:153-169.

Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy. 2011. Perceived predation risk reduces the number of offspring songbirds produce per year. *Science* 334:1398-1401.

FIGURE LEGEND

FIGURE 1. Daily survival rates (DSR) of nests of the Tawny-bellied Seedeaters (*Sporophila hypoxanta*) during three breeding seasons (2007-2010), according to nest age (a; through the 21-day nesting cycle: 12 of incubation and 9 of nestling) and day of nesting season (b; respecting a linear time trend), calculated with program MARK by means of candidate models that include each predictor variable.

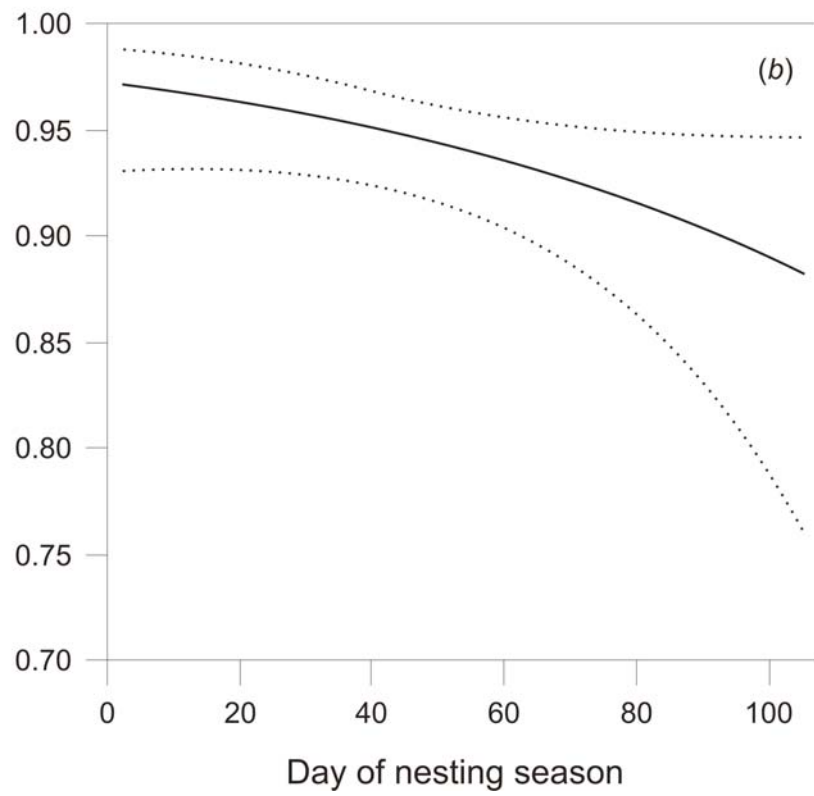
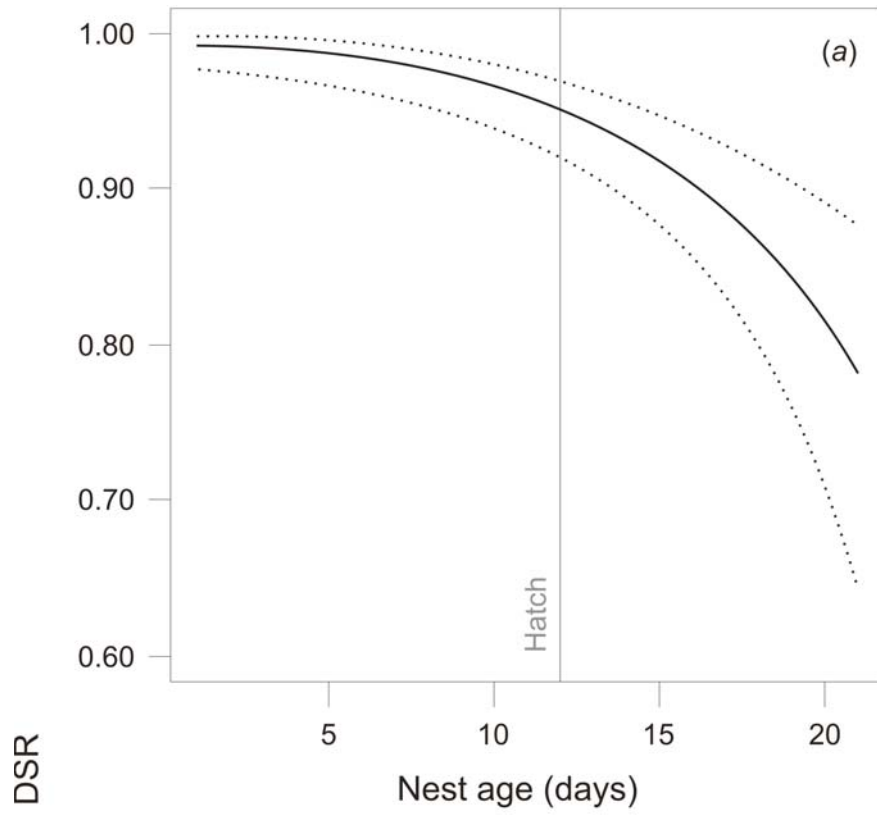


TABLE 1. Support for candidate models of daily survival for nests of Tawny-bellied Seedeaters (*Sporophila hypoxantha*) in south Brazilian grasslands, over three breeding seasons (2007-2010). Models were based on Akaike's Information Criterion corrected for small sample sizes (AIC_c). We excluded models with values less than those of the null model. See Methods for explanation of covariates.

Model	ΔAIC_c	w_i	K	Deviance
First set (time trend)				
S_T	0.00 ^a	0.49	2	110.30
S_{TT}	1.00	0.29	3	109.27
$S_{(.)}$	1.74	0.20	1	114.06
Second set (covariates)				
S_{age}	0.00 ^b	0.34	2	103.78
$S_{T+ageDay1}$	1.78	0.14	3	103.53
$S_{T+age+study\ site}$	2.19	0.11	4	101.90
$S_{T+age+nest\ concealment}$	3.51	0.05	4	103.22
$S_{T+age+nest\ height}$	3.52	0.05	4	103.23
$S_{T+age+plant\ height}$	3.75	0.05	4	103.46
$S_{T+age+plant\ cover}$	3.82	0.05	4	103.53
$S_{T+age+year}$	4.19	0.04	5	101.85
$S_{T+age+study\ site+nest\ concealment}$	4.21	0.04	5	101.88
$S_{T+age+year+study\ site}$	4.57	0.03	6	100.17
$S_{T+age+plant\ species}$	4.74	0.03	5	102.40
$S_{T+age+year+study\ site+nest\ concealment}$	6.62	0.01	7	100.15
$S_{T+age+year+plant\ species}$	7.99	0	7	101.52
S_{global}	11.59	0	11	96.74
S_T	19.27	0	2	123.05
$S_{T+study\ site}$	19.87	0	3	121.62
$S_{(.)}$	20.70	0	1	126.50

^a $AIC_c = 114.33$. ^b $AIC_c = 107.81$. ΔAIC_c = difference between AIC_c of each model and the top model; K = number of parameters; w_i = Akaike weight; T = linear time trend; TT = quadratic time trend; $(.)$ = null model. Notations follow Dinsmore et al. (2002).

CAPÍTULO 3

Nest-site selection by Tawny-bellied Seed eaters *Sporophila hypoxantha* in
south Brazilian dry grasslands

Artigo a ser submetido para publicação no periódico *Bird Conservation International*

Nest-site selection by Tawny-bellied Seed eaters *Sporophila hypoxantha* in south Brazilian dry grasslands

ISMAEL FRANZ and CARLA S. FONTANA

Running Head: Nest-site selection by Tawny-bellied Seed eaters

Author Head: I. Franz and C. S. Fontana

Summary

Sporophila seed eaters are important elements in South American grasslands, but little is known about their ecological requirements and preferred reproductive habitats. In 2008 and 2009, we conducted a study in dry grasslands in the state of Santa Catarina, southern Brazil (28°18'40"S 50°17'50"W), evaluating the floristic composition and vegetation structure in monitored breeding areas of Tawny-bellied Seed eaters (*Sporophila hypoxantha*). We used plots of 4 m² in areas of nest sites (one at the nest plant and four 10 m distant) and non-nest sites (n = 130 in each group). We measured 10 variables divided into three previously identified strata, classified according to grassland type, and counted and identified the plant species in each plot. We performed univariate (Mann-Whitney *U*-test) and multivariate analyses (Principal Coordinates Analysis and MANOVA). Nest sites had a lower % bare-ground cover, lower % low-stratum cover, higher % mid-stratum cover, lower % high-stratum cover, higher low-stratum maximum height, higher mid-stratum maximum height, lower slope, higher % low-horizontal obstruction and lower % high-horizontal obstruction. The PCoA found that Axis 1 explained 21.7% of the data variation, and Axis 2 12.8% (*P* = 0.006). Some of the plant species associated with nest sites were *Andropogon lateralis*, *Saccharum*

angustifolium and *Baccharis caprariffolia*; species associated with non-nest sites were *Eupatorium multicrenulatum*, *Escallonia megapotamica* and *Eryngium horridum*. The MANOVA revealed that the species selects certain grassland typologies within the grassland matrix. Tawny-bellied Seedeaters avoid nesting in areas with a dense high stratum (> 1 m), selecting grasslands with a dense middle stratum, abundant grass clumps and low shrubs (Asteraceae).

Introduction

Twenty years ago, Collar *et al.* (1992) warned of the near-total destruction of open grasslands in south-east Brazil, indicating that 6.3% of the world's threatened birds are grassland species. In the southern region, 25% of natural grasslands have been lost over the past 30 years due to expansion of agricultural activities (Overbeck *et al.* 2007). This loss and alteration of grassland habitats has had serious consequences for obligate grassland birds (Bencke *et al.* 2003, Bencke 2009). Similarly to occurrences in North America, several species of South American grassland breeders have suffered declines in their populations (Vickery *et al.* 1999, Askins *et al.* 2007). Prominent examples of these declines and local extinctions are the Pampas Meadowlark (*Sturnella defilippii*; Tubaro & Gabelli 1999), Strange-tailed Tyrant (*Alectrurus risora*; Di Giacomo & Di Giacomo 2004) and *Sporophila* seedeaters, which are among the most characteristic elements of the South American grassland avifauna (Silva 1999).

The poor or completely non-existent knowledge of ecological and habitat requirements of several species of South American grassland birds impede decision-making related to their conservation (Cody 1985, Collar *et al.* 1992, Vickery *et al.* 1999). *Sporophila* seedeaters, for example, inhabit grassy and shrubby areas, marshes and the forest edge (Schauensee 1952). The “capuchinos” group is composed of

obligate grassland specialists (Vickery *et al.* 1999) that breed in tall and dense grasslands (Bencke 2009), in both dry and wet habitats. The Tawny-bellied Seedeater (*Sporophila hypoxantha*) is migratory, wintering in the grasslands of the Cerrado of central Brazil (Silva 1999), and moves in October/November to breed in southern Brazil, returning in February and March (Franz & Fontana 2012a). This seedeater reproduces in dry shrubby grasslands and in marshes or wet grasslands (Areta & Repenning 2011), but no study has evaluated in detail its selection of nest sites and other habitat requirements of the species.

David Lack highlighted the role of habitat selection in speciation from congeneric taxa and adaptive radiation (Lack 1940), which occurred rapidly in the group of capuchinos (Lijtmaer *et al.* 2004, Campagna *et al.* 2009, Campagna *et al.* 2011). Traits related to ecology, especially the preferred habitats, have been widely used as tools for understanding the evolutionary relationships and identity of members of the genus *Sporophila*, particularly among the capuchinos (see Areta 2008, Repenning *et al.* 2010, Areta & Repenning 2011, Areta *et al.* 2011).

The aim of this study was to describe and characterise in detail the habitat at sites selected for nesting by Tawny-bellied Seedeaters, considering aspects of the composition, density and structure of vegetation. This information can serve as a basis for defining conservation and management measures to mitigate possible harm to the species in southern Brazilian grasslands.

Methods

We conducted the study in an area of hilly dry grasslands along the Lava-Tudo River, cities of São Joaquim and Lages, Santa Catarina state, southern Brazil (central point: 28°18'40"S 50°17'50"W). We covered a contiguous area of approximately 400 ha,

with altitudes ranging from 800 to 1,000 m. The vegetation is composed of a wide diversity of shrubs and herbs (Asteraceae), prominently *Vernonia* spp., *Eupatorium* spp. and *Baccharis* spp., grasses (Poaceae) such as *Paspalum* spp., *Sorghastrum* spp., *Andropogon* spp. and *Piptochaetium* spp., "caraguatás" (*Eryngium horridum*), and scattered small trees. A detailed description of the study site was provided by Franz & Fontana (2012a, b).

Nests of Tawny-bellied Seedeaters were found and monitored in three reproductive seasons from November 2007 to March 2010 (see Franz & Fontana 2012a). In March 2008 and 2009, at the end of the breeding season, we conducted expeditions to assess floristic composition and vegetation structure in breeding areas of the species. We use plots of 4 m² (2 x 2 m) as the sample unit, marked on the ground with a rope. For 26 of 69 nests found, we established a central plot and four satellites, 10 m distant from the center in each of the cardinal directions (Figure 1). The central plot of each set, which had its center at the support plant where the nest was built, was considered the nest site, and the other four, the nest patch (*sensu* Jones & Robertson 2001). For each set of five plots in the area used for nesting, we evaluated five control plots, randomly marked in the same grassland matrix, but in areas that were not used for nesting in each breeding season assessed (often close neighbors of nest sites). These control plots did not include different environments of the matrix (non-grassland), were within a distance of <100 m from the limits of the nearest occupied territory, and were within the sampling area of ~400 ha. Thus, the same number of plots for occupied and unoccupied areas for nesting were sampled (n = 130 in each group), so that these environments represented used *vs.* not used for nesting by the seedeaters.

In each plot (n = 260), we measured variables of grassland structure and floristic composition. We distinguished three vertical strata of the vegetation, with boundaries

clearly seen in the plots, namely: low, the lower part, which consisted of grasses, small herbs and creepers, not exceeding 30 cm high; mid, the layer with a high density of shrubs and grass clumps, usually not more than 1 m high; and high, the emerging stratum, composed of high grass stems (e.g., *Saccharum* spp.), sawgrass stems (*Eryngium horridum*) and sparse trees, rich in perches, sometimes exceeding 2 m in height. We measured % bare ground cover, % low-stratum cover, % mid-stratum cover and % high-stratum cover. The method for estimating the coverage was adapted from the Daubenmire Frame (Daubenmire 1959; "canopy-coverage method"), which assesses the occupancy of each species in a vertical projection of a predetermined area at intervals of defined percentage. We estimated the coverage by noting how much of each plot of 4 m² was occupied by each band in vertical projection, but with a continuous value (not intervals), with zero indicating absent and 100% indicating that this type of cover extended over the entire plot. The height of each stratum, low, mid and high, was measured with a pole of known length. We estimated lateral/horizontal vegetation cover with a coloured plate 100 cm high by 80 cm wide, set vertically from the ground on the line on one side of the plot. On the opposite side (2 m distant), an observer read from a viewpoint of ~80 cm from the ground (down observer), the occupation by vegetation in the lower part (up to 50 cm) and the high part (higher than 50 to 100 cm) of the plate, scored as zero (without visual obstruction) and 100% (completely blocked visually, with the plate fully obstructed). We adapted this method from the Robel Pole (Robel *et al.* 1970), which uses a pole rather than a plate. The slope in each plot was measured with a clinometer, 5 m from the plot, perpendicular to the hill face occupied. In addition to these ten numeric variables, we classified the plots according to each of the three types of grasslands found in the region: (1) dry grasslands, the most common type, marked by a rich diversity of species of herbs, herbaceous plants, shrubs, grasses and

sparse small trees; (2) rocky grasslands, characterised by shallow soil with basalt outcrops and lower vegetation density; and (3) wet grasslands, consisting of patches of wet grasslands near streams, composed of plants characteristic of wetlands. The floristic composition was assessed by counting the number of individuals of each species of plant present in the plots. When it was not possible to determine the species in the field, herbarium specimens were prepared to send to appropriate specialists for identification. We considered individual vegetative parts of plants, in some cases (e.g., grasses and *Eryngium* spp.) counting the number of clumps and stems, which are structurally distinct, separately. All variables were measured in plots with a nest (nest sites and nest patches) and no nest. The same observer evaluated each variable throughout the study.

We analysed the nest-site and nest-patch plots together (five plots = nest area) and separately (variation within the territory) and compared them with non-nest plots. To determine the degree of simple association between the numeric variables related to vegetation structure at nest and non-nest sites, we used the nonparametric tests of Mann-Whitney (or Wilcoxon-Mann-Whitney *U*-test or Wilcoxon rank-sum test), using the BioEstat 5.0 software (Ayres *et al.* 2007). The same test was used to compare portions of the nest site to the nest patch. We considered *P* values <0.05 as significant. With the variables of floristic composition and abundance, we performed a multivariate analysis using the software Multiv v.2.4 (Pillar 2006). Initially, we added the numbers of individuals of each species of plant in each set of five plots. we excluded from the analysis, plants with $n < 30$ individuals sampled in all plots, except for small trees, which are scarce in the grasslands but have an important role in vegetation structure because of their size. Then, the data of the original matrix (52 sampling units [26 nest and 26 non-nest] and 27 variables [plant species]) were submitted to vectorial transformation by double adjustment (deviations from expected values via marginal

totals). The measure of similarity between the sampling units used was Euclidean Distance. The values were plotted in an ordination by Principal Coordinates Analysis (PCoA), considering up to three axes of ordination, run with 1000 iterations of bootstrap resampling. Finally, to test the significance of these treatments of floristic-composition data, we conducted a MANOVA using randomisation testing, according to the method described by Orlóci & Pillar (1996). Means are presented as value \pm standard deviation.

Results

Of the 130 plots of nest sites evaluated, 63 (48%) were in dry grasslands and 67 (52%) in rocky grasslands; and of the 130 plots of non-nest sites, 34 (26%) were in dry grassland, 91 (70%) in rocky grassland, and 5 (4%) in wet grassland. There was no significant difference (Table 1) of the variables for habitat structure between the central portions (nest site) and satellites (nest patch), so that each set of five plots in the area (nest site + nest patch) could be grouped to form the samples of real nest sites. Among non-nest sites and nest sites, univariate analysis found nine of 10 structural variables with significant differences (Table 2). Of these, five variables showed a strong difference ($P < 0.0001$): % bare-ground cover (lower in nest sites), % mid-stratum cover (higher in nest sites), % high-stratum cover (lower in nest sites), mid-stratum maximum height (higher in nest sites) and slope (lower at nest sites). Also, % low-stratum cover was lower at nest sites, low-stratum maximum height was higher, % low-horizontal obstruction was higher, and % high-horizontal obstruction was lower at nest sites. The distinction of strata (low-grassy, mid-shrubby and high-emergent) to collect data on the structure of grassland vegetation has proven effective in identifying variations on a finer-scale habitat.

We counted 9,137 plants of 91 species in the 260 plots analysed. Of the 27 species with $n > 30$ individuals (including small trees) used in the analysis ($n = 8,868$), we counted 5,274 (59%) individuals in portions of nest sites, and 3594 (41%) in portions of non-nest sites (Table 3). In nest sites, the most abundant species were *Andropogon lateralis* ($n = 1,223$ individuals), *A. virgatus* ($n = 745$), *Saccharum angustifolium* ($n = 431$), *Vernonia chamaedrys* ($n = 387$), *Baccharis caprariifolia* ($n = 373$) and *Eupatorium polystachyum* ($n = 334$). In non-nest sites, *A. lateralis* ($n = 473$) and *A. virgatus* ($n = 455$) were also most abundant, followed by *Eryngium horridum* ($n = 411$), *V. chamaedrys* ($n = 287$), *Eupatorium multicrenulatum* ($n = 245$) and *E. polystachyum* ($n = 218$).

The Principal Coordinates Analysis (PCoA) found that ordination Axis 1 explained 21.7% of the variation in the data, and ordination Axis 2 explained 12.8% (Figure 2). The randomisation test of the similarity measure (Euclidean Distance) showed that nest-site and non-nest-site groups differed significantly, with P value = 0.006. Original descriptors with the highest correlation coefficients ($> 50\%$) on Axis 1 were *Andropogon lateralis* (-0.86), *A. virgatus* (0.69), *Baccharis cognata* (0.67), *Schizachyrium* sp. (0.64), *Eryngium elegans* (0.62) and *Saccharum angustifolium* (0.51). On Axis 2, these were *Eupatorium multicrenulatum* (0.73), *Baccharis caprariifolia* (-0.67), *Eryngium horridum* (0.57), *Escallonia megapotamica* (0.57) and *Eupatorium laevigatum* (0.56).

Therefore, the plants characteristic of nest sites are the grasses *Andropogon lateralis*, *A. virgatus* and *Saccharum angustifolium*, which were part of the structure of the mid-stratum with its clumps, and *Eryngium elegans*, a small sawgrass, some herbs and shrubs of the genus *Baccharis*, especially *B. caprariifolia*, and the shrubs *Vernonia chamaedrys* and *Eupatorium polystachyum*, which are abundant in dry grasslands. In

the plots of non-nest sites, the most prominent species were scattered small trees, especially *Escallonia megapotamica*, and the caraguatá *Eryngium horridum*, an abundant and visible component in the landscape; and the open shrub *Eupatorium multicrenulatum*, which occurs on steep rocky grasslands.

Discussion

Tawny-bellied Seedeaters avoid nesting in areas marked by a greater density of the upper stratum (vegetation above 1 m in height), selecting the portions where the grassland has a dense middle stratum, resulting from the greater abundance of grass clumps and low shrubs (<1 m). Clumps of *Andropogon* spp. and *Saccharum* spp. as well as the shrubs *Vernonia chamaedrys*, *Baccharis caprariifolia* and *Eupatorium polystachyum* (the plants most often used as nest support; Franz & Fontana 2012a) are very common elements in the study area. Even though they also occur in non-nest sites (it is difficult to find areas without these species in the region), in nest sites they were especially dense. The dry shrubby grasslands of this region could be called "*Vernonia/Eupatorium* grasslands", interspersed with patches of "guamirim (*Escallonia megapotamica*) grasslands", a small tree typical of the region, which is clearly avoided by *Sporophila hypoxantha*. In a more widely recognised classification, these grassland types chosen by the capuchinos consist of so-called "campo limpo" (= open grasslands without trees), and secondarily "campo sujo" (grasslands with scattered small trees). However, these are not completely natural types, because their dynamics have been affected by management activities such as burning and grazing, and in some areas are mixed. The species also avoids nesting where the density of "sawgrasses/eryngos" such as the rosette species called caraguatá (*Eryngium horridum*) is high, since the presence of sawgrasses reduces the occurrence of the preferred shrubs.

Non-nest sites occurred mainly in rocky grasslands (70%), even though dry grasslands were the most common type in the area. Rocky grasslands are characterised by a steeper slope and lower floristic diversity, where *Eupatorium multicrorenulatum* is prominent. Areas with these characteristics, associated with the variable percentage of bare ground cover (always higher in rocky grasslands), were avoided by Tawny-bellied Seedeaters. Half of the nest-site plots were in rocky grasslands, but in parts that were clearly more similar to the dry grasslands. The shrubs selected by this seedeater rarely occur in rocky grasslands, as well as in areas with a high density of grass clumps, so that this type of grassland probably provides less camouflage for the nests and fewer support plants for nests. The sites chosen for nesting were therefore concentrated in the flatter areas of the hills, where, possibly because of deeper soil, the plant density/biomass and species richness are higher. In the study area, steep areas with rocky grasslands and high densities of *E. megapotamica* are commonly used as a nest site by the congeneric Plumbeous Seedeater (*Sporophila plumbea*; I. Franz pers. obs.), indicating probable spatial segregation. Segregation between sympatric species by differences in vegetation structure is common among birds of grassland and open habitats (Cody 1985). In *Sporophila* seedeaters, habitat segregation is perhaps the most important isolating barrier (Sick 1967).

Tawny-bellied Seedeaters are known to nest both in dry and wet grasslands, but are more commonly associated with wet sites (Ridgely & Tudor 1989, Belton 1994, Sick 1997, Azpiroz 2001, Bencke *et al.* 2003). On a macro scale, the species prefers to breed in dry grasslands with shrubs rather than in marshes or wet grasslands (Areta & Repenning 2011). According to these authors, the preferred breeding habitat varies geographically, congruent with the five “regiolects” known, and this differentiation may have been favored by the wide distribution of dry shrubby grasslands. In this study, as

seen, we confirmed the dependence of the species (“southeastern Brazil regiolect”) on dry grasslands rich in shrubs. In the Reserva El Bagual, Formosa Province, Argentina, the species nests in two types of grasslands, tall grasslands dominated by *Imperata brasiliensis* and *Elionurus muticus* or *Andropogon lateralis*, and low wetlands of *Paspalum intermedium* and *Sorghastrum pellitum* (Di Giacomo 2005). Ninety percent of the nests found by Di Giacomo were of the first type, which may indicate a preference for dense dry grasslands. Another capuchino, the Black-bellied Seedeater (*Sporophila melanogaster*), which reproduces only in southern Brazil, showed a similar trend when selecting nest sites with a dense mid-stratum, in both dry grasslands and wetlands (Rovedder 2011), but apparently preferred the latter (Repenning *et al.* 2010). In the study area, this sympatric species occurs in smaller numbers than *S. hypoxantha* and nests mainly in patches of wet grasslands (I. Franz pers. obs.). Marsh Seedeaters (*S. palustris*) reproduce exclusively in marshy or wet grassland habitats, while Chestnut Seedeaters (*S. cinnamomea*) use preferably “undulating” grasslands (grasslands on dry ridges, valleys and slopes), also marsh or wet grasslands and Caraguatal-Cardal grasslands (dry grasslands dominated by *Eryngium horridum* and *Cardus* spp.), according to Areta (2008). The latter is the preferred habitat of the Dark-throated Seedeater (*S. ruficollis*), which also breeds in depressed Pampas grasslands, “undulating” grasslands, and annual crops (Areta *et al.* 2011).

Since males of the species immigrate before the females and soon defend well-established territories (Franz & Fontana 2012a, b), the vegetation types that later correspond to the nest patch (the broader territory area surrounding the nest) are selected only by the males. Immigrant females select males based on, among other factors apparently, the quality of nest sites (Franz & Fontana 2012b), and are responsible for choosing the area closest to the nest (nest site itself) and the support

plant. Thus, although this subject has not yet been investigated and tested, it seems that nest-site selection is an important attribute of sexual selection in this and probably other species of capuchinos (see Introduction).

In southern Brazil, one of the most important economic activities conducted in areas of natural grasslands is livestock grazing (Nabinger *et al.* 2000). The intensity of grazing and associated management practices (use of fire) directly affect the grassland dynamics, and therefore should be considered because they influence the reproduction of grassland birds. According to Behling & Pillar (2007), under low grazing intensity, grassland environments eventually come to be dominated by tall grasses (e.g., *Andropogon* spp. and *Schizachyrium* spp.) together with shrubs such as *Vernonia* spp. and *Baccharis* spp. (Asteraceae), among others. As seen here, these plants are locally important for the breeding of Tawny-bellied Seed eaters, suggesting that low-intensity grazing can be beneficial to the species. Regarding the use of fire to control the development and renovation of pasture, it seems that this activity must affect the species, since, for example, *Baccharis* spp., important shrubs in the choice of nesting sites, thrive in the absence of burning for extended periods (Müller *et al.* 2007); while a plant that is more abundant in non-nest sites, *Eryngium horridum*, is associated with disturbances in the pastures, increasing its reproductive capacity and quantity after burning (Fidelis *et al.* 2008). Franz & Fontana (2012b) found that cattle trampling and burning were responsible for 9% of unsuccessful nests in the same area. Considering that with total exclusion of grazing and burning, the *Araucaria angustifolia* forest tends to expand over the grassland (Oliveira & Pillar 2006), moderate livestock grazing could provide ideal conditions for the capuchinos and other grassland species. Intensive agriculture is not tolerated by these species, according to Filloy Bellocq (2006). The authors found that *Sporophila hypoxantha*, as well as another capuchino, the Dark-

throated Seedeater, were unable to adapt to increases in agricultural lands by 20 and 60%, respectively. Overgrazing negatively affects capuchinos, but moderate grazing appears to be tolerated and is thus a less harmful alternative land use than agriculture or forestry, in the opinion of Areta (2008).

Adding the available knowledge about the breeding biology (Di Giacomo 2005, Facchinetti *et al.* 2008, Franz & Fontana 2012a) to the data from the present study, we conclude that the Tawny-bellied Seedeater depends on dry or wet grasslands rich in low shrubs of the family Asteraceae to breed, in addition to a high density of grasses. Although it is associated with several open habitats, more-detailed analysis reveals that the species selects certain grassland typologies within the matrix. Initiatives aimed at the conservation of this species, for example in the form of establishing protected areas, should therefore consider management techniques that favor the perpetuation of shrubby grasslands.

Acknowledgements

We thank Ilsi I. Boldrini and his team (Departamento de Botânica, UFRGS) for identifying hundreds of plant species. André de Mendonça Lima (Departamento de Ecologia, UFRGS) for help with data analysis in Multiv. The Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES for providing funding for IF. The Fundação Grupo Boticário de Proteção à Natureza (project no. 0795-20082) and Neotropical Grassland Conservancy for funding and support of the project. Cristiano E. Rovedder, Márcio Repenning and Mariana L. Gonçalves for their untiring assistance in the field and friendship. Joaquim and Nair, Antônio and Ivonete for logistical support and permission to work in their particular areas.

References

- Arete, J. I. (2008) Entre Ríos Seedeater (*Sporophila zelichi*): a species that never was. *J. Field. Ornithol.* 79(4): 352-363.
- Arete, J. I. & Repenning, M. (2011) Systematics of the Tawny-bellied Seedeater (*Sporophila hypoxantha*). I. Geographic variation, ecology, and evolution of vocalizations. *Condor* 113(3): 664-677.
- Arete, J. I., Noriega, J. I., Pagano, L. & Roesler, I. (2011) Unraveling the ecological radiation of the capuchinos: systematics of Dark-throated Seedeater *Sporophila ruficollis* and description of a new dark-collared form. *Bull. Brit. Orn. Club* 131: 4-23.
- Askins, R. A., Chávez-Ramírez, F., Dale, B. c., Haas, C. A., Herkert, J. R., Knopf, F. L. & Vickery, P. D. (2007) Conservation of Grassland Birds in North America: Understanding Ecological Processes in Different Regions: "Report of the AOU Committee on Conservation". *Ornithol. Monogr.* 64: 1-46.
- Ayres, M., Ayres Jr., M., Ayres, D. L. & Santos, A. A. (2007) *BioEstat*. Version 5.0. São Paulo, Brazil: USP.
- Azpiroz, A. B. (2001) *Aves del Uruguay: Lista e introduccion a su biologia y conservacion*. Montevideo, Uruguay: GUPECA- Aves Uruguay.
- Behling, H. & Pillar, V. D. (2007) Late Quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern *Araucaria* forest and grassland ecosystems. *Phil. Trans. R. Soc. B* 362: 243-251.
- Belton, W. (1994) *Aves do Rio Grande do Sul: distribuição e biologia*. São Leopoldo, Brazil: Universidade do Vale do Rio dos Sinos.

- Bencke, G. A. (2009) Diversidade e conservação da fauna dos Campos do Sul do Brasil. Pp. 101-121 in V. D. Pillar, S. C. Müller, Z. M. S. Castilhos & A. V. A. Jacques, eds. *Campos sulinos: conservação e uso sustentável da biodiversidade*. Brasília, Brazil: MMA.
- Bencke, G. A., Fontana, C. S., Dias, R. A., Maurício, G. N. & Mähler Jr., J. K. F. (2003) Aves. Pp. 189-479 in C. S. Fontana, G. A. Bencke & R. E. Reis, eds. *Livro vermelho da fauna ameaçada de extinção no Rio Grande do Sul*. Porto Alegre, Brazil: EDIPUCRS.
- Campagna, L., Lijtmaer, D. A., Kerr, K. C. R., Barreira, A. S., Hebert, P. D. N., Loughheed, C. S. & Tubaro, P. L. (2009) DNA barcodes provide new evidence of a recent radiation in the genus *Sporophila* (Aves: Passeriformes). *Mol. Ecol. Resour.* 10(3): 449-458.
- Campagna, L., Benites, P., Loughheed, S. C., Lijtmaer, D. A., Di Giacomo, A. S., Eaton, M. D. & Tubaro, P. L. (2011) Rapid phenotypic evolution during incipient speciation in a continental avian radiation. *Proc. R. Soc. B*. Available online before print.
- Cody, M. L. (1985) *Habitat selection in birds*. California, USA: Academic Press.
- Collar, N. J., Gonzaga, L. P., Krabbe, N., Madrono Nieto, A., Naranjo, L. G., Parker III, T. A. & Wege, D. C. (1992) *Threatened birds of the Americas*. Washington DC, USA: Smithsonian Institution Press.
- Daubenmire, R. (1959) A canopy-coverage method of vegetational analysis. *Northwest Sci.* 33: 43-64.
- Di Giacomo, A. G. (2005) Aves de la Reserva El Bagual. Pp 201-465 in A. G. Di Giacomo & S. F. Krapovickas, eds. *Historia natural y paisaje de la Reserva El*

- Bagual*. Temas de Naturaleza y Conservación 4. Buenos Aires, Argentina: Asociación Ornitológica del Plata.
- Di Giacomo, A. S. & Di Giacomo, A. G. (2004) Extinción, historia natural y conservación de las poblaciones del Yetapá de Collar (*Alectrurus risora*) en la Argentina. *Ornitol. Neotrop.* 115: 145-157.
- Facchinetti, C., Di Giacomo, A. G. & Reboresda, J. C. (2008) Parental care in Tawny-bellied (*Sporophila hypoxantha*) and Rusty-collared (*S. collaris*) Seedeaters. *Wilson J. Orn.* 120(4): 879-883.
- Fidelis, A., Overbeck, G. E., Pillar, V. D. & Pfadenhauer, J. (2008) Effects of disturbance on population biology of the rosette species *Eryngium horridum* Malme in grasslands in southern Brazil. *Plant Ecol.* 195: 55-67.
- Filloy, J. & Bellocq, I. (2006) Spatial variations in the abundance of *Sporophila* seedeaters in the southern Neotropics: contrasting the effects of agricultural development and geographical position. *Biodiversity Conserv.* 15: 3329-3340.
- Franz, I. & Fontana, C. S. (2012a) Breeding biology of the Tawny-bellied Seedeater (*Sporophila hypoxantha*) in south Brazilian upland grasslands. *Chapter 1* - this study.
- Franz, I. & Fontana, C. S. (2012b) Reproductive success of Tawny-bellied Seedeaters (*Sporophila hypoxantha*) in Brazilian subtropical grasslands: strong influence of time-specific factors on nest survival. *Chapter 2* - this study.
- Jones, J. & Robertson, R. J. (2001) Territory and nest-site selection of Cerulean Warblers in eastern Ontario. *Auk* 118(3): 727-735.
- Lack, D. (1940) Habitat selection and speciation in birds. *Br. Birds* 34: 80-84.

- Lijtmaer, D. A., Sharpe, N. M. M., Tubaro, P. L. & Loughheed, S. C. (2004) Molecular phylogenetics and diversification of the genus *Sporophila* (Aves: Passeriformes). *Mol. Phylogenet. Evol.* 33(3): 562-579.
- Müller, S. C., Overbeck, G. E., Pfadenhauer, J. & Pillar, V. D. (2007) Plant functional types of woody species related to fire disturbance in forest-grassland ecotones. *Plant Ecol.* 189: 1-14.
- Nabinger, C., Moraes, A. & Maraschin, G. E. (2000) Campos in southern Brazil. Pp. 355-376 in G. Lemaire, J. G. Hodgson, A. Moraes & G. E. Maraschin, eds. *Grasslands ecophysiology and grazing ecology*. Wallingford, UK: CABI Publishing.
- Oliveira, J. M. & Pillar, V. D. (2004) Vegetation dynamics on mosaics of Campos and Araucaria forest between 1974 and 1999 in southern Brazil. *Community Ecol.* 5(2): 197-202.
- Overbeck, G. E., Müller, S. C., Fidelis, A., Pfadenhauer, J., Pillar, V. D., Blanco, C. C., Boldrini, I. I., Both, R. & Forneck, E. D. (2007) Brazil's neglected biome: The South Brazilian Campos. *Perspect. Plant Ecol.* 9: 101-116.
- Pillar, V. D. (2006) *MULTIV: Multivariate exploratory analysis, randomizing testing and bootstrapping resampling*, users guide v. 2.4. Porto Alegre, Brazil: Universidade Federal do Rio Grande do Sul.
- Pillar, V. D. & Orłóci, L. (1996) On randomization testing in vegetation science: multifactor comparisons of relevé groups. *J. Veg. Sci.* 7: 585-592.
- Repenning, M., Rovedder, C. E. & Fontana, C. S. (2010) Another color morph of *Sporophila* Seed eater from the capuchinos group (Aves, Emberizidae). *Iheringia, Sér. Zool.* 100(4): 369-378.

- Ridgely, R. E. & Tudor, G. (1989) *The birds of South America*. Vol. 1 - The oscine passerines. Austin, USA: University of Texas Press.
- Robel, R. J., Briggs, J. N., Dayton, A. D. & Hulbert, L. C. (1970) Relationships between visual obstruction measurements and weight of grassland vegetation. *J. Range Manage.* 23: 295-297.
- Rovedder, C. E. (2011) *História natural de Sporophila melanogaster (Pelzeln, 1870) (Aves: Emberizidae) com ênfase em sua biologia reprodutiva*. MSc. Dissertation. Porto Alegre, Brazil: Pontifícia Universidade Católica do Rio Grande do Sul.
- Schauensee, R. M. 1952. A review of the genus *Sporophila*. *Proc. Acad. Nat. Sci. Philadelphia* 54: 153-198.
- Sick, H. (1967) "Bico de Ferro" - overlooked seedeater from Rio de Janeiro (*Sporophila*, Fringillidae, Aves). *An. Acad. Bras. Ciênc.* 39: 307-314.
- Sick, H. (1997) *Ornitologia brasileira: uma introdução*. Rio de Janeiro, Brazil: Nova Fronteira.
- Silva, J. M. C. (1999) Seasonal movements and conservation of seedeaters of the genus *Sporophila* in South America. *Stud. Avian Biol.* 19: 272-280.
- Tubaro, P. L. & Gabelli, F. M. (1999) The decline of the Pampas Meadowlark: difficulties of applying the IUCN criteria to Neotropical grassland birds. *Stud. Avian Biol.* 19: 250-257.
- Vickery, P. D., Tubaro, P. L., Silva, J. M. C., Peterjohn, B. G., Herkert, J. R. & Cavalcanti, R. B. (1999) Conservation of grassland birds in the western hemisphere. *Stud. Avian Biol.* 19: 2-26.

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Table 1. Univariate comparisons (Mann-Whitney *U*-test) between plots of nest site (n = 26) and nest patch (n = 104) of Tawny-bellied Seed eaters (*Sporophila hypoxantha*) based on habitat variables in south Brazilian dry grasslands. Values are presented as mean \pm SD (range).

Habitat variable	Nest site	Nest patch	<i>P</i>
Bare ground cover (%)	3.0 \pm 5.4 (0-22)	3.4 \pm 7.1 (0-55)	0.4
Low-stratum cover (%)	13.2 \pm 16.8 (0-55)	19.2 \pm 22.9 (0-90)	0.3
Mid-stratum cover (%)	84.5 \pm 16.7 (45-100)	76.9 \pm 22.1 (10-100)	0.1
High-stratum cover (%)	2.1 \pm 1.6 (0-5)	3.7 \pm 6.1 (0-43)	0.2
Low-stratum max. height (cm)	14.0 \pm 9.3 (0-30)	14.6 \pm 10.4 (0-35)	0.2
Mid-stratum max. height (cm)	96.1 \pm 15.7 (70-140)	94.7 \pm 18.8 (35-180)	0.4
Vegetation max. height (cm)	151.7 \pm 39.9 (85-200)	146.1 \pm 45.6 (70-250)	0.4
Low (0-50 cm) horiz. obstruction (%)	75.6 \pm 22.8 (25-100)	67.3 \pm 26.4 (5-100)	0.07
Up (50-100 cm) horiz. obstruction (%)	17.6 \pm 20.1 (0-95)	19.6 \pm 20.5 (0-100)	0.4
Slope (°)	10.0 \pm 7.4 (0-31)	10.5 \pm 7.7 (0-35)	0.4

Table 2. Univariate comparisons (Mann-Whitney *U*-test) between plots of nest sites (n = 130) and non-nest sites (n = 130) of Tawny-bellied Seed eaters (*Sporophila hypoxantha*), based on habitat variables in southern Brazilian dry grasslands. Values are presented as mean \pm SD (range). In bold, the statistically significant values ($P < 0.05$).

Habitat variable	Nest site	Non-nest site	<i>P</i>
Bare ground cover (%)	3.3 \pm 6.8 (0-55)	11.2 \pm 16.8 (0-96)	< 0.0001
Low-stratum cover (%)	18.1 \pm 21.9 (0-90)	27.4 \pm 30.4 (0-95)	0.038
Mid-stratum cover (%)	78.4 \pm 21.3 (10-100)	50.2 \pm 31.6 (2-100)	< 0.0001
High-stratum cover (%)	3.4 \pm 5.6 (0-43)	21.6 \pm 30.4 (0-98)	< 0.0001
Low-stratum max. height (cm)	14.5 \pm 10.2 (5-35)	10.9 \pm 9.5 (0-40)	0.002
Mid-stratum max. height (cm)	95.0 \pm 18.2 (35-180)	84.6 \pm 14.8 (35-120)	< 0.0001
Vegetation max. height (cm)	147.2 \pm 44.4 (70-250)	159.3 \pm 60.8 (50-350)	0.077
Low (0-50 cm) horiz. obstruction (%)	68.9 \pm 25.8 (5-100)	59.8 \pm 28.5 (1-100)	0.006
Up (50-100 cm) horiz. obstruction (%)	19.2 \pm 20.4 (0-100)	37.3 \pm 35.8 (0-100)	0.001
Slope (°)	10.4 \pm 7.6 (0-35)	19.0 \pm 13.8 (0-53)	< 0.0001

Table 3. Mean and total numbers of individuals of each plant species between plots of nest sites (n = 130) and non-nest sites (n = 130) of Tawny-bellied Seedeaters (*Sporophila hypoxantha*) in southern Brazilian dry grasslands.

Plant species	Nest site		Non-nest site	
	Mean \pm SD	Total	Mean \pm SD	Total
Shrubs				
<i>Eupatorium polystachyum</i>	2.5 \pm 3.7	334	1.6 \pm 2.2	218
<i>Eupatorium multicrenulatum</i>	0.7 \pm 2.7	99	2.0 \pm 4.1	265
<i>Eupatorium serratum</i>	0.1 \pm 0.8	22	0.2 \pm 0.9	34
<i>Eupatorium laevigatum</i>	0	0	0.4 \pm 1.4	56
<i>Vernonia chamaedrys</i>	2.7 \pm 2.7	387	2.2 \pm 3.3	287
<i>Baccharis caprariifolia</i>	2.8 \pm 3.4	373	1.0 \pm 2.6	130
<i>Baccharis cognata</i>	1.0 \pm 2.6	135	0.4 \pm 1.4	61
<i>Baccharis dracunculifolia</i>	0	1	0.3 \pm 1.7	45
<i>Baccharis coridifolia</i>	0.6 \pm 2.0	85	0.3 \pm 2.0	46
<i>Baccharis rufescens</i>	1.4 \pm 2.4	198	1.3 \pm 2.4	170
<i>Baccharis stenocephala</i>	0.5 \pm 1.5	68	0.5 \pm 1.6	64
<i>Baccharis trimera</i>	0.4 \pm 2.1	61	0.6 \pm 1.8	88
<i>Baccharis ochracea</i>	0.4 \pm 1.4	52	0.3 \pm 1.5	43
Grasses				
<i>Andropogon lateralis</i>	9.2 \pm 10.3	1,223	3.6 \pm 5.6	473
<i>Andropogon virgatus</i>	5.7 \pm 8.4	745	3.5 \pm 6.0	455
<i>Saccharum angustifolium</i> (clump)	3.3 \pm 4.7	431	1.3 \pm 2.5	175
<i>Saccharum angustifolium</i> (stem)	1.9 \pm 3.0	248	1.2 \pm 2.5	159
<i>Schizachyrium</i> sp.	1.3 \pm 6.8	170	1.1 \pm 9.7	150
<i>Eriochrysis cayennensis</i>	0.4 \pm 1.5	63	0.5 \pm 2.1	63
“Sawgrasses/eryngos”				
<i>Eryngium horridum</i>	1.8 \pm 2.9	263	3.1 \pm 3.8	411
<i>Eryngium elegans</i>	1.5 \pm 4.8	199	0	0
<i>Eryngium pristis</i>	0.5 \pm 3.2	75	0	0
Small trees				
<i>Schinus terebinthifolius</i>	0	4	0.1 \pm 0.6	17
<i>Lithraea brasiliensis</i>	0	0	0	5
<i>Escallonia megapotamica</i>	0	11	0.8 \pm 1.9	108
Herbs				
<i>Cunila incana</i>	0	2	0.2 \pm 1.1	31
<i>Pterocaulon polystachyum</i>	0.1 \pm 0.7	25	0.3 \pm 0.9	40

Figure Captions

Figure 1. Schematic illustration of the method used for marking and assessment of nest-site and non-nest-site plots of Tawny-bellied Seedeaters (*Sporophila hypoxantha*) in southern Brazilian dry grasslands. Each plot is 4 m² and the dashed lines represent measurements.

Figure 2. Ordination of 26 plant species (numbers, see below) present in nest-sites (black dots) and non-nest sites (gray dots) of Tawny-bellied Seedeaters (*Sporophila hypoxantha*) in southern Brazilian dry grasslands. The scatter diagram is defined by ordination Axis 1 and 2 generated by Principal Coordinates Analysis (PCoA) using the Euclidean Distance from each species abundance data. The percentage of total variation represented by the Axis is indicated. Plant species: 1 *Eupatorium polystachyum*, 2 *Eupatorium multicrenulatum*, 3 *Eupatorium serratum*, 4 *Eupatorium laevigatum*, 5 *Vernonia chamaedrys*, 6 *Baccharis caprariifolia*, 7 *Baccharis cognata*, 8 *Baccharis dracunculifolia*, 9 *Baccharis coridifolia*, 10 *Baccharis rufescens*, 11 *Baccharis stenocephala*, 12 *Baccharis trimera*, 13 *Baccharis ochracea*, 14 *Andropogon lateralis*, 15 *Andropogon virgatus*, 16 *Saccharum angustifolium* (clump), 17 *Saccharum angustifolium* (stem), 18 *Schizachyrium* sp., 19 *Schinus terebinthifolius*, 20 *Lithraea brasiliensis*, 21 *Escallonia megapotamica*, 22 *Eryngium horridum*, 23 *Eryngium elegans*, 24 *Eryngium pristis*, 25 *Cunila incana*, 26 *Pterocaulon polystachyum*, 27 *Eriochrysis cayennensis*.

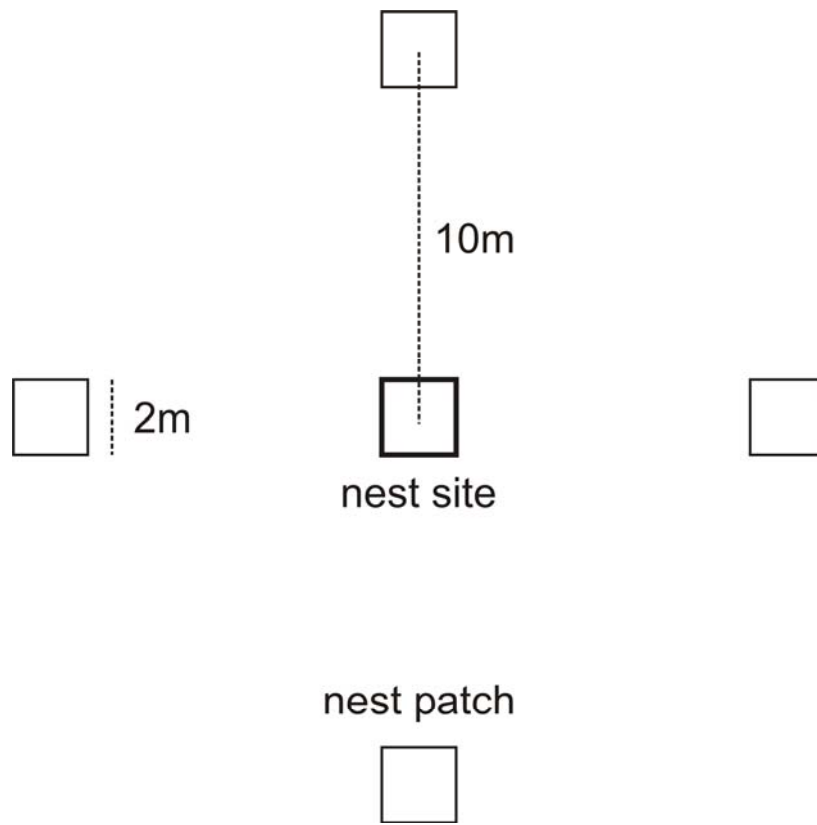


Figure 1

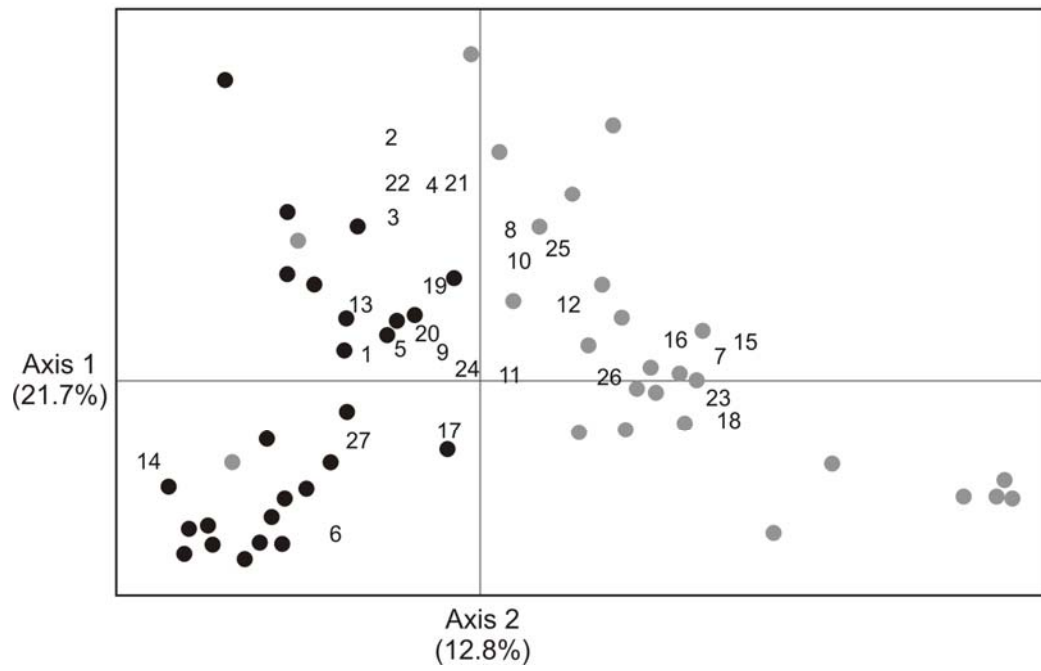


Figure 2

CAPÍTULO 4

Plumage of one and voice of another: an apparent hybrid between
Black-bellied (*Sporophila melanogaster*) and Tawny-bellied (*S.*
hypoxantha) Seedeaters

Artigo a ser submetido para publicação no periódico *The Wilson Journal of Ornithology*

RRH: *Franz et al.* • APPARENT HYBRID BETWEEN *SPOROPHILA* CAPUCHINOS

PLUMAGE OF ONE AND VOICE OF ANOTHER: AN APPARENT HYBRID BETWEEN
BLACK-BELLIED (*SPOROPHILA MELANOGASTER*) AND TAWNY-BELLIED (*S.*
HYPOXANTHA) SEEDEATERS

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ABSTRACT.—Some questions on the relationships and limits between groups and species in the diverse genus *Sporophila* remain unclear, and the study of hybrids can make an additional contribution to clarifying them. We recorded an individual with hybrid phenotype between the Black-bellied Seedeater *Sporophila melanogaster* and the Tawny-bellied Seedeater *S. hypoxantha* in Lages, Santa Catarina, southern Brazil, in an area of sympatry characterized by dry and hilly grasslands. The individual showed the plumage pattern and coloration of one species (*S. melanogaster*) and the voice of the other (*S. hypoxantha*). The most likely hypothesis to explain the existence of this apparent hybrid is that there was a social couple (*S. hypoxantha*) and an external genetic father (*S. melanogaster*), with the occurrence of extrapair copulation. Nevertheless, we do not reject the possibility of to represent a case of interspecific song learning, a subject that needs more studies within capuchinos. Presumed hybrids between these species were unknown until this study.

The study of hybrids may help to elucidate the pattern of evolution of a group (Short 1969a). A few cases of hybridization have been recorded within the seedeaters (genus *Sporophila*, Emberizidae), mostly based on captive specimens with known parentage or on museum skins (see Sick 1963). We did not find any reports of *Sporophila* hybrids recorded and studied directly in the wild. McCarthy (2006) mentioned the record of hybrids between 21 different “species” of seedeaters. In the “capuchinos” group (in Spanish, or “caboclinhos” in Portuguese), which includes species with a similar pattern of male plumage coloration (Ouellet 1992) and low genetic divergence (Lijtmaer et al. 2004), hybridization is known only between *Sporophila hypochroma* x *S. castaneiventris* and *S. castaneiventris* x *S. minuta* (Short 1969b). In addition, two possible cases of capuchinos x non-capuchinos interbreeding were identified (*S. bouvreuil pileata* x *S. lineola* and *S. b. bouvreuil* x *S. plumbea*; Sick 1963).

In this study, we describe a case of apparently natural hybridization between two capuchinos: the Black-bellied (*Sporophila melanogaster* [Pelzeln, 1870]) and the Tawny-bellied (*S. hypoxantha* Cabanis, 1851) Seedeaters, recorded in a sympatric zone in southern Brazil. The main goals are to report this information supporting the proximity among the members of the group, present this new and previously unknown hybrid, and contribute to studies of the diversity of seedeaters.

METHODS

Field studies involving the natural history of birds of the genus *Sporophila* were initiated in 2007 in the region of the southern Brazilian upland wetlands and grasslands (called “Campos de Cima da Serra” in Portuguese). An intensive field effort was expended during the breeding seasons of 2007/08, 2008/09, and 2009/10 (approximately 1,000 h by

each of 3 researchers). Among the focus species of the study were the Tawny-bellied Seedeater and the Black-bellied Seedeater. In one of our study areas, both species coexist, but the Tawny-bellied Seedeater occurs in much larger numbers. This site is located in the “Coxilha Rica” locality (central point: UTM 22J 0570495 / 6868162, altitude ranging from 800 to 1,000 m), part of the municipalities of Lages and São Joaquim, state of Santa Catarina, southern Brazil. The hilly landscape matrix is characterized by shallow soil covered by dry grasslands, composed of a rich flora with diverse species of Asteraceae shrubs (e.g., *Eupatorium* spp., *Vernonia* spp.), “caraguatás” (*Eryngium horridum*), and various grasses (e.g., genera *Piptochaetium*, *Andropogon*, *Setaria*, *Paspalum* and *Sorghastrum*).

In this area, an adult capuchino male with plumage features of one species and vocal patterns of another was recorded and analyzed as having a possible hybrid origin. It was first recorded on 19 November 2008. On that day, we obtained documentation in the form of photography, film and audio recordings. Vocalizations were sampled with a Sony TCD-5M recorder and a Sennheiser ME-66 directional microphone. The recorded segments were digitalized, and spectrograms were produced using Raven Pro 1.4 software (Charif et al. 2006). In the following year, the male, recognized by voice and plumage characteristics, immigrated to the same territory and was captured on 18 December 2009. We used playback of the species’ calls (Tawny-bellied Seedeater and Black-bellied Seedeater, obtained from birds of that same area) to evaluate the response of the individual.

RESULTS

Visually, the bird was easily recognized as a typical Black-bellied Seedeater male. However, its vocalizations belonged to the Tawny-bellied Seedeater repertoire. Below, we describe the individual according to their plumage, voice, habitat, and behavior.

Plumage coloration

The underparts are generally blackish, with some grayish and brownish feathers (Fig. 1). Gray extends up the back sides of the body toward the breast, leaving the black part as a discontinuous streak, fully visible in frontal view. The well-defined cheek is gray. The gray color that predominates on the back is the same as that found in adult males of the Black-bellied Seedeater, with a more standard bluish-gray. The rump is grayish-brown, the same color as some back feathers. In males of Tawny-bellied Seedeater, the tawny ventral part extends to the flanks, occupying the entire front side of the body. The cheek is tawny, the same color as the throat and the rest of the frontal part. The back is a more opaque, darker gray. The rump is the same color as the belly. Thus, the hybrid in question has breeding plumage completely similar to that of adult *Sporophila melanogaster* males, marked by typical color blocks (cheeks, flanks, and gray rump), with no marking that belongs exclusively to the pattern of *S. hypoxantha*. In the following year (after capture), the plumage retained the same general color pattern (Fig. 1).

Vocalizations

The main vocal repertoire of the possible hybrid was well documented, with a song type and at least three types of calls identified. The voice of this individual has all the

characteristics of the patterns of *Sporophila hypoxantha* (Fig. 2). No shape of the notes resembles those of the *S. melanogaster* vocal repertoire. This song lasts 6 s and includes seven main groups of notes, with a short *tsiilp* making the connection between some of these (appearing as vertical ticks in the spectrogram).

Habitat and behavior

The environment in which the individual was recorded is dry grasslands, with basalt outcrops at some points, and small isolated wetlands. The lower and middle vegetation strata are dense, consisting mainly of clumps of grasses and *Eupatorium* spp. shrubs, and the upper stratum is characterized by a high concentration of *Eryngium horridum* with inflorescences up to 1.60 m tall. The male showed territorial behavior (singing continuously on the higher perches) and responded aggressively to playback of Tawny-bellied Seedeater, by rapidly approaching. The playback of the Black-bellied Seedeater call did not have any effect. Throughout the period of observation (one month), the hybrid defended the same territory, which was measured at 0.31 ha. It was located contiguously to territories defended by Tawny-bellied Seedeater ($n = 3$) and Black-bellied Seedeater ($n = 1$). No indication of pairing was observed. In the following year, the individual defended a territory at the same site.

DISCUSSION

Two main characters, plumage and vocalizations, were used to distinguish the presumed hybrid described here. We suggest three possibilities for mating to produce these individual. The simplest would be (1) a couple formed by the two species interbred and created the clutch, which inherited the mother's plumage and the voice from the social and

genetic father. This hypothesis seems reasonable, but we noted that in the wild females usually reject foreign males when already paired, demonstrating a strong signal of selection and social isolation, and are therefore less likely to choose a male of another species. The second hypothesis is that (2) an already paired female was mated forcibly (extrapair copulation) by a male of another species (we have observed this behavior within both species). The same-species couple would raise the chicks, which would learn the song of the social father and inherit the plumage characters from the genetic father. The possibility that (3) they are not hybrids, and when young, learned the song of a neighbor male of the other species is a little more remote, since the entire repertoire belongs to a parental species (no elements combined) and males are in general aggressive and dedicated to territory defense, not allowing external males to approach easily. Territories are maintained dynamically and possibly the tutor accompanies the young for a considerable time during the fledgling period, with directed, not accidental training. Therefore, the second hypothesis seems to be the most appropriate to combine theory with the knowledge derived from observation of many capuchino pairs in nature. According to this, the apparent hybrid would have a social mother and father of *Sporophila hypoxantha* and an external (genetic) father of *S. melanogaster*. Nevertheless, we do not totally reject the possibility of to represent a case of interspecific song learning (hypothesis 3), because there are strong indications that the song is learned in seedeaters (Areta 2008, Sick 1963). We consider that this subject needs more practical studies within capuchinos.

The bird has exclusively plumage of Black-bellied Seedeater (color tonality and color distribution blocks). We think that a capuchino hybrid could inherit the color distribution of one parental species and the color tonality from another, or an intermediate pattern. So, we expected to find some individuals showing these distinct combinations. Ryan et al. (1994)

studied two species of *Nesospiza* buntings in the Tristan da Cunha archipelago and found that hybrids, in general, have a propensity to show the color of one or other of the parental species, except for a few cases of intermediate patterns.

Sympatric species can be genetically more similar than allopatric species as a result of introgressive hybridization (Grant and Grant 1996). The southern capuchinos group (8 species, south of the Amazon River), which includes the two species in question (*Sporophila hypoxantha* and *S. melanogaster*), shows an extremely low mean genetic divergence, suggesting a rapid radiation in the last half-million years (Lijtmaer et al. 2004). This proximity between species could increase the likelihood of producing hybrids. However, the idea that hybridizing species must be closely related is “dead”, according to Gill (1998). In Gill’s opinion, what would define the capacity of two species to interbreed would be social recognition, making speciation also a cultural phenomenon. In the capuchinos, this may be an important process, considering the strong sexual selection marked by pronounced dimorphism between males and females. Still, the close similarity of phenotypes among females of some species such as Tawny-bellied Seedeater and Black-bellied Seedeater can act as a factor favoring interbreeding through forced copulation (an action already seen in the field). Thus, these and possibly several other species of capuchinos are presumably able to interbreed in the wild.

The fact that the presumed hybrid was recorded in areas of sympatry that stand out in the matrix (around areas where only Tawny-bellied Seedeater occurs) defending a territory surrounded by both Tawny-bellied Seedeaters and Black-bellied Seedeaters, may indicate that it were born nearby and returned as adults to the same area. Natal philopatry occurs in both species (pers. comm., subject being studied). So this area could be considered a zone of overlap and hybridization (not a hybrid zone), where parental phenotypes occur together with

hybrids. It is important to monitor this type of area to seek new hybrids. The existence of several intrageneric hybrids may be further evidence for their relatively close relationship (Short 1969a).

There is an unnatural facilitator of hybridization between seedeaters in nature. Knowingly all species of the genus *Sporophila* are appreciated by aviculturists and also widely captured today. The removal of large quantities of males from habitats may be affecting the sexual selection and facilitating the interbreed, for having fewer adult males, and females (in general, morphologically very similar) will remain active in greater numbers. In São Paulo, *Sporophila crassirostris* was virtually extinct in nature and the remaining females accept males of *S. angolensis* still present (Lordello 1957). The natural environment degradation and suppression are concomitant problems apparently also shove the contact of closely species and influencing the habitat segregation, an important mechanism of speciation (Sick 1967, 1997).

Finally, we note that a satisfactory knowledge on this subject and many others still uncertain involving complex groups and species within the genus *Sporophila* only will be achieved with greater field effort. Still, we consider the possibility of testing in laboratory some situations and trends (as suggested by Sick 1963), such as the acceptance and selection of males by females, song learning, transmission and inheritance of morphological traits, among others.

ACKNOWLEDGMENTS

Our project on the biology of seedeaters was funded by Fundação Grupo Boticário de Proteção à Natureza and received financial support from Neotropical Grassland Conservancy,

to whom we are very grateful. To couple friends Joaquim and Nair, Antônio and Ivonete, we thank for hospitality and essential logistic support in the study area. To Cristiano E. Rovedder for field work assistance and friendship. Reviews by Robin Restall and Juan I. Areta consistently improved an earlier version of the manuscript.

LITERATURE CITED

- Areta, J. I. 2008. Entre Ríos Seedeater (*Sporophila zelichi*): a species that never was. *Journal of Field Ornithology* 79(4):352-363.
- Charif, R. A., D. W. Ponirakis, and T. P. Krein. 2006. Raven Lite 1.0. Cornell Laboratory of Ornithology, Ithaca, NY.
- Gill, F. B. 1998. Hybridization in birds. *The Auk* 115(2):281-283.
- Grant, P. R., and B. R. Grant. 1996. Speciation and hybridization in island birds. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 351:765-772.
- Lijtmaer, D. A., N. M. M. Sharpe, P. L. Tubaro, and S. C. Loughheed. 2004. Molecular phylogenetics and diversification of the genus *Sporophila* (Aves: Passeriformes). *Molecular Phylogenetics and Evolution* 33(3):562-579.
- Lordello, L. G. E. 1957. Duas aves híbridadas da fauna do Brasil. *Revista Brasileira de Biologia* 17:139-142.
- McCarthy, E. M. 2006. *Handbook of avian hybrids of the World*. Oxford University Press, Oxford, UK.
- Ouellet, H. 1992. Speciation, zoogeography and taxonomic problems in the Neotropical genus *Sporophila* (Aves: Emberizinae). *Bulletin of the British Ornithological Club Centenary Supplement* 112a:225-235.

- Ryan, P. G., C. L. Moloney, and J. Hudon. 1994. Color variation and hybridization among *Nesospiza* Buntings on Inaccessible Island, Tristan da Cunha. *The Auk* 111(1):314-327.
- Short, L. L. 1969a. Taxonomic aspects of avian hybridization. *The Auk* 86:84-105.
- Short, L. L. 1969b. Relationships among some South American seedeaters (*Sporophila*), with a record of *S. hypochroma* for Argentina. *The Auk* 81(2):216-219.
- Sick, H. 1963. Hybridization in certain Brazilian Fringillidae (*Sporophila* and *Oryzoborus*). *Proceedings of the XIII International Ornithological Congress* 161-170.
- Sick, H. 1967. "Bico de Ferro" - Overlooked seedeater from Rio de Janeiro (*Sporophila*, Fringillidae, Aves). *Anais da Academia Brasileira de Ciências* 39:307-314.
- Sick, H. 1997. *Ornitologia brasileira*. Ed. Nova Fronteira, Rio de Janeiro.

FIGURE CAPTIONS

FIG. 1. Apparent hybrid between *Sporophila melanogaster* and *S. hypoxantha* recorded in Santa Catarina, Brazil. Above: specimen recorded on 19 November 2008 and (below) the same in the next year, captured on 18 December 2009.

FIG. 2. Comparative spectrograms of songs of an apparent hybrid between *Sporophila melanogaster* and *S. hypoxantha* (above) and a typical male of *S. hypoxantha* (below). These songs were recorded respectively on 19 November 2008 and 28 November 2008, both in the same area (Coxilha Rica, Lages, Santa Catarina, Brazil). The last note that appears on the spectrogram above, preceded by a *tsiilp* connection, is a call not belonging to the song.



FIG. 1

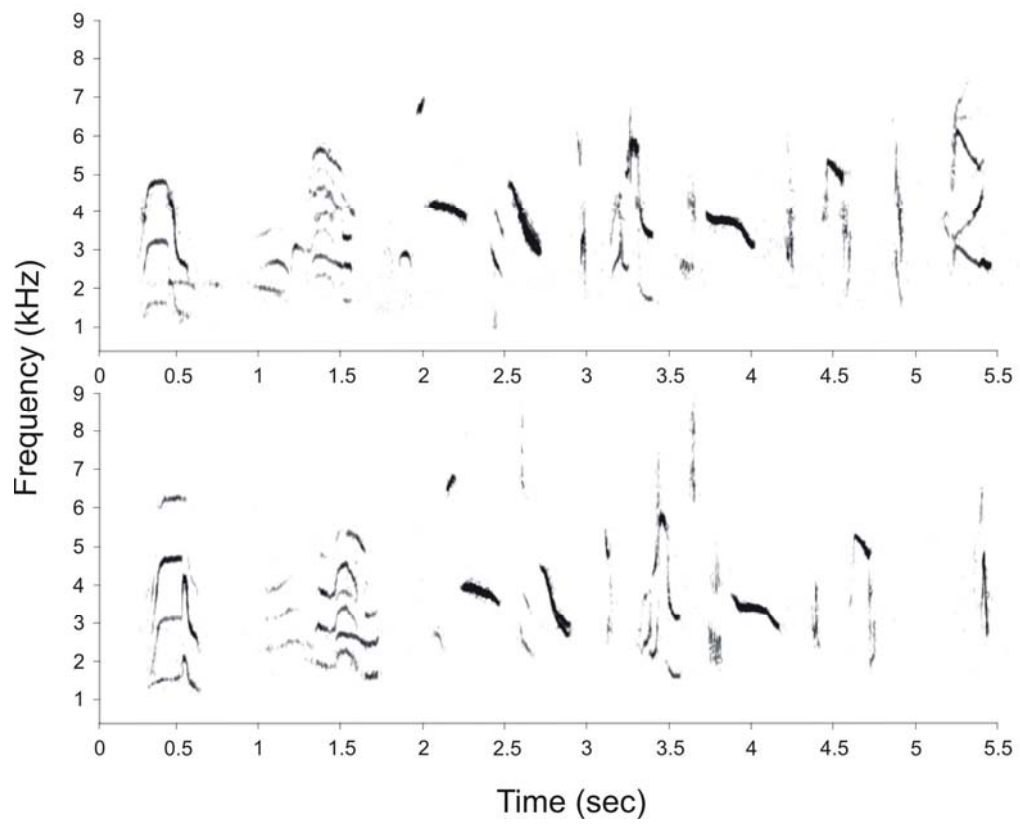


FIG. 2

CONCLUSÕES GERAIS

Este estudo abordou a história natural, ou história de vida, de uma população do caboclinho-de-barriga-vermelha (*Sporophila hypoxantha*) que todos os anos migra para o sul do Brasil para reproduzir. A maioria das informações apresentadas, mesmo algumas básicas, é inédita. O estudo, portanto, representa o primeiro passo para uma melhor compreensão das necessidades ecológicas e características biológicas da espécie. Com base nele e nas importantes pesquisas disponíveis da Argentina, novas hipóteses e algumas lançadas aqui poderão ser delineadas e testadas. Por exemplo, existe diferença na aptidão (*fitness*) entre os casais que reproduzem no início da temporada (que fornece maior chance de sucesso) em relação aos reprodutores do final da temporada? A fecundação extra-par, que parece tão evidente, realmente ocorre? E qual a influência disso tudo na seleção sexual? Essas e outras questões permanecem desprovidas de resolução. Pesquisas de cunho mais básico são o ponto de partida para se alcançar perguntas mais elaboradas e buscar testá-las.

Consideramos o caboclinho-de-barriga-vermelha um modelo muito interessante para investigações biológicas, ecológicas e evolutivas com variados enfoques, uma vez que apresenta distribuição ampla, linhagens distintas distribuídas de forma descontínua (os “regiolects”), populações residentes e migratórias, fidelidade aos sítios reprodutivos (filopatRIA), parâmetros biológicos aparentemente variáveis no espaço, entre outros. Estudar comparativamente o modo de vida das populações nos extremos de distribuição da espécie, como na Bolívia, no Paraguai, nordeste da Argentina (onde se concentram os estudos pioneiros), Uruguai e sul do Brasil, não apenas seria interessante do ponto de vista da história natural, mas também contribuiria para esclarecer importantes lacunas acerca da sua história evolutiva. Por que não, ainda, da história dos próprios caboclinhos, como um grupo em plena diversificação.

Aspectos estudados, como a sobrevivência de ninhos e fatores associados e a seleção de sítios de nidificação, são escassos para as aves brasileiras e neotropicais como um todo. No grupo dos papa-capins, são virtualmente inexistentes. Cuidado biparental apenas na fase tardia de ninhegos surge como sendo uma característica que talvez possa acontecer de forma geral nos caboclinhos. Mas apenas com mais estudos será possível confirmar esse indício. Estudos sobre biologia de *Sporophila ruficollis*, *S. palustris*, *S.*

hypochroma, *S. bouvreuil* e *S. pileata* seriam muito bem vindos, assim como com o extremamente ameaçado *S. nigrorufa*. Comparando aspectos reprodutivos entre populações residentes e migratórias de *S. hypoxantha* (Argentina vs. Brasil), encontramos um padrão interessante de temporada reprodutiva mais curta e atividade parental acelerada nas migratórias. O sucesso reprodutivo foi mediano, mas a produtividade baixa. Fatores temporais influenciaram a sobrevivência de ninhos, que decaí ao longo do ciclo de nidificação e durante a temporada reprodutiva. Para nidificar na área de estudo, verificamos que os casais selecionam campos secos com estrato médio denso, ricos em arbustos como *Vernonia chamaedrys*, *Eupatorium polystachyum* e *Baccharis caprariifolia*. Evitam campos muito íngremes e com estrato superior denso a ponto de se sobrepor ao estrato médio. Outros resultados encontrados foram: (1) apenas a fêmea constrói (3-6 dias) o ninho e incuba (12 dias) os ovos, assistida de perto pelo macho; (2) a ninhada habitual é de dois ovos, e ninhadas de três parecem ocorrer no início da temporada; (3) machos passam a alimentar ninhegos após cinco dias de vida; (4) filhotes deixam os ninhos com 9-10 dias; (5) com um mês de vida tornam-se independentes, e permanecem próximos do ninho até o momento de emigrar; (6) predação é a principal causa de perda de ninhadas, seguida de abandono e parasitismo por *Philornis seguyi*, e essa última atinge mais da metade dos ninhos com ninhegos, mas causa poucas perdas; (7) arbustos da família Asteraceae são essenciais para a espécie, tanto como planta suporte de ninhos quanto como elementos da fisionomia da vegetação campestre.

Existem mais de 30 espécies do gênero neotropical *Sporophila*, das quais pelo menos *S. hypoxantha*, *S. melanogaster*, *S. plumbea*, *S. telasco*, *S. collaris*, *S. lineola* e *S. caeruleascens* já tiveram a biologia reprodutiva estudada com certo detalhamento. Outras como *S. leucoptera*, *S. nigricollis*, *S. americana*, *S. schistacea*, *S. intermedia* e *S. albogularis* foram estudadas com menos amostras e informações. O grupo como um todo demonstra forte potencial como modelo para estudos ecológicos e evolutivos. Recomendamos, assim sendo, que se dê continuidade para as pesquisas sobre a história de vida das espécies que compõem o grupo.

O possível híbrido entre a espécie estudada e *Sporophila melanogaster* apresentava fenótipo compartilhado: voz da primeira e plumagem da segunda. Mesmo que aprendizagem interespecífica de canto seja uma hipótese alternativa para explicar a existência desse espécime, esperávamos um canto com elementos combinados, nesse

caso. A comprovada incapacidade em se distinguir espécies de caboclinhos com base em moléculas dificulta de sobremaneira a comprovação da identidade do espécime registrado.

Como amplamente visto e discutido, o conhecimento da história natural das aves neotropicais é não somente insuficiente, mas pode ser considerado apenas iniciado. As informações levantadas no Cerrado brasileiro, desde a década de 1980, exemplificam como o esforço pontual direcionado para o conhecimento geral pode “gerar bons frutos” (ou seriam ovos?). Partindo de informações básicas sobre as principais espécies daquele bioma, foi possível identificar novos questionamentos e ir além, respondendo-os. A criação de redes de cooperação seria uma iniciativa bastante apreciável, de modo a aprimorar as técnicas de coleta e, principalmente, análises de dados. Isso parece, em passos lentos, estar sendo iniciado. Sem dúvida esta década será chave no desenvolvimento dos estudos com história natural de aves brasileiras. Na região subtropical, ainda, parcerias com pesquisadores de países vizinhos, como Argentina, Uruguai e Paraguai, seriam benéficas para todos os envolvidos.

As maiores discussões norteadoras da ciência que trata da história de vida das aves têm como base dados envolvendo espécies do hemisfério norte. Padrões em aves tropicais foram buscados por importantes estudiosos, como Alexander Skutch, desde a década de 1940, e os estudos produzidos por eles ainda servem como a principal base para as discussões correntes. Parece-nos tão claro, por exemplo, que as espécies que vivem entre os trópicos pouco podem ser equiparadas com as espécies das regiões subtropicais. As duas espécies de caboclinhos do norte (“tropicais”), *Sporophila minuta* e *S. castaneiventris*, nunca foram propriamente estudadas. Seus parâmetros reprodutivos acompanhariam a aparente distância filogenética com os caboclinhos do sul? Se negativo, qual a influência do clima e ambiente tropical sobre sua biologia? Com essas e outras perguntas que parecem ter suas respostas tão distantes não temos o intuito de desprezar o conhecimento atual sobre biologia de aves neotropicais. Ao contrário, representa um apelo para que esse se torne um campo de pesquisa cada vez mais crescente e difundido.

Por fim, discutimos brevemente algumas implicações que as informações coletadas têm para a conservação do caboclinho-de-barriga-vermelha. Embora esteja presente em várias localidades desde a Argentina e sul do Brasil até a Bolívia e o Brasil central, habitando alguns ambientes distintos (campos secos ou banhados, principalmente), a

espécie apresenta uma clara tendência em selecionar microhabitats na matriz campestre que sejam mais planos e tenham um denso estrato médio (a parte arbustiva do campo que não ultrapassa muito 1m de altura), para nidificar. Tanto campos muito ralos quanto aqueles adensados de árvores pequenas (*e.g. Escallonia megapotamica*) são evitados. Intensidade muito elevada de manejo com cargas de gado acima da média associadas à queimadas mais severas e frequentes favoreceria a manutenção de campos baixos com menos arbustos e plantas herbáceas, prejudicando a espécie. Em contraponto, a exclusão total do pastejo favorece o desenvolvimento de uma vegetação alta demais, além dos limites tolerados pelo caboclinho. A aplicação de queimadas tem o limiar entre benefício e prejuízo para a espécie desconhecido, de modo que representa um foco de pesquisa importante a se considerar. Portanto, a utilização da pecuária extensiva, com baixa carga e intensidade moderada, parece ser compatível com a conservação e manutenção em longo prazo do caboclinho-de-barriga-vermelha nos campos sul-brasileiros.

APÊNDICE FOTOGRÁFICO



Espécie foco do estudo: *Sporophila hypoxantha* Cabanis, 1851 (caboclinho-de-barriga-vermelha). Machos (B e C) e fêmeas (D e F) típicos, macho em fase de muda de penas, (E, plumagem pré-eclipse) e bando monoespecífico reunido pouco antes da emigração (A).



Área de estudo: campos ao longo do rio Lava-Tudo (A), em São Joaquim e Lages, Santa Catarina, Brasil. Campos secos densos, habitat de nidificação preferencial (B), coxilhas ricas em caraguatás *Eryngium horridum* (C), campos rochosos (D) e campos limpos manejados (E).



Plantas mencionadas no estudo: *Vernonia chamaedrys*, principal planta suporte de ninhos (A), *Escallonia megapotamica*, típica de habitats evitados para nidificação (B), campos manejados ricos em caraguatás *Eryngium horridum* (C), campos de *Sorghastrum setosum*, característicos do início da temporada reprodutiva - novembro (D) e campos de *Andropogon selloanus*, típicos do fim da temporada - fevereiro (E).



Alguns dos principais impactos e usos da terra nos Campos de Cima da Serra: queima de arbustos importantes, como *Eupatorium polystachyum* (A), gado em capinzal denso (B), silvicultura nos campos íngremes (C), plantio de forrageiras e silvicultura (D), queimadas na área de estudo (E, Coxilha Rica, Lages/SC), drenagem de campos úmidos (F), queimadas recentes em campo seco (G) e monocultura de pinheiros exóticos em estágio inicial (H).



Exemplo de regeneração pós-fogo (queimada de nível severo) em campos secos na área de estudo (Coxilha Rica, Lages/SC): antes (acima, dezembro/2008) e após 14 meses (fevereiro/2010).



Alguns dos métodos empregados no estudo: captura com gaiola-alçapão e espécime cativo (A) e rede de neblina (B), marcação de parcelas para análise de vegetação (C), tomada de medida de cobertura lateral da vegetação (D), observação de atividade nos ninhos com luneta (E) e filmagem remota (H), ninhego com sete dias recém anilhado (G) e tomada de dados biométricos de adultos (F).