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SPECIAL SECTION

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SPECIALIZATION ON BAMBOO BY NEOTROPICAL BIRDS

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Ornithologists have long marveled at the many species of neotropical forest birds found in close association with woody bamboos (Poaceae: Bambuseae). Over 400 species of woody bamboos occur in the neotropics, a total second only to southeast Asia, which has nearly 1000 species (Bystrakova et al. 2003, 2004). Woody bamboos may grow in the open with a compact shrubby aspect, clamber up trees into the forest canopy, stand erect and self-supported up to 30 m tall, arch over and extend outward, or form dense tangles that carpet the ground, providing a diverse array of microhabitats (McClure 1966, Judziewicz et al. 1999). Their clonal reproduction allows many of them to colonize disturbed areas quickly, forming stands large enough to hold one or more territories of specialist birds (Kratter 1997, Judziewicz et al. 1999, Gagnon and Platt 2008). The synchronous seed production of many bamboos provides abundant and nutritious food for granivores, while bamboos' fast growth, often hollow stems, and dense tangled habit support diverse arthropod communities that provide food for insectivores (Janzen 1976, Reid et al. 2004, Lebbin 2007). However, specialization by birds on woody bamboos is hindered by dramatic changes in resource availability over time and space. Most neotropical woody bamboos grow vegetatively for 30–40 years, then flower synchronously over large areas and die (Judziewicz et al. 1999). It has long been a mystery how so many species of neotropical birds specialize on such a fluctuating resource, and, more recently, concerns have been raised about how to conserve these species and their interaction relationships in the face of widespread deforestation.

Bamboo specialist birds can be grouped according to their foraging strategy and hypothesized response to bamboo flowering cycles (C. Sánchez 2005, Areta and Cockle 2012). The majority of species are insectivores that forage for insects in live or dead bamboo during the long vegetative phase. These birds may open bamboo internodes or probe in existing holes

to capture ants, larvae, or aquatic insects, glean arthropods off bamboo surfaces including culms, leaves, and trapped litter, or capture insects in flight within bamboo stands (Parker 1982, Pierpont and Fitzpatrick 1983, Fitzpatrick and Willard 1990, Rodrigues et al. 1994, Parker et al. 1997, Lane et al. 2007, Laverde and Stiles 2007). They enjoy a stable and productive bamboo habitat over many years, but as the bamboo flowers, dies, and disappears, they must switch to alternative habitat, disperse in search of new bamboo habitat, or experience population declines. Much rarer are the bamboo-seed specialists, granivores that specialize on bamboo seeds that often are produced in short, widespread pulses of masting after many years of vegetative growth (Neudorf and Blanchfield 1994, Olmos 1996, Sick 1997, Areta et al. 2009). These birds take advantage of the huge pulses of food resources offered by bamboo mast but must also experience long periods of food scarcity and travel widely in search of flowering bamboos. A third group of birds, mixed strategists, usually feed on bamboo shoots, leaves, and insects but consume bamboo seeds when available, taking advantage of bamboo resources in both the vegetative and flowering phases (Bertoni 1919, Hilty et al. 1979).

Parker et al. (1996) listed 102 species of neotropical birds in 54 genera as associated or probably associated with bamboo microhabitat; however, these classifications were based on limited field data, mostly anecdotal. Kratter's (1997) seminal study revealed 19 bamboo-specialist birds at just one site in western Amazonia. In the past decade, new species of bamboo-specialist birds have been described, known species have been identified as bamboo specialists, and bamboo specialists have been studied in greater detail, revealing relationships with specific species of bamboos (e.g., Lentino and Restall 2003, Bodrati and Cockle 2006, Lane et al. 2007, Lebbin 2007, Areta and Bodrati 2008, Tobias et al. 2008). However,

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even today many potential bamboo specialists remain unidentified as such, or their relationship with bamboo species is understood poorly (Bodrati and Areta 2006).

In this special section, a collection of four field studies from the neotropics contributes to understanding the ecology and conservation of bamboo-specialist birds in light of their fluctuating habitat: through the long vegetative phase (Leite et al. 2013, Lebbin 2013), the flowering phase (Areta et al. 2013), and after the bamboo dies (Socolar et al. 2013). In the first article in this collection, Leite et al. (2013) show that the critically endangered Kaempfer's Woodpecker (*Celeus obrieni*) specializes on the bamboo *Guadua paniculata*, where it forages by perforating the internodes to capture ants of the genera *Camponotus* and *Azteca*. They further propose that the distribution of this woodpecker in its cerrado habitat is limited by the distribution of *G. paniculata*. When this bamboo habitat is scarcest, after die-offs or wildfires, the authors suggest that survival of Kaempfer's Woodpecker depends critically on the species' ability to disperse between viable bamboo patches.

To understand occupancy of bamboo patches by specialist insectivorous birds, a critical question is how large the patches of bamboo need to be. In the second paper in this collection, Lebbin (2013) addresses this question by examining which of 38 species of bamboo-specialist insectivores occupied 13 patches of *Guadua* ranging from 0.15 to 48 ha in the Amazon of southeastern Peru. Specialist species dropped out of the community in a nested fashion as patch size declined; that is, smaller patches supported a nested subset of the species present in incrementally larger patches. Although the smallest patch supported only one (facultative) bamboo specialist, patches of just a few hectares were large enough to support many bamboo-specialist insectivores, suggesting that the availability of bamboo habitat for these species may be underestimated when only large patches of bamboo are considered.

For the highly vagile bamboo-seed specialists, which move between patches of seeding bamboo, occupancy of bamboo patches depends mostly on the timing of seed production and species-specific traits of bamboo seeds. One of the first cases to receive attention was that of the Magpie Mannikin (*Lonchura fringilloides*), which seemed to follow episodes of seeding of Bindura Bamboo (*Oxytenanthera abyssinica*) in Africa (Jackson 1972). In the neotropics, supposed bamboo-seed specialists have been reported feeding on bamboo seeds and breeding in seed-bearing stands of several bamboo genera (Davis 1945, J. E. Sánchez and Hernández 1990, J. E. Sánchez 1993, Neudorf and Blanchfield 1994, Olmos 1996, Stutchbury et al. 1996, C. Sánchez 2005, Vasconcelos et al. 2005, Greeney et al. 2007, Areta and Bodrati 2008, Areta et al. 2009, Cestari and Bernardi 2011). Areta et al. (2009) recently showed that three bamboo-seed specialists have been recorded in Argentina only at times and places when and where *Guadua* bamboos were masting; however, bamboo-seed specialists are also recorded occasionally outside of bamboos, probably

while searching for new pulses of masting (Lentino and Restall 2003, J. E. Sánchez et al. 2006, Areta et al. 2009). Until now, there has been little information about where the bamboo-seed specialists go and how they survive while specializing on such a boom-and-bust resource. The third paper in this special section (Areta et al. 2013) addresses these questions through a study of two globally threatened *Sporophila* seedeaters that are bamboo specialists across the southern and western Atlantic forest in Brazil, Paraguay, and Argentina. The authors show that bamboo-seed availability is likely to be the main factor limiting reproduction of these birds, which breed even during a cold winter if enough bamboo seeds are available. These authors suggest that the seedeaters maintain their populations at a regional scale by moving among patches of flowering of different species of bamboos, with large-seeded bamboos acting as strong population pumps and small-seeded bamboos acting as maintenance stations.

One of the biggest mysteries regarding all three groups of bamboo-specialist birds—insectivores, seed specialists, and mixed strategists—is what happens to these species when the bamboo dies (Lane et al. 2007). Anecdotal evidence suggests that some species decline regionally, while others move to alternative bamboos or alternative nonbamboo habitats (Neudorf and Blanchfield 1994, Areta and Bodrati 2008, Areta et al. 2009, 2013, Bodrati et al. 2010, 2012). The fourth paper in this special section is, to our knowledge, the first study to measure quantitatively the changes in a bird community following death of bamboo. Socolar et al. (2013) compare spot maps from two patches of *Guadua* bamboo in the Peruvian Amazon, 16 years before and 7 years after the bamboo flowered and died. By the post-die-off census, trees had grown up in the areas formerly occupied by bamboo, creating two patches of second growth in the matrix of mature forest. Although a few species of bamboo-specialist birds persisted in the die-offs, twelve specialist species disappeared from the area, and almost no species had colonized, specialist or not. The species that disappeared from the bamboo die-offs were those Lebbin (2013) found to be most restricted to large or high-quality bamboo patches; in contrast, species that remained in the die-offs without any bamboo were those Lebbin (2013) found also present in marginal bamboo patches. Although these species were present in habitat without bamboo, they continued to rely on habitat generated by bamboo (successional habitat after the die-off) and should still be considered bamboo specialists. Importantly, bamboo die-off led to a sharp decrease in avian species richness at the level of the patch but little difference at the broader scale of the stand.

The four papers in this special section show that the presence of woody bamboos adds to regional bird diversity in the neotropics by supporting a taxonomically and ecologically diverse suite of specialists. The conservation of these birds depends critically on the preservation of bamboo habitats, made difficult by the strong spatial and temporal fluctuations of bamboo resources generated by the bamboos' cycle

of flowering. We hope that this special section draws attention to the important role of bamboos in the conservation of neotropical birds. We believe that bamboo should be recognized as a critical habitat that deserves specific conservation measures through networks of reserves that provide continuous resources for all groups of bamboo specialists. We further hope this set of papers will inspire ornithologists, birders, and students to pay close attention to the natural history and ecology of the birds and bamboos they observe in the field and to study the fascinating relationships between these specialist animals and their fluctuating resources.

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