Revista Brasileira de Ornitologia 25(1): 54–59.
March 2017

ARTICLE

The invasive species rules: competitive exclusion in forest avian mixed-species flocks in a fragmented landscape

Marcos Maldonado-Coelho[1,4], Miguel Ângelo Marini[2], Fábio Raposo do Amaral[1] & Rômulo Ribon[3]

[1] Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Paulo, CEP 09972-270, Diadema, SP, Brazil.
[2] Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade de Brasília, CEP 70910-900, Brasília, DF, Brazil.
[3] Museu de Zoologia João Moojen de Oliveira, Departamento de Biologia Animal, Universidade Federal de Viçosa, CEP 36570-000, Viçosa, MG, Brazil.
[4] Corresponding author: maldonadocoelhom@gmail.com

Received on 30 September 2016. Accepted on 26 May 2017.
This study contains Supplementary Information (Table S1) available only online.

ABSTRACT: Evidence of checkerboard patterns of species' distribution in avian mixed-species flocks suggest that competition is one of the forces shaping the composition and structure of these associations. However, evidence of competition among flock species comes from studies performed in well-preserved regions and no study has reported the interactions between invasive and native flocking species in human-modified landscapes. Such studies are important because evidence show that avian social systems such as mixed-species flocks suffer several negative impacts of habitat fragmentation. In this study, it is shown that an invasive woodcreeper (*Lepidocolaptes angustirostris*) from open areas of central and western South America is: 1) expanding its range into that of a native Atlantic Forest woodcreeper (*L. squamatus*); 2) using the same forest fragments in which the native woodcreeper occurs; 3) regularly joining Atlantic Forest mixed-species flocks that contain the native woodcreeper; 4) overlapping in foraging height with the native woodcreeper during flocking; and 5) engaging in aggressive encounters and excluding the native woodcreeper from flocks. We suggest that this aggressive behavior is a consequence of the overlap in foraging height between the invasive and native species in their original habitats and that their contact has so recently been established. This study suggests that competitive interactions mediated by aggressive behaviors of invasive species may have a negative impact on the fitness of native mixed-species flock species in a fragmented landscape.

KEY-WORDS: Atlantic Forest, biological invasion, foraging behavior, habitat fragmentation, multispecific interactions.

INTRODUCTION

Interspecific competition and aggression mediate species' spatial segregation and occupation in a number of avian communities (*e.g.* Robinson & Terborgh 1995, Jankowski *et al.* 2010). Evidence of assembly patterns suggest that these deterministic processes also shape the composition and structure of avian mixed-species flocks (*e.g.* Graves & Gotelli 1993, Colorado & Rodewald 2015). Mixed-species flocks are mutualistic associations between two or more species, and hypothesized advantages for birds that join such flocks are decreased predation risks and/or increased foraging efficiency (*e.g.* Morse 1977, Powell 1985). However, direct aggressive interactions in these associations can lead to local exclusion of subordinate bird species by the dominant species (Pierpont 1986, Graves & Gotelli 1993). Thus, avian mixed-species flocks offer an exceptional opportunity to investigate species interactions as many species, including closely related ones, can be found in the same flock. Evidence of competition among avian mixed-species flocking species come from research programs performed in relatively well-preserved regions (*e.g.* Graves & Gotelli 1993, Colorado & Rodewald 2015) and no study has yet documented the interactions between invasive and native flocking species in human-modified landscapes. This is relevant because Neotropical avian social systems such as mixed-species flocks and army ant followers are known to be negatively affected by habitat disturbance, including forest fragmentation (Stouffer & Bierregaard-Jr. 1995, Maldonado-Coelho & Marini 2004, Mokross *et al.* 2014). In this study, we show that the Cerrado Woodcreeper, *Lepidocolaptes angustirostris* (hereafter "invasive woodcreeper") is: 1) expanding its range into that of the native Atlantic Forest woodcreeper, *Lepidocolaptes squamatus* (hereafter "native woodcreeper"); 2) using the same forest fragments in which the native woodcreeper occurs; 3) regularly joining Atlantic Forest mixed-species flocks containing the native woodcreeper; 4) overlapping in foraging height with the native woodcreeper during flocking; and 5) engaging in aggressive encounters and excluding the native woodcreeper from flocks. The invasive species

either aggressively interfere with foraging activities or completely exclude the subordinate native species from the flocks. We discuss how these negative interactions could affect the fitness of the native species.

METHODS

Species studied, study area and mixed-species flock observations

The native woodcreeper is commonly observed foraging in the canopy and sub-canopy of primary and secondary growth of moist, semideciduous and dry forests in eastern Brazil, where it regularly participates in mixed-species flocks (Develey & Peres 2000, Maldonado-Coelho & Marini 2004). The invasive woodcreeper has a broader geographic distribution, inhabiting semi-open and forested vegetation physiognomies of the Cerrado, Chaco and Caatinga Biomes (Sick 1997). It is a regular species in mixed-species flocks in open habitats in central South America (Alves & Cavalcanti 1996). The invasive woodcreeper is slightly larger (average 31 g, Marini *et al.* 1997) than the native woodcreeper (average 30 g, M.Â.M, unpubl. data). In the Atlantic Forest, the invasive woodcreeper is expanding its distribution in the wake of forest destruction (Sick 1997).

The study region is located in the municipality of Viçosa and Paula Cândido (20°42'30" – 20°50'00"S; 42°48'45" – 42°56'15"W), southeastern state of Minas Gerais, Brazil (Fig. 1). This region was covered by pristine forest until the middle 1800's, when scattered farms producing food for the gold mines of the municipality of Ouro Preto, Minas Gerais, began to appear (Brandt 2004). Several habitat sensitive Atlantic Forest endemic birds were still present in the area in the 1930's (Ribon *et al.* 2003). Currently, the original Atlantic Forest is highly fragmented (33.5% of native forest remains) and the forest remnants are second-growth forests embedded in a matrix of pastures and crops. Details on the studied area, on the bird communities, and on mixed-species flock sampling can be found in previous published works (Ribon *et al.* 2003, Maldonado-Coelho & Marini 2004).

Geographic expansion of the invasive woodcreeper

We did not rely on geographic distributions described in field guides as these may present large inaccuracies on species' ranges (*e.g.* Lopes 2008). For example, range maps of the invasive woodcreeper in the most popular Neotropical guide (Ridgely & Tudor 1994) is misleading, as it shows an erroneous historical (*i.e.* prior to deforestation) occurrence of this species in the Atlantic Forest. Instead, we used an extensive database that includes geographical localities from museum specimens (Bolívar-Leguizamón & Silveira 2015) and from reliable photographic records deposited in the Wikiaves database (Table S1, Supplementary Information).

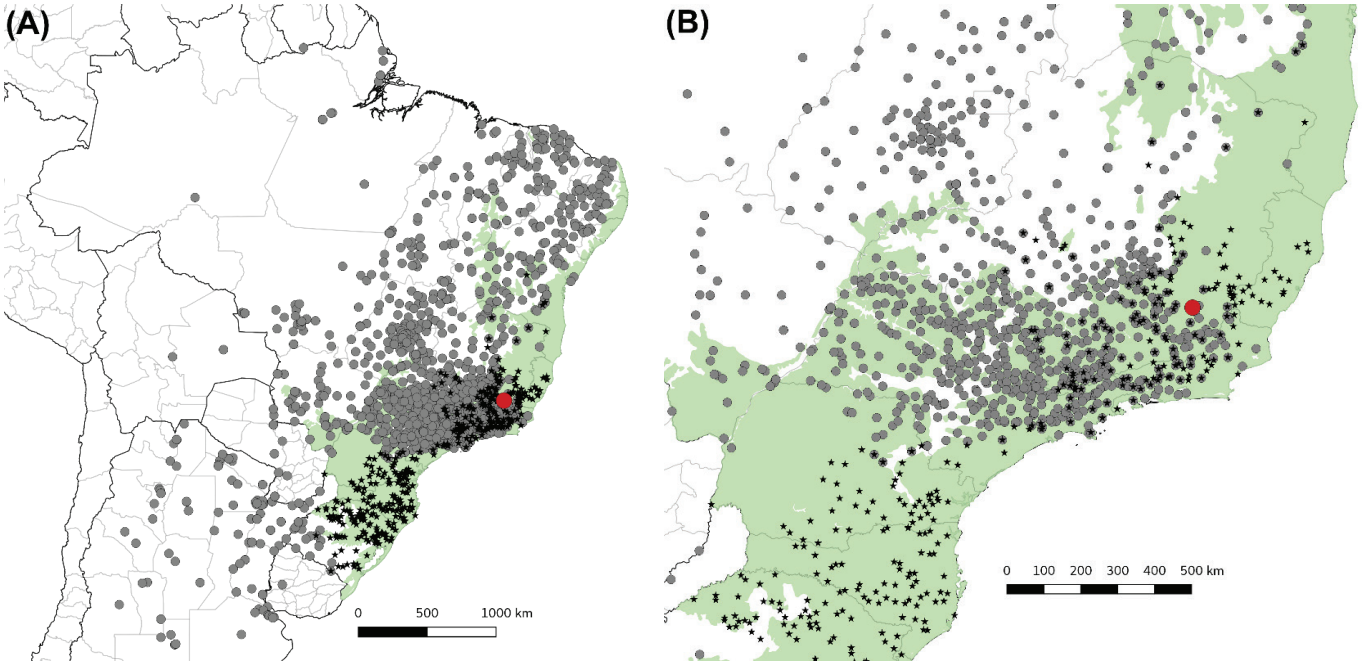

Figure 1. Geographic distribution of the invasive woodcreeper (gray dots), *Lepidocolaptes angustirostris*, and the native woodcreeper (black stars) (**A**). The native woodcreeper is represented by the two Atlantic Forest species of the complex *Lepidocolaptes squamatus/falcinellus/wagleri*. The distribution of the third member of this species complex, *L. wagleri*, from the dry forests of central Brazil is not presented here. In (**B**), region of sympatry between the invasive and the native woodcreepers in the Atlantic Forest. The red circle represents the study area and the green shaded area depicts the historical distribution of the Atlantic Forest, before large-scale deforestation. See Table S1 (Supplementary Information) for records used and descriptions of coordinate sources.

Forest fragment use and abundance of the invasive and native woodcreepers

From May 1996 to November 1999, 236 points located in 41 forest fragments were sampled six times each. Forest fragment sizes ranged from 1 to 384.5 ha. All the point counts were located by at least 50 m from forest fragment borders and were separated from one another by at least 150 m. All the birds seen or heard were recorded, independently of their distance from the observer (unlimited point-count). Counting birds lasted 10 min at each sampling point, starting at sunrise to about 10:00 h and from 16:00–17:00 h to sunset. No sampling was conducted under rain or strong wind. A bird was only recorded when the observer was sure that it was inside the forest fragment. An index of abundance per point (IAP) for both species was obtained by dividing the detected number of individuals of each species by the total number of samples (*i.e.* point-counts) in each fragment. IAP was plotted against fragment size to show the distribution and abundance of both species in forest fragments in the studied region.

Mixed-species flocks participation by the invasive woodcreeper

The forest fragments studied had sizes of 3.6, 7.6, 9.4, 38.8, 45.1, 75.0, 120.0, 181.2 and 384.5 ha. These forest fragments were included in the same set of fragments sampled by point-counts. Mixed-species flock observations were performed during the rainy (October 1998–January 1999) and dry (May–August 1999) seasons and flock observations were conducted between 06:30 h and 12:00 h and between 15:00 h and 18:00 h. The invasive woodcreeper was observed interacting with the native woodcreeper species in flocks in the forest fragment of 9.4 ha. From the nine forest fragments studied, this was the only forest fragment in which the invasive woodcreeper was observed participating in mixed-species flocks - probably because of its recent colonization in the region (R.R., pers. obs.).

Foraging height use pattern of the invasive and native woodcreepers

The foraging observations on the native woodcreeper were carried out in all nine forest fragments in which flocks were studied, whereas foraging behavior of the invasive woodcreeper and all interactions between the two species were observed only in the 9.4 ha forest fragment (see above). Foraging observations were performed during the rainy and dry seasons and foraging heights were only obtained when the species were associated in mixed-species flocks. In a comparison of foraging height use, the aim was to assess if the two woodcreeper species presented any differences in behavior when associated in mixed-species flocks. Seven 2 m classes of foraging heights were defined and estimated by eye. Information on each foraging bout was collected in intervals of 5 minutes to avoid pseudoreplication. In all recorded foraging bouts, the individuals were always searching for prey on tree trunks; hence, the foraging heights recorded were assumed to represent the actual foraging heights, even though individuals were only occasionally seen capturing prey.

RESULTS

Geographic expansion of the invasive woodcreeper

When mapping the invasive woodcreeper records onto the historical distribution of the Atlantic Forest (prior to forest destruction), a clear colonization pattern into this biome emerges (Fig. 1). A detailed account of the colonization history of the invasive woodcreeper is beyond the scope of this study, but two important aspects uncovered here are that: 1) this species has invaded the Atlantic Forest Biome in the central and southeastern regions (Fig. 1); and 2) currently, this species overlaps extensively with the native woodcreeper in central Atlantic Forest (Fig. 1).

Forest fragment use and abundance of the invasive and native woodcreepers

The invasive woodcreeper was recorded in only a few forest remnants and, in all instances, had low abundance. On the other hand, the native woodcreeper was widespread in the studied area and its abundance was not affected by the area of forest fragments (r^2 = 0.011, $P > 0.05$; Fig. 2).

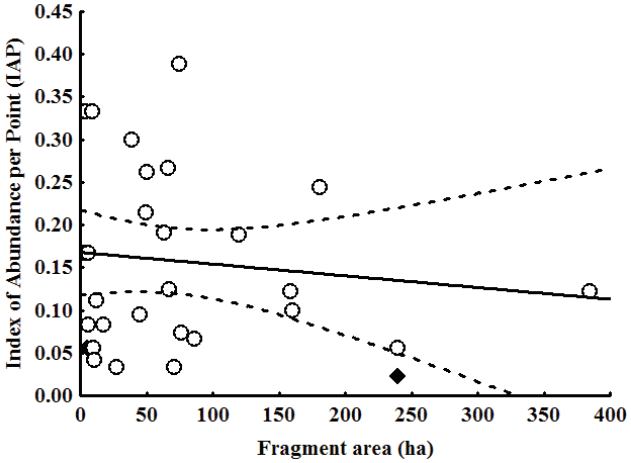

Figure 2. Abundance of the invasive (*Lepidocolaptes angustirostris*, black diamonds) and native (*Lepidocolaptes squamatus*, open circles) woodcreepers as a function of forest fragment size in the area of study. Unbroken and broken lines represent respectively the fit of a linear model and associated confidence intervals.

Foraging height use pattern of the invasive and native woodcreepers

The analysis indicates that the two species differed in foraging height distribution (Kolmogorov-Smirnov two-sample test; D = 0.289, $P < 0.05$; $n_{\text{invasive-woodcreeper}} = 64$, $n_{\text{native-woodcreeper}} = 94$; Fig. 3). This difference in foraging height distribution is because individuals of the invasive woodcreeper did not show preferences in foraging height classes whereas individuals of the native woodcreeper exhibited a preference for the upper levels of trees. In the second comparison of foraging height use, the goal was to assess if there were any detectable behavioral shifts in foraging height of the native woodcreeper in response to the presence of the invasive woodcreeper in mixed-species flocks. That is, we wanted to assess if individuals of the native woodcreeper exhibited a pattern of ecological character displacement (Pfennig & Pfennig 2009). Native woodcreepers in mixed-species flocks in which the invasive woodcreeper participated did not show differences in foraging height distribution from native woodcreepers in mixed-species flocks in which the invasive woodcreeper was absent (*i.e.* in the other eight forest fragments; Kolmogorov-Smirnov two-sample test; D = 0.131, $P > 0.05$; $n_{\text{9.4 forest fragment}} = 94$, $n_{\text{other forest fragments}} = 323$; Fig. 3).

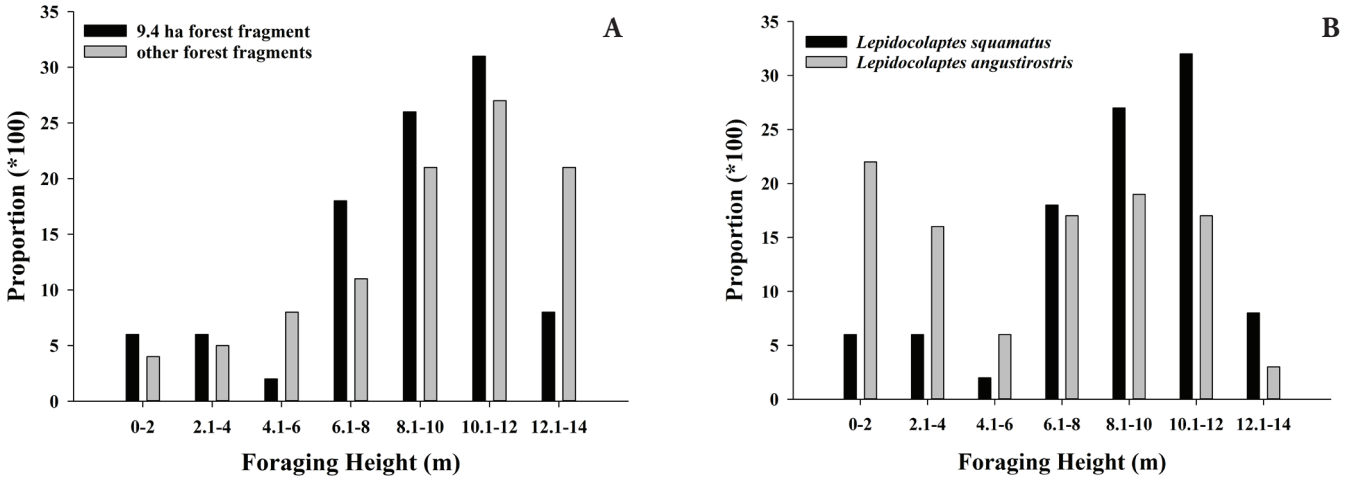

Figure 3. Proportion of foraging height distribution use for the two *Lepidocolaptes* species when associated with mixed-species flocks in the 9.4 ha forest fragment (**A**). Proportion of foraging height distribution use for the native woodcreeper (*L. squamatus*) individuals when associated with mixed-species flocks in the 9.4 ha forest fragment and for individuals of this species when associated with mixed-species flocks in the other eight forest fragments (**B**).

Agonistic interactions between the invasive and native woodcreepers

Twenty-nine mixed species flocks were followed in the 9.4 forest fragment. The invasive woodcreeper was observed joining six flocks, all in which the native woodcreeper was participating. Six aggressive interactions in different flocks were observed between the two species. In two of the interactions, the native woodcreeper was excluded completely from the flocks after being attacked by the invasive woodcreeper and it was not observed rejoining the flocks after the next two hours of observation. In the remaining four interactions, the native woodcreeper shifted foraging height and branch ($n = 2$) or tree ($n = 2$) when attacked by the invasive woodcreeper.

DISCUSSION

Competitive exclusion by more aggressive bird species is a common pattern in mixed-species flocks and over army ants. In such social organizations, the larger species will often be dominant (Willis & Oniki 1978, Pierpont 1986, Graves & Gotelli 1993). The invasive woodcreeper is only slightly larger than the native woodcreeper; hence, its dominance over the native species could be mediated by some behavioral aspect such as a stronger interspecific territoriality. The invasive woodcreeper was regularly observed in isolated trees along pastures and agricultural lands surrounding the 9.4 ha forest fragment. Most Cerrado bird species that join flocks (*sensu* Alves & Cavalcanti 1996) and Cerrado mixed-species flocks themselves are absent from the region. Thus, one possibility is that, in order to gain the two main benefits of mixed-species flocking—predator avoidance and increased foraging efficiency (Morse 1977, Powell 1985)—the invasive woodcreeper enters the forest fragment to join flocks. It is noteworthy that five out of the six records of the invasive woodcreeper in mixed-species forest flocks were made in the dry season, a period of food shortage for insectivorous birds in the Atlantic Forest (Develey & Peres 2000). Thus, the invasive woodcreeper likely increases its frequency of participation in forest flocks during this season to augment food intake. However, a consequence

of its mixed-species forest flock attendance is disturbance and exclusion of the subordinate native woodcreeper.

Sympatric species may be under selective pressures to avoid the negative effects of competition and consequently evolve differences in habitat use, foraging behavior and body dimensions (Schoener 1965, Murray-Jr. 1971). Species that interact in mixed-species flocks in any region could have co-evolved syntopically for thousands of generations and hence could have had enough time to evolve ecological segregation in one or more dimensions. Although the two woodcreeper species exhibited distinct foraging height distributions, the overlap was extensive. The observed interspecific aggression in this study can be a transitory phase given the short period of contact between them (Murray-Jr. 1971). In fact, it is expected that the frequency in which negative interactions occur will decrease over time. As such, interactions can be energetically costly for both subordinate and dominant species. Thus, that the two woodcreepers only recently came into contact implies that ecological segregation (*i.e.* character displacement) have not had time to evolve. Evidence in support of this idea is the overlapping foraging height distributions of native woodcreepers in flocks in which the invasive woodcreeper is absent and in which it is present.

In the present study, we have shown that the process of Atlantic Forest fragmentation has led to the invasion of an aggressively dominant species from the adjacent Cerrado Biome. We have also shown that the native woodcreeper, which regularly join mixed-species flocks all year round (Maldonado-Coelho & Marini 2003), experiences foraging interference and flock exclusion as a result of agonistic interactions with the invasive species. It is reasonable to expect that such foraging interference and competitive exclusion will result in reduced fitness in the native woodcreeper, as the benefits of participating in mixed-species flocks would be lost or largely diminished. Those individuals disturbed when foraging, and certainly those excluded from flocks, are likely to experience a decrease in foraging efficiency and an elevated risk of predation. This can be critical because: i) the frequency of the invasive woodcreeper in flocks were higher during the period of food shortage (*i.e.* the dry season), ii) competitive exclusion from flocks can be detrimental to the fitness of the native species mainly in small and potentially food depleted forest fragments (*e.g.* Zanette *et al.* 2000), and iii) sympatry between the two woodcreepers is extensive in southeastern Atlantic Forest, and ongoing competition can be pervasive across their area of overlap. However, one positive finding of this study is the reduced abundance and occurrence of the invasive woodcreeper in the sampled forest fragments. This implies that the negative interactions reported here could have an impact on the native woodcreeper at the level of interacting individuals, but they may not be extensive at the population level. Future studies should assess this possibility by comparing fitness of native woodcreeper individuals in the presence and absence of the invasive woodcreeper.

Finally, two caveats of this study are the lack of replicates of fragments in which the invasive and native woodcreepers interact in mixed-species flocks and the small sample size of their agonistic interactions. Although this limits the generalization of our study, the preliminary evidence of negative interactions in flocks highlights the importance of additional studies, both in the Atlantic Forest and elsewhere in the Neotropics.

ACKNOWLEDGEMENTS

Funding was provided by *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES)* to M.M.-C. at the Graduate Program in Ecology and Evolution from Federal University of São Paulo (UNIFESP-Diadema), Fundação *de Amparo à Pesquisa do Estado de São Paulo (FAPESP)* and the Biota Program (2010/05445-2 and 2015/18287-0 to M.M.-C.; 2011/50143-7, 2011/23155-4 and 2013/50297-0 to F.R.A.) and National Science Foundation DOB 1343578 (F.R.A). We thank World Wildlife Fund (WWF) and the Graduate Program of Ecology, Conservation and Wildlife Management (ECMVS) from Federal University of Minas Gerais (UFMG) for financial support. The *Conselho Brasileiro de Desenvolvimento Científico e Tecnológico (CNPq)* provided fellowships to all authors. M.Â.M. received a researcher fellowship from CNPq. R.R. is thankful to *Programa Natureza e Sociedade* WWF/SUNY projeto CSR 142-00, CNPq, CAPES, *PROBIO-Ministério do Meio Ambiente*/ World Bank/Global Environmental Facility. M.M.-C., M.Â.M., F.R.A. and R.R. conceived the idea, design, experiment (supervised research, formulated question or hypothesis) and wrote the paper. M.M.-C., F.R.A. and R.R. performed the experiments and analyzed the data (collected data, conducted the research). This study was carried out in strict accordance with the recommendations in the use of animals for research in Brazilian universities.

REFERENCES

Alves M.A.S. & Cavalcanti R.B. 1996. Sentinel behavior, seasonality, and the structure of bird flocks in a Brazilian savanna. *Ornitología Neotropical* 7: 43–51.

Bolívar-Leguizamón S. & Silveira L.F. 2015. Morphological variation and taxonomy of *Lepidocolaptes angustirostris* (Vieillot, 1818) (Passeriformes: Dendrocolaptidae). *Papéis Avulsos de Zoologia, São Paulo* 55: 281–316.

Brandt A. 2004. Desbravamento, caminhos antigos e povoamento dos Sertões do Leste: uma aventura de pioneiros. Viçosa: Centro de Referência do Professor.

Colorado G.J. & Rodewald A.D. 2015. Assembly patterns of mixed-species avian flocks in the Andes. *Journal of Animal Ecology* 84: 386–395.

Develey P.F. & Peres C.A. 2000. Resource seasonality and the structure of mixed species bird flocks in a coastal Atlantic Forest of southeastern Brazil. *Journal of Tropical Ecology* 16: 33–53.

Graves G.R. & Gotelli N.J. 1993. Assembly of avian mixed-species flocks in Amazonia. *Proceedings of the National Academy of Sciences of the United States of America* 90: 1388–1391.

Jankowski J.E., Robinson S.K. & Levey D.J. 2010. Squeezed at the top: interspecific aggression may constrain elevational ranges in tropical birds. *Ecology* 91: 1877–1884.

Lopes L.E. 2008. The range of the Curl-crested Jay: lessons for evaluating bird endemism in the South American Cerrado. *Diversity and Distributions* 14: 561–568.

Maldonado-Coelho M. & Marini M.Â. 2003. Composição de bandos mistos de aves em fragmentos de Mata Atlântica no sudeste do Brasil. *Papéis Avulsos de Zoologia, São Paulo* 43: 31–54.

Maldonado-Coelho M. & Marini M.Â. 2004. Mixed-species bird flocks from Brazilian Atlantic Forest: the effects of forest fragmentation and seasonality on their size, richness and stability. *Biological Conservation* 116: 19–26.

Marini M.Â., Motta-Junior J.C., Vasconcellos L.A.S. & Cavalcanti R.B. 1997. Avian body masses from the Cerrado region of central Brazil. *Ornitología Neotropical* 8: 93–99.

Mokross K., Ryder T.B., Côrtes M.C., Wolfe J.D. & Stouffer P.C. 2014. Decay of interspecific avian flock networks along a disturbance gradient in Amazonia. *Proceedings of the Royal Society of London B: Biological Sciences* 281: 20132599.

Morse D.H. 1977. Feeding behavior and predator avoidance in heterospecific groups. *BioScience* 27: 332–339.

Murray-Jr., B.G. 1971. The ecological consequences of interspecific territorial behavior in birds. *Ecology* 52: 414–423.

Pfennig K.S. & Pfennig D.W. 2009. Character displacement: ecological and reproductive responses to a common evolutionary problem. *Quarterly Review of Biology* 84: 253–276.

Pierpont N. 1986. *Interspecific aggression and the ecology of woodcreepers (Aves: Dendrocolaptidae)*. Ph.D. Thesis. Princeton: Princeton University.

Powell G.V.N. 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics, p. 713–732. In: Buckley P.A., Foster M.S., Morton E.S., Ridgely R.S. & Buckley F.G. (eds.). *Neotropical ornithology. Ornithological Monographs* 36: 713–732.

Ribon R., Simon J.E. & Mattos G.T. 2003. Bird extinctions in Atlantic Forest fragments of the Viçosa region, southeastern Brazil. *Conservation Biology* 17: 1827–1839.

Ridgely R.S. & Tudor G. 1994. *The birds of South America, v. 2, the Suboscine Passerines*. Austin: University of Texas Press.

Robinson S.K. & Terborgh J. 1995. Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology* 64: 1–11.

Schoener T.W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. *Evolution* 19: 189–213.

Sick H. 1997. *Ornitologia Brasileira*. Rio de Janeiro: Editora Nova Fronteira.

Stouffer P.C. & Bierregaard-Jr. R.O. 1995. Use of Amazonian Forest fragments by understory insectivorous birds. *Ecology* 76: 2429–2445.

Willis E.O. & Oniki Y. 1978. Birds and army ants. *Annual Review of Ecology and Systematics* 9: 243–263.

Zanette L., Doyle P. & Trémont S.M. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81: 1654–1666.

Associate Editor: Gustavo S. Cabanne.