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NATURAL HISTORY, DISTRIBUTION, AND CONSERVATION OF TWO NOMADIC *SPOROPHILA* SEEDEATERS SPECIALIZING ON BAMBOO IN THE ATLANTIC FOREST

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Abstract. Semelparous woody bamboos flower fairly synchronously and in clocklike fashion after many years, providing abundant and nutritious seeds. However, this resource is ephemeral, localized, and unpredictable from the perspective of birds that feed on those seeds. Birds specializing on bamboo seeds track this food source and are nomadic. We recorded Temminck's Seedeater (*Sporophila falcirostris*) at 29 localities and the Buffy-fronted Seedeater (*S. frontalis*) at 23 localities in Argentina, Paraguay, and southeastern Brazil. In these species, nomadism is unassociated with any seasonal factor: birds may persist year round over several consecutive years if the seed supply is constant enough. Most occurrences and all breeding records were related to masting of bamboo; records of isolated birds away from seeding bamboo must represent individuals searching for bamboo patches. We report winter breeding of these species for the first time and demonstrate that the supply of bamboo seeds is the main limitation to their breeding. On a broad spatiotemporal scale, large-seeded bamboos (e.g., *Guadua* spp.) may function as strong population pumps, small-seeded bamboos (e.g., *Chusquea* spp.) as maintenance stations. Both species fed mostly on bamboo seeds, occasionally on bamboo flowers, and rarely on alternative food sources. They consumed insects frequently and occurred in mixed-species flocks, especially during autumn and winter. Creation of a network of protected areas is essential to preserve bamboo patches that flower at different times and localities in sufficiently large quantities to guarantee the long-term survival of the peculiarly dynamic populations of bamboo seedeaters.

Key words: Argentina, Brazil, Chusquea, Guadua, Merostachys, nomadism, Paraguay, Sporophila falcirostris, Sporophila frontalis.

Historia Natural, Distribución y Conservación de Dos Especies Nómades de *Sporophila* que se Alimentan de Semillas de Bambú en la Selva Atlántica

Resumen. Los bambúes leñosos semélparos florecen de manera bastante sincrónica y de modo cronométrico cada muchos años, proveyendo semillas abundantes y nutritivas. Sin embargo, este recurso es efímero, local e impredecible desde la perspectiva de las aves que se alimentan de estas semillas. Las aves que se especializan en semillas de bambú, como *Sporophila falcirostris* y *S. frontalis*, rastrean este recurso y son nómades. Registramos a *S. falcirostris* en 29 localidades y a *S. frontalis* en 23 localidades en Argentina, Paraguay y sudeste de Brasil. En estas especies, el nomadismo no está asociado a ningún factor estacional: las aves permanecerán durante todo el año a lo largo de varios años si la provisión de semillas es lo suficientemente constante. Todos los registros de reproducción y la mayoría de las presencias corresponden a momentos de producción masiva de semillas de bambú; los registros de individuos aislados lejos de bambúes deben interpretarse como individuos en búsqueda de parches de bambú. No se conocen poblaciones estables conformadas por individuos residentes en ninguna parte de la distribución geográfica de estas especies. Reportamos por primera vez reproducción invernal en estas especies y demostramos que la disponibilidad de semillas es la principal limitante para su reproducción. En una escala espaciotemporal amplia, los bambúes con semillas grandes (e.g., *Guadua* spp.) funcionarían como bombas poblacionales fuertes, mientras que los bambúes con semillas pequeñas (e.g., *Chusquea* spp.) serían estaciones de mantenimiento. Ambas especies se alimentaron mayormente de semillas de bambú, ocasionalmente de flores de bambú y raramente de fuentes alternativas de alimento. Consumieron insectos frecuentemente y formaron parte de bandos mixtos, especialmente durante otoño e invierno. La creación de una red de áreas protegidas es esencial para preservar parches de bambúes floreciendo en diferentes momentos y localidades en cantidades suficientes para garantizar la supervivencia a largo plazo de las poblaciones peculiarmente dinámicas de los semilleritos de bambú.

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INTRODUCTION

Bamboo-specialist birds are tightly dependent on the life histories of the bamboos on which they specialize. The life cycle of a typical woody bamboo includes (1) a long vegetative (clonal) growth phase, (2) a short flowering/seeding phase, and (3) a senescence/recruiting phase of intermediate length (Gadgil and Prasad 1984, Kratter 1997, Gagnon and Platt 2008). Many woody bamboos are long-lived and semelparous, growing vegetatively for many years, then making a single massive investment in sexual reproduction, which provides an abundant source of nutritious food for seed-eating birds before the plant's death (Seifrizz 1920, 1950, McClure 1966, Gadgil and Prasad 1984). The "predator-satiation hypothesis" maintains that mass masting of bamboo satiates predators, producing more seeds than predators can take, permitting the survival and growth of remaining seeds (Janzen 1976).

Overabundance of seeds is ephemeral, and birds' specialization on bamboo seeds seems to be rare worldwide (Jackson 1972, Restall 1995, Sick 1997, Robson 2004). But why is this so? For a bird to learn inductively when bamboo will mast, it would need to attend two previous episodes of masting in the same area. Since bamboo cycles are typically much longer than the lives of individual birds, there is no chance for seed-specialist birds to learn when and where bamboo seeds will be available in the future. Therefore, although bamboo seed availability is ecologically predictable (i.e., seeds are always available after the same length of time in roughly the same area), seed availability is unpredictable to individual birds (Areta et al. 2009). During their lifetime, most individual bamboo-seed specialists must face a lack of their preferred food supply, at which time they must wander to survive, as do other nomadic birds that follow ephemeral food resources (Keast 1961, Neudorf and Blanchfield 1994, Dean 1997, Kratter 1997, Sick 1997, Areta and Cockle 2012).

Bamboo-seed specialization seems to have evolved rarely, and three conditions have been identified that may allow its evolution from adequate precursors: (1) high species richness of bamboos, (2) bamboo species with energetically rewarding seeds that compensate for the high cost of wandering, and (3) masting of different bamboos occurs close enough together in time and space to ensure a reasonably continuous supply of seeds for nomadic birds (Areta and Cockle 2012). The Atlantic Forest of South America meets these criteria (Bystriakova et al. 2004, Filgueiras and Gonçalves 2004, Areta et al. 2009) and harbors four endemic bamboo-seed specialists: the Purple-winged Ground Dove (*Claravis geoffroyi*), Uniform Finch (*Haplospiza unicolor*), Temminck's Seedeater (*Sporophila falcirostris*), and Buffy-fronted Seedeater (*S. frontalis*) (Stotz et al. 1996).

The little-known *S. falcirostris* and *S. frontalis* have been reported to occur patchily in northeastern Argentina, southeastern Brazil, and eastern Paraguay (Collar et al. 1992, Ridgely and Tudor 1989). While most species of *Sporophila* live in grasslands or along forest borders, these bamboo

seed eaters are regularly found in bamboo stands well within forests. They presumably travel long distances, searching for stands of seeding bamboo and feeding on alternative food sources when no bamboo is available (Areta et al. 2009, Areta and Cockle 2012). Although their strong flight capacity may enable them to cross large gaps in forest (Sabel 1990, Sick 1997), the disturbance of the quasi-cycles of bamboo-seed availability on a wide regional scale and the lack of alternative food resources resulting from forest loss may pose the most serious threats to their long-term survival (Areta et al. 2009, Areta and Cockle 2012). Both species are considered vulnerable by BirdLife International (2011).

The strict relationship of *S. falcirostris* and *S. frontalis* with bamboo masting is poorly understood, as there is little information on these birds' breeding, population movements, population sizes, foraging, and preferences for species of bamboo. Areta et al. (2009) showed that all records of these species in Argentina from 1957 to 2008 coincided in time and place with episodes of seeding of *Guadua* bamboos, but the dependence on bamboos may vary geographically, as both species have been recorded *en masse* at masting of *Meurostachys* in Brazil (Sick 1997) and feeding upon *Chusquea* and other bamboos (Vasconcelos et al. 2005, Areta et al. 2009). Here, we provide new data on these seed eaters' distribution, abundance, breeding, territoriality, foraging, and plumages from Argentina, Paraguay and Brazil, to (1) clarify some aspects of their dynamic biogeography, (2) elucidate their true breeding season and ecological factors that condition it, (3) evaluate the contribution of different bamboo species to the final size of a population (i.e., pumping vs. maintenance bamboos), (4) test their use of alternative food sources, and (5) discuss their conservation problems on the basis of a dataset significantly larger than hitherto available.

METHODS

BIRD SAMPLING

Our data are the result of surveys from 1998 to 2011 at numerous localities in the southernmost portion of the Atlantic Forest in Argentina, Paraguay, and Brazil. These surveys include both specific searches for bamboo-specialist birds at some localities that we visited repeatedly and random encounters during general avifaunal surveys. Whenever we found *S. falcirostris* and *S. frontalis* we recorded data on habitat use, abundance, appearance, and behavior (for localities and dates see Appendix 1, available at <http://dx.doi.org/10.1525/cond.2012.120064>). In addition to our records, we compiled and mapped published and unpublished third-party records from the southern portion of the ranges of *S. frontalis* and *S. falcirostris*. We identified the species of bamboo where we found the seed eaters and recorded the life stage of the bamboo stands. Bamboo specimens from Brazil are deposited at the herbarium of the Universidade Regional de Blumenau, Santa Catarina, Brazil.

We followed Remsen and Robinson (1990) in describing foraging maneuvers. We tape-recorded voices and photographed birds when possible. Our recordings are deposited at the Macaulay Library of Natural Sounds (JIA, AB, MV; www.macaulaylibrary.org) and at Xeno-Canto (GT, AER; www.xeno-canto.org). Photographs archived at www.wikiaves.com.br are cited with the acronym “WA” followed by the corresponding catalog number.

We recorded 400 min of nest-building behavior of *S. falcirostris* at Apepú, Misiones, Argentina (8 September 2008, 11:37–12:37, 60 min; 9 September 2008, 17:07–18:17, 70 min; 10 September 2008, 6:00–8:40, 160 min; 10 September 2008, 12:57–14:37, 100 min). We visited a second nest presumably with eggs being incubated five times over 2 days at Avancini, Misiones, Argentina (18–19 September 2008).

THE BAMBOOS

Most of our bird records were associated with six bamboo species, whose life histories and structural features that we consider relevant to their use by *Sporophila* seedeaters are summarized in Table 1. Given the problems inherent in estimating the intervals between episodes of masting, we detail the key data on which these estimates are based. The intermast period of two specimens of *G. chacoensis* grown from seedlings was ~28 years, and on the basis of numerous records it has been estimated at ~28–30 years in nature (Vega and Cámara Hernández 2008, Areta et al. 2009). The flowering cycle of *G. tigoara* has not been firmly established. On the basis of herbarium specimens Clark and Londoño (2002) considered that species polycarpic, flowering every 2 years with a few culms of a clump flowering simultaneously and the individuals not dying after flowering. Alves (2007), however, found massive fairly synchronous flowering followed by death and lack of sexual maturity in 2-year old individuals. The intermast period is still to be determined but may range from 10 to 36 years (Alves 2007). Sendulsky (2001) proposed the intermast period of *Merostachys neesii* to be 31–33 years on the basis of three consecutive mastings. We estimate the intermast period of *Merostachys multiramea* at 30 years on the basis of records of four consecutive mastings (Sendulsky 1995, Schmidt and Longhi-Wagner 2009, Areta et al. 2009). The intermast period of *Chusquea ramosissima* is still to be determined, but at most localities it flowers irregularly and asynchronously with flowering and nonflowering clumps occurring simultaneously. At a landscape scale the spatial pattern of flowering is discontinuous with flowering and nonflowering sites widely interspersed (Areta et al. 2009, Montti et al. 2011). Despite these difficulties, some evidence suggests that the intermast period is 23 years (Dutra 1938, Montti et al. 2011). Clark (2001) proposed the intermast period of *Chusquea capituliflora* to be 16 years, although this species may also flower sporadically.

RESULTS

DISTRIBUTION

We obtained records of *S. falcirostris* at 33 localities and of *S. frontalis* at 29 localities in Argentina, Paraguay, and southern Brazil, distributed in an eastern and a western cluster (Fig. 1, Appendix 1). Our own records represent over 1100 Temminck’s Seedeaters and 120 Buffy-fronted Seedeaters, the vast majority for times and places with seeding bamboos (Appendix 1, Table 2).

The records in the western cluster in Argentina, Paraguay, and the interior of southeastern Brazil from 2004 to 2011 (Appendix 1) were related to the masting of *G. chacoensis*. Most records pertain to *S. falcirostris*, only a few records to *S. frontalis*. Although a few birds were observed feeding on the sporadically flowering *C. ramosissima*, the overwhelming majority fed on *G. chacoensis*. Neither *S. falcirostris* nor *S. frontalis* was found on mast-seeding *Merostachys clausenii* (see Areta et al. 2009 for details).

The records in the eastern cluster in coastal southeastern Brazil from 2005 to 2011 (Appendix 1) were related to four consecutive episodes of bamboo masting. First, *M. multiramea* flowered from the second half of 2005 to 2006 throughout the montane and subtropical ombrophylous forest of Santa Catarina, usually above 400 m above sea level. We observed only *S. frontalis* using this resource. Second, *C. capituliflora* flowered from September 2006 to July 2007, mainly in the Médio Vale do Itajaí. We observed only *S. falcirostris* feeding on this resource. Third, *C. capituliflora* flowered asynchronously in two areas from March 2008 to March 2009, beginning with some clumps in the Médio Vale do Itajaí, and continuing along all the Atlantic scarp of northeastern Santa Catarina, Vale do Itajaí, and the northeastern Grande Florianópolis region from 0 to ~500 m above sea level. This resource was used by both *S. falcirostris* and *S. frontalis*, which we sometimes observed together. Fourth, *G. tigoara* flowered from at least October 2010 to September 2011 at Pedra d’Ampolar, and it was also used by both seedeaters.

ABUNDANCE

At several localities, the two seedeaters’ abundance fluctuated widely in direct relation to seed availability (Appendix 1). For example, in Parque Nacional Iguazu, the abundance of *S. falcirostris* was directly related to the percentage of seeding bamboo: for equivalent percentages of bamboos seeding larger numbers of birds were counted in the right tail of the distribution of bird abundance than in the left tail (Appendix 1). This is expected given the abundance of birds during the peak of seeding, which contrasted with the lack of birds before the bamboo seeded. Likewise, at Morro da Turquia, records were concentrated during the peak of seeding and few birds were noted at the beginning and end of seeding (Appendix 1). Although *S. falcirostris* was formerly abundant at Avancini, there were

TABLE 1. Structural and natural-history features of six Atlantic Forest bamboos used by Temminck's Seedeater (*Sporophila falcirostris*) and the Buffy-fronted Seedeater (*S. frontalis*) in Argentina, Brazil, and Paraguay. See Methods for details of masting.

	<i>Guadua chacoensis</i>	<i>Guadua tagoara</i>	<i>Merostachys neesii</i>	<i>Merostachys multiramea</i>	<i>Chusquea ramosissima</i>	<i>Chusquea capituliflora</i>
Distribution	southeastern Bolivia, southern Brazil, eastern Paraguay, and north-east Argentina	Brazil (Bahia to Rio Grande do Sul)	Brazil (Rio de Janeiro to São Paulo)	southeastern Brazil (São Paulo to Rio Grande do Sul) and northeastern Argentina (Misiones)	southeastern Brazil (Bahia to Rio Grande do Sul), northeastern Argentina (Misiones), eastern Paraguay, and northern Uruguay	Brazil (Rio de Janeiro to Rio Grande do Sul)
Altitudinal range (m above sea level)	75 to 450 m	50 to 1200 m	~700 to 1200 m	10 to ~700 m	5–700 m	10–700 m
Height	10–20 m	10–15 m tall (up to 20 m)	10 m	6–9 m (up to 12 m)	3–6 m	5 m
Culm diameter	8–15 cm	5–10 cm	3 cm	3–4 cm	0.5–1.5 cm	0.7–2 cm
Habit	culms erect below and arching apically	culms erect at base but arching above foliage; secondary branches leaning on or pendant from trees	culms erect below, arching above, and hanging apically	culms erect below, arching above, and hanging apically	climbing; frequently hanging	climbing; frequently hanging and forming curtains of foliage
Intermast period	28–30 years	10–36 years?, polycarpic?	31–33 years	30 years	23 years?, asynchronous	16 years?, sporadically?
Seed size	11–22 mm	12–14 mm	10 mm	10 mm	7–9 mm	6–10 mm
References	Londoño and Peterson 1992, Vega and Cámara Hernández 2008, Areta et al. 2009, Schmidt and Longhi-Wagner 2009	Clark and Londoño 2002, Alves 2007, Schmidt and Longhi-Wagner 2009	Sendulsky 2001, Filgueiras and Shirasuna 2009, Cestari and Bernardi 2011, pers. obs.	Sendulsky 1995, Rugolo de Agrasar and Rodriguez 2002, Schmidt and Longhi-Wagner 2009	Dutra 1938, Judziewicz et al. 1999, Clark 2001, Schmidt and Longhi-Wagner 2009, pers. obs.	Judziewicz et al. 1999, Clark 2001, Schmidt and Longhi-Wagner 2009, pers. obs.

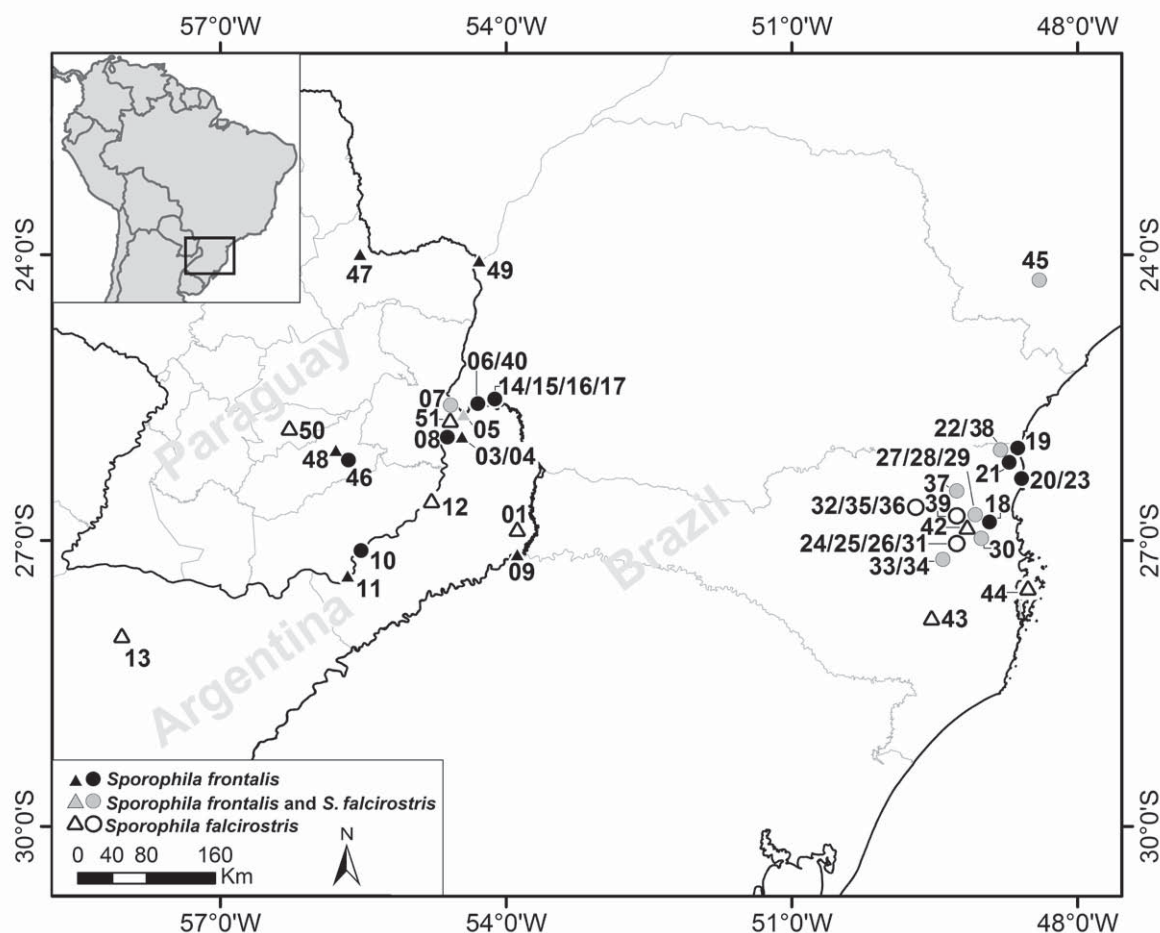


FIGURE 1. Distribution of Temminck's Seedeater (*Sporophila falcirostris*) and Buffy-fronted Seedeater (*S. frontalis*) in Argentina, southern Brazil, and Paraguay (from data in Appendix 1). Triangles = literature records, circles = new records.

TABLE 2. Sum of maximum number of birds per locality and habitat and number of localities (in parentheses) in which Temminck's Seedeater (*Sporophila falcirostris*) and the Buffy-fronted Seedeater (*S. frontalis*) were recorded during this study in Argentina, Brazil, and Paraguay. Ratio of number of birds/localities in square brackets. Data from Appendix 1.

	<i>S. falcirostris</i>	<i>S. frontalis</i>
Bamboo habitats		
<i>Guadua</i>		
<i>G. chacoensis</i>	1006 (12) [84]	3 (3) [1]
<i>G. tigoara</i>	6 (1) [6]	41 (2) [20.5]
<i>Merostachys</i>		
<i>M. multiramea</i>	—	10 (1) [10]
<i>M. neesii</i>	—	34 (2) [17]
<i>Chusquea</i>		
<i>C. ramosissima</i>	13 (2) [6.5]	—
<i>C. capituliflora</i>	97 (7) [14]	76 (7) [11]
Nonbamboo habitats	12 (8) [1.5]	5 (3) [2]

none and no seeds of *G. chacoensis* by 15 February 2010, but other seed-eating birds such as the Double-collared Seedeater (*Sporophila caerulescens*), Chestnut-bellied Seed-finch (*Oryzoborus angolensis*), and Saffron Finch (*Sicalis flaveola*) were still present in the same abundance as on previous visits, evidencing a null response to availability of seeds of *G. chacoensis* (Appendix 1). Similarly, at Puerto Bemberg, 14–17 August 2010, we heard single Temminck's Seedeaters calling daily as they moved for long distances over the crown of the higher trees, presumably looking for bamboo seeds after the seeding was over, calling only a few times at each spot and never singing, and none was detected on later visits, 1–4 December 2010 and 5–8 April 2011 (Appendix 1; see also Bodrati et al. 2012).

The large masting of *G. chacoensis* in the western cluster attracted more than 100 Temminck's Seedeaters to three localities: Apepú in Parque Nacional Iguazú and Avancini and Peterson on Península Andresito, while concentrations at mastings of *G. tigoara* and *C. capituliflora* (eastern cluster) and *C. ramosissima*

(western cluster) never exceeded this number. The largest concentration occurred at Apepú, where we counted at least 734 individuals between 28 and 31 July 2008 (Appendix 1, Table 2). Even though the standard deviation is large, the simple ratio of number of birds per locality provides a rough estimation of the attraction that each bamboo exerts on each species of seedeater (Table 2).

FOOD AND FORAGING

Bamboos. We recorded *Sporophila falcirostris* feeding upon green and ripe seeds and flowers of *G. chacoensis* and upon ripe seeds and flowers of *C. ramosissima* in Argentina, on seeds of *G. chacoensis* in Paraguay and on seeds of *G. chacoensis*, *G. tagoara*, and *C. capituliflora* in Brazil (Appendix 1). Most foraging of *S. falcirostris* consisted of gleaning seeds of *Guadua*. By far the most common maneuver was “gleaning” with a lesser proportion of attacks performed by “reaching” and a minor number of attempts by “hanging down on vertical and horizontal branches” and by “hanging up.” Overall, *S. falcirostris* is neither a very active nor an acrobatic bird, remaining still for long periods of time in the same place and taking seeds from the stalks while perching vertically. We have repeatedly found birds of both sexes grasping bamboo spikelets with their feet (“clasp”). Usually they first took spikelets from the stalk with the beak, then transferred them to one foot, turned them facing upward and proceeded to extract the seed with the bill. The remaining cover of the seed was discarded. Occasionally a bird even flew from one perch to another holding a bamboo seed in its foot, then consumed it after landing. Only once, at Parque Nacional Iguazu, did we see a female *S. falcirostris* descending from a low perch to take seeds from a spikelet on the ground. After taking the seeds she flew back to the same perch. The sequence was repeated several times. Some adult birds were observed “hovering,” and others hovered to take seeds from the stalks (9 September 2008, Appendix 1). The strong preference for bamboo seeds was exemplified on 2 August 2008, where in a large area of Península Andresito, the only bamboo in sight, a single *G. chacoensis* with 21 seeding culms, attracted a singing adult male and four female/young birds that fed on its seeds; the birds were absent when no seeds were available (Appendix 1). At several localities, *S. falcirostris* occurred with *Haplospiza unicolor* and the Sooty Grassquit (*Tiaris fuliginosus*), all three species feeding on the seeds of *G. chacoensis* (Appendix 1).

Feeding on some species of bamboo was easier than on others. Evidently, it was much more difficult for *S. falcirostris* to reach seeds of *C. ramosissima* than those of *G. chacoensis*. When at Parque Nacional Iguazu a group of ~8 individuals fed upon *C. ramosissima* seeds and perched on the weaker seed stalks, these stalks bent, obliging the birds to engage in maneuvers more acrobatic than those required from the horizontal perches that they enjoyed when feeding on *G. chacoensis*. On 13 June 2008, for example, a female stretched so much in an attempt to reach the flowers of *C. ramosissima* that she fell from the perch.

We recorded lone individuals or groups of *S. falcirostris* as they appeared to search for bamboo seeds (see Abundance above, Appendix 1). On 16 January 2008 at Parque Nacional Iguazú we observed an adult male and two female-plumaged birds passing through then leaving a stand of *G. chacoensis* without seeds, suggesting that these birds were actively looking for seeds. At Güirá-Pe, in a marshy area surrounded by forest without bamboo, we heard a nomadic individual passing only once, 19 April 2009, despite our stay of 11 days in the area (Appendix 1). At Avancini on 23 November 2008, a group of 25–30 Temminck’s Seedeaters was moving in one direction but asynchronously, with birds dispersed over multiple culms and searching for seeds among clusters formed mostly by oddly shaped, densely packed spikelets. The birds searched for a few seconds then moved on, as if searching communally to optimize bamboo-seed discovery. They kept in contact by their calls but did not sing (Appendix 1).

We recorded *S. frontalis* feeding on seeds of *G. chacoensis* in Argentina and on seeds of *G. tagoara*, *M. multiramea*, *M. neesii*, and *C. capituliflora* in Brazil (Appendix 1). At Parque Estadual Intervales, an episode of large-scale masting of *Merostachys neesii* was over on 20 August 2010 when we located a group of 5 or 6 Buffy-fronted Seedeaters in the canopy associating with a group of 6–8 Uniform Finches in the understory as they searched for seeds on a dead bamboo clump where no seeds were available (Trilha Mirante das Antas). The birds flew past this area, where there was also a large patch of vegetative *G. tagoara*, and were not seen over the next two days. At a distant spot on the same trail, we heard a male singing twice as it moved through the canopy. The next day, on a distant trail, we heard a male *S. frontalis* singing sporadically as it moved through the canopy, and we found a presumed pair feeding on the few seeds left in a small patch of *M. neesii*; although a pair of *H. unicolor* was accompanying them, they did not feed on the seeds and left the area promptly while the seedeaters were feeding. The pair of *S. frontalis* grasped 3–5 stalks simultaneously in order to support their weight, after which they were able to take seeds directly from them by hanging down, clinging, or stretching. We also observed the male hovering to take a seed. Local guide Faustino Avelino (pers. comm.) mentioned seeing *S. frontalis* eating seeds of *G. tagoara* (taquarussu), *M. neesii* (taquara-poca), and possibly *Chusquea* (lambe-papo). Accordingly, we recorded both seedeaters from 2002 to 2005 during the seeding of *G. tagoara* (Appendix 1).

Near Blumenau, when foraging communally on *C. capituliflora*, both *S. falcirostris* and *S. frontalis* crushed husk by husk until they found an edible seed (Appendix 1). Once all the husks of a spikelet were crushed, both species cut it off and moved to another spikelet.

Insects. Most of our observations of *S. falcirostris* feeding on insects were in stands of *Guadua* in Iguazú and Iguazú national parks (Appendix 1). The birds foraged for insects in three ways: chasing insects in flight (“flutter-chase”), directly

“gleaning” small arthropods from the base of *G. chacoensis* leaves, and “hovering” to take insects from the bamboo stems. For example, on 30 July 2008, when a rain began along the road at Apepú, only *S. falcirostris* chased insects in flight; neither *H. unicolor* nor *T. fuliginosus*, which were in the same stand of seeding *G. chacoensis*, did so. On 29 July 2008, a group of four Temminck’s Seedeaters foraged among the green leaves of *C. ramosissima* and in the foliage of a small 5-m shrub, and a female-like bird looked for insects in a white and foamy ball of spider web. On 18 January 2008 a female took insects from the base of *G. chacoensis* leaves. On 6 September 2007 an adult male captured insects in flight, returning to its perch, and in descending flights, changing perches; when doing so, he reached the lowest altitude at which we saw him (5 m), though he kept higher (10–14 m) when foraging on *G. chacoensis* seeds. On 13 September 2008 a young male *S. falcirostris* looked for insects on the side of the main trunk of a group of isolated very mossy trees at Parque Nacional do Iguazu. This bird passed its bill laterally on the mosses on one side of the tree and looked into and probed a diverse array of epiphytes such as ferns, small bromeliads, and especially *Tillandsia* sp. The trees were almost devoid of leaves but their trunks and branches were festooned with moss and epiphytes. The bird clung almost vertically to the surface of the main trunk either parallel or perpendicular to it. We recorded two mixed-species flocks in which *S. falcirostris* was feeding exclusively upon insects (flocks 11, 12, see Appendix 2, available at <http://dx.doi.org/10.1525/cond.2012.120064>).

Alternative food sources. We observed *S. falcirostris* feeding on two alternative sources of seeds in disturbed areas near forest borders in the eastern cluster: rice (*Oryza sativa*; road PR-412, 30 August 2003), and a grass (*Panicum* sp.) at Vila da Glória, 21 December 1999. Also, it was probably feeding on an unidentified grass species when no bamboo species were

masting (road SC-415, 27 October 2010; see Appendix 1). We observed *S. frontalis* feeding on rice and once on the dry fruits of an unidentified species of native tree in Parque Nacional da Serra do Itajaí, Indaial, in the eastern cluster, 17 July 2007

Mixed-species flocks. During winter and, especially, autumn we recorded *S. falcirostris* in mixed-species flocks in and away from bamboo stands (Appendix 2). Our only record of *S. frontalis* in a mixed-species flock is of an adult male in a winter canopy flock (no species list available), foraging on what looked like small insects and on some fruits or seeds of an unidentified tree at a forest edge without seeding bamboo (Parque Nacional da Serra do Itajaí, Indaial, 17 July 2007).

TERRITORIALITY AND TERRITORY SIZE

The vast majority of the territories of *S. falcirostris* and *S. frontalis* were near or within stands of seeding bamboo and were defended aggressively against conspecifics (Tables 2, 3). The easiest way to detect (and many times also to identify) *S. falcirostris* and *S. frontalis* is by listening for their voices. The loud vocalizations of both species and their small territories of $\sim 30 \times 30$ m allowed males to cover the whole territory at once while singing from a central perch. We found territorial birds year round, and lack of territoriality was related either to foraging flocks or to lack or scarcity of bamboo seed (Appendices 1, 2). Details of territorial behavior and number of territories found appear below (see Table 3 for summary).

On 29 July 2008, *S. falcirostris* had established at least 6 territories within ~ 200 m near the house at Apepú; on 1 September 2008 we located 5 territories each occupying $\sim 30 \times 30$ m. On 30 July 2008, of over 700 Temminck’s Seedeaters recorded at Apepú, we found only 12 more than 150 m away from any seeding bamboo. Here, on 11 September 2008, we estimated that 90% of the over 200 territories of *S. falcirostris* were

TABLE 3. Summary of new records of breeding of Temminck’s Seedeater (*Sporophila falcirostris*) and the Buffy-fronted Seedeater (*S. frontalis*) in Argentina and Brazil; b = building, f = fledgling, n = nest, t = territorial birds. See Breeding and Appendix 1 for details.

Bamboo species and locality	<i>S. falcirostris</i>	<i>S. frontalis</i>
<i>Guadua chacoensis</i>		
Parque Nacional Iguazu: Apepú	January 2008 [f], July 2008 [t], September 2008 [t/b/n], November 2008 [t/f]	—
Península Andresito: Avancini	August 2008 [t/n], September 2008 [t/n], November 2008 [t/f]	—
Península Andresito: Peterson	August 2008 [t/n]	—
Península Andresito: Güirá-Pé	July 2008 [f]	—
<i>Guadua tagoara</i>		
Pedra d’Amolar	July 2011 [t/f]	July 2011 [t/f]
<i>Chusquea capituliflora</i>		
Morro da Turquia	August 2008 [t]	August 2008 [t/f/n]
Área de Proteção Ambiental municipal das Ilhas Fluviais do Rio Itajaí-Açu	September 2006 [t], October 2006 [t], November 2007 [f], May 2008 [f]	—
Bairro da Velha	—	August 2008 [t/f]

within stands of seeding *G. chacoensis*, 5% were 50–200 m from such stands, and another 5% were over 200 m from them (although there may have been seeding bamboo nearby that went undetected, especially on the Brazilian shore of the Iguazu river). On 9 September 2008, an additional 15 territorial pairs defended areas of $\sim 30 \times 30$ m at Apepú, while on 18 September 2008, 13 territories (no size estimate) were in two *G. chacoensis* stands at Avancini. In ~ 300 m of the trail that descends to the waterfalls at Parque Nacional do Iguazú, on 13 September 2008 we found 10 territories of *S. falcirostris*, all within 50 m of seeding *G. chacoensis*.

Although at Parque Nacional Iguazu males were territorial year round, on 28 July 2008 males of *S. falcirostris* sang much more in seeding *G. chacoensis* than when they were in mixed species flocks in *C. ramosissima*, and they fed much more on *G. chacoensis* than on *C. ramosissima* (see Food and foraging). At Avancini on 4 August 2008, many Temminck's Seed-eaters, including several in female-like plumage, were singing the full complex song intensely. At least three times we found two males singing continuously; while one sang the complex song the other uttered the trill. We never observed serious agonistic encounters between these males, though we were able to tape-record the voices of two birds chasing in flight. We also observed two birds (presumably male and female) with the male chasing the female for 5 min but always at close range and without fighting; we suspect this was a sexual chase.

Both members of a pair that was feeding on *G. chacoensis* seeds at Parque Nacional Iguazu responded to playback by approaching the sound source in silence and later vocalizing at close range. The male sang a trill on an even pitch, but every time we played song at it, it flew toward the sound source, landing closer to us, after which it raised its wings to the sides and vibrated them rapidly with the tail upright as it uttered a very soft trill. The female was also observed performing the same threat display. A second pair in a more distant *G. chacoensis* stand called softly while engaged in sexual chases. They engaged in a fight and fell rolling in the air with tangled beaks and feet from 6 to 1.5 m from the ground, when they separated, flying off in opposite directions. A few seconds later, the male fed the female sporadically, and she shook her wings and uttered a soft churring call when fed with *G. chacoensis* seeds. Birds were much more widely spaced and territorial on 7 September 2008 during late winter than during early winter (see Breeding).

At Pedra d'Amolar on 5 and 7 July 2011, three territorial male Buffy-fronted Seed-eaters with adjacent territories of $\sim 30 \times 30$ m sang the full song intensely, each from its preferred perch. In response to playback, two of them approached the sound source unobtrusively (descending a few meters in the same trees) and changed from the full song to the call. A fourth, isolated, territorial male responded aggressively to playback, approaching to within 2 m of the observers, and began calling loudly from a perch at close range. On 5 July 2011, at the "creche" in a stand of *G. tagoara* (see Breeding),

we tape-recorded an impressive burst of calls by a large flock of *S. frontalis*. Some minutes later, while the calls continued, small parties ranging from 2 to 5 and totaling ~ 30 individuals flew across a large open area of ~ 1 km to the other side of the mountain valley.

A pair of *S. frontalis* foraging on the few remaining seeds of *M. neesii* at Parque Estadual Intervales, 21 August 2010, ignored the playback of calls and songs, indicating nonterritorial behavior (see Foraging). Groups sang as they moved through the forest canopy searching for bamboo seeds despite not being territorial, 20 August 2010. The same behavior was observed on 2 September 2008 at Área de Proteção Ambiental das Ilhas Fluviais do Rio Itajaí-Açu, where small flocks sang intensely while moving at 50 m from the ground in the canopy.

BREEDING

We recorded breeding of *S. falcirostris* and *S. frontalis* only during episodes of bamboo masting irrespective of the season of the year, as we detail below (see Table 3 for summary).

Study nests. We found nest 1 of *S. falcirostris* on 8 September 2008 at Apepú. It was located 5 m above the ground in a fork of a *Eugenia involucrata* tree, on a lateral branch 50 cm in from the outer edge of the tree. The outer portion of the nest was built from the creeping rhizome of a climbing *Microgramma*-like fern from which the fronds were removed. The translucent cup was made up of few such fibers, which also tied the nest to the fork. The fern was gathered at a nearby tree, 5 m from the nest. Early in the morning when we found the nest, the sides were more developed than the bottom, but later on that day the bottom became more solid.

Only the female took part in nest building as the male escorted her back and forth. To reach the nest, the female used two or three different perches, which were at the same height as the nest or from 0.5 m to slightly above 1 m higher. The female entered the nest and built it by tying knots or adding and manipulating fibers and lichens from inside the nest or when perched on its rim. The female shaped the nest by pressing the inner walls with the body and pressing from inside and outside with the wings as she sat inside. The male, with the female already in the nest, approached the nest by short leaps and then while perched on the nest rim or at a distance of 5–20 cm delivered an evenly pitched trill and a series of soft calls. He generally reached the nest 5–10 sec after the female, even when both arrived at the nest tree simultaneously. The male sang within a 30-m radius of the nest while other males vocalized just beyond this radius. Although only the female brought material and built the nest, on at least two occasions the male sat on the nest and left hastily as if nervous. The single day that we were able to study the nest before sunrise, construction began at 07:40, when the female removed a leaf that had fallen inside the nest and incorporated it into the nest structure. The female's rate of construction was low at 0.025 visits min^{-1} or 1.35 visits hr^{-1} over 9 visits. On all but

one of the visits the male was singing and trilling either on the nest tree (usually ~2 m above and ~2 m to the side of the nest) or on a neighboring tree while the female built; in all instances the male and female arrived together at the nest tree or a neighboring tree and both flew out of the nesting area together. Only once did we hear the male singing without the female being engaged in construction.

Nest 2 of *S. falcirostris* we found on 18 September 2008 at Avancini. It was built with black fibers inside and with the same tree-fern fibers as nest 1 outside and below. It was attached to a climbing ivy by these ferns and placed in a multipronged fork of the same ivy where it contacted the main trunk of a *Cecropia pachystachya* from which the ivy hung. The *Cecropia* was 7.5 m high, and the nest was at 4.5 m from the ground. The female was apparently incubating, as she was sitting in the nest on all four of our visits. While female sat, the male sang at a moderate rate and intensity.

When flushed from the nest, the female uttered a soft, shrill peep, much softer than that of the males (tape-recorded). After being flushed, she joined the male and both foraged together on *G. chacoensis* seeds, calling each other within a 15-m radius of the nest. The male and female flew together very close to each other and frequently descended to 2–3 m from the ground while uttering their peeps nervously. Besides the calls, the male also emitted the evenly pitched trill and an arrested version of the full song. On one occasion, while the pair was foraging, they were scared by a rapid flight of a large group of White-eyed Parakeet (*Aratinga leucophthalma*) that was foraging and descended in free fall from 10 m to ground level, hiding in the dense understory. The next day, we tape-recorded the male singing as the female incubated.

Other nests. At Peterson we found two nests of *S. falcirostris* under construction. The first nest was placed 5 m high, wedged between the culm and a branch of *G. chacoensis* and was just a ring of black rootlets. A female flew away from this structure. A second nest was a small cup very well hidden at 10 m from the ground, and a female was taking material to it. On 2 August 2008 we also encountered several nestlike structures that appeared to be old nests of *S. falcirostris* near each other on dry branches of *G. chacoensis*. The next day at Avancini we found two other nestlike structures.

At Apepú on 9 September 2008 we filmed a nervous pair low in the vegetation, the male singing as low as 20 cm from the ground. Some 5 m away from this point, we found an almost finished nest on the ground that we presumed belonged to this pair. As we approached the fallen nest, the female made a free-fall flight, passing by us at very high speed, and the male flew so close to us that he almost touched our heads. The outer rim and lower portion of the nest were built of *Microrhizoma*-like creeping rhizome, the outside of leaves and seeds of *G. chacoensis* and small unidentified fern fronds and moss on the outside, and the inside of reddish-brown arched fibers.

Fledglings and indirect evidence of breeding. On 4 September 2007 in Parque Nacional Iguazú we found a presumably nesting pair of *S. falcirostris* moving low through the forest, keeping in close contact. From 16 to 18 January 2008 we found ~20 fledglings being fed by female-plumaged birds in the same park. We never observed male-plumaged birds feeding the fledglings. Fledglings were exclusively fed seeds of *G. chacoensis* regurgitated by the adult female. Fledglings frequently gathered in groups, but we also encountered pairs accompanied by two fledglings, suggesting a clutch size of at least two. On one occasion, while the female fed fledglings with seeds, the male captured insects in flight. We tape-recorded these fledglings' begging calls, which were accompanied by a fast and shallow wing vibration; fledglings followed the female through the bamboo stands begging for food. The decreased vocal activity of males of *S. falcirostris* between September–November 2007 and January 2008, and the presence of fledglings in mid January 2008, strongly suggest that most breeding took place between September and November and there was little or no breeding in January.

At Apepú, large foraging groups of *S. falcirostris* were characteristic of the winter, but by 9 September 2008 they had broken up and we found pairs segregated in territories of roughly 30 × 30 m. We observed at least 15 such pairs moving low in the understory, in some cases the females carrying or looking for nesting material. Females were always accompanied by males.

We tape-recorded several fledglings of *S. falcirostris* at Apepú on 22 November 2008. At Avancini on 23 November 2008 where we noted 4 fledglings and ~40 other individuals of *S. falcirostris*, we heard only imperfect renderings of songs (young birds?) a couple of times; most of the time the birds were calling.

Winter breeding. In early July 2008 at Güirá-Pé, J. Mazzochi, P. Bertotto, and R. Ymbernon (pers. comm.) observed a pair with the female feeding fledglings over two consecutive days. Although there are no patches of *G. chacoensis* in this private reserve, there is a small patch in a neighboring property and several bamboo stands in the Península Andresito as a whole.

From 5 to 7 July 2011 we found evidence of massive winter breeding at Pedra d'Amolar: at least 10 fledglings of *S. frontalis*, 4 of *S. falcirostris*, 3 of *T. fuliginosus*, and 2 of *S. caerulea* in a particularly stunted (4-m-high) stand of *G. tigoara* that was bordered by a pasture in a very steep area. Most fledglings were confined to this area, which acted as a multi-species "creche," presumably because of both the large number of seeds and the ease with which birds may escape predators. At least twice, we saw three *S. frontalis* fledglings begging from a single female, suggesting that the clutch consisted of at least three eggs. Females with the mouth full of (and overflowing with) seeds were encountered several times. We tape-recorded the begging calls of all these species. Females of *S. frontalis* uttered a peculiar metallic call that apparently functioned to

generate cohesion with the family (fledglings). We also tape-recorded voices of a male *S. frontalis* learning to sing. On the basis of their very short tails, we estimate that the youngest fledglings of that species had left the nest less than 6 days earlier. The bills of fledglings of *S. falcirostris* were all very dark and appeared to be darker than those of the adult females, and fledglings also appeared to have bills smaller than those of the adults. All fledglings of *S. frontalis* had well developed orange wing bands, and some also had an incipient short pale eyebrow (see also Sabel 1990), while those of *S. falcirostris* were plain-winged and plain-faced. The rictus of fledglings of both species was fleshy yellow.

During winter (August 2008) at Morro da Turquia, adult males of *S. falcirostris* and *S. frontalis* vocalized intensely in fixed territories. The report by a local inhabitant of 15 nests of *S. frontalis* placed in a stand of seeding *C. capituliflora* and the observation of a female *S. frontalis* feeding a fledgling suggest that both species were breeding during the masting of *C. capituliflora*.

There is apparently no seasonality in the appearance of eclipse (nonbreeding) plumage, as several males of *S. falcirostris* observed and photographed during winter in Pedra d'Amolar had fully developed yellow bills and gray plumage. Some fully gray males of *S. falcirostris* had bright yellow nails [e.g., WA288950, WA289069], a feature that seems under-reported in the literature but has been mentioned for *S. schistacea* (Sick 1997, Restall 2006). We never observed *S. frontalis* with yellow nails.

ROOSTING

At Avancini on 23 November 2008, two adult male Temminck's Seedeaters roosted 8 m from the ground on a dry horizontal *G. chacoensis* branch that was covered by dense ivy. They occasionally opened their eyes without moving their bodies. We left the area at 19:55 when it was almost totally dark and the two birds were asleep.

DISCUSSION

DISTRIBUTION

Both *S. falcirostris* and *S. frontalis* are nomadic. Their nomadism is not associated with any seasonal factor: birds were present throughout the year over several consecutive years where the supply of bamboo seed was constant enough. The south-to-north wave of flowering of *G. chacoensis* in the western cluster resulted in birds remaining in the region longer than expected if the flowering in this area was absolutely synchronous (Areta et al. 2009). In the eastern cluster, four consecutive pulses of bamboo masting allowed birds to remain in the region for several consecutive years. The lack of records between the eastern and western clusters may be explained by lack of surveys in the area, lack of bamboo and forest in a highly disturbed landscape or both. In light of these findings, the records of single or few individuals not

directly associating with bamboo seeding can be interpreted as representing individuals searching for bamboo patches or as occurrences due to recent bamboo seeding nearby. No stable populations formed by resident individuals are known in any part of these species' ranges, which has important implications for their conservation (see below). The records of transient birds (recorded for a single or a few consecutive days) at several places near the beginning or after the end of a nearby massive burst of seeding, and the records of flocks searching for seeds on the few remaining dry and dead bamboo culms left in some areas provide strong evidence of their food-related displacement.

Both *S. falcirostris* and *S. frontalis* can be considered regional nomads (sensu Areta and Cockle 2012) since they completely vacate large regions in the absence of their preferred food resources. Interestingly, the extent of nomadism may vary from the center to the edges of the species' ranges. Areas in the center of any bird's range should, logically, have a greater chance of being visited by a bird in transit to a bamboo patch.

Davis (1945) included two bamboo-seed specialists, *S. frontalis* and *H. unicolor*, rather ambiguously in his two presumably exclusive categories of migratory and nomadic birds. At Fazenda Boa Fé, he recorded *S. frontalis* in December 1942 (4 birds), January 1943 (76), February 1943 (7), and March 1943 (1) and *H. unicolor* from November to May, peaking abruptly also in January 1943 with 185 birds. Both birds "came in to feed on the seeds of the small bamboo" (Davis 1945:279). Sick (1997) suggested that *S. falcirostris* may be migratory, as the birds disappeared periodically, but also mentioned that *S. falcirostris* and *S. frontalis* "migrated" to feed on bamboo seeds; although he never used the term "nomadism" he seemed to be aware of such behavior since he mentioned that the long cycles of masting would not have allowed a single bird to feed more than once in its life on a bamboo at a single locality. Sigrist (2009) mentioned that *S. falcirostris* has "migratory habits," which we consider to be wrong.

The total geographic range of bamboo-seed specialists must be understood as an incidental effect of the accumulation of the birds' occurrences at different points. In this sense, the boundaries of the range are more dynamic than are those of resident and migratory species. The total range is greater than the realized range because it represents the limits of where nomadic birds may be expected.

Although on a coarse scale *S. frontalis* and *S. falcirostris* are ecologically similar and sympatric across most of their distributions, *S. falcirostris* has been recorded regularly in large numbers in the interior Atlantic Forest of Argentina, Paraguay, and Brazil, while *S. frontalis* has seldom been observed far from the coastal Atlantic Forest of Brazil with few records (none properly documented) for Argentina and Paraguay. In our study area, altitudinal records of *S. frontalis* range from 35 to 1060 m above sea level (most between 300 and 850 m), while those of *S. falcirostris* range from 5 to 850 m (most between 50 and 300 m). We therefore propose that there is an intrinsic

difference in habitat preference and geographic distribution between these seedeaters, with *S. falcistrostris* favoring lowland and mid-elevation forests in the coastal mountains and interior and *S. frontalis* preferring mid- and high-elevation forests in Brazilian coastal mountains, rarely extending >100 km inland. Although *S. falcistrostris* has been considered less abundant than *S. frontalis*, being at best uncommon at any locality (Ridgely and Tudor 1989, Collar et al. 1992), our data from Argentina challenge this view and instead point toward these habitat/altitudinal preferences as the main explanation for the species' differences in local abundance.

The dynamic and clumped distribution of these seedeaters precludes the calculation of (and makes meaningless) any estimate of their population densities over their entire distribution. For example, although BirdLife International (2011) estimated "0.5–2.5 individuals/km² × 4,100 km² (10% EOO) = 2,050–10,250," it is virtually impossible to attach a biological meaning to this value. Moreover, given that a large part of the population may be concentrated in high density at a few spots at any given moment, the extrapolation of a mean density to the whole range lacks any solid basis and should be avoided. The spatial pattern of abundance of nomadic bamboo seedeaters is not appropriately described by average values.

In Brazil, *S. falcistrostris* is known from Bahia to Paraná (Sick et al. 1981, Ridgely and Tudor 1989—see documented records in www.wikiaves.com.br). Our records are the first documentation of *S. falcistrostris* for the state of Santa Catarina and extend the southern limit of the species' range south about 100 km. Previous undocumented records from northeastern Santa Catarina either without specific localities (Straube et al. 2004) or from Guaruva and Itapoá (Machado et al. 2008) were in need of confirmation (Silveira et al. 2009). In Brazil, *S. frontalis* occurs from southern Bahia to Rio Grande do Sul; Bencke et al. (2003) considered it probably extirpated from the latter state. Despite the number of records for Santa Catarina, ours are the first observations of large flocks foraging and breeding during masting of bamboo in that state.

FOOD AND FORAGING

Our abundant field data reinforce and substantiate the widely held notion that *S. falcistrostris* and *S. frontalis* are bamboo-seed specialists that depend on the cycles of bamboo flowering and seeding. The largest concentrations of *S. falcistrostris* were observed in northern Misiones during the seeding of *G. chacoensis*, suggesting that it is the true attractor of seedeaters into the area and that they feed on seeds and flowers of *C. ramosissima* only opportunistically.

We observed *S. falcistrostris* and *S. frontalis* clasping seeds with their feet. The Magpie Mannikin (*Lonchura fringilloides*), a partial bamboo-seed specialist, is also known to hold bamboo spikelets with its feet to feed on them (Restall 1995), suggesting that grasping with the foot might be an

important behavior of some bamboo-seed specialists that feed on large seeds (see Baptista 1976). The cutting off of spikelets of *C. capituliflora* of which all husks have been crushed may represent an adaptation to reduce energy expenditure and search time for energy-poor sources. Birds feeding on seeds of *C. aff. meyeriana* may also cut spikelets off; Olmos (1996) reported *H. unicolor* crushing many empty husks before finding an edible seed.

Bamboo-seed specialists may feed on alternative food sources when no bamboo seed is available (Areta et al. 2009). For example, Sick (1997) reported *S. falcistrostris* feeding on seeds of *Hypolirum* sp. (Cyperaceae) in forest clearings, and Pimentel and Olmos (2011) noted *S. frontalis* feeding on seeds of cf. *Scleria* sp. (Cyperaceae) on the ground and in forest clearings after seeds of *Guadua* were exhausted. These sedges tend to dominate the forest floor once bamboo dies, and their seeds may be an important food for seedeaters once the masting of bamboo is over (F. Olmos, in litt.). Our data on other alternative food sources is in agreement with this conceptual framework. Historical and modern records of *S. frontalis* and *S. falcistrostris* feeding on rice (Berlepsch and Ihering 1885, Sick 1997, present work) coincide with what is known of *S. schistacea* (Fernandes and Deslandes 2008) and of southeast Asian bamboo-seed specialists, which are frequently recorded feeding on rice (Restall 1995). Rice is closely related to the woody bamboos (Kelchner and Clark 1997, Zhang 2000) and must be considered an introduced alternative food source in the neotropics (see Conservation). In the neotropics several species of wild rice may provide a regular food source in, for example, the large swamps along the coastal of southeastern and southern Brazil (F. Olmos, in litt.).

Flocking with other species has seldom been reported in these two seedeaters. Davis (1946) reported two Buffy-fronted Seedeaters with a mixed-species flock in forest at Fazenda Boa Fé in December, considering that species an accidental migratory member of such flocks during the nonbreeding season. Sick (1997) reported both species joining a winter flock of seedeaters including the Capped (*S. bouvreuil*) and Collared (*S. collaris*) at Lagoa Juparanã in July. Despite this, we have frequently encountered both *S. falcistrostris* and *S. frontalis* feeding on insects and bamboo seeds and flowers in mixed species flocks of varied composition at low, middle, and upper levels of riparian and mountain forests during autumn and winter.

These seedeaters' frequent pursuit of insects in flight and their feeding of nestlings with insects at least in captivity support the suspected relationship of rictal bristles to the importance of insects in their diet (Areta et al. 2009, see also Partridge 1964). A presumed female *S. frontalis* has been photographed preying upon a spider in Reserva Ecológica Guapiaçú (Dingain 2011).

In captivity, *S. falcistrostris* has been observed stripping the bark off small green branches and *Sambucus* trees and chewing *Ligustrum* and "Japanese bamboo," which were

taken as possible explanations for the peculiarly shaped bill (Sabel 1990). However, bill shape seems to be closely related to feeding on bamboo seeds (Areta et al. 2009).

BREEDING

On 5 August 1958, at Arroyo Uruguay-i, Misiones, W. H. Partridge collected a male *S. falcirostris* with enlarged testes, indicating the initiation of sexual development, while the ovary of a female collected that same day did not show signs of sexual activity (Navas and Bó 1987). The only previous report of *S. falcirostris* breeding in Argentina (Castelino 1990) was of a nest under construction during the seeding of *G. trinitii* at Parque Nacional Iguazú 15–17 August 1988. The nest was a cup made of moss placed 5 m from the ground on a *Sorocea ilicifolia* (= *S. bonplandii*) tree; as we observed, only the female carried material while the male escorted her. In Brazil, Collar et al. (1992) reported the gonads of two March specimens from São Paulo were inactive, and Sick (1997) reported nests placed high up in the vegetation at forest edge. The report of a male *S. falcirostris* (American Museum of Natural History 319136, Tibagy, Fazenda Monte Alegre, elevation 1000 m, Paraná, Brazil) with testes fairly enlarged in March (Collar et al. 1992) must be discarded. Our examination of this specimen shows that it belongs to an undescribed species, usually considered to be a “yellow-billed” Plumbeous Seedeater (*Sporophila plumbea*) (see Belton 1974).

In captivity, the male of *S. falcirostris* starts building the nest and the female completes it (Sabel 1990). Females lay two whitish eggs with reddish-brown blotches and smaller spots especially on the blunt end; although there are occasionally blackish markings, they never form the striations present on the eggs of *S. frontalis* (Sabel 1990). Incubation lasts 12 days, and chicks become independent after some 30 days. Females can lay a second clutch while young birds have not yet attained independence (Sabel 1990). In captivity, chicks were frequently fed flying insects and diverse nonflying arthropods like spiders, mealworm larvae, and ant pupae (Sabel 1990).

Although previous information suggests that the breeding season of *S. frontalis* is mostly spring as in other birds in its range (gonads inactive in June and August, enlarging in September, active in October, and regressing in December; Davis 1945, Collar et al. 1992), our records of massive winter breeding contradict this notion. Moreover, Davis (1945) recorded *S. frontalis* only from December to March, so his data are useless for evaluating winter breeding, as implied by Collar et al. (1992). The concentration of “thousands” of *S. frontalis* at Itatiaia during June and July 1952 during the seeding of *Merostachys* (Sick 1997) and that of hundreds (if not thousands) at the same place in September and October 1985 (Parker in Collar et al. 1992), perhaps due to the seeding of the same species, must have resulted in ample opportunities for breeding during winter and spring.

The report of a presumed female *S. frontalis* building ball-like nests of grasses in pine trees near a stand of seeding bamboo (Parker in Collar et al. 1992) is at odds with data from captivity, in which males build cup-shaped nests (Partridge 1964, Sabel 1990), and may stem from a misidentification, since it is in agreement with available data on *Tiaris fuliginosus* (Marcondes-Machado 1974, 1994, Areta and Bodrati 2008). In that species females build spherical nests of grasses and frequent plantations of exotic trees near stands of seeding bamboo, where they feed (Sick 1997, Sigrist 2009; pers. obs.).

Data on *S. frontalis* in captivity indicate that either the male alone builds the cup-shaped nest, leaving all the incubation and chick-rearing to the female, which does not allow the male near the nest (Partridge 1964), or that males choose where to place the nest, build the first portion of the nest, and later attract the female, which finishes the nest (Sabel 1990). Females lay 2 or 3 (most frequently 3) light gray to whitish eggs with neat light and dark brown spots accompanied by blackish filiform stripes and incubate for 12 days (Partridge 1964, Sabel 1990). Chicks feed alone at 26 days and become independent at ~30 days. Both sexes, but primarily the male, feed the fledglings (Sabel 1990). Females can lay a new clutch within 10 days of having fledged young (Partridge 1964), and once, 2 days after the chicks had left the nest, a female finished building a nest that the male had started, feeding the fledglings up to the moment when the third egg was laid, when the male alone took over the task (Sabel 1990). In captivity, a female *S. frontalis* fed the nestlings and herself mostly on flies that she caught in flight rather than with other nonflying protein sources (aphids and ant eggs) or seeds (Partridge 1964); another female fed on ant larvae and even took the larvae from her fledglings' bills if they were not swallowed quickly (Sabel 1990). Birds bred mostly from June to August after molting; however, after four consecutive clutches, there were chicks even in September. Some September eggs were infertile (Sabel 1990).

We interpret the capacity of *S. falcirostris* and *S. frontalis* for rapid breeding as a way of taking advantage of the episodic hyper-abundance of bamboo seeds in natural settings. In these species the division between breeding and nonbreeding seasons seems largely contingent on the availability of bamboo seeds. Although in captivity both species are sensitive to cold wet weather that coincides with their molt (Sabel 1990), we found them breeding during cold and rainy weather (Appendix 1). For bamboo-seed specialists, an abundant supply of bamboo seeds is analogous to spring, while lack of bamboo seeds can be said to constitute their winter. Despite the year-round breeding of bamboo-seed specialists, their substantial participation in winter mixed-species flocks and their nonterritorial winter concentrations to feed on seeding bamboos suggest that the role of bamboo-seed availability is secondarily modified by climatic factors (i.e., more birds are likely to breed during spring than during winter, if the supply of bamboo seed is held constant).

PLUMAGES

Plumage variation seems greater in the bamboo-seed specialists *S. falcirostris*, *S. schistacea*, and *S. frontalis* than in any other species of *Sporophila* (pers. obs., Sick 1997). Whether this has to do with sexual selection or it is a mere by-product of the protracted acquisition of the fully mature male's ornamental plumage is unknown. Given the explosive initiation of breeding, birds able to breed rapidly may have an advantage over those that take longer to mature. The complex plumages and variation in bill color may represent a signaling system of great complexity indicating age and breeding status.

Although brown-plumaged and yellow-billed Temminck's Seedeaters have been considered females (e.g., Chebez 2008), we contest this identification and suggest that these birds are sexually mature males that, for an unknown reason (arrested development, delayed maturation, polymorphism, etc.) have not acquired the normal gray plumage. We base our conclusion on several such birds' defending territories and singing the full song. Moreover, the relative scarcity of gray-plumaged birds, our repeated observations of pairs consisting of one dark-billed and one yellow-billed bird, and our observations of nests at which the female was always dark-billed and the male was always yellow-billed are all consistent with the interpretation of brown-plumaged, yellow-billed birds as males. Restall (2006) considered an equivalent plumage the "intermediate male, citron morph" in *S. schistacea*, sister species to *S. falcirostris* (Parker 1982, Lijtmaer et al. 2004), whose plumage maturation has been shown to take at least 5 years and which also is extremely variable.

Successful hybridization between *S. frontalis* and *S. falcirostris* is known in captivity, but the resulting phenotype is undescribed (Sick 1997:762). The copulation-solicitation positions of females of the two species are very similar, and in captivity a single female *S. falcirostris* produced seven chicks through hybridization with a male *S. frontalis* (Sabel 1990). She later produced three hybrid chicks with a male Yellow-bellied Seedeater (*S. nigricollis*), two of which lived for less than 1 year and one reached an age of 5 years. All the hybrids of *falcirostris* × *nigricollis* resembled their mother in coloration and bill shape. This same female was also observed copulating with a male Band-tailed Seedeater (*Catamenia analis*), indicating her acceptance of a wide range of male plumages (Sabel 1990). At Schroeder, Santa Catarina, 6 February 2011, Sydney Vargas photographed (WA 293096, 293116) an apparent hybrid with features that seem consistent with both *S. frontalis* and *S. falcirostris*. The frantic breeding activity in areas where both species are found together may result in occasional hybridization between them. However, we were unable to confirm hybridization in the wild at our study sites.

Although with captives in Germany Sabel (1990) reported *S. falcirostris* to molt in winter and *S. frontalis* to molt twice a year, March–May and September–November, in nature all plumage types may appear at any time of the year, making it

difficult to establish a seasonal pattern of molt and plumage acquisition. Indeed, there seems to be none. Although Sick (1997) reported an eclipse (post-breeding or nonbreeding) plumage, its appearance may depend largely on the particular environmental conditions the bird faces (i.e., abundance or lack of bamboo seeds) instead of following a cyclical seasonal pattern.

BIRDS AND BAMBOOS

The bulk of records of *S. falcirostris* and *S. frontalis* in our study area and elsewhere to the north are from seeding bamboos of the genera *Guadua*, *Merostachys*, and *Chusquea* (see Appendix 1, www.wikiaves.com.br). The geographic distribution of records and observations of feeding and nesting in *Guadua* strongly suggest that it was masting of that genus, rather than of *Merostachys* or *Chusquea*, that allowed the birds to occur sporadically over 50 years in the western cluster in Argentina (Areta et al. 2009, this work). The continued presence and winter breeding of *S. falcirostris* and *S. frontalis* during the masting of *G. tangoara* in the eastern cluster (this work) is evidence that *G. tangoara* is an important food source. Both seedeaters were also present during seeding of *Guadua* spp. at Reserva Ecológica Guapiaçú (Rio de Janeiro, Brazil), where *S. frontalis* was more common than *S. falcirostris* (Pimentel and Olmos 2011). During masting of a species of *Guadua*, *S. frontalis* occurred at Itatiaia (Rio de Janeiro, Brazil), where extended masting ended in June 2010 (F. Olmos, in litt.), and Teresópolis (Rio de Janeiro, Brazil). But in Minas Gerais during masting of one species of *Merostachys* and two of *Chusquea*, September–November 2007, only one *S. falcirostris* was detected (M. F. Vasconcelos in Areta et al. 2009). Neither *S. falcirostris* or *S. frontalis* was found during masting of *Parodiolyra micrantha* and *Chusquea attenuata* in the Serra do Espinhaço, Minas Gerais, indicating that these species may have extirpated from the area by habitat destruction or may not feed on the bamboo species studied (Vasconcelos et al. 2005).

On an unspecified date, Sigrist (2009) reported both *Sporophila* species feeding together on seeds of "taquari" (*Chusquea?*, *Merostachys?*) at Juquiá, São Paulo, at ~200 m above sea level along forest borders in the mountains. This bamboo is said to flower every year and to grow in isolated clumps.

During a masting of *C. capituliflora*, we observed both species feeding on seeds and presumed they were breeding. We have a few records of *S. falcirostris* feeding on *C. ramosissima*. Likewise, both *S. frontalis* and *S. falcirostris* have been photographed at masting of *Chusquea* (subgenus *Rettbergia*) at Ubatuba, São Paulo, consuming its seeds; many males of *S. falcirostris* were singing from the treetops (G. Trivelato in Areta et al. 2009). Silva e Silva and Olmos (2007) recorded *S. frontalis* in numbers with *H. unicolor* during seeding of a small scandent bamboo (*Chusquea?*) in the mangroves of Santos e Cubatão, São Paulo, but only a solitary individual in

restinga habitat away from bamboo. Although *S. frontalis* was present during masting of *Chusquea* aff. *meyeriana* at Fazenda Intervalles, São Paulo, it did not feed on the seeds of this bamboo, suggesting that it must specialize on other bamboos, probably *Merostachys* or *Guadua* (Olmos 1996). Confirming this hypothesis, *S. frontalis* was abundant in this same area during the seeding of *M. neesii*, remaining even to the end of the masting (Cestari and Bernardi 2011, this work).

The seeds of *C. ramosissima* and *C. tenella* (7–9 mm) are smaller than those of *Guadua trinii*, *G. chacoensis*, and *M. clausenii* (11–22 mm), and this may be an important factor in the specialization of *S. falcistrostris* and *S. frontalis* on *Guadua* in Argentina (Areta et al. 2009). The small seeds of *C. capituliflora* (6–10 mm) were widely used by both species. At least two small-seeded bamboos, *C. aff. meyeriana* (Olmos 1996) and *C. capituliflora* (this work), have many empty husks in their spikelets, increasing the cost/benefit ratio for seedeaters foraging on their seeds and discouraging their consumption.

Small-seeded bamboos (e.g., *Chusquea* spp.) flower at shorter intervals, are more difficult to forage on, provide a low energy return in relation to the cost of foraging, and allow breeding on only a moderate scale. Large-seeded bamboos (e.g., *Guadua* spp. and *Merostachys* spp.) flower at longer intervals, are easier to forage on, provide a high return of energy in relation to the cost of foraging, and allow for mass breeding. Thus, while small-seeded bamboos may not be the preferred food resource, they may be the best at hand at a given moment and may offer a better return in energy than do food sources other than bamboo. In sum, on a broader spatio-temporal scale, large-seeded bamboos may be seen as strong population pumps and small-seeded bamboos as maintenance (steady-state) stations.

“The presence of slightly allopatric mast-seeding bamboos with unsynchronized cohorts is the ideal circumstance for the evolution of eruptive nomadic behavior by seed predators” (Janzen 1976:375). In Misiones, Argentina, both species of *Guadua* seem to flower out of phase and in a wave from south to north, *G. trinii* in inner Misiones and along the Uruguay River and *G. chacoensis* along the Paraná River and in the Iguazú (Areta et al. 2009). Thus these two bamboo species on whose seeds *S. falcistrostris* is known to feed extensively fulfill the two conditions of slight allopatry and asynchronous mast seeding. Alternatively, the presumed variation in life history of *G. tagoara* and its asynchronous seeding over a wide range may provide a fairly continuous food supply over time within a single species. These slight departures from strict synchrony in the form of waves of flowering (Jaksic and Lima 2003, Franklin 2004) or in geographic mosaics of asynchronous seeding (Montti et al. 2011) are key to understand the biology of bamboo-seed specialists (Areta et al. 2009, this work).

CONSERVATION

The main threat to long term conservation of *S. falcistrostris* and *S. frontalis* is habitat loss. More than 90% of the

original extent of the Atlantic forest (and hence of the seedeaters’ potential habitats) has been replaced by anthropogenic habitats (Galindo-Leal and Câmara 2003). Habitat replacement may extirpate populations through various mechanisms: loss of bamboo habitat, loss of alternative food sources, and loss of connectivity (Areta and Cockle 2012). Among the habitats that have replaced lowland forest in Brazil, rice fields may affect the seedeaters’ populations in three ways. First, by reducing forest and suitable bamboo habitats; second, since rice is an alternative food resource, its presence may disrupt the natural pattern of nomadism; third, the massive application of pesticides may result in extensive population losses, making rice fields an ecological trap (Battin 2004).

Both species are highly prized as cage birds in Brazil but not in Argentina or Paraguay. For example, during our visits to the environs of Corupá during the seeding of *G. tagoara* we noted both as cage birds, and near Blumenau during the seeding of *C. capituliflora* we observed recently caged birds many times. Along forest edges, in fragments, and in highly degraded areas bamboos such as *C. capituliflora* may have contradictory effects on these seedeaters. On one hand, they may reduce the effects of habitat loss, but on the other they may attract a large number of individuals to places where they are easily captured. For example, some residents of the Blumenau area mentioned capturing 30 Temminck’s Seedeaters in just one day in their backyard.

Our most important conservation message is that, periodically, many parts of the ranges of *S. falcistrostris* and *S. frontalis*, one or a few at a time, will play an important role in the maintenance of viable populations. Perhaps the most difficult task is to incorporate this long-term thinking into conservation planning for the benefit of bamboo-seed specialists. It is difficult to identify and protect key sites for these species that are absent most of the time from any area likely to be key. Our records show that these seedeaters use no large protected area continuously, the bulk of records for times and places where bamboos are seeding (Appendix 1). It is clear that protected areas do not suffice to ensure the long-term preservation of nomadic bamboo seedeaters that require a large area in which the habitat is intermittent. Nothing is permanent and everything is contingent in the life histories of birds that specialize on bamboo seeds. As their movements are erratic and unpredictable, their conservation will depend on maintaining areas that are likely to be important at some point in time. It is thus essential to create and preserve a network of habitat (formally protected and nonprotected) to preserve bamboo patches flowering at different times and localities in quantities large enough to guarantee the long-term endurance of the seedeaters’ peculiarly dynamic populations. As we learn more about the timing and geographic patterns of bamboo flowering and the birds’ preferences for seeds, their apparently unpredictable movements will become more predictable.

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