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ARTICLE

Behavioral responses of urban birds to human disturbance in urban parks at Curitiba, Paraná (Brazil)

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ABSTRACT: Proximity to humans can influence behaviors that are essential in birds' life, such as breeding, foraging and flight. In urban parks, which are important natural shelters to birds, human activity varies broadly in time such that attentiveness and escaping behavior of birds may be intensified as humans' density increases. In this study, we tested this hypothesis in six urban parks at Curitiba, southern Brazil, using three common bird species as models, the Rufous Hornero (*Furnarius rufus*), the Southern Lapwing (*Vanellus chilensis*) and the Rufous-bellied Thrush (*Turdus rufiventris*). Specifically, we tested if foraging rate, alert distance (AD), flight initiation distance (FID) and flight distance (FD) were related to human density at birds' surroundings. We found no influence of humans on birds foraging rate, whereas AD, FID and FD decreased with human density in the area. We also found differences in birds escaping strategy; "flying" strategy was associated with higher AD, FID and FD than "walking". Results also indicate that humans' presence temporally affected birds' vigilance and flight responses, evident through their constant foraging rate irrespective of human density, *i.e.* increased tolerance to human proximity. Our study provides evidence of behavioral plasticity of the model species to the intensity of human use of their living area, which also highlights the importance of further efforts in creating refuges within urban parks to minimize negative anthropic impacts on urban species.

KEY-WORDS: approaching experimental trial, escaping strategy, flight initiation distance, foraging rate, human density.

INTRODUCTION

Many bird species are sensitive to environmental change, but several can cope with anthropic activities. Thus, parks and other green areas become important shelter especially to birds in human-altered environments (Fernández-Juricic *et al.* 2001), because ecological and environmental conditions may match with the natural contexts where these species have evolved. However, human use of green areas for leisure or touristic activities can also cause profound impacts in wildlife (Collins-Kreiner *et al.* 2013). For instance, the presence of humans may cause foraging area reduction and increasing stress hormone levels in urban animals that can affect parental care (*e.g.*, *Haematopus ostralegus*, Verhulst *et al.* 2001), hatching success and chick development (*e.g.*, *Opisthocomus hoazin*, Mullner *et al.* 2004 and *Pygoscelis adeliae*, Giese 1996), high mortality rates (Blumstein 2006) and, ultimately, local species extinction. Even though selection has favored agile escape behaviors in birds to overcome potential threats (*e.g.* predators, Ydenberg & Dill 1986), individual habituation to human co-occurrence can be decisive for survival and may represent an important filter selecting individuals and species less sensitive to urbanization.

The escape behavior to human approach reflects a bird innate response to guarantee survival. Individual responses involve an optimal decision-making that maximizes foraging and daily general activities (*e.g.* mating and nesting) while reducing any potential threat (Blumstein *et al.* 2003, Piratelli *et al.* 2015). Three important metrics to assess an individual habituation and risk avoidance agility are the alert distance (AD), flight initiation distance (FID) and flight distance (FD). The first indicates birds' visual and auditory orientation when detecting an approaching threat (Blumstein 2006, Weston *et al.* 2012). Specifically, the alert state in birds is easily recognized through behaviors like head raise (Whitfield *et al.* 2008), continuous surroundings scan (Schlacher *et al.* 2013) and momentarily interruption of activities. The second indicates the distance in relation to a potential threat at which the individual begins to escape by walking or flying away (Cooper-Jr. & Pérez-Mellado 2011), and the third represents the actual distance travelled for escaping.

Optimized alertness and escape responses, measured as AD, FID and FD, may allow birds to accomplish their daily activities in a non-ideal condition for many species. Indeed, birds exposed to human proximity tend to have lower AD, FID and FD, indicating tolerance to human approach likely due to habituation (Miller *et al.* 2001, Ikuta & Blumnstein 2003, Cooper-Jr. & Pérez-Mellado 2011). However, even low levels of human disturbance can be threatening to birds (Bötsch *et al.* 2017). For that reason, these metrics may allow measuring the impacts of the human disturbance in birds living in a given area and how these animals cope with it. To better understand how urban birds deal with human proximity, we experimentally tested the hypothesis that birds respond to humans' presence through shifting AD, FID, FD, and their foraging rate in correlation to the amount of humans that occupy or approach to their foraging areas.

To do so, we had as models three common ground foraging urban species, the Rufous Hornero (*Furnarius rufus*), the Southern Lapwing (*Vanellus chilensis*) and the Rufous-bellied Thrush (*Turdus rufiventris*). Considering urban birds may habituate to humans' presence (Miller *et al.* 2001, Ikuta & Blumnstein 2003, Cooper-Jr. & Pérez-Mellado 2011), in days with denser human population in urban green areas we expected that these birds would thus have lower AD, FID, and FD. In addition, increasing number of people using the green areas would reduce the time window for food search by birds since they would have to spend more time in alert posture than foraging. Therefore, we expected an inverse relationship between foraging rate and human density.

METHODS

Study area

We collected data in 25 sampling days from August to September 2016, in six green areas at Curitiba, the most populous city in Paraná state, south Brazil: Jardim Botânico (25°26'31''S; 49°14'27''W), Parque Barigui (25°25'32''S; 49°18'58''W), Parque São Lourenço (25°23'13''S; 49°16'10''W), Passeio Público (25°25'32''S; 49°16'11''W), Campus Centro Politécnico of the Universidade Federal do Paraná (25°27'6''S; 49°13'55''W) and Fazenda Experimental Canguiri of the Universidade Federal do Paraná (25°27'34''S; 49°15'54''W).

Behavioral observations and approaching experiment

We searched for individuals of the three model-species foraging in each green area. We counted the number of humans within a sampling plot with 20 m radius (1256.64 m^2) around each spotted bird either before and after each observation trial and used their average number to represent human density at each trial in the analyses. We ensured variable human density values across all samples by collecting data both in weekdays and weekends. During five minutes of observation we calculated each individual foraging effort as the number of pecks/min, irrespective of their success in each capturing attempt.

We conducted an approaching experiment by walking towards each bird at a constant walking pace (0.5–1.0 m/s) in a straight trajectory. We then marked and measured with a measuring tape the researcher position when the bird displayed the alert behavior (AD) and when it walked or flew away (FID, Fig. 1). We acquired FD by measuring the distance between the researcher position when the bird initiated its flight and the refuge or landing position (Fig. 1). To standardize all experimental trials, we set the researcher initial distance (ID) to the bird before any approach to be of at least 20 m (Fig. 1) and run all trials in non-rainy days. Since subjects were unmarked, we run the experiments in alternated days and local regions within each green area to avoid sampling each individual repetitively and to prevent birds to get habituated to the experiment. To avoid biases, the same researcher (T.V.P.) made all trials.

Statistical analysis

We tested data for normality using Shapiro-Wilk test and transformed AD, FID, FD and foraging rate to their square root to approximate to a normal distribution. Because AD, FID, and FD were correlated (AD-FID, $r = 0.77$; AD-FD, $r = 0.54$, and FID-FD, $r = 0.64$; $P < 0.001$ and $df = 129$ in all cases), we included them in a principal component analysis (PCA) and used the first principal component (PC1, explained variance = 77%) as response variable. Higher PC1 values represented lower values of AD, FID and FD (loadings: -0.40, -0.50 and -0.77, correlations with PC1: -0.77, -0.85 and -0.93, respectively).

We used two Analysis of Covariance (ANCOVA) to test for the relationship between (*i*) PC1 and human density and escape strategy (walking or flying), and (*ii*) between foraging rate and human density. We validated

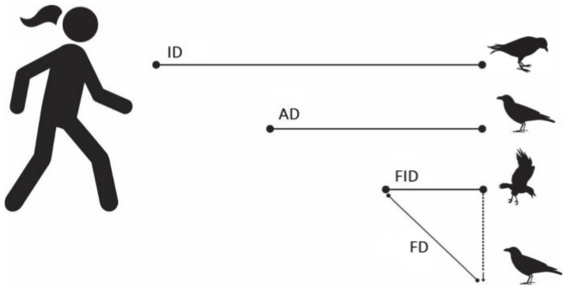

Figure 1. Schematic representation of recorded distances during approaching experiments to the birds. Dashed line indicates bird movement trajectory. ID: researcher initial distance; AD: bird alert distance; FID: flight initiation distance; and FD: flight distance.

Table 1. Foraging rate, alert distance (AD), flight initiation distance (FID) and flight distance (FD) recorded for each bird species in urban parks at Curitiba, Brazil. Values are mean ± SD.

Species	Sample size	Foraging rate (pecks/min)	AD (m)	FID (m)	FD (m)
Rufous Hornero	51	44.6 ± 29.8	4.7 ± 1.98	2.6 ± 1.6	5.6 ± 5.5
Rufous-bellied Thrush	35	24.7 ± 21	6.5 ± 2.4	4.2 ± 2.3	7.9 ± 5.5
Southern Lapwing	45	12.3 ±13.6	7.9 ± 3.3	5.3 ± 3.3	8.3 ± 3.8

the models by plotting residuals versus fitted values. We run all statistical analyses in R 3.4.2 (R Core Team 2016).

RESULTS

We made 133 records of foraging rate and approaching experiments to individuals of the three species: 51 Rufous Horneros, 45 Southern Lapwings and 35 Rufous-bellied Thrushes. Foraging rates were unrelated to human density ($\beta \pm SE = -0.009 \pm 0.011$, $n = 131$, $t = -0.84$, $P = 0.40$), indicating lack of human influence on food-searching behavior by birds (Fig. 2). We found variation in AD, FID and FD between species (Table 1; Fig. 3 left), supporting the inclusion of species as an additional fixed effect term in the models. PC1 was positively related to human density ($\beta \pm SE = 0.04 \pm 0.01$, $n = 131$, $t = 4.09$, $P < 0.0001$, Fig. 3), and indicated that AD, FID and FD reduced as human density increased. In other words, as the number of humans increased on birds surroundings, consequently reducing the area free of people, birds started escaping at shorter distances, but went to closer distances to the observer than in scenarios of low density of humans. PC1 values were smaller when birds flew to escape ($\beta_{flight} \pm SE = -1.04 \pm 0.16$, $n = 131$, $t = -6.46$, $P < 0.0001$) in comparison to the walking escape strategy (Fig. 3). Altogether, this indicates that AD, FID and FD values were higher when birds escaped on the wing, meaning that when humans' density was high, birds preferred walking instead of flying escapes, thus allowing closer approach of the observer and evading to a nearer refuge as opposed to when humans were denser in the area and birds avoided their proximity by flying to a farther refuge.

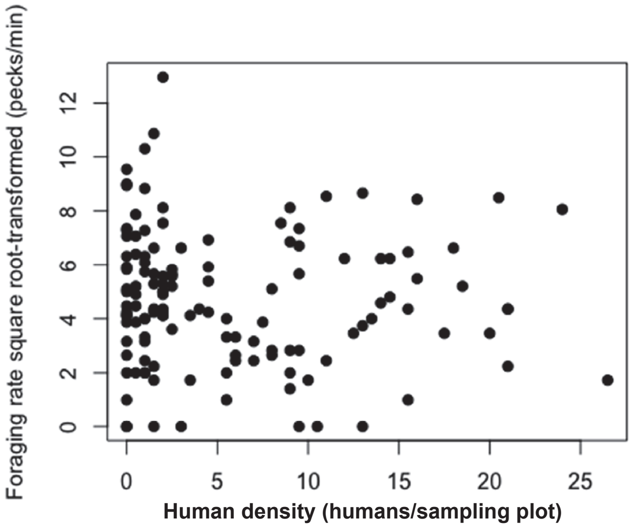

Figure 2. Bird's foraging rate in relation to human density per sampling plot (1256.64 m^2) drawn with birds at its center.

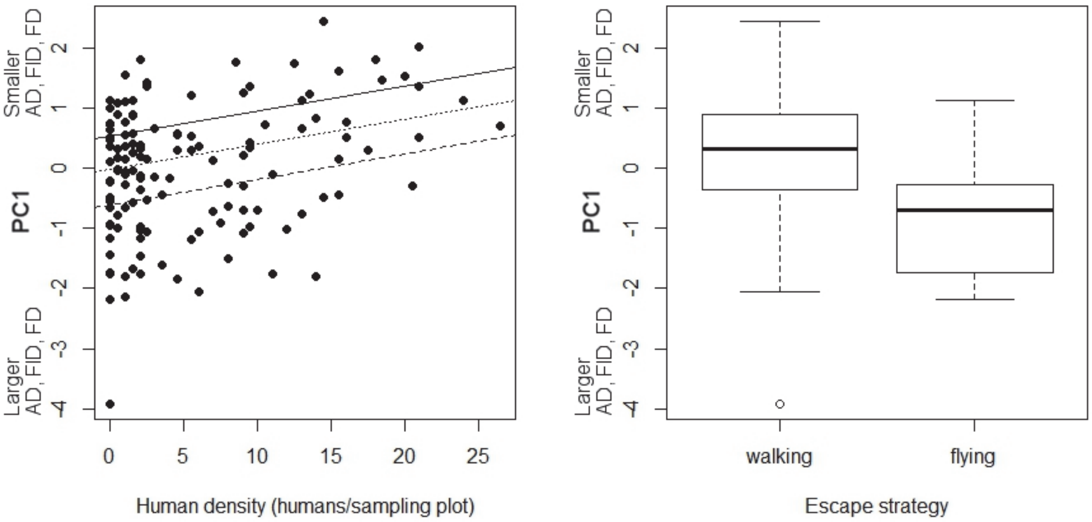

Figure 3. First principal component scores (PC1) of a Principal Component Analyses including AD, FID and FD in relation to humans' density per sampling plot (1256.64 m^2; left; Rufous Hornero: solid line; Southern Lapwing: dashed line; Rufous-bellied Thrush: dotted line) and to escape strategy (right). Higher values of PC1 represents lower AD, FID and FD.

DISCUSSION

In this study we tested the hypothesis that individuals of Rufous Horneros, Southern Lapwings and Rufous-bellied Thrushes in urban parks would adjust their foraging and escaping behavior according to the number of humans on their proximity. We showed that birds of the three studied species kept foraging at the same rate irrespective of humans' density. Nevertheless, AD, FID and FD were shorter when more humans were at bird's surroundings, situation in which birds allowed a closer approach of the observer and flew to a closer safe-distance in the approaching experimental trials.

The unpredicted result of human density unaffecting birds' foraging rate reveals a few plausible strategies birds adopt to survive in urban environments. Bird hunting and trapping are illegal activities in Brazil (Brasil 1967), therefore urban birds could have been associating humans' approximation as a non-threatening behavior (*e.g.* Blumstein 2006, Weston *et al.* 2012, Guay *et al.* 2013), ultimately leading to steady foraging rate. Furthermore, the reduction on their adverse reactions to humans may result from a foraging strategy optimized for ensuring proper spatial and temporal exploration of resources in human populated habitats. When high number of humans occupy the parks, foraging may be hampered by the restricted amount of unoccupied foraging areas. To overcome this problem, our data suggest that urban birds maximize their foraging efforts by keep searching for food despite of increased human proximity. This coincides to previous findings that birds become more tolerant to people when human encounter events are more frequent (Samia *et al.* 2015), but our results add that this occur even when the variation of encounter rates occurs within the same location. In other words, birds sustain constant foraging rates through shifting AD and FID to their minimum when human's density increases, thus expressing a finer trade-off equilibrium between energy intake and safety, extending to at least these three tropical species such strategy already reported for some temperate birds (Prieto *et al.* 2009, Lin *et al.* 2012, Jimenez *et al.* 2013) and even other taxa (*e.g.* lizards, Cooper-Jr. 2010).

Interestingly, our results contradict previous findings from temperate region studies, where foraging activity of urban- and seabirds was negatively related to the presence of humans (*e.g.* Fernández-Juricic & Tellería 2000, Velando & Munilla 2011). It is plausible that the increased diversity, and thus abundance of food, at our tropical study sites (Brown 2014) allows birds to sustain foraging rates even in a more confined area. Besides resource availability, future investigations should also include a wider timeframe, thus allowing assessments of individual variation across time and the adaptive value of this response.

Escaping from an imminent threat requires prompt muscular response. In birds, flying is the fastest way of moving away, but also more energy demanding than running (Harrison & Roberts 2000). For this reason, birds should use flight over running for escaping solely when the risk is higher, thus allowing a faster response and reaching the farthest safe distances from the threat, as supported by our results.

Survival in urban habitats requires that birds cope with frequent interactions with humans, which ultimately lead to birds becoming more tolerant to that. Despite of that, our results show that syntopy with humans ultimately affects birds' foraging strategy and always result in birds escaping using a plastic response that varies according to human's density in the surrounding areas. By that, it is obvious that living in urban parks causes inherent stress responses in birds (*e.g.* raised heart rate, and escaping flight, Steven *et al.* 2011), which may ultimately affect individual fitness and population survival. Therefore, we highlight that to improve the chances of native urban-inhabitant bird species conservation it is important to ensure that parks have human-free areas, in which birds could find refuge for foraging and resting especially in days when the density of visitors increases such as during weekends.

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ARTICLE

Ecology of mixed-species flocks of birds across gradients in the Neotropics

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ABSTRACT: Mixed-species flocks of birds have been studied for more than a century, but investigation efforts are historically unbalanced towards certain types of habitats, such as woodlands and lowland forests. Here we provide a first glance of bird flocks' patterns across different gradients in recent studies conducted within the Neotropics. We summarize a symposium where a series of independent studies that approached the topic, some of them making use of techniques that were seldom applied in previous decades in Neotropical systems. We discuss bird flocks' patterns across a latitudinal gradient, social network patterns in bird flocks' across elevational gradients in local and regional scale, and, finally, patterns of flocking response to different levels of human disturbance. Altogether, these studies offer a larger and diverse panorama of possible patterns of response and diversity of mixed-species flocks of birds in the Neotropical region, and provide a rich ground where future studies with bird flocks in the Neotropics may rely on.

KEY-WORDS: altitude, anthropogenic disturbance, facilitation, habitat fragmentation, mixed parties of birds, positive interactions.

INTRODUCTION

More than a century ago, every naturalist and ornithologist who penetrated the tropical humid forests would be mesmerized by the "mixed parties of birds", to judge from the fascinating description of Bates in 1863 (p. 334–335): "*One may pass several days without seeing many birds; but now and then the surrounding bushes and trees appear suddenly to swarm with them. There are scores, probably hundreds of birds, all moving about with the greatest activity (…) in a few minutes the host is gone, and the forest path remains deserted and silent as before*". Bird flocks may account of more than a hundred individuals (Diamond 1987), and these "bird waves" have been the focus of many investigations.

Mixed-species flocks of birds (MSF henceforth) are associations of individual birds from different species in which participants actively maintain a connection over time, move together searching for resources and foraging (Morse 1970, Sridhar *et al.* 2009, Harrison & Whitehouse 2011). They are a prevailing social system in almost every terrestrial ecosystem on earth, from tropical forests – where many passerine birds detected in an area can be observed in MSFs and the aggregation is prevalent year-round (Goodale *et al.* 2009), to temperate forests – where flocking species primarily integrate mixed-species flocks during winter, when resources are scarce and birds are typically outside the breeding season (Morse 1970). MSF members are hypothesized to benefit from joining these associations by two main mechanisms: (*i*) improve feeding efficiency and/or (*ii*) reduce risk of predation (Morse 1977, Sridhar & Shanker 2014, Goodale *et al.* 2015). The benefits, however, may vary among species (Hino 2000), and be dependent of habitat context and group organization (Sridhar *et al.* 2012).

From an ecological perspective, MSFs represent "community modules" (*sensu* Holt 1997), in which competition and positive interactions are highly concentrated in space and time (Sridhar *et al.* 2012). Because of the intricate biological interactions acting upon MSFs, they are considered among the most complex multi-specific associations of terrestrial vertebrates (Munn 1985). Furthermore, they have been proposed as an ideal study system to test for community assembly hypotheses and community responses to disturbance in ecological time scales (Graves & Gotelli 1993, Sridhar *et al.* 2012, Zuluaga & Rodewald 2015). A new interest for the study of these social systems has recently raised, potentially triggered by a new venue for statistical analyses, new computational power and access to large-scale datasets

(Sridhar *et al.* 2009, Sridhar *et al.* 2012, Mokross *et al.* 2014).

The phenomenon of MSF has been studied under many different perspectives, from the comprehension of composition and structure (Bates 1863, Goodale *et al.* 2009, Goodale *et al.* 2015) to understanding species roles and dynamics through experimental studies (*e.g.*, Dolby & Grubb-Jr. 1998, Forsman *et al.* 1998, Krams 2001). Nevertheless, studies are not equally distributed throughout the globe. Historically, much more attention has been given to forested habitats, such as temperate broadleaf forests and to tropical rainforests, whereas fewer studies have been conducted in other environments, such as savannah and dry shrublands (Alves & Cavalcanti 1996, Jones & Bock 2003, Amaral & Ragusa-Netto 2008, Zarco & Cueto 2017).

This directional tendency of studies originated mainly two kinds of biases: between (temperate *vs.* tropical ecosystems) and within climatic regions (*e.g.*, lowland *vs.* highland in the Neotropics). The first is noticeable when comparing flock diversity: in temperate ecosystems, flocks show a lower species diversity compared to tropical flocks, and species in temperate flocks tend to join seasonally and perform well-defined functions within the mixed flocks (Morse 1970, Farley *et al.* 2008). This condition allows researchers to test for specific hypotheses on benefits and consequences of species loss on the overall flock. However, in tropical systems, investigations may increase in complexity, because some species do not have clear established functions within MSF (Greenberg 2000, Zuluaga 2013, Fanjul 2016). The second bias is especially evident in the Neotropical region by the fact that most of our understanding of tropical flocks comes from lowland ecosystems, particularly from the Amazonia, where MSFs seem to be more stable in space and time (*e.g.*, Graves & Gotelli 1993, Martínez & Robinson 2016), and are dominated by certain groups of species (*e.g.*, antbirds).

Additionally, within the Neotropics there are comparatively fewer studies in other non-forested environments such as grasslands, shrublands and mangroves (but see Zarco & Cueto 2017, Ferrari & Motta-Junior 2018), and studies investigating how the structure of mixed flocks vary across natural gradients (*e.g.*, elevational gradient in Andean ecosystem) are even more scarce (but see Marín-Gómez & Arbeláez-Cortés 2015). Finally, MSFs may be affected by several kinds of anthropogenic disturbances, from fragmentation to urbanization, but the first was far more investigated (Maldonado-Coelho & Marini 2000, Mokross *et al.* 2014, Cordeiro *et al.* 2015, see further references in Goodale *et al.* 2015), in detriment of studies on the impacts of deforestation and habitat degradation, or the combination of both. Thus, similar to the Wallacean shortfalls in biodiversity, it is clear that we face basic knowledge shortfalls on mixed-species flocks of birds in the Neotropics.

The importance of the Neotropical region is undeniable: it encompasses a great latitudinal extension, including 181 terrestrial ecoregions and 11 biomes (Olson *et al.* 2001), that ranges from extremely moisture habitats to deserts and xeric shrublands. A major physiographic feature of the region is the mountain ranges that run from south to north along the west, which separates the Pacific from the Amazon Basins. The Neotropical region not only harbors the largest remnant of tropical rainforest in the globe, but also the driest desert, the desert of Atacama, plus one of the rainiest places, the Choco Biogeographic Region to the west. MSF are widespread in the Neotropics, occurring virtually in all its ecoregions. Additionally, MSF have been proposed as systems that promote high species diversity in Neotropical avifauna, leading to higher species packing within communities (Graves & Gotelli 1993). Unfortunately, a considerable part of the pristine environments in the Neotropical region had already been altered (Gibson *et al.* 2011) and is still under pressure of forest loss and habitat change due to human activities (Wright *et al.* 2009). Additionally, climate change effects highlight the need of further understanding of the ecology and dynamics of the highly diversified Neotropical biota (Joly 2008).

Here, we examine the ecological response of mixed-species flocks to natural and anthropogenic gradients in the Neotropical region. We do not intend to conduct a comprehensive bibliographic review, but to discuss current advances in studies with flocks in the Neotropics, and to provide guidelines for further progress on this topic. The studies summarized here were presented during the Symposium "Mixed-species flocks of birds: ecology and evolution" at the XII Ornithological Congress of the Americas, held at Puerto Iguazú, Argentina, from 8 to 11 August 2017. This document is organized in two sections. First, we describe the three most important gradients in the Neotropical region: the latitudinal gradient, the elevational gradient and the gradient of human disturbances. Second, we present a section with conclusions and guidelines for future research largely inspired in the discussion following the symposium and in the interaction among participants.

Mixed-species flocks and latitudinal gradients

A well-documented biogeographic pattern is the change of richness and diversity along latitudinal gradients, which shows a progressive decrease from the tropics to the temperate regions (Pianka 1966, Ruggiero 2001, Willig *et al.* 2003, Hillebrand 2004). Rabinovich & Rapoport (1975) observed that the spatial variation of bird richness is explained by climatic and topographic variables. Most studies point to climate regimes as the main drivers of latitudinal gradients of bird diversity, which affect various aspects of the ecology of the species directly or indirectly, including diets, use of available microhabitats and behavior (Ruggiero & Lawton 1998, Ruggiero 2001, Salisbury *et al.* 2012).

There are numerous studies that evaluate patterns in structure, composition and social role of the species that participate in flocks in the Neotropics (Munn & Terborgh 1979, King & Rappole 2000, Tubelis 2007, Amaral & Ragusa-Netto 2008, Knowlton & Graham 2011, Fanjul & Echevarria 2015), but virtually none of them investigates latitudinal effects. The subtropical mountain forest of the Yungas in Argentina is distributed from northern Salta (limit with Bolivia) to the north of Catamarca province encompassing approximately 700 km of extension. A pattern of decreasing diversity along latitude was observed in this forest in different *taxa*, including birds (Nores 1989, Blendinger & Alvarez 2009), mammals (Ojeda *et al.* 2008) and trees (Morales *et al.* 1995, Blundo *et al.* 2011). This pattern would be related mainly to latitudinal climatic impoverishment caused by the decrease in temperature and precipitation that influence the structure of the local vegetation (Brown *et al.* 2001, Ojeda *et al.* 2008, Blundo *et al.* 2011, Bellard *et al.* 2012). Considering these findings, Fanjul (2016) examined the potential role of the latitudinal gradient on the composition and structural variables of MSF (number of flocks, number of species and individuals participating) along the Yungas Forest of Argentina.

In this symposium, Fanjul demonstrated that whereas there was an effect of the latitudinal gradient on the composition of species, there was no effect on structural variables of MSF. However, species composition changed along the latitudinal gradient, dividing the Argentine Yungas in three sectors (north, center and south).

The structure and composition of mixed flocks are intimately related to the type of environment where flocks occur (Mokross *et al.* 2014), varying between regions, localities and habitats (Powell 1985). Although there is a turnover of individuals and species within a flock across space and time, most flocks' general structure will not change, unless the environment is altered (Zhang *et al.* 2013, Marín-Gómez & Arbeláez-Cortés 2015). In such case, these results could indicate that flocks maintain their structure independently of an inherent species turnover across the latitudinal gradient.

Mixed-species flocks of birds and elevational gradients

Species diversity and community composition are known to change with elevation in a somehow predictable fashion: overall species diversity decreases with elevation, not necessarily following a linear pattern (McCain 2009, McCain & Grytnes 2010). Elevational gradients result in significant changes in many environmental conditions (*e.g.*, temperature, precipitation, oxygen levels), with lower temperatures and more seasonal climatic regimes characterizing higher elevations. Because environmental characteristics change within relatively short distances in mountains, they have been used as model systems to evaluate the relative importance of ecological and evolutionary processes in community structure (Sundqvist *et al.* 2013, Graham *et al.* 2014, Read *et al.* 2014). Harsh conditions at higher elevations are expected to act as a filter, allowing only species that are well adapted to these conditions to persist. On the other hand, at lower elevations, biological interactions (*e.g.*, species interactions) are expected to be a more important force shaping communities (Weiher *et al.* 2011). In a much smaller scale, topography may also cause variation in vegetation composition and determine overall species distribution (Cintra & Naka 2012) within a relatively small area.

Despite the great ubiquity of mixed-species flocks and their early recognition as good study models to test ecological hypotheses (Graves & Gotelli 1993), research focusing on ecological structure of flocks along elevational gradients are still scarce. This gap is clear when conducting a bibliographic search on ISI Web of Science v.5.27 (10 December 2017) with "mixed species flocks" AND "elevation" OR "altitude" as key words in the article topic: results returned only 19 studies between 1900 and 2017. Further examination on each of these studies indicates that only six of them focus on elevation, either testing for MSF composition changes with elevation (Greenberg *et al.* 2001, Arbeláez-Cortés & Marín-Gomez 2012, Marín-Gómez & Arbeláez-Cortés 2015, O'Donnell 2017), or including elevation as a predictor while testing for the effect of other habitat characteristics on flocks (Brandt *et al.* 2009, Goodale *et al.* 2009). Therefore, we attempted to analyze the effect of small and large amplitude of elevational variation in flock's network properties.

In this symposium, Montaño-Centellas presented an example of flock variation along a well-preserved elevational gradient in Bolivia. This study used network theory to test for the effect of elevation on the structure of social networks in mixed-species flocks of birds, along a continuous transect (2000–3550 m a.s.l.) that largely lacks human presence and dissects a protected area (Montaño-Centellas & Garitano-Zavala 2015). She found that species composition, species richness in flocks, as well as network-level metrics vary with elevation. As expected, the number of species participating in flocks decreased with elevation, with an average of six species above 3250 m a.s.l. and an average of nine species at 2000 m a.s.l. (Montaño-Centellas *in prep.*). At the species-level metrics, she found that whereas there were no significant differences in degree (the number of connections each species maintains with other species), weighted degree (the sum of the frequency of interspecific associations for each node) changed across elevations. These results suggest that the overall role of any given species within flocks might change across elevations as well as its position within the network. At the network-level metrics, she found that networks at higher elevations were less modular (*e.g.*, had less community structure), had lower strength (*e.g.*, average of the weighted degrees) and had lower skewed degree distributions than networks at lower elevations. Overall, these findings suggest that networks at higher elevations are less complex, more evenly distributed as they do not include "sub-units" within the flocks, and are potentially less resilient, as long tail degree distributions are characteristic of networks that are more resilient (Thébault & Fontaine 2010).

This study exemplifies the examination of flocks as components of the community along a broad environmental gradient, where abiotic characteristics (*e.g.*, temperature) strongly correlate with elevation and are important predictors of community changes. However, elevation may also affect communities at smaller scales, modifying local environmental characteristics and creating natural gradients within otherwise climatically "homogeneous" and stable habitats (*i.e.* non-seasonal when compared with temperate regions), such as the Amazonian lowland *terra firme* Forests (Karr & Freemark 1983, Cintra & Naka 2012). This idea would not be conceivable for lowland forests, where species richness was once believed to show a remarkable constancy in a variety of Amazonian sites (Cohn-Haft *et al.* 1997).

Because mixed-species flocks of birds represent "community modules" (*sensu* Holt 1997), flocks are expected to respond as communities to small changes, with little or no differences among MSF that occur in the same habitat. However, in this symposium, Kajiki demonstrated that mixed-species flocks of birds differed along a discrete environmental gradient in *terra firme* forest, both in richness and species position within the network. She examined the effect of environmental variables (elevation and NDVI index) in species richness and structure of mixed species flocks in a *terra firme* forest in the Brazilian Amazon, where elevation varied by less than 130 m between highest and lowest point. By employing network analysis to understand general network properties of flocks, she found that only weighted degree was affected by the environmental gradient: MSF at lower elevations presented higher frequencies of interspecific interactions. Furthermore, species richness was also affected by this gradient, with richer MSF in mid-elevation sites, which presented higher NDVI values. These results suggest that birds are responding to small-scale environmental heterogeneity (Cintra & Naka 2012) and that even small differences in elevation can result in different network properties.

Mixed-species flocks of birds' response to anthropogenic disturbances

Of the world's rapidly vanishing tropical forests, Neotropical forests are not an exception (Bierregaard-Jr. & Lovejoy 1989, Pimm & Raven 2000). This is of great concern because the Neotropics harbor several biodiversity hotspots (Myers *et al.* 2000), and a great amount of information on natural history of Neotropical species, as well as ecological data of these biological communities, are still missing. The main reason behind the rapid vanishing of tropical forest is the expansion and intensification of agricultural frontier, which leads to forest loss and fragmentation (Foley *et al.* 2005, Laurance *et al.* 2014). As fragmentation increases, the surface of native environments and the size of the remnant fragments decrease, with the subsequent increment in isolation. Removal of native forests and replacement by crops with different architecture and phenology result in changes in several environmental conditions in newly created landscapes. For instance, air temperature, temperature range within the day and albedo increase due to changes in the radiation balance within fragments, which leads to higher desiccation rates (Foley *et al.* 2005, Laurance *et al.* 2014). Higher radiation and desiccation levels in forest fragments may lead to decreased prey availability, reducing foraging opportunities for birds and alter their natural cycles (Saunders *et al.* 1991, Laurance 2004). Furthermore, fragmented landscapes limit movements of understory passerines (Tellería & Santos 1995, Develey & Stouffer 2001), increase nest predation (Kattan *et al.* 1994, Renjifo 1999, 2001) and facilitate the establishment of raptors associated with forest gaps (Thiollay 1999). These changes in forest configuration and the associated mechanisms reduce habitat quality for birds, causing an overall loss of biodiversity (Stouffer & Bierregaard-Jr. 1995, Maldonado-Coelho & Marini 2004).

Nevertheless, the consequences of deforestation and habitat degradation extend beyond the loss of bird diversity, and affect ecological interactions (Brandt *et al.* 2009, Mokross *et al.* 2014). Because MSF are an important functional component of bird communities it is imperative to better understand the complex social structure of this type of group association (Greenberg 2000). Furthermore, MSF may be a good predictor of habitat quality, as there is a positive relationship between habitat quality and flock attributes (*e.g.*, well-preserved habitats contain richer mixed flocks; Zuluaga & Rodewald 2015).

In this respect, Mangini showed in her presentation that for seasonal forests in Salta, northwest of Argentina, birds attended mixed-species flocks in both continuous and fragmented forests, following the same seasonal pattern, and reaching the highest number of recorded mixed flocks during the Austral fall and winter. However, some species with similar abundances in both types of forest configuration had a higher flocking propensity within forest fragments, while other species showed this pattern in continuous forest (Mangini *et al.* in prep.). Furthermore, the number of flocks, as well as their species richness and number of individuals, were smaller within forest fragments when compared with continuous forest.

Even though fragmentation is a key factor for the loss of both biodiversity and interactions, flocks may be affected by factors acting simultaneously at different scales. As Colorado showed in his presentation, a multi-scale factor (*i.e.* landscape and local scale) seems to be affecting different attributes of mixed-species flocks recorded in one area. In this study conducted in several countries across the Andes, the remaining amount of forest at a regional level interacted with the type of habitat and microhabitat structure to shape the frequency of occurrence, richness and abundance of mixed flocks in a particular area (Zuluaga & Rodewald 2015). In general, deforestation, loss of habitat structure and conversion of high quality to poorer habitats (*e.g.*, silvopasture) resulted in the loss of some species and guilds (*e.g.*, understory specialists and insectivores) that do not exist in disturbed, less-complex habitats.

Along with the fragmentation process and habitat degradation mediated by anthropogenic causes, there is not only a biodiversity loss, but also a loss of poorly understood interactions such as those occurring in mixed-species flocks. Since mixed-species flocking is proposed as a behavior to improve the foraging efficiency and to enhance predation avoidance of their members (Miller 1922, Buskirk 1976, Morse 1977, Goldman 1980, Sridhar & Shanker 2014), the formation of mixed flocks can act as a mechanism to cope with difficult conditions (Morse 1970, Mangini & Areta 2018). Thus, MSF comprise social interactions that should not be understood as simple congregation of different species together in one place, and rather as a social interaction that allows bird species to obtain certain benefits. In this way, we do not know to what extent the loss of interactions, manifested by smaller and less diverse mixed flocks in degraded habitats will affect ecological dynamics of bird communities in mid to long-term.

Conclusion and future directions

Altogether, the presentations in this symposium demonstrate how mixed-species flocks respond to various environmental gradients in different scales. Environmental gradients affect not only general assembly patterns, such as species composition, but also network properties and species interactions within MSF. In general, MSF composition changed across the three gradients analyzed here, and structural properties of MSF (number of flocks, number of species and individuals within flocks) varied significantly across the elevational and the anthropogenic gradients. Furthermore, it was possible to detect changes in network properties of flocks across the elevational gradient, with less complex networks with fewer interspecific interactions at higher elevations. Interestingly, responses of MSF to environmental gradients were detected at different scales, suggesting flocks can be a good study system to further test ecological hypothesis.

The studies presented in this symposium represented a good overview of the current research on MSF in the Neotropics. Here we mention a number of opportunities for improvement. Studies were conducted in different environments and biomes: Yungas' foothill and montane forest, primary Andean montane Forest, Amazonian lowland Forest, and silvopasture. However, as a reflection of Wallacean shortfalls in biodiversity inventories in the Tropics, much of what we know on MSF is concentrated in certain regions, such as areas next to urban centers, populated municipalities, research institutes or environments that received more attention by their high biodiversity. Consequently, we still lack basic information on MSF in other environments such as subtropical forests, grasslands and shrublands that represent a significant amount of the geographic area in the Neotropical region.

In addition, advances in technology and computational power allowed the development of new equipment for tracking animal movements, and enabled the use of social network analysis with biological data. Population ecology explored these tools for a long time. However, only recently social network theory has been used to respond questions in MSF research through the analysis of emerging properties in MSF (see Farine 2014 and Mokross *et al.* 2014 for some examples). The method is powerful for assembling and depicting patterns of social interactions, which usually are not easy to detect or perceive. It enables inferences on the strength of those interactions, and analyses of species or individual's social functions within the group. Future investigations should consider including social network analysis in their methodological framework as a more accurate way of detecting social interactions and relationships among species. Furthermore, future studies should examine these interactions within mixed flocks and with their environment, integrating species-specific research and species-habitat relationships to disentangle the mechanisms that promote and maintain mixed flocks formations. Further experimental approaches to study the gain of benefits of joining MSF are also scarce in tropical areas and should be a fruitful arena for future research in the region. Finally, although much conservation attention is given for species as a unit, from a functional perspective, conservation efforts should be directed to preserve interactions rather than solely species, including those among birds in MSF.

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ARTICLE

Advocating better habitat use and selection models in bird ecology

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ABSTRACT: Studies on habitat use and habitat selection represent a basic aspect of bird ecology, due to its importance in natural history, distribution, response to environmental changes, management and conservation. Basically, a statistical model that identifies environmental variables linked to a species presence is searched for. In this sense, there is a wide array of analytical methods that identify important explanatory variables within a model, with higher explanatory and predictive power than classical regression approaches. However, some of these powerful models are not widespread in ornithological studies, partly because of their complex theory, and in some cases, difficulties on their implementation and interpretation. Here, I describe generalized linear models and other five statistical models for the analysis of bird habitat use and selection outperforming classical approaches: generalized additive models, mixed effects models, occupancy models, binomial N-mixture models and decision trees (classification and regression trees, bagging, random forests and boosting). Each of these models has its benefits and drawbacks, but major advantages include dealing with non-normal distributions (presence-absence and abundance data typically found in habitat use and selection studies), heterogeneous variances, non-linear and complex relationships among variables, lack of statistical independence and imperfect detection. To aid ornithologists in making use of the methods described, a readable description of each method is provided, as well as a flowchart along with some recommendations to help them decide the most appropriate analysis. The use of these models in ornithological studies is encouraged, given their huge potential as statistical tools in bird ecology.

KEY-WORDS: binomial mixture models, classification trees, generalized additive models, generalized linear models, mixed models, occupancy models, regression trees.

HABITAT USE AND SELECTION IN BIRDS: FROM THEORY TO MODEL FIT

In the last decades, habitat use and selection has emerged as a basic aspect of bird ecology, due to its importance in natural history, distribution, response to environmental changes, management and conservation of bird species (Cody 1985, Guisan & Thuiller 2005, Engler *et al.* 2017). Despite the long tradition of the study of habitat use and selection in birds, however, almost 20 years ago, Jones (2001) had noticed ornithologists usually tended to be inconsistent of what habitat use and selection represent, with major implications on their hypothesis and conclusions about bird ecology (Jones 2001). Currently, some confusion between these terms still persists as a general issue in animal ecology (Lele *et al.* 2013, Boyce *et al.* 2016, McGarigal *et al.* 2016). Here, "habitat" is defined as a distinctive set of physical environmental factors that a species uses for survival and reproduction (Jones 2001, Lele *et al.* 2013). "Habitat use" refers to the way in which an individual or species uses habitats to meet its life history needs (Jones 2001). "Habitat selection", by contrast, refers to a hierarchical process of behavioral responses that may result in the disproportionate use of habitats to influence survival and fitness of individuals (McGarigal *et al.* 2016). Therefore, habitat selection refers to a process, whereas habitat use refers to the pattern resulting from habitat selection (Jones 2001).

In the field, standard approaches to assess bird habitat use or selection involve: (1) sampling the presence or abundance of individuals of a species across sampling units (typically transects or point counts; Bibby *et al.* 2000) across different habitat types, (2) comparing presence locations with random locations where the species could potentially be present across different habitat types (use-availability or case-control approach; Jones 2001, Keating & Cherry 2004, Johnson *et al.* 2006), or (3) using tracking devices on individual birds to acquire location data and compare them to available locations where the species was not recorded (Burger & Shaffer 2008, Wakefield *et al.* 2009, Bridge *et al.* 2011). With the rise of powerful statistical methods and the advancement of computing facility, more complex designs have been developed to assess habitat use and selection. For instance, these approaches can be extended to make repeated visits at the same sampling sites (temporal dependence), repeated observations on the same individuals (*e.g.* individuals tracked) or sampling many sites located nearby (spatial dependence). Notwithstanding, a plethora of statistical models outperforming classical linear models and which have been used for a while in other research areas (*e.g.* generalized linear and additive mixed models, Hastie & Tibshirani 1990, Bolker *et al.* 2009, Zuur *et al.* 2009; classification and regression trees, De'ath 2002, 2007; Ecological Niche Factor Analysis, Hirzel *et al.* 2002, Basille *et al.* 2008; quantile regression, Cade & Noon 2003; regularization methods such as ridge regression and LASSO, Reineking & Schröder 2006, James *et al.* 2013; Artificial Neural Networks, Lek & Guégan 1999; Flexible Discriminant Analysis, Hastie *et al.* 1994; Support Vector Machines, Kecman 2005; Bayesian approaches, Ellison 2004) are still not widespread among ornithologists. Some of these methods (*e.g.* generalized additive models, mixed models), nevertheless, have been widely used in some particular bird groups, such as seabirds (Wakefield *et al.* 2009, Engler *et al.* 2017). This phenomenon may be partly due to their relatively complex theory, and in some cases, difficulties on their implementation and interpretation (Bolker *et al.* 2009, Zuur *et al.* 2009, Dahlgren 2010). This is accentuated for Bayesian modeling, which represents a completely different statistical paradigm (Dennis 1996, Dorazio 2016). Moreover, early-career researchers tend to be reluctant to new analytical methods, as a result of self-perceived lack of quantitative training (Barraquand *et al.* 2014). Despite these issues, the methods mentioned typically both offer greater insight than classical approaches and represent no longer a problem in terms of statistical assumptions (Elith *et al.* 2006, Bolker *et al.* 2009, Elith & Graham 2009, Shabani *et al.* 2016).

From a statistical view, habitat use models aim to identify environmental variables linked to a species presence or abundance, and are species distribution models by definition (Guisan & Zimmerman 2000). On the other hand, habitat selection models link environmental variables with some proxy of fitness (nest site location, territories, reproductive output; Jones 2001). Although both types of models represent a correlative relationship between a bird species and its habitat, they are often expressed as a causal relationship, where the environment influences or explains the presence or abundance of a certain species:

$$\hat{Y} = b_0 + f\left(x\right)$$

where $\hat{Y}$ is the probability of occurrence or abundance of a bird species, b_0 is the intercept, x is an environmental variable, which may be represented by a categorical (different habitat types), ordinal or quantitative variable (*e.g.* environmental gradient), and $f(x)$ is a function of x. This simple model is suited for both habitat use and habitat selection studies, as it makes no assumptions of underlying processes, but just represents relationships between variables. It depends on the researcher whether this model is to be considered a habitat use or selection model (see Jones 2001). Beyond this theoretical discussion, the aim of this work is to describe some statistical methods appropriate for modeling the relationship between birds and their environment. As stated before, there is a myriad of methods that identify important environmental variables within a model, such as generalized additive models, mixed effects models, occupancy models, binomial mixture models and decision trees (classification and regression trees, bagging, random forests and boosting). In particular, these methods allow dealing with non-normal distributions (presence-absence and abundance data typically found in habitat use and selection studies), heterogeneous variances, non-linear relationships among variables, lack of statistical independence and imperfect detection. Here, I review these methods in order to (1) show the basics of each model with a readable description, (2) encourage ornithologists who are unfamiliar with the benefits of these methods to apply some of these analyses in their studies, and (3) help them to decide on which model to fit.

All graphs and models were built in R 3.3.1 (R Core Team 2016) using the packages lme4 (Bates *et al.* 2015), mgcv (Wood 2006), unmarked (Fiske & Chandler 2011), rpart (Therneau *et al.* 2015) and rpart.plot (Milborrow 2017).

REVIEW OF MODELING METHODS

Classical approaches: Generalized Linear Models

Generalized Linear Models (GLM) extend the classical linear regression approach by allowing different error distributions (not only normal) and the inclusion of non-homogeneous variances (Nelder & Wedderburn 1972). Every GLM has three basic components: (1) an error structure or random component, (2) a linear predictor or systematic component, and (3) a link function. The error structure corresponds to the distribution probability of the residuals (*i.e.* observed – predicted values), whereas the linear predictor represents the set of environmental variables. Finally, the link function $g\left(\hat{Y}\right)$ is a function of the response variable that links the error structure with the linear predictor, and makes the function linear (Dobson 2002):

$$g\left(\hat{Y}\right) = b_0 + b_1 x$$

where $\hat{Y}$ is the predicted occurrence or abundance of a bird species, $g\left(\hat{Y}\right)$ is a function of $\hat{Y}$, x is an environmental variable, and b_0 and b_1 represent model coefficients. This simple model can be expanded to include non-linear effects through quadratic and interaction terms:

$$g(\hat{Y}) = b_0+b_1x_1+b_2x_2+b_3x_1^2+b_4x_2^2+b_5x_1x_2$$

where x_1 and x_2 represent environmental variables and b_i's represent model coefficients. Although GLMs can provide non-linear fits by including quadratic or cubic terms, they must use a high degree to produce flexible fits. Presence-absence data follow a binomial distribution (Pearce & Ferrier 2000), whereas count data may follow a Poisson, negative binomial or zero–inflated distributions (Welsh *et al.* 1996, Guisan *et al.* 2002, Ver Hoef *et al.* 2007). For the univariate case, binomial and Poisson GLMs are expressed, respectively, as:

$$\hat{Y} = \frac{\exp\left(b_0 + b_1x\right)}{1+\exp\left(b_0 + b_1x\right)}$$

$$\hat{Y} = \exp\left(b_0 + b_1x\right)$$

where b_0 and b_1 are model coefficients. Link functions transforming both models into a straight line are the logit $\log\left(\frac{\hat{Y}}{1-\hat{Y}}\right)$ and the log function, respectively (Dobson 2002):

$$\log\left(\frac{\hat{Y}}{1-\hat{Y}}\right) = b_0 + b_1x$$

$$\log\left(\hat{Y}\right) = b_0 + b_1x$$

The binomial GLM predicts the probability of occurrence of a species (Fig. 1), but the measured outcome is often codified as 0 (absent) and 1 (present). This model describes a logistic curve, and indeed, aroused independently from linear regression under the name of logistic regression (Hosmer-Jr. *et al.* 2013). The Poisson GLM, in contrast, predicts values between 0 and +∞, as the response is represented by count data (Fig. 1). By using a Poisson distribution, heterogeneous variances are controlled, given that the expected value (mean) equals the variance. Thus, the larger the $\hat{Y}$, the larger the variance of the residuals (Fig. 1). However, in ecological data it is common for the variance to be larger than expected under a Poisson distribution (*e.g.* clumped distributions), which is termed "overdispersion" (Ver Hoef & Boveng 2007, Richards 2008, Lindén & Mäntyniemi 2011). Overdispersion may lead to wrong conclusions as it inflates *P*-values, and thus it is imperative to control for it (Zuur *et al.* 2009). There are several ways to do so, which depends on the kind of data and amount of overdispersion. Essentially, it can be corrected by either including an overdispersion parameter (quasi-Poisson GLM) or using another distribution (negative binomial or zero-inflated; Potts & Elith 2006, Ver Hoef & Boveng 2007).

Examples of GLMs applied to birds include Oppel *et al.* (2012), who compared five modeling techniques, including GLMs, to predict the distribution of the Balearic Shearwater *Puffinus mauretanicus*. Rodríguez-Pastor *et al.* (2012) used a Poisson GLM to assess habitat use of the invasive Monk Parakeet *Myiopsitta monachus* in an urban area from Mexico, and Shahan *et al.* (2017) assessed the importance of local and landscape variables on grassland bird occurrence of prairie fragments using binomial GLMs.

Beyond linearity: Generalized Additive Models

GLMs establish relationships between the response and the environmental variables in a linear fashion. However, it is common for a species to show non-linear relationships with environmental variables, where species select environmental conditions in which they can survive and reproduce optimally. As a result, the presence or abundance of a species along an environmental gradient is usually unimodal (Austin 1987, Palmer & Dixon 1990). Generalized Additive Models (GAMs) extend GLMs by allowing the estimation of non-linear relationships between the response and the environmental variables, without assuming an *a priori* shape (Hastie & Tibshirani 1990, Yee & Mitchell 1991, Guisan *et al.* 2002). They are said to be data-driven instead of model-driven (like GLMs). A GAM is expressed as:

$$g(\hat{Y}) = b_0+f(x)$$

where $f(x)$ is a non-linear function of x. Therefore, this model assumes no particular relationship between the response and the environmental variables. Like GLMs, GAMs can also use the same error distributions to model presence-absence and abundance data (binomial, Poisson, negative binomial, zero-inflated distributions) and link functions (logit, log; Yee & Mitchell 1991, Barry & Welsh 2002). Therefore, for presence-absence and count data, respectively, univariate GAMs are expressed as:

$$\hat{Y} = \frac{\exp\left[b_0 + f\left(x\right)\right]}{1+\exp\left[b_0 + f\left(x\right)\right]}$$

$$\hat{Y} = \exp\left[b_0 + f\left(x\right)\right]$$

Basically, GAMs fit a smoothing curve by dividing the data into regions called “windows” at certain point locations called “knots”, and then fit individual functions called splines within each window (Hastie & Tibshirani 1990, Zuur *et al.* 2009, James *et al.* 2013). There are many types of splines, but the most common involve cubic regression and smoothing splines. Cubic regression splines are cubic polynomials which are then joined together to form a smoothing curve (Zuur *et al.* 2009, James *et al.* 2013). Smoothing splines (also called penalized splines or *P*-splines) arise in a different situation, in which the aim is to find a function $f(x)$ minimizing a residual sum of squares (*RSS*) subject to a smoothness penalty (Zuur *et al.* 2009, James *et al.* 2013):

$$\sum\left[Y-f\left(x\right)\right]^{2}+\lambda J\left(f\right)$$

The first term is the *RSS* and measures the fit between the observed Y and expected values $f(x)$. Minimizing only this term would lead to a function $f(x)$ that exactly interpolates the data (James *et al.* 2013). Such a curve would be extremely rough, zigzagging among the different observed values, and with low predictive value. The second term is a penalty term measuring the degree of smoothness of the function $f(x)$ (James *et al.* 2013), which is the product of a smoothness or tuning parameter λ and

$$J\left(f\right)=\int f''\left(x\right)^{2}dx$$

where $f''(x)$ is the second derivative of $f(x)$. In practical terms, $J(f)$ is a summed curvature of $f(x)$, which means it is a measure of roughness: it is large if $f(x)$ is very wiggly, and it is zero if it is a straight line (James *et al.* 2013). If $\lambda = 0$, the penalty term has no effect, and $f(x)$ will exactly interpolate the data. When λ is large, $f(x)$ will be perfectly smooth (*i.e.* a straight line). Whatever type of spline is used, the result is that each environmental variable is

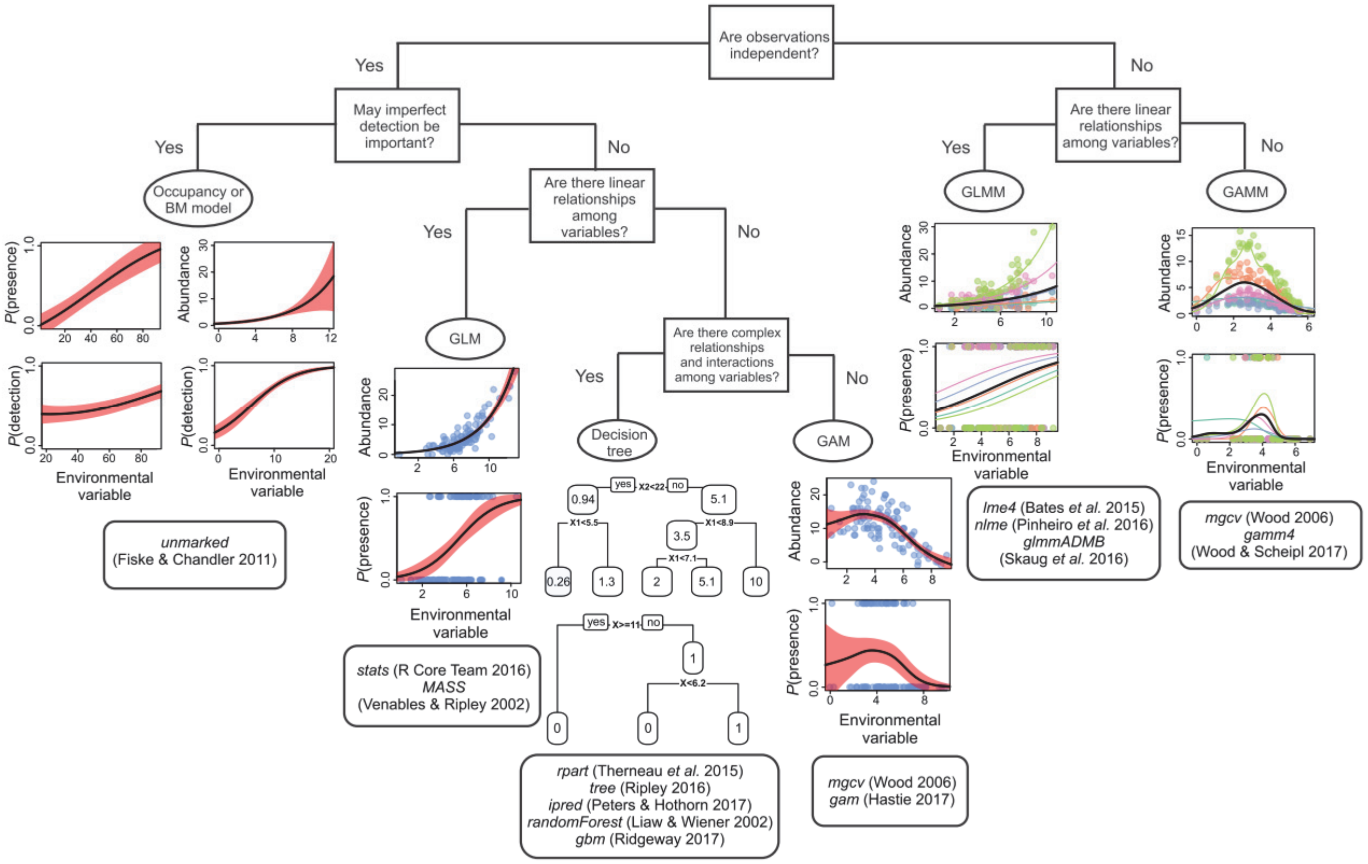

Figure 1. Flowchart illustrating how to select appropriate habitat use and selection models according to data properties. Rectangles hold questions, and ellipses contain recommended models. For most models (except for the classification tree), a hypothetical example using only one environmental variable is shown for the two most common data types in habitat models: presence-absence and abundance data. Points depict observations, black lines depict overall fitted models and red bands represent 95% confidence intervals. In decision trees, *Xs* represent environmental variables and values inside boxes, predicted values. Different colors in mixed models (GLMM and GAMM) indicate different levels of random effects (*e.g.* individuals, transects, point counts, etc.). Rounded corner boxes include R packages to perform the analysis. This is not a comprehensive review, but merely a guide to aid ornithologists to use an appropriate method. To choose a model, the researcher should also accompany this flowchart with data exploration, model validation and selection (see text for further details). BM - Binomial Mixture, GLM - Generalized Linear Model, GLMM - Generalized Linear Mixed Model, GAM - Generalized Additive Model, GAMM - Generalized Additive Mixed Model.

included in the model as a non-parametric smoothing function (Fig. 1). This only applies for numeric and ordinal data; nominal variables are included like in GLMs, in which case it is called a semi-parametric model, since it includes both non-parametric and parametric terms (James *et al.* 2013):

$$g(\hat{Y}) = b_0 + f(x_1) + b_1 x_2$$

where x_1 and x_2 are numeric and nominal, respectively, variables, and b_1 is a parametric coefficient.

GAMs, in contrast to GLMs, provide non-linear fits by increasing the number of knots but keeping the degree fixed (James *et al.* 2013). The main drawback of GAMs is that the fitted model is represented by a complex equation, and no coefficient estimates and standard errors are provided (Wood 2006, Zuur *et al.* 2009, Hegel *et al.* 2010). Instead, the significance of the model itself and the environmental variables is assessed, and a graphical display of the model relating environmental with response variables is often more useful (Wood 2006, Hegel *et al.* 2010).

Seabird ecology, contrary to terrestrial bird ecology, has often used GAMs as part of its statistical toolbox (Wakefield *et al.* 2009). As an example, Olivier & Wotherspoon (2006) assessed habitat selection in Wilson's Storm Petrel (*Oceanites oceanicus*) in both ice and ice-free areas where it nests. By using remote-sensing data, Fauchald *et al.* (2017) applied GAMs to relate foraging locations of Antarctic Petrels (*Thalassoica antarctica*) with melting ice and primary production. Pereira *et al.* (2018) used a combination of different models, including GAMs, to predict 30 seabird distributions as a function of different environmental stressors (fishing intensity, ship density and oil pollution risk). An example of the use of GAMs in terrestrial birds is Whitaker *et al.* (2015), who investigated the habitat use of the threatened Newfoundland Gray-cheeked Thrush (*Catharus minimus minimus*) at both local and landscape scales.

When assumptions of classical models are not met: mixed effects models

In habitat use and selection studies, it is often the case for ornithologists to take repeated samples of the same units (individual birds, point counts, transects, nests) over time (within a year, across years) or to have hierarchical or nested data (*e.g.* several samples of the same bird on different times). Under these scenarios of statistical non-independence, GLMs and GAMs are no longer valid, as these assume independence among observations (Hastie & Tibshirani 1990, Dobson 2002, Zuur *et al.* 2009). To cope with this, mixed effects models (or just mixed models; Bolker *et al.* 2009, Dingemanse & Dochtermann 2013, Schielzeth & Nakagawa 2013) treat some factors grouping several observations that do not represent a directly measured effect (*e.g.* individual, point count, year, date, site, etc.) as random variables (*i.e.* random factors or effects). For the sake of simplicity, I will consider only one random factor (*e.g.* individuals or point counts with repeated observations). Fixed effects, on the contrary, represent the effects that explanatory variables have on the response variable and are supposed to be determined or fixed by the researcher (Bolker *et al.* 2009, Dingemanse & Dochtermann 2013), here represented by the environmental variables. Models are termed “mixed” because they include both random and fixed effects (Dingemanse & Dochtermann 2013) and are particularly valuable for identifying the source of unobserved variability and accounting for it, thus reducing the overall variance of the model (Bolker *et al.* 2009). Overall, mixed models extend GLMs and GAMs by including random effects, which are called, respectively, Generalized Linear Mixed Models (GLMMs) and Generalized Additive Mixed Models (GAMMs). As extensions of GLMs and GAMs, mixed models may use the same error and link functions.

In the simplest case, GLMMs and GAMMs can be expressed, respectively, as:

$$g\left(\hat{Y}\right) = b_0 + b_1 x + \gamma$$

$$g\left(\hat{Y}\right) = b_0 + f\left(x\right) + \gamma$$

Here, the intercept b_0 represents the grand mean of average individual or point count responses, whereas γ is each individual›s or point count›s unique average response (random effect) with γ coefficients normally distributed with a certain variance (Zuur *et al.* 2009, Dingemanse & Dochtermann 2013). In this model, the contribution of individuals or point counts is estimated as the difference from the population line by including intercepts for each individual or point count and keeping slopes constant (Dingemanse & Dochtermann 2013). This is called a random intercept model, as the intercepts of the individuals or point counts are assumed to be normally distributed with mean zero and variance σ^2 (Zuur *et al.* 2009, Dingemanse & Dochtermann 2013). This σ^2 represents the variance across random intercepts of individuals or point counts. In other words, in a random intercept GLMM there is an overall trend represented by the first two terms of the model (fixed effect), and one line fitted to each individual or point count parallel to the population fitted line (random effect), whose intercepts are assumed random (Fig. 1).

We may further suspect that the relationship between the environmental variables and the response is different for each individual or point count (*i.e.* they have different intercepts and slopes). By extension, intercepts

γ_1 and slopes γ_2 can vary randomly by assuming normal distributions with means zero and variances σ_1^2 and σ_2^2, respectively. This is called a random intercept and slope model (Zuur *et al.* 2009; Fig. 1):

$$g\left(\hat{Y}\right)=\left(b_0+b_1x\right)+\left(\gamma_1+\gamma_2z\right)$$

$$g\left(\hat{Y}\right)=\left[b_0+f\left(x\right)\right]+\left(\gamma_1+\gamma_2z\right)$$

The first two terms represent the average relationship between presence or abundance and an environmental variable x, whereas the last two terms represent now individual curves for each of the point counts or individuals, whose intercepts γ_1 and slopes γ_2 vary randomly. In this model, z may be represented by different environmental variables including x, but this notation is used to distinguish the fixed component from the random one. The decision between both kinds of models is based on model selection or in biological meaning (see below; Zuur *et al.* 2009). It is worth mentioning that more complex designs exist, that allow including nested random factors, as well as spatial and temporal autocorrelation (nearby sampling units in space or time) commonly found in ornithological studies (Zuur & Ieno 2016). A comprehensive review is beyond the scope of this work. Under these scenarios, readers are encouraged to see Dormann *et al.* (2007), Zuur *et al.* (2009) and Zuur & Ieno (2016).

Mixed models have been used to fit the abundance and/or occurrence of birds to environmental variables. As examples, Paiva *et al.* (2010, 2013a, 2013b) analyzed foraging habitat use of different populations of Cory's Shearwater (*Calonectris diomedea borealis*) using Gaussian or binomial GLMMs with foraging trip nested within individual bird as random factor. Palacio (2016) assessed the habitat use of the Tufted-tit Spinetail (*Leptasthenura platensis*) in several forest remnants using a binomial GLMM with forest patch as random factor grouping occurrence records. Heldbjerg *et al.* (2017) analyzed GPS-location use of different land cover types as a function of the distance to the nest in the European Starling (*Sturnus vulgaris*) using a binomial GLMM with the identity of the individual as random factor. As in the case of GAMs, seabird ecologists have often used GAMMs to model habitat use and selection (Wakefield *et al.* 2009). Paiva *et al.* (2017), for instance, compared foraging habitat use derived from GPS-loggers between female and male Cory's Shearwaters in six breeding seasons. An example of GAMM applied to terrestrial birds is Sitters *et al.* (2014), who assessed the relationship between forest bird occurrence of 15 bird species, habitat structure and time since fire in a 70-year chronosequence using binomial GAMMs and specifying landscape (units of 100 ha separated by at least 3 km) and site (transects within landscapes) as random factors.

Accounting for imperfect detection: occupancy and binomial *N*-mixture models

So far, all the models described assume that detection of a species is perfect, that is, that every individual in the field is recorded. True absences are virtually impossible to assure, given the different sources of variation that may cause false negatives (a species may occur unnoticed either due to low abundance, cryptic or elusive habits, misidentification, or erroneous sampling designs; MacKenzie *et al.* 2005, Zuur *et al.* 2009, Guillera-Arroita 2017). Failure to account for imperfect detection may bias model parameter estimates, as the proportion of sites with presences (occupancy) will always underestimate the true occupancy, even with low levels of non-detection (Gu & Swihart 2003). Occupancy models account for imperfect detection by estimating both an occupancy probability ψ and a detection probability p based on making multiple visits at the same sample sites (called "detection histories"; MacKenzie *et al.* 2005, Guillera-Arroita 2017; Fig. 1). Mathematically, imperfect detection means $p < 1$. The essence of the method is that if a species is recorded in a given site (usually coded as 1), and then it is undetected (usually coded as 0), it is assumed that the site is occupied and the absences represent non-detections. As probabilities, both occupancy and detection are assumed to be binomially distributed (MacKenzie *et al.* 2005). In turn, each parameter may be constant or a function of one or more environmental variables, alike a binomial GLM (Welsh *et al.* 2013):

$$\psi=\frac{\exp\left(b_0+b_1x\right)}{1+\exp\left(b_0+b_1x\right)}$$

$$p=\frac{\exp\left(\gamma_0+\gamma_1x\right)}{1+\exp\left(\gamma_0+\gamma_1x\right)}$$

where ψ is occupancy probability, p is detection probability (given the species is present in a certain sampling site), x is an environmental variable (it may be the same or not for both occupancy and detection), and b_0, b_1, γ_0 and γ_1 are model coefficients (Fig. 1). This occupancy model may be one of the simplest approaches, and several extensions have been developed to expand this framework (*e.g.* multi-season: MacKenzie *et al.* 2003; multi-species: Dorazio *et al.* 2006, Richmond *et al.* 2010, Rota *et al.* 2016; alternative sampling designs: Lele *et al.* 2012, Specht *et al.* 2017).

A similar idea may be applied to deal with abundance instead of presence-absence data. Binomial *N*-mixture models (or *N*-mixture models) estimate both abundance N and detection probability p from abundance data

(Dodd-Jr. & Dorazio 2004, Kéry *et al.* 2005, Royle *et al.* 2005; Fig. 1). As before, p is assumed to be binomially distributed, whereas N is assumed to follow some distribution for count data (Poisson, negative binomial, zero inflated; Kéry 2008, Joseph *et al.* 2009). Assuming a Poisson distribution with mean λ, both λ and p can be modeled as functions of environmental variables:

$$N \sim Poisson(\lambda)$$
$$\lambda = \exp\left(b_0 + b_1 x\right)$$
$$p = \frac{\exp\left(\gamma_0 + \gamma_1 x\right)}{1 + \exp\left(\gamma_0 + \gamma_1 x\right)}$$

where N is the expected number of individuals, λ is the mean expected abundance, p is detection probability, x is an environmental variable, and b_0, b_1, γ_0 and γ_1 are model coefficients.

Models accounting for imperfect detection have several assumptions, the most important being the independence among sampling sites and the closed state of occupancy or demographic closure (Kéry *et al.* 2005, MacKenzie *et al.* 2005), which means that occupancy does not change at a site within the sampling period. Despite being promising tools, occupancy models suffer from several caveats. The estimating equations often have multiple solutions and the estimates are unstable when data are sparse, making accurate inference difficult (Welsh *et al.* 2013). Most importantly, when detection depends on abundance, model estimates are biased with similar magnitude to those biases obtained when ignoring non-detection (Welsh *et al.* 2013). As Welsh *et al.* (2013) has shown in a simulation study, occupancy modeling is not always applicable and should not be used indiscriminately to account for imperfect detection. In particular, sparse data (*i.e.* low number of occupied sites) results in extreme fits (0 or 1) for both detection and occupancy, because small changes in the data have large effects on the estimated parameters. Also, when detection is suspected to depend on abundance, occupancy models perform poorly (Welsh *et al.* 2013; but see Guillera-Arroita *et al.* 2014). Recently, however, Specht *et al.* (2017) proposed an alternative sampling design in which each of the sites is visited once, and sites where the species is encountered in the first survey are visited an additional number of times to better estimate detection probability. This conditional design expending a greater relative effort at occupied sites leads to improved parameter estimates (Specht *et al.* 2017).

In the last years, numerous applications of occupancy modeling and, to a lesser extent, N-mixture models have been applied to bird habitat use and selection. For instance, Parashuram *et al.* (2015) related Forest Thrush (*Turdus lherminieri*) abundance to forest structure using a binomial N-mixture model, and Suwanrat *et al.* (2015) applied a beta-binomial mixture model to estimate the abundance of the secretive Siamese Fireback (*Lophura diardi*) from camera trapping data in pristine and degraded forests. Glisson *et al.* (2017) and Huber *et al.* (2017) modeled the occupancy probability of the endangered wetland bird Yuma Ridgeway's Rail (*Rallus obsoletus yumanensis*) and the Wood Warbler (*Phylloscopus sibilatrix*), respectively, as a function of different environmental and anthropogenic disturbance variables.

Complex interactions among variables but simple decision rules: decision trees

Additional tools to identify important environmental variables in habitat use and selection models are decision trees (Breiman *et al.* 1984, De'ath & Fabricius 2000, De'ath 2002). Decision trees are non-parametric models that predict responses by recursively splitting the space of predictors (environmental variables) into a number of simple regions, giving as a result a dichotomous branching tree showing the hierarchy of importance of predictors as well as the nature of interactions between variables (Breiman *et al.* 1984, De'ath & Fabricius 2000, De'ath 2002). The tree is built by repeatedly splitting the data, defined by a simple rule based on a single explanatory variable (Fig. 1). At each split, the data is partitioned into two mutually exclusive groups, each being as homogeneous as possible. At each level of the tree, the mean of the observations in the region to which it belongs is used to make predictions (De'ath & Fabricius 2000). If the predicted response is presence-absence data, the tree is called classification tree; if the response is quantitative the tree is named regression tree (Breiman *et al.* 1984, Zuur *et al.* 2007; Fig. 1). A major advantage of decision trees is their simple and attractive graphical output (Fig. 1). As such, there is some terminology associated with trees, much alike phylogenetic trees. The root represents the top of the tree and initial split, and the terminal nodes are called leaves. The interpretation of the tree is made as follows: start at the root, and ask a sequence of questions about the environmental variables. The interior nodes are labeled with questions, and the edges or branches between them labeled by the answers (Fig. 1). Usually, each question refers to only a single variable, and has a yes/no answer. Arbitrarily, if the answer is "yes", we proceed to the left branch; otherwise, we proceed to the right branch (Fig. 1). The mean value of a group of observations is given as a prediction at the end of a branch.

A major issue to deal with is that decision trees tend to overfit, as a result of high complexity (*i.e.* many leaves). Overfitting leads to poor predictions, but using a small tree might also result in a poor fit (James *et al.* 2013).

A common approach to reduce overfitting is to grow a very complex tree and then apply an algorithm to prune it (Breiman *et al.* 1984). Intuitively, the aim is to find a sequence of subtrees of decreasing size, each of which is the best of all trees of its size, and then select the tree that gives better predictions. Pruning may be carried out through a cost-complexity approach. The cost can be defined by a metric such as the residual sum of squares (*RSS*) with a complexity penalty based on the size of the tree (Zuur *et al.* 2007):

$$RSS + cp \times tree\ size$$

The *RSS* measures data fit (see also GAMs), and *cp* is called complexity parameter ($cp \geq 0$). If the size of the tree is large, the *RSS* is relatively low and *vice versa* (recall that more complex trees tend to overfit thus reducing the *RSS*). The essence is to obtain a sequence of best subtrees as a function of *cp*, and then select the best subtree. *cp* values can be selected by cross-validation (Zuur *et al.* 2007, James *et al.* 2013), in which data are split in K (typically $K = 10$) subsets (K-fold cross validation). Each of these subsets is left out in turn, and a tree is computed for the remaining $(K - 1)/K$ percent of the data (90% if $K = 10$). Once the optimal tree size is calculated for a given *cp* value using the 90% subset, predictions are made and compared to observed values in the remaining 10% subset. The sum of squared differences between the observed and mean values per leaf is the prediction error. This process is applied for each of the $K = 10$ cross validations, giving 10 values of prediction errors. These 10 values are averaged for each *cp* value, and the *cp* value that minimizes the average prediction error is chosen (James *et al.* 2013).

Building a classification tree is quite similar to building a regression tree. However, *RSS* cannot be used in classification trees, as the outcome is 0 or 1. The Gini impurity index G can be used instead (Breiman *et al.* 1984):

$$G = \sum p\left(1 - p\right)$$

where p is the proportion of observations that belong to a given class. It is a measure of total variance across the K classes; if all observations belong to one class, $G = 0$ (no variance) and the node is considered "pure" as we can be pretty certain that the predicted values is either 0 or 1.

Main advantages of decision trees are: (1) their non-parametric nature, as they make no distributional assumptions about the data, (2) their simplicity and usefulness for interpretation, which make them ideal to explain to non-scientists (James *et al.* 2013), and (3) better at dealing with non-linearity and complex relationships between explanatory variables than other approaches (GLM, GAM and mixed models; Zuur *et al.* 2007, James *et al.* 2013). On the other hand, they are less competitive in terms of statistical accuracy than other methods (*e.g.* GAMs). However, by aggregating many decision trees with methods like bagging, random forests, and boosting, the predictive performance of trees can be substantially improved (James *et al.* 2013).

A consequence of overfitting is that decision trees suffer from high variance. This means that splitting a dataset at random and fitting decision trees to each subset may give rather different results. To overcome this, bagging uses bootstrapping techniques to generate N different datasets (typically 100–1000), and then averages resulting predictions from each tree (Breiman 1996, De'ath 2007, James *et al.* 2013). Although bagging results in improved accuracy over prediction of a single tree, it is no longer possible to represent the results using one tree, and it is no longer clear which variables are the most important ones (James *et al.* 2013). However, it is possible to obtain a summary of the importance of each environmental variable by computing the decrease in *RSS* (regression trees) or Gini index (classification trees) due to splits over a given explanatory variable, averaged over all trees; a large value indicates an important predictor.

Now suppose the following setting: there is one very strong explanatory variable in the data set, and a number of other moderately strong predictors. In the set of bagged trees, most or all of the trees will use this strong predictor as first split. Consequently, all of the bagged trees will be similar to each other, and their predictions will be highly correlated. Averaging many highly correlated values does not substantially decrease variance as averaging many uncorrelated quantities. Another tree-based technique, called random forests, provides an improvement over bagging, as a way to reduce correlations between predictions of different trees (Breiman 2001, Cutler *et al.* 2007, James *et al.* 2013). As in bagging, a number of decision trees are built on bootstrapped samples, but each time a split in a tree is considered, a random sample of m predictors is chosen from the full set of p predictors. The number of m random predictors is typically fixed at $\sqrt{p}$.

A third approach for improving predictions of decision trees is boosting, also called boosted trees, in which each tree is grown sequentially using information from previous trees to improve error (De'ath 2007, Elith *et al.* 2008, James *et al.* 2013). Boosting assigns a weight to each model based on classification error. At each iteration, weights are increased on the incorrectly classified classes to focus the algorithm on these cases. The basic method proceeds as follows: given a current model, a decision tree is fitted using the residuals of the models as response. This new decision tree is added into the fitted function in order to update the residuals. Each of these trees can be small, with a few leaves. By fitting small trees to the residuals, the function is slowly improved in areas where it does not perform well. Boosting does not involve bootstrapping; each tree is fitted on a modified version of the original dataset instead. For a detailed description of the method see De'ath (2007).

Decision trees applied to birds have been typically used in Ecological Niche Modeling (Engler *et al.* 2017). Examples include Marini *et al.* (2009, 2010), Quillfeldt *et al.* (2017), and Krüger *et al.* (2018), who used several models, including GAMs, classification trees, boosting and random forests to predict the abundance of the Red-spectacled Amazon (*Amazona pretrei*), 26 bird species from South America, the Black-browed Albatross (*Thalassarche melanophris*), and seven large seabird species of the Southern Ocean, respectively. Carrasco *et al.* (2017) used random forests to analyze the presence of breeding colonies in six species of herons and egrets as a function of land-use variables, and Steel *et al.* (2017) assessed habitat use in 15 terrestrial birds across a vineyard-matorral landscape using boosted classification trees.

HOW TO CHOOSE THE RIGHT MODEL?

After presenting some methods to analyze bird habitat use and selection, the obvious question is: "Which model should I fit to my data?" In an attempt to answer this question, I provide some general guidelines for ornithologists to decide on which model to use, partly summarized in Fig. 1. In the next sections, I will also briefly describe three broad issues in order to help researchers to recognize, at least, an appropriate model: (1) data types, sampling design and biological knowledge, (2) data exploration and model validation, and (3) model selection. Researchers must be aware that more than one model may be used to fit a particular dataset. Alternatively, and although I have tried to cover the most important types of data and designs in ornithological studies, none of the methods presented could fit a dataset well. Under these circumstances, researchers are encouraged to see also other methods mentioned in the current review.

Data types, sampling design and biological knowledge

The nature of the data gathered will undoubtedly have consequences on the type of model it can be applied, since it leads immediately to a subset of possible probability distributions to be handled. The two most common data types in habitat models are presence-absence and count data. As stated above, presence-absence data follow a binomial distribution, whereas count data may follow a Poisson, negative binomial or zero-inflated distributions. Zero-inflated Poisson (ZIP) or negative binomial (ZINB) distributions will be particularly useful for cryptic and rare birds, in which there are an excess of zeroes and a low number of records (Welsh *et al.* 1996, Martin *et al.* 2005, Zuur *et al.* 2012). Extensions to account for imperfect detection have also been developed (Wenger & Freeman 2008, Joseph *et al.* 2009, Dénes *et al.* 2015). Although both data types are, by far, the most widely used in habitat models, they are not the only ones. In seabirds, for example, it is common to assess habitat use using proxies of foraging activity and distribution (*e.g.* trip duration, time required for a bird to pass through a circle with a given radius–first passage time duration–, foraging area, home ranges of foraging excursions; Pinaud 2007, Paiva *et al.* 2013b, 2017), which are continuous variables following Gaussian or beta distributions.

Sampling design and field methods are other major drivers of the model to be applied (Zuur & Ieno 2016). In bird habitat selection studies, it is common to have one or more sources of dependency. For example, transects or point counts are usually visited multiple times within a season, a year or between different years. These multiple visits represent a source of dependency, which may be modeled by mixed models (Zuur *et al.* 2009), occupancy or binomial *N*-mixture models. The same applies to repeated foraging observations of individual birds, in which the individual must be included as a random factor in a mixed model. Another valuable method used to model bird habitat selection is GPS tracking of individual birds, in which individual locations are dependent observations (Wakefield *et al.* 2009, Singh *et al.* 2016, Paiva *et al.* 2017). In this case, the individual bird is treated as a random factor in a mixed model.

Biological knowledge on the species under study has also implications for choosing a given model (Burnham *et al.* 2011). For instance, occupancy and binomial *N*-mixture models are ideal for terrestrial birds, for which there are many sources of variation impairing detection (see above), and, in particular, for cryptic or elusive species, for which $p << 1$ (Wenger & Freeman 2008). More rarely, occupancy models have been applied to seabirds. This is because the absence of vegetation and the size and conspicuousness of nesting colonies allows p being considered nearly or equal to 1 (Passuni *et al.* 2016). As an example, Passuni *et al.* (2016) assessed habitat selection with occupancy models in breeding colonies of three tropical seabird species and its relationship with oceanographic conditions and prey availability. In mixed models, for instance, if a bird appears in flocks (or any other groups, such as colonies, roosts or leks, namely areas where males aggregate to perform competitive displays for the females) then the flock should be treated as a random factor, since the presence and abundance of a species depends on the movement of other individuals in the group (Avilés & Bednekoff 2007, Xu *et al.* 2010, Végvári *et al.* 2016).

Data exploration and model validation

A fundamental step in data analysis is data exploration, as it provides insight into the data and their limitations, helps the researcher to identify appropriate models and allows checking model assumptions (Zuur *et al.* 2010). In this sense, graphical tools are advocated as the most important devices for data exploration, whereas certain statistical tests are warned against (Quinn & Keough 2002, Läärä 2009). Zuur *et al.* (2010) provide a protocol for data exploration covering important issues in exploratory data analysis, such as heterogeneity of variance, dependence among observations, zero inflation in GLMs and types of relationships between the response and explanatory variables. In particular, visualization of model residuals represents a key step to check whether a model meets its assumptions (*i.e.* model validation; Quinn & Keough 2002, Zuur *et al.* 2010, Zuur & Ieno 2016). To this end, a plot of residuals *vs.* fitted values, residuals *vs.* each environmental variable, and residuals *vs.* time or space coordinates, if relevant, must be made (Zuur *et al.* 2009, 2010). In all these plots, residual variation should be similar, showing no pattern. Although sometimes the researcher may think observations are *a priori* independent (which justifies the use of a GLM, GAM, occupancy models or binomial *N*-mixture models, Fig. 1), residuals may show some pattern. In these cases, a GLMM or GAMM should be a better choice (Fig. 1; Zuur *et al.* 2009, Zuur & Ieno 2016). Under temporal or spatial dependence, a GLMM or GAMM with temporal or spatial autocorrelation structure may be needed (Zuur *et al.* 2009). Finally, the choice between a linear and an additive model is based on the type of relationship between the response and the environmental variables (Fig. 1). If the relationship is linear or quadratic, consider using a GLM or GLMM; for more complex relationships consider applying a GAM or GAMM (Fig. 1; Zuur *et al.* 2009, Zuur & Ieno 2016). For complex relationships and interaction effects, decision trees are appropriate models. Although these assume no independence among observations, however, they are sensitive to autocorrelation effects (Segurado *et al.* 2006).

Model selection

A great body of literature has been devoted to the topic of model selection in ecology during the last decade (Burnham & Anderson 2004, Johnson & Omland 2004, Whittingham *et al.* 2006, Diniz-Filho *et al.* 2008, Burnham *et al.* 2011, Warren & Seifert 2011, Aho *et al.* 2014, Mac Nally *et al.* 2018). Once the researcher has identified an appropriate habitat model, he/she must choose one or several alternatives among a set of candidate models. To this, there are major two algorithms: (1) stepwise model selection (Whittingham *et al.* 2006) and (2) information-theoretic approaches (IT approaches; Burnham & Anderson 2002). Stepwise selection *sensu lato* operates by successive addition or removal of significant or non-significant terms (forward selection or backward selection, respectively). Others operate by forward selection but also check the previous term to see if it can now be removed (stepwise selection *sensu stricto*; Whittingham *et al.* 2006). Stepwise selection is considered a poor procedure and is not recommended anymore, because it includes bias in parameter estimation, inconsistencies among model selection algorithms, the problem of multiple hypothesis testing, and an inappropriate focus or reliance on a single best model (Whittingham *et al.* 2006). Also, they are not able to compare non-nested models. For all these reasons, I will focus on IT approaches.

IT methods provide measures of the strength of evidence for a set of hypotheses (*i.e.* statistical models) given the data (Burnham & Anderson 2002). These are called "information-theoretic" because they are based on Kullback-Leibler (K-L) information (also called K-L distance or divergence). In essence, K-L information represents the information loss when model g_i is used to approximate reality f (process that generated observed data), or, in other words, the distance between g_i and f (Burnham *et al.* 2011). Thus, the idea is to select the model in the set of R models that minimizes K-L information loss (Burnham *et al.* 2011). Akaike (1973) found a simple expression describing the information loss when fitting a model, called Akaike's Information Criterion (AIC):

$$AIC = -2\ln L + 2K$$

L is the likelihood, *i.e.* the probability of a model given the data, and K is the number of parameters in the model. Conceptually, the expression describes a trade-off between goodness-of-fit (first term with a negative effect on AIC) and complexity (second term with a positive effect on AIC). So, the higher the fit and the lower the number of parameters, the lower the AIC (*i.e.* principle of parsimony). In practice, AIC is computed for each of the R candidate models and the model with the smallest AIC value is selected as "best" (Burnham *et al.* 2011). Thus, it is the AIC differences (ΔAIC) that are important for ranking the models:

$$\Delta AIC_i = AIC_i - AIC_{min} \qquad \text{for } i = 1, 2, 3, \ldots, R.$$

where AIC_{min} is the minimum of the AIC values for the R models. Akaike weights w_i are a measure of strength of evidence and represent the probability of each model given the data and the R models under consideration (Burnham *et al.* 2011). In the literature, it is common to discard models with ΔAIC < 2. This arbitrary cutoff rule is now known to be poor, and models within the 2–7 range have support and should rarely be dismissed

(Arnold 2010, Burnham *et al.* 2011). After this procedure, nevertheless, there might be substantial model selection uncertainty, which is quantified by Akaike weights (*e.g.* the best model has probability 0.3). Under these circumstances, inferences should be based on all the models in the set of best models, which can be done with model averaging (Burnham & Anderson 2002). Grueber *et al.* (2011) suggest model averaging when w_i of the best model < 0.9. Basically, average coefficients result from a weighted average of the coefficients that appear in the best models, where the weights are represented by Akaike weights (Grueber *et al.* 2011). At this point, there are two approaches to compute these averages (Grueber *et al.* 2011): (1) full-model averaging or zero method, in which parameters not included in a model are set to zero and included when averaging the coefficient estimates, or (2) conditional-model averaging or natural average method, in which only those parameters included in a model are used for averaging (Burnham & Anderson 2002). The choice between both approaches depends on the aim of the study; Nakagawa & Freckleton (2011) recommend full-model averaging when the aim of the study is to determine those factors with the strongest effect on the response variable. On the other hand, when there is a particular factor of interest and it is possible that this factor may have a weak effect compared to other covariates, conditional-model averaging should be used to avoid shrinkage towards zero (Nakagawa & Freckleton 2011).

As AIC provides a relative measure of model fit, many different types of models may be compared. The comparisons are only valid for models fitted to the same response variable, so nested or non-nested models can be compared (Burnham & Anderson 2002, Grueber *et al.* 2011). Model 1 is said to be nested in model 2 if the parameters in model 1 are a subset of the parameters in model 2. For instance, a random intercept GLMM with one environmental variable is nested within another random intercept GLMM with the same environmental variable plus a quadratic term of the same variable. Another example is a random intercept GAMM and a random intercept and slope GAMM with the same environmental variable. Thus, different structures of random factors may be compared in mixed models (Zuur *et al.* 2009). It should be noted, however, that comparisons between mixed models is an active area of research, as there is no current consensus of how to handle random factors (Müller *et al.* 2013, Schielzeth & Nakagawa 2013, Rocha & Singer 2018, Sciandra & Plaia in press). Following the previous reasoning, GLMs are nested within GLMMs (GLMs with random factors), GAMs are nested within GLMMs (GAMs with parametric coefficients and random factors), and GAMMs encompass all these types of models (GLMs, GAMs and GLMMs), which means that all these are nested (Zuur *et al.* 2009). In contrast, a GAM and a regression tree represent non-nested models, but they also can be compared using AIC. Thereby, IT approaches are a useful way to compare the different models presented in this review.

Overall, some basic principles guiding the use of AIC may be summarized: (1) AIC is a relative measure of model parsimony, so it only has meaning when comparing AIC values for different models; lower AIC indicates a more parsimonious model, relative to a model with a higher AIC (Burnham & Anderson 2002, Burnham *et al.* 2011), (2) nested, as well as non-nested, models can be compared (Burnham & Anderson 2002, Grueber *et al.* 2011), (3) too many models should not be compared, because a model with the lowest AIC, that is not the most appropriate model, might be found by chance; competing models should be based on biological meaning (Burnham *et al.* 2011), (4) it is possible to have multiple models performing similarly to each other, which may lead or not to model averaging (Grueber *et al.* 2011), (5) models with small sample sizes (as a rule of thumb, when n/K < 40) should be compared with the AIC corrected for small sample sizes (AIC_c; Hurvich & Tsai 1989), which penalizes stronger for the number of parameters in the model than AIC:

$$AIC_c = AIC + \frac{2K\ (K+1)}{n-K-1}$$

where n is sample size, and (6) the model identified as the "best" model may still have low explanatory or predictive power, so its adequacy needs to be addressed (Mac Nally *et al.* 2018); this can be achieved with different measures of explained variance (pseudo-R^2, R^2_{GLMM}; Nakagawa *et al.* 2017) coupled with cross-validation (Mac Nally *et al.* 2018).

Finally, AIC is not the only information criterion to determine the amount of information contained in a given model, but at present, it is by far the most widely used in ecology (Symonds & Moussalli 2011, Mac Nally *et al.* 2018). Other alternatives proposed include the Bayesian information criterion (BIC), the deviance information criterion (DIC), and the Watanabe-Akaike information criterion (WAIC), among others (see Box 1 in Grueber *et al.* 2011). For the criticisms of these indices, readers are encouraged to see Spiegelhalter *et al.* (2002) and Murtaugh (2009).

CONCLUDING REMARKS

This review presents powerful tools to model habitat use and habitat selection in ornithological studies. A comprehensive review of the methods available is beyond the scope of this work. Instead, this contribution is intended to give a broad overview of some of the most relevant approaches to analyze relationships between birds and its environment, some of which still remain underused by ornithologists. Many other methods are available to model bird habitat use or selection, some of which require presence-only data such as Environmental Envelope Models (Hijmans & Graham 2006), Maximum Entropy (Elith *et al.* 2011, Merow *et al.* 2013) or Ecological Niche Factor Analysis (Hirzel *et al.* 2002, Basille *et al.* 2008). Other promising but more complex algorithms derived from machine-learning theory are Artificial Neural Networks (Lek & Guégan 1999, Yen *et al.* 2004) and Support Vector Machines (Guo *et al.* 2005, Kecman 2005). Hopefully, this work will attract ornithologists' interest in using some of the techniques presented, who will undoubtedly achieve a quality leap. Overall, the use of these models in ornithological studies is encouraged, given their huge potential as statistical tools in bird ecology.

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ARTICLE

Using MacKinnon lists and mist-netting simultaneously: maximizing the efficiency of rapid surveys of bird populations in the Atlantic Forest of northeastern Brazil

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ABSTRACT: The Brazilian Atlantic Forest has been transformed into a mosaic of forest fragments that impacts local populations of vertebrates, in particular birds. In the state of Sergipe, Brazil, while only approximately 10% of the original forest remains, ornithological research is still incipient, and basic data are still lacking. In this context, the present study investigated the bird community of a remnant of Atlantic Forest in the municipality of Japoatã using complementary methods in a rapid survey approach. The composition of the community and its trophic guilds was defined and compared with other localities in Sergipe, and Atlantic Forest sites in other Brazilian states. Data were collected in October 2016, by mist-netting and the compilation of MacKinnon lists. A total of 118 bird species were recorded during 1088 net-h and in 60 MacKinnon lists. Four of these species are under some risk of extinction, and one of these is endemic to the region. The most diverse families were Thraupidae, Tyrannidae, Trochilidae, and Thamnophilidae, with the relative contribution of each family varying according to the the sampling method used. The most common species were *Manacus manacus* (Linnaeus, 1766) and *Coereba flaveola* (Linnaeus, 1758). The omnivores were the largest guild (*n* = 301 individuals), followed by the insectivores (*n* = 236) and the frugivores *n* = 146). The combined survey approach proved effective, increasing the number of bird species known to occur in the study area to 165, with an increase of more than 40% in comparison with previous surveys in the same area. Overall, the results of the present study reinforce the need for further ornithological surveys in the region, and the value of combining complementary approaches for a more comprehensive inventory during rapid surveys.

KEY-WORDS: avifauna, bird conservation, MacKinnon lists, mist-netting, trophic guilds.

INTRODUCTION

The Atlantic Forest originally covered more than 1.3 million square kilometers of the eastern coast of Brazil (Fundação SOS Mata Atlântica & INEP 2016), and is now considered to be one of the world's 35 biodiversity conservation hotspots (Williams *et al.* 2011). The Atlantic Forest extends over more than 20 degrees of latitude, ranging from equatorial to subtropical regions, which generates a considerable diversity of habitats and ecosystems (Tabarelli *et al.* 2005) that contributes to its considerable biodiversity (Myers *et al.* 2000, Faria *et al.* 2006, Pereira & Alves 2007). This biome has suffered extensive deforestation, and ongoing impacts have reduced its cover to no more than 15% of its original area (Fundação SOS Mata Atlântica & INEP 2016). In the Brazilian state of Sergipe, the Atlantic Forest, which originally covered almost half of the state, has been reduced to approximately 10% of its original area. The municipality of Japoatã, location of the present study, was the state's third most degraded in 2000–2014, and currently has only 9.6% of its original forest cover (Fundação SOS Mata Atlântica & INEP 2015).

The expansion of farmland and urban development typically transforms forests into a mosaic of habitats (Gascon *et al.* 2000, Guerra *et al.* 2015), with forest fragments persisting within a matrix of agricultural land. In Sergipe, this matrix is often composed of plantations of sugarcane (*Saccharum* sp.) and eucalypt (*Eucalyptus* sp.). The fragmentation of the forest has a number of negative impacts, including an increase in edge effects, and exposure to fires and chemical substances, such as herbicides, applied to the surrounding matrix (Gascon *et al.* 2000, Piratelli *et al.* 2005, Pereira &

Alves 2007). Dário *et al.* (2002) concluded that habitat fragmentation is especially problematic where dispersal is interrupted, the habitat is of poor quality or the fragments are too small to support viable populations. Dislich *et al.* (2001) emphasize the need for inventories for the understanding of the dynamics of these impacted environments.

Birds are an important component of tropical forest ecosystems (Ortega *et al.* 2003), and almost two thousand different species are found in Brazil (Piacentini *et al.* 2015). A total of 891 species are found in the Atlantic Forest (Moreira-Lima 2013), of which, 213 are endemic, and 147 are considered to be under some risk of extinction. Forest-dwelling birds are especially vulnerable to habitat fragmentation, whereas the populations of more generalist species may increase in response to the expansion of the agricultural matrix and edge effects (Piratelli *et al.* 2005).

The variation in the ecological characteristics of birds, such as their life history and behavior, and the relatively ease of collecting reliable field data make these animals useful indicators of environmental impacts, and they are often the principal focus in studies of environmental monitoring (Uezu *et al.* 2005). In Brazil, a number of studies have demonstrated the impacts of environmental degradation on the diversity of bird communities (Anjos & Boçon 1999, Gimenes & Anjos 2000, Dário *et al.* 2002, Piratelli *et al.* 2005, Faria *et al.* 2006, Paglia 2007, Franz *et al.* 2010), although few data are available on the bird fauna of the state of Sergipe (Sousa 2009, Ruiz-Esparza *et al.* 2015).

Ecological research in the Neotropical region is often hampered by both the complexity of the ecosystems and the scarcity of resources and trained personnel (MacLeod *et al.* 2011). In this context, a rapid survey approach can be extremely lucrative, especially when a relatively large volume of data can be obtained during a short period of time (MacLeod *et al.* 2011, Cavarzere *et al.* 2012, Ruiz-Esparza *et al.* 2016). The present study evaluated the effectiveness of combining complementary approaches, specifically mist-netting and MacKinnon lists (Bibby *et al.* 1998, Ribon 2010), for the collection of data during rapid surveys, in the Atlantic Forest of eastern Sergipe. While both methods provide relatively robust samples of bird diversity, mist-netting tends to provide records of more cryptic, understory species rarely recorded in MacKinnon lists, whereas these lists provide records of many, typically larger, high-flying species, that are almost never captured in mist-nets. The two methods were evaluated separately, and as a combined approach for the inventory of the bird fauna of the Fazenda Santana, a large sugarcane plantation in the municipalities of Japoatã and Pacatuba.

METHODS

Study area

Data were collected between 20–29 October 2016, in remnants of seasonal semi-deciduous Atlantic Forest in eastern Sergipe, Brazil. The study site is located on the Fazenda Santana (10°32'S; 36°45'W), a sugarcane plantation administered by the Brazilian Sugar and Alcohol Company (CBAA), in the municipalities of Japoatã and Pacatuba (Fig. 1).

The local climate is humid coastal, with annual

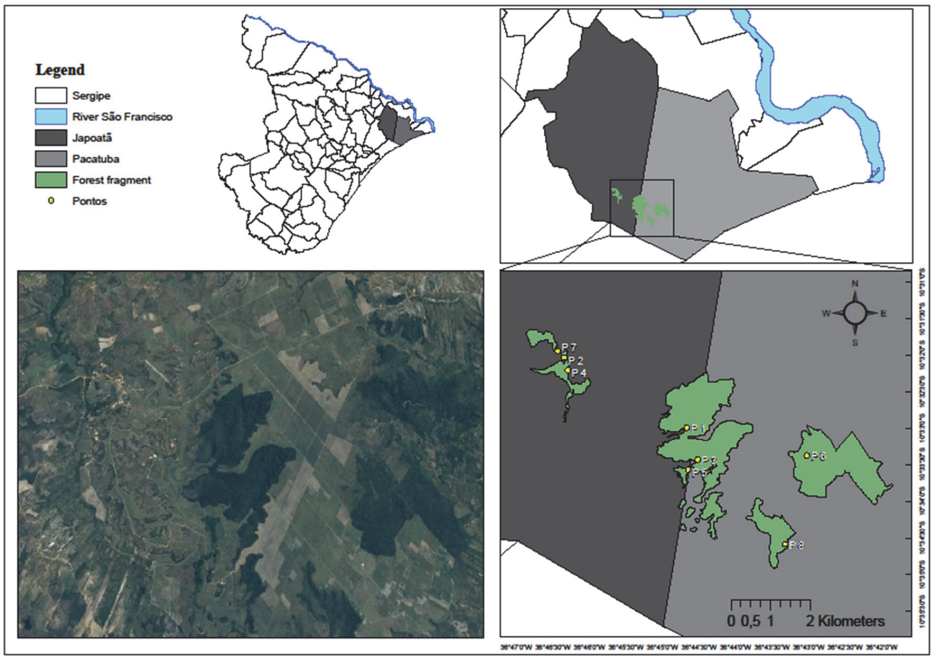

Figure 1. Location of the sampling points on the Fazenda Santana, in the municipalities of Japoatã and Japaratuba, in Sergipe, Brazil.

precipitation of between 1000 mm and 1400 mm (Santos 2009, Aragão *et al.* 2013). The forest patches of the Fazenda Santana straddle the border between the municipalities of Japoatã and Pacatuba, with a total area of approximately 700 ha, surrounded by a matrix of sugarcane. Most of the forest is secondary, having suffered repeated impacts from deforestation and successive sugarcane harvests, which involve the burning off of the plantations prior to harvesting the cane (Sousa 2009).

Data collection

Two complementary techniques were used simultaneously to collect data on the avian fauna of the study area – mist-netting and MacKinnon lists (MacKinnon & Phillipps 1993). A total of 12 mist-nets (12 m × 2.5 m, total area of 360 m^2) were set at eight different sampling points (Fig. 1) to sample the different habitats found within the study area (fragment edge and interior, open and closed habitats). The nets were set along pre-existing trails in morning (05:00–10:00 h) and afternoon (15:00–19:00 h) sessions, and were monitored every 20 min for the prevention of deaths (Ruiz-Esparza *et al.* 2012). The time of capture of each individual in the mist-nets was recorded, for the analysis of daily activity patterns.

All birds captured were ringed with standardized aluminum bands provided by the Brazilian Center for Avian Research and Conservation, CEMAVE (authorization 3905), processed according to the CEMAVE (1994) protocol, and then released at the capture site. Each bird was removed from the net, and placed in a cotton bag to be weighed using Pesola® spring balances (models 10100 and 41000). Prior to the release of each specimen, fecal samples were collected in eppendorf tubes containing 10% formaldehyde for the analysis of the composition of the diet, used to classify guilds. The collection of all biological material was authorized by the Brazilian Federal Biodiversity Information System (SISBIO), through license number 8286-1.

The MacKinnon lists were collected following the recommendations of Ribon (2010), with lists of 10 species being compiled. The birds were identified by an experienced ornithologist using binoculars (8 × 40) and a field guide (Sigrist 2015), supported by vocalizations, whenever appropriate.

While somewhat limited, the inventory of Sousa (2009) was used as a baseline for the compilation of species occurrences, together with the study of Ruiz-Esparza *et al.* (2015). The taxonomy was based on the Brazilian list of Ornithological Records (Piacentini *et al.* 2015), and the conservation status of the species was obtained from IUCN (2017). Birds that were observed or heard outside the systematic sampling were recorded as present at the study site, but they were not included in the statistical analyses.

Data analysis

The relative frequency (Fr) of each species or guild captured in the mist-nets was determined by $Fr = (n/T)*100$, where n = the number of individuals of the target species/group, and T = the total number of individuals recorded in the sample. For the MacKinnon lists, the relative frequency (IFL: Index of Frequency in the Lists) was determined by $IFL = (l/Lt)*100$, where l = the number of lists in which the species appears, and Lt = the total number of MacKinnon lists obtained during the study period.

The Jackknife I estimator was used to estimate the total species richness of the study area. This procedure was run in EstimateS 9.1.0 (Colwell *et al.* 2012). Rarefaction curves were also plotted in PAST (Hammer *et al.* 2001) to verify the relative effectiveness of the different survey methods. A cluster analysis based on the Jaccard coefficient was also run in PAST to compare the results of the present study with those of previous surveys in Sergipe (Sousa 2009, Ruiz-Esparza *et al.* 2015).

The species were classified in trophic guilds based on the available data (Wilman *et al.* 2014), together with foraging observations in the field and fecal analyses recorded during the present study. The species were classified in eight guilds: Carnivore (C), Frugivore (F), Granivore (G), Insectivore (I), Nectarivore (N), Scavengers (S), Omnivore (O), and Piscivore (P). The relative abundance of each guild was calculated as above, and the biomass of each group was also determined.

RESULTS

The mist-netting resulted in a total of 1088 net-h of sampling, during which a total of 280 individuals were captured, representing 61 species belonging to 23 families. The Thraupidae was the most diverse family, with 13 species, followed by the Tyrannidae (6 species), and the Trochilidae (5 species). These three families together accounted for 39.3% of the species captured in mist-nets. The Jackknife 1 analysis estimated a total of 89 species for the study area based on these data (Fig. 2), which was statistically different from the number actually recorded (t = -8.35; P = 0.0001).

A total of 599 individuals were recorded in 60 MacKinnon lists, representing 97 species in 33 families. Once again, the Thraupidae was the most diverse family (15 species), followed by the Tyrannidae (10 species), Trochilidae (8 species), and Thamnophilidae (6 species), which together contributed 40.2% of all sightings. The Jackknife 1 analysis of the data estimated a total of 120 species for the study area (Fig. 3), significantly different from the number actually observed (t = -8.69; P = 0.0001). The reduced number of MacKinnon lists is a result of

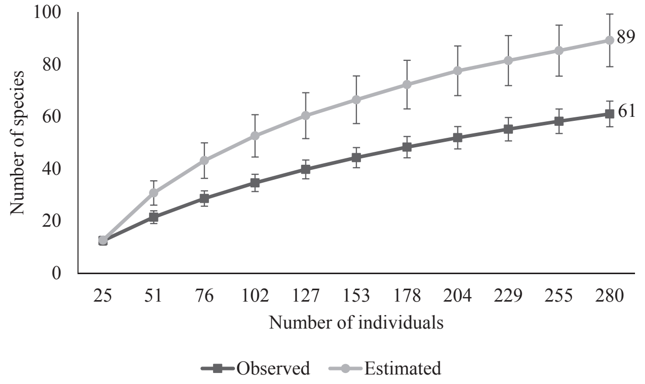

Figure 2. Bird species richness observed and estimated according to the Jackknife 1 procedure, based on the records collected during mist-netting at Fazenda Santana in Japoatã and Pacatuba, Sergipe, Brazil. The records are based on a total of 1080 net-h of sampling effort.

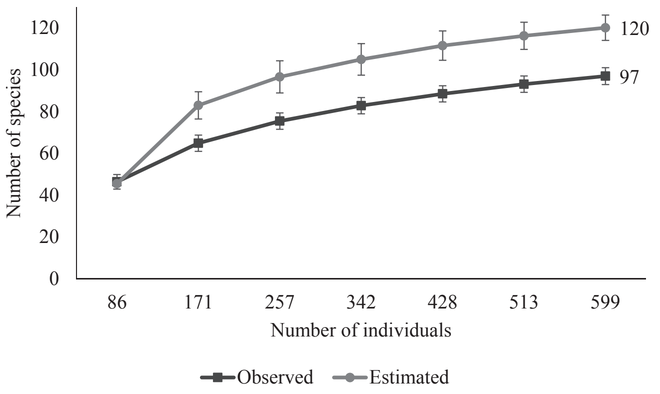

Figure 3. Bird species richness observed and estimated according to the Jackknife 1 procedure, based on the records collected in the MacKinnon lists at Fazenda Santana in Japoatã and Pacatuba, Sergipe, Brazil. Each sample point consists of six lists.

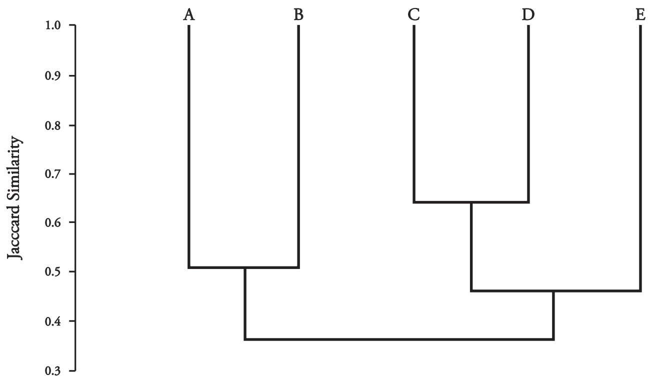

Figure 4. Cluster plot based on the Jaccard similarity index. A = Fazenda Santana (present study); B = Mata do Junco (Ruiz-Esparza *et al.* 2015); C = Mata da Santana (Sousa 2009); D = Mata do Junco (Sousa 2009); E = Mata do Crasto (Sousa 2009).

the low species richness of the study site. However, the number of lists compiled during the present study was more than proportional to the study period, given that approximately 200 lists have been compiled during six other, more recent excursions to the study area (unpub. data).

The cluster analysis (Fig. 4) indicated a relatively high degree of similarity between the results of the present study and those of Ruiz-Esparza *et al.* (2015) at the Mata do Junco reserve (Jaccard index J' = 0.506), located in the municipality of Capela, which borders Japoatã (Fig. 4B). All other studies returned indices of less than 0.4 for the comparison with the present study, and Mata do Crasto, located in the southern extreme of Sergipe, was the least similar (J' = 0.319), which is consistent with its geographic distance from the present study site (Fig. 4). The rarefaction curves plotted for the two methods used in the present study (MacKinnon lists and mist-netting) indicated that the MacKinnon lists provided a more effective inventory of the local avifauna, with an additional 36 species being recorded during the course of the study period (Fig. 5).

A further six species – *Aramides cajaneus* (Statius-Muller, 1776), *Crypturellus noctivagus* (Wied, 1820), *Euscarthmus meloryphus* Wied, 1831, *Nyctibius griseus* (Gmelin, 1789), *Pseudastur polionotus* (Kaup, 1847), and *Pyriglena atra* (Swainson, 1825) – were recorded only during non-systematic observations. Of the total of 118 species recorded at the Fazenda Santana during the present study, only four are listed by the IUCN (2017), two (*C. noctivagus* and *P. polionotus*) are listed as "Near Threatened", one (*Herpsilochmus pectoralis* Sclater, 1857) as "Vulnerable", and one (*P. atra*) as "Endangered".

The most abundant species captured in the mist-nets were *Manacus manacus* (Linnaeus, 1766) (*n* = 60 records; 21.4% of the total), *Dacnis cayana* (Linnaeus, 1766) (n

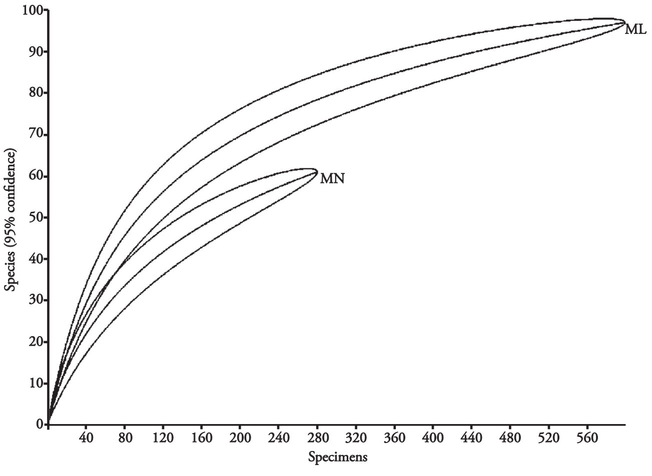

Figure 5. Rarefaction curves comparing the two survey methods used in the present study. ML = MacKinnon lists; MN = Mist-nets.

= 25; 8.9%), *Tangara cayana* (Linnaeus, 1766) (*n* = 17; 6.1%), *Turdus leucomelas* Vieillot, 1818 (*n* = 14; 5.0%), *Hydropsalis albicollis* (Gmelin, 1789) (*n* = 12; 4.3%) and *Tachyphonus rufus* (Boddaert, 1783) (*n* = 12; 4.3%). Together, these six species contributed almost half of all the individuals captured (Table 1).

The most common species recorded in the MacKinnon lists were *Coereba flaveola* (Linnaeus, 1758) (IFL = 46.7%), *Amazona aestiva* (Linnaeus, 1758) (IFL = 41.7%), *Cyclarhis gujanensis* (Gmelin, 1789) (IFL = 36.7%), *Tangara palmarum* (Wied, 1821) (IFL = 33.3%), *Columbina talpacoti* (Temminck, 1810) (IFL = 31.7%), and *D. cayana* (IFL= 31.7%). All other species were recorded less frequently (Table 1).

Based on the timing of the captures in the mist-nets, the birds were most active during the early morning (5:00–10:00 h), when 73.9% of the captures were recorded (during 55.5% of the sampling effort). During the afternoon sessions (15:00–19:00 h), 26.1% of the individuals were captured. After sunset (18:00 h), only birds with nocturnal habits were captured in the mist-nets (Fig. 6).

Considering all records (mist-net captures and MacKinnon lists), the largest guild was that of the omnivores, with 301 individuals (34.2% of the total), followed by the insectivores (*n* = 236; 26.8%), frugivores (*n* = 146; 16.6%), granivores (*n* = 94; 10.6%), nectarivores (*n* = 68; 7.7%), carnivores (*n* = 24; 2.7%), scavengers (*n* = 9; 1.0%), and piscivores (*n* = 1 or 0.1%) (Fig. 7). A similar pattern was recorded in terms of biomass (Fig. 8), although the predominance of the omnivores increased even further, whereas the nectarivores were relegated to penultimate position due to their exceptionally small individual body size.

DISCUSSION

The 118 bird species recorded in the present study represent approximately 43% of the 276 species known to occur in the Atlantic Forest of the state of Sergipe (Ruiz-Esparza *et al.* 2015), and in particular, add 45 species to Sousa (2009) original inventory of the study site. This indicates that the rapid survey approach adopted in the present study provided a reliable sample of the local avian fauna, and represents an important advance in the data available for the study area (Sousa 2009, Moreira-Lima 2013).

Jaccard's index analysis reflected a low similarity (38.9%) between the findings of the present study and the inventory of Sousa (2009). This may be related to the different sampling methods used in the two studies. Sousa (2009) recorded 114 species during 12 visits to the study area between 2001 and 2007, but did not apply a standardized sampling protocol, and included surveys of non-forested areas. This contrasts with the more systematic, complementary approach adopted in the present study. In a similar comparative study, O'Dea *et al.* (2004) found that MacKinnon lists provided much more

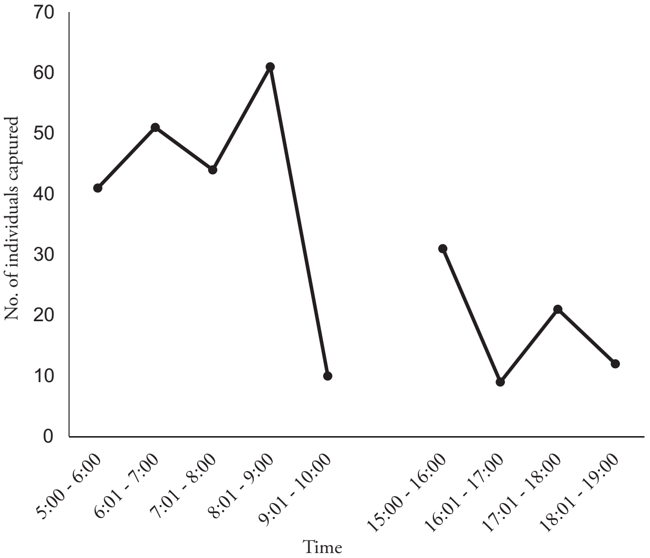

Figure 6. Number of individuals captured in the mist-nets at different times of day.

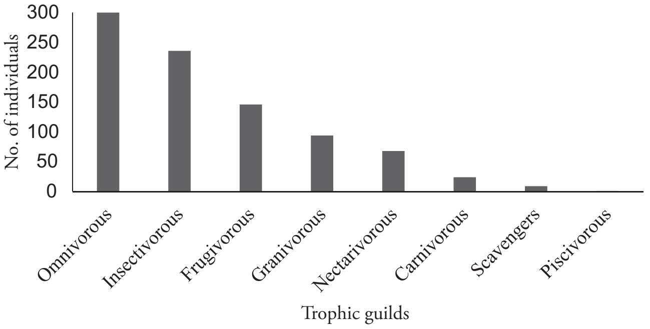

Figure 7. Number of individuals recorded in the present study by trophic guild.

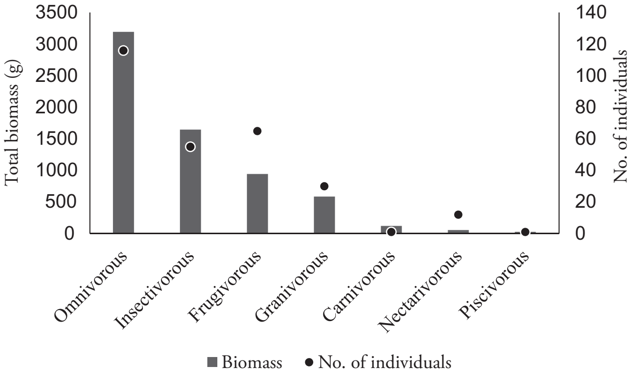

Figure 8. Abundance of individuals, and accumulated biomass by trophic category, collected during the mist-netting.

Table 1. Bird species recorded between 20–29 October at the Fazenda Santana, Japoatã, Sergipe, Brazil. The classification and nomenclature follow the Brazilian Ornithological Records Committee (Piacentini *et al.* 2015). Method: mist-net (MN), MacKinnon list (ML), occasional records (OR). Guild: carnivorous (C), scavengers (S), frugivorous (F), granivorous (G), insectivorous (I), nectarivorous (N), omnivorous (O), piscivorous (P). Number in MacKinnon lists (nML), number in mist-net (nMN), number in occasional records (nOR), total number (*n*), index of frequency in lists (IFL), relative frequency (RF).

Family / Species	Common name	Method	Guild	nML	nMN	nOR	*n*	IFL	RF
Accipitriformes									
Accipitridae									
Geranospiza caerulescens (Vieillot, 1817)	Crane Hawk	MN	C	2	0	0	2	0.03	–
Pseudastur polionotus (Kaup, 1847)	Mantled Hawk	OR	C	0	0	1	1	–	–
Rupornis magnirostris (Gmelin, 1788)	Roadside Hawk	MN	C	6	0	0	6	0.10	–
Apodiformes									
Trochilidae									
Anthracothorax nigricollis (Vieillot, 1817)	Black-throated Mango	MN	N	1	0	0	1	0.02	–
Chlorostilbon lucidus (Shaw, 1812)	Glittering-bellied Emerald	MN–ML	N	9	1	0	10	0.15	0.36
Chlorostilbon notatus (Reich, 1793)	Blue-chinned Sapphire	MN–ML	N	4	2	0	6	0.07	0.71
Chrysolampis mosquitus (Linnaeus, 1758)	Ruby-topaz Hummingbird	MN	N	1	0	0	1	0.02	–
Eupetomena macroura (Gmelin, 1788)	Swallow-tailed Hummingbird	MN	N	4	0	0	4	0.07	–
Hylocharis cyanus (Vieillot, 1818)	White-chinned Sapphire	MN	N	3	0	0	3	0.05	–
Phaethornis pretrei (Lesson & Delattre, 1839)	Planalto Hermit	ML	N	0	2	0	2	–	0.71
Phaethornis ruber (Linnaeus, 1758)	Reddish Hermit	MN–ML	N	2	1	0	3	0.03	0.36
Thalurania glaucopis (Gmelin, 1788)	Violet-capped Woodnymph	MN–ML	N	4	2	0	6	0.07	0.71
Caprimulgiformes									
Caprimulgidae									
Antrostomus rufus (Boddaert, 1783)	Rufous Nightjar	ML	I	0	1	0	1	–	0.36
Chordeiles pusillus (Gould, 1861)	Least Nighthawk	ML	I	0	1	0	1	–	0.36
Hydropsalis albicollis (Gmelin, 1789)	Common Pauraque	MN–ML	I	2	12	0	14	0.03	4.29
Hydropsalis torquata (Gmelin, 1789)	Scissor-tailed Nightjar	ML	I	0	1	0	1	–	0.36
Cariamiformes									
Cariamidae									
Cariama cristata (Linnaeus, 1766)	Red-legged Seriema	MN	C	1	0	0	1	0.02	–
Cathartiformes									
Cathartidae									
Cathartes aura (Linnaeus, 1758)	Turkey Vulture	MN	S	5	0	0	5	0.08	–
Cathartes burrovianus Cassin, 1845	Lesser Yellow-headed Vulture	MN	S	2	0	0	2	0.03	–
Coragyps atratus (Bechstein, 1793)	Black Vulture	MN	S	2	0	0	2	0.03	–
Charadriiformes									
Charadriidae									
Vanellus chilensis (Molina, 1782)	Southern Lapwing	MN	O	3	0	0	3	0.05	–
Columbiformes									
Columbidae									
Columbina squammata (Lesson, 1831)	Scaled Dove	MN–ML	G	5	1	0	6	0.08	0.36
Columbina talpacoti (Temminck, 1810)	Ruddy Ground-Dove	MN–ML	G	19	4	0	23	0.32	1.43
Leptotila verreauxi Bonaparte, 1855	White-tipped Dove	MN–ML	G	16	1	0	17	0.27	0.36
Patagioenas cayennensis (Bonnaterre, 1792)	Pale-vented Pigeon	MN	F	5	0	0	5	0.08	–
Patagioenas picazuro (Temminck, 1813)	Picazuro Pigeon	MN	G	5	0	0	5	0.08	–

Family / Species	**Common name**	**Method**	**Guild**	**nML**	**nMN**	**nOR**	***n***	**IFL**	**RF**
Coraciiformes									
Alcedinidae									
Chloroceryle americana (Gmelin, 1788)	Green Kingfisher	ML	P	0	1	0	1	–	0.36
Cuculiformes									
Cuculidae									
Crotophaga ani Linnaeus, 1758	Smooth-billed Ani	MN–ML	O	7	1	0	8	0.12	0.36
Guira guira (Gmelin, 1788)	Guira Cuckoo	MN	O	1	0	0	1	0.02	–
Piaya cayana (Linnaeus, 1766)	Squirrel Cuckoo	MN–ML	O	3	1	0	4	0.05	0.36
Falconiformes									
Falconidae									
Caracara plancus (Miller, 1777)	Southern Caracara	MN	C	7	0	0	7	0.12	–
Herpetotheres cachinnans (Linnaeus, 1758)	Laughing Falcon	MN	C	2	0	0	2	0.03	–
Milvago chimachima (Vieillot, 1816)	Yellow-headed Caracara	MN	C	5	0	0	5	0.08	–
Galbuliformes									
Galbulidae									
Galbula ruficauda Cuvier, 1816	Rufous-tailed Jacamar	MN–ML	I	6	5	0	11	0.10	1.79
Galliformes									
Cracidae									
Ortalis araucuan (Spix, 1825)	East Brazilian Chachalaca	MN	F	2	0	0	2	0.03	–
Penelope superciliaris Temminck, 1815	Rusty-margined Guan	MN	F	1	0	0	1	0.02	–
Passeriformes									
Dendrocolaptidae									
Xiphorhynchus fuscus (Vieillot, 1818)	Lesser Woodcreeper	ML	I	0	1	0	1	–	0.36
Xiphorhynchus guttatus (Lichtenstein, 1820)	Buff-throated Woodcreeper	MN	I	3	0	0	3	0.05	–
Fringillidae									
Euphonia chlorotica (Linnaeus, 1766)	Purple-throated Euphonia	MN	F	8	0	0	8	0.13	–
Euphonia violacea (Linnaeus, 1758)	Violaceous Euphonia	ML	F	0	2	0	2	–	0.71
Furnariidae									
Furnarius figulus (Lichtenstein, 1823)	Wing-banded Hornero	MN	I	2	0	0	2	0.03	–
Furnarius rufus (Gmelin, 1788)	Rufous Hornero	ML	O	0	2	0	2	–	0.71
Synallaxis albescens Temminck, 1823	Pale-breasted Spinetail	MN	I	2	0	0	2	0.03	–
Synallaxis frontalis Pelzeln, 1859	Sooty-fronted Spinetail	MN–ML	I	1	1	0	2	0.02	0.36
Hirundinidae									
Progne chalybea (Gmelin, 1789)	Gray-breasted Martin	MN	I	3	0	0	3	0.05	–
Stelgidopteryx ruficollis (Vieillot, 1817)	Southern Rough-winged Swallow	MN	I	1	0	0	1	0.02	–
Icteridae									
Icterus cayanensis (Linnaeus, 1766)	Epaulet Oriole	ML	O	0	1	0	1	–	0.36
Icterus pyrrhopterus tibialis Swainson, 1838	Variable Oriole	MN	O	1	0	0	1	0.02	–
Molothrus bonariensis (Gmelin, 1789)	Shiny Cowbird	MN	O	1	0	0	1	0.02	–
Nyctibiidae									
Nyctibius griseus (Gmelin, 1789)	Common Potoo	OR	I	0	0	1	1	–	–
Parulidae									
Myiothlypis flaveola Baird, 1865	Flavescent Warbler	MN	I	10	0	0	10	0.17	–

Family / Species	**Common name**	**Method**	**Guild**	**nML**	**nMN**	**nOR**	***n***	**IFL**	**RF**
Passerellidae									
Arremon taciturnus (Hermann, 1783)	Pectoral Sparrow	MN–ML	O	13	8	0	21	0.22	2.86
Pipridae									
Chiroxiphia pareola (Linnaeus, 1766)	Blue-backed Manakin	MN–ML	F	7	2	0	9	0.12	0.71
Manacus manacus (Linnaeus, 1766)	White-bearded Manakin	MN–ML	F	12	60	0	72	0.20	21.43
Neopelma pallescens (Lafresnaye, 1853)	Pale-bellied Tyrant-Manakin	MN–ML	O	1	5	0	6	0.02	1.79
Platyrinchidae									
Platyrinchus mystaceus Vieillot, 1818	White-throated Spadebill	MN–ML	I	1	2	0	3	0.02	0.71
Polioptilidae									
Polioptila plumbea (Gmelin, 1788)	Tropical Gnatcatcher	MN	I	12	0	0	12	0.20	–
Rallidae									
Aramides cajaneus (Statius Muller, 1776)	Gray-necked Wood-Rail	OR	O	0	0	1	1	–	–
Rhynchocyclidae									
Hemitriccus margaritaceiventer (d'Orbigny & Lafresnaye, 1837)	Pearly-vented Tody-tyrant	MN	I	8	0	0	8	0.13	–
Hemitriccus nidipendulus (Wied, 1831)	Hangnest Tody-Tyrant	MN–ML	I	1	3	0	4	0.02	1.07
Leptopogon amaurocephalus Tschudi, 1846	Sepia-capped Flycatcher	MN–ML	I	1	2	0	3	0.02	0.71
Todirostrum cinereum (Linnaeus, 1766)	Common Tody-Flycatcher	MN–ML	I	4	1	0	5	0.07	0.36
Tolmomyias flaviventris (Wied, 1831)	Yellow-breasted Flycatcher	MN–ML	I	10	2	0	12	0.17	0.71
Thamnophilidae									
Formicivora grisea (Boddaert, 1783)	White-fringed Antwren	ML	I	0	1	0	1	–	0.36
Formicivora melanogaster Pelzeln, 1868	Black-bellied Antwren	MN	I	2	0	0	2	0.03	–
Formicivora rufa (Wied, 1831)	Rusty-backed Antwren	MN	I	2	0	0	2	0.03	–
Herpsilochmus pectoralis Sclater, 1857	Pectoral Antwren	MN–ML	I	14	1	0	15	0.23	0.36
Pyriglena atra(Swainson, 1825)	Fringe-backed Fire-eye	OR	I	0	0	1	1	–	–
Taraba major (Vieillot, 1816)	Great Antshrike	MN–ML	I	6	5	0	11	0.10	1.79
Thamnophilus caerulescens Vieillot, 1816	Variable Antshrike	MN	I	1	0	0	1	0.02	–
Thamnophilus pelzelni Hellmayr, 1924	Planalto Slaty-Antshrike	MN–ML	I	11	2	0	13	0.18	0.71
Thraupidae									
Coereba flaveola (Linnaeus, 1758)	Bananaquit	MN–ML	N	28	4	0	32	0.47	1.43
Conirostrum speciosum (Temminck, 1824)	Chestnut-vented Conebill	MN–ML	O	1	1	0	2	0.02	0.36
Dacnis cayana (Linnaeus, 1766)	Blue Dacnis	MN–ML	O	19	25	0	44	0.32	8.93
Hemithraupis guira (Linnaeus, 1766)	Guira Tanager	MN	O	1	0	0	1	0.02	–
Lanio cristatus (Linnaeus, 1766)	Flame-crested Tanager	MN	O	2	0	0	2	0.03	–
Nemosia pileata (Boddaert, 1783)	Hooded Tanager	MN	O	3	0	0	3	0.05	–
Ramphocelus bresilius (Linnaeus, 1766)	Brazilian Tanager	ML	O	0	4	0	4	–	1.43
Saltator maximus (Statius Muller, 1776)	Buff-throated Saltator	MN–ML	O	4	5	0	9	0.07	1.79
Schistochlamys ruficapillus (Vieillot, 1817)	Cinnamon Tanager	MN–ML	G	1	1	0	2	0.02	0.36
Sporophila bouvreuil (Statius Muller, 1776)	Copper Seedeater	MN	G	1	0	0	1	0.02	–
Sporophila leucoptera (Vieillot, 1817)	White-bellied Seedeater	ML	G	0	5	0	5	–	1.79
Sporophila lineola (Linnaeus, 1758)	Lined Seedeater	ML	G	0	6	0	6	–	2.14
Sporophila nigricollis (Vieillot, 1823)	Yellow-bellied Seedeater	MN–ML	G	3	5	0	8	0.05	1.79
Tachyphonus rufus (Boddaert, 1783)	White-lined Tanager	MN–ML	O	14	12	0	26	0.23	4.29
Tangara cayana (Linnaeus, 1766)	Burnished-buff Tanager	MN–ML	O	8	17	0	25	0.13	6.07

Family / Species	**Common name**	**Method**	**Guild**	**nML**	**nMN**	**nOR**	***n***	**IFL**	**RF**
Tangara palmarum (Wied, 1821)	Palm Tanager	MN–ML	O	20	2	0	22	0.33	0.71
Tangara sayaca (Linnaeus, 1766)	Sayaca Tanager	MN	O	7	0	0	7	0.12	–
Volatinia jacarina (Linnaeus, 1766)	Blue-black Grassquit	MN–ML	G	14	7	0	21	0.23	2.50
Tinamidae									
Crypturellus noctivagus (Wied, 1820)	Yellow-legged Tinamou	OR	O	0	0	1	1	–	–
Tityridae									
Pachyramphus polychopterus (Vieillot, 1818)	White-winged Becard	MN–ML	I	4	2	0	6	0.07	0.71
Troglodytidae									
Pheugopedius genibarbis (Swainson, 1838)	Moustached Wren	MN–ML	O	13	1	0	14	0.22	0.36
Troglodytes musculus Naumann, 1823	Southern House Wren	MN–ML	I	3	1	0	4	0.05	0.36
Turdidae									
Turdus leucomelas Vieillot, 1818	Pale-breasted Thrush	MN–ML	O	15	14	0	29	0.25	5.00
Tyrannidae									
Camptostoma obsoletum (Temminck, 1824)	Southern Beardless-Tyrannulet	MN–ML	I	6	4	0	10	0.10	1.43
Elaenia cristata Pelzeln, 1868	Plain-crested Elaenia	MN–ML	O	14	3	0	17	0.23	1.07
Elaenia flavogaster (Thunberg, 1822)	Yellow-bellied Elaenia	ML	O	0	6	0	6	–	2.14
Elaenia spectabilis Pelzeln, 1868	Large Elaenia	MN	O	1	0	0	1	0.02	–
Euscarthmus meloryphus Wied, 1831	Tawny-crowned Pygmy-Tyrant	OR	I	0	0	1	1	–	–
Megarynchus pitangua (Linnaeus, 1766)	Boat-billed Flycatcher	MN	O	6	0	0	6	0.10	–
Myiarchus ferox (Gmelin, 1789)	Short-crested Flycatcher	MN–ML	I	5	2	0	7	0.08	0.71
Myiarchus swainsoni Cabanis & Heine, 1859	Swainson's Flycatcher	MN	I	3	0	0	3	0.05	–
Myiophobus fasciatus (Statius Muller, 1776)	Bran-colored Flycatcher	MN–ML	I	1	1	0	2	0.02	0.36
Myiozetetes similis (Spix, 1825)	Social Flycatcher	MN–ML	O	4	8	0	12	0.07	2.86
Pitangus sulphuratus (Linnaeus, 1766)	Great Kiskadee	MN	O	15	0	0	15	0.25	–
Tyrannus melancholicus Vieillot, 1819	Tropical Kingbird	MN	I	15	0	0	15	0.25	–
Vireonidae									
Cyclarhis gujanensis (Gmelin, 1789)	Rufous-browed Peppershrike	MN–ML	I	22	2	0	24	0.37	0.71
Vireo chivi (Vieillot, 1817)	Chivi Vireo	MN–ML	I	12	2	0	14	0.20	0.71
Piciformes									
Picidae									
Campephilus melanoleucos (Gmelin, 1788)	Crimson-crested Woodpecker	MN	I	1	0	0	1	0.02	–
Colaptes melanochloros (Gmelin, 1788)	Green-barred Woodpecker	MN	I	1	0	0	1	0.02	–
Picumnus exilis (Lichtenstein, 1823)	Bahia Piculet	MN	I	2	0	0	2	0.03	–
Veniliornis passerinus (Linnaeus, 1766)	Little Woodpecker	MN	I	2	0	0	2	0.03	–
Psittaciformes									
Psittacidae									
Amazona aestiva (Linnaeus, 1758)	Turquoise-fronted Parrot	MN	F	25	0	0	25	0.42	–
Eupsittula aurea (Gmelin, 1788)	Peach-fronted Parakeet	MN	F	12	0	0	12	0.20	–
Forpus xanthopterygius (Spix, 1824)	Blue-winged Parrotlet	MN–ML	F	9	1	0	10	0.15	0.36
Strigiformes									
Strigidae									
Megascops choliba (Vieillot, 1817)	Tropical Screech-Owl	ML	C	0	1	0	1	–	0.36
Tinamiformes									
Tinamidae									

Family / Species	**Common name**	**Method**	**Guild**	**nML**	**nMN**	**nOR**	***n***	**IFL**	**RF**
Nothura maculosa (Temminck, 1815)	Spotted Nothura	MN	I	1	0	0	1	0.02	–
Trogoniformes									
Trogonidae									
Trogon curucui Linnaeus, 1766	Blue-crowned Trogon	MN	O	8	0	0	8	0.13	–

reliable species counts than those obtained at listening points in highland forest in Ecuador, which they attributed to the more comprehensive, active nature of the searches used to compile the MacKinnon lists. The lists do not record abundance data, however, although relative species abundance can be inferred through the IFL (Bibby *et al.* 1998, Ribon 2010). The greater similarity (J' = 50.6%) found between the results of the present study and those of the survey of Ruiz-Esparza *et al.* (2015) may be related to the use of a similar, complementary approach by these authors.

The rarefaction curves further reinforce the effectiveness of the complementary methods for bird inventories in a rapid survey approach, as recommended by Ribon (2010). In the Mata do Junco, Ruiz-Esparza *et al.* (2015) recorded a bird community dominated by Tyrannidae and Thraupidae, as observed in the present study, and in other studies in the Atlantic Forest (Dário *et al.* 2002, Faria *et al.* 2006, Almeida *et al.* 2012, Crestani *et al.* 2015). This reflects the overall diversity of the Thraupidae (157 species) and Tyrannidae (114 species) in the Neotropics (Sick 1997, Piacentini *et al.* 2015), and may reflect the adaptability of both groups to a range of environments, including anthropogenic habitats (Telino-Júnior *et al.* 2005).

The local bird community was dominated by omnivores and insectivores, as observed at other Atlantic Forest sites in the region (Magalhães *et al.* 2007, Ruiz-Esparza *et al.* 2015). At many other sites, however, insectivores predominate over omnivores (Matarazzo-Neuberger 1995, Silveira *et al.* 2003, Telino-Júnior *et al.* 2005, Ruiz-Esparza *et al.* 2016), which may reflect variations in local habitats. Anjos (1998) concluded that omnivorous birds may be more tolerant to habitat fragmentation, due to their greater ecological flexibility, allowing these species to predominate in impacted environments. It is, nevertheless, important to note that while omnivores were more abundant in the present study, the insectivore species richness was higher. The granivores, in turn, may have been favored by the abundance of open habitats within the general study area, which may favor these species (Telino-Júnior *et al.* 2005).

Overall, results of the present study indicate that the combination of complementary sampling techniques provided a more reliable inventory of the bird fauna of the study area than either method on its own, and was especially effective in the context of the rapid survey approach, when compared with the existing data for the study area. Despite these findings, analyses indicate that further research will confirm the occurrence of additional species at the site, using both techniques, which was expected, given the limited perspective of the rapid survey approach.

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ARTICLE

Bird surveys in grasslands: do different count methods present distinct results?

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ABSTRACT: We compared two methods routinely used to conduct bird community surveys: point counts and transects. Our aim was to look for differences between these two methods regarding detection of bird richness and abundances. Additionally, we analyzed if one of the methods provided higher correlation of bird data with vegetation structure as an important habitat descriptor. From September 2014 to January 2015, we surveyed birds in 264 point counts and 258 transects spread across the southern Brazilian grasslands. We conducted one method in direct sequence of the other, in the same place with the same observers and at the same weather conditions. We standardized data to eliminate the effort bias caused by area covered and time employed in each method. Total abundance of birds recorded by the two methods did not differ (point counts 4753 and transects 4436, $P = 0.31$), but we found a significant difference in species richness (point counts 187 and transects 173, $P = 0.01$). Abundance of birds sampled with the transect method showed a slightly higher correlation with vegetation height ($r^2 = 0.07$; $P = 0.004$) than the point counts method ($r^2 = 0.03$; $P = 0.05$). While results from both methods were similar, richness detection was more effective in point counts, indicating that this method might be more useful than it currently is. We discuss potential factors that may influence effectiveness of both methods and suggest issues that should be addressed in further research in order to develop standardized sampling methods for bird communities.

KEY-WORDS: Brazil, fixed-radius point-counts, fixed-width transects, SESA grasslands, standard survey, vegetation parameters.

INTRODUCTION

Grasslands are one of the most threatened ecosystems of the Earth (Azpiroz *et al.* 2012). Precise information about grassland degradation and its effects on biodiversity, ecosystem services and economic potential can support conservation and management plans, thus contributing to the conservation of habitats, plant and animal populations. Birds are an important part of the grasslands' biodiversity and, due to their sensitivity to environmental changes, a good indicator of degradation (Mekonen 2017).

To better comprehend the impacts of land use change on birds, studies are required at both local and regional scales. In South America recent efforts have addressed important questions about the effects of agriculture, urbanization, livestock and exotic trees forestation on grassland birds (Codesido *et al.* 2008, Dias *et al.* 2013, Isacch *et al.* 2014, Cardoni *et al.* 2015, Silva *et al.* 2015, Azpiroz & Blake 2016, Dotta *et al.* 2016, Fontana *et al.* 2016). Currently, however, researches apply different field methods for their bird censuses. This makes it difficult to measure additional impacts on bird communities and/or populations or even compare results at a wider spatial scale.

The application of different methods to survey and measure bird species richness and abundances, limiting the potential for comparisons among studies, is a frequent concern in ornithology (see Buckland 2006, Iknayan *et al.* 2014, Matsuoka *et al.* 2014 for different approaches). So far, point counts (*e.g.*, fixed radius method) and line transects (*e.g.*, fixed width method) figure as the two most used methods to census birds (Diefenbach *et al.* 2003). Attempts to standardize the usage of those methods and a complete description of them were published by Ralph & Scott (1981), Ralph *et al.* (1995), Bibby *et al.* (2000), and reviewed by Matsuoka *et al.* (2014).

The point count method, first descripted by Blondel *et al.* (1970) to census forest birds, is considered the most widely used technique to survey terrestrial birds in North America. The method requires an experienced observer and consists in recording all birds detected in a specific amount of time (*e.g.*, 5, 10, 15 or 20 min) within an unlimited or limited distance (point radius) (Diefenbach *et al.* 2003). The line transect method has been suggested as a more suitable method for sampling open landscapes. It also requires experienced observers, but in this case the sampling is active: by using one or several lines the researcher walks through the pre-determined distance, recording all birds. This method can be applied with different distances, widths and different number of transects (Järvinen 1978, Järvinen & Väisänen 1979).

Despite some controversy on the usefulness of both techniques to assess bird populations, in consequence of the specific detectability of each bird species (Buckland *et al.* 2001, Buckland 2006), point counts and/or transects (with their different versions), continue to be used to estimate abundances of birds. Both methods likely are much used due to their easy applicability in different habitat types and because they are unpretentious and cheap techniques. For their application, only one good observer and good binoculars are required, and they can be easily adapted according to the researcher's specific goals. However, standardization seems useful to define optimal protocols for the methods that allows for comparable results.

In this study, conducted in the south Brazilian grassland region, our main goal is to compare bird survey data gathered by point and transect methods regarding species richness and relative abundance value and, with this, to evaluate how comparable the results are. As structure and composition of bird communities are frequently linked to habitat characteristics, such as vegetation structure (Recher 1969, Karr & Roth 1971, Willson 1974, Marone 1991, Patterson & Best 1996, Marone *et al.* 1997, Azpiroz & Blake 2016), we additionally recorded parameters that describe physical features of the grasslands to test if the two methods for bird sampling resulted in differences regarding the relation of bird data and habitat parameters. We predict that if the bird community parameters were similar using point counts or transects, then the results on the effect of habitat variables should show similar patterns. In this case, independent of the bird census method used, results would be comparable and applicable for bird population monitoring.

METHODS

We conducted fieldwork from October of 2014 to January of 2015 in areas under good conservation status spread throughout the entire south Brazilian grassland region (from Paraná to Rio Grande do Sul states) (Fig. 1). This region encompasses the grasslands in the south of the Atlantic Forest Biome and in the Pampa Biome, covering the different grassland physiognomies of the south Brazilian grasslands (Overbeck *et al.* 2007). A general description of the study region can be found in Azpiroz *et al.* (2012) who use the term "northern Campos" for the Pampa grasslands and the term "Brazilian upland

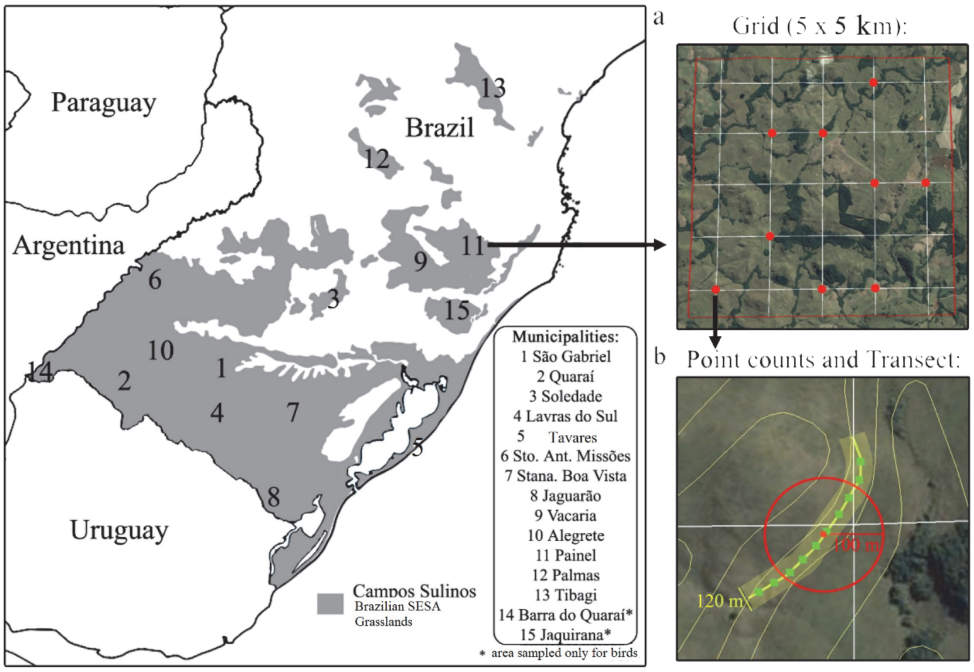

Figure 1. Distribution of the study sites in the Campos Sulinos grasslands in southern Brazil (part of the SESA grasslands) and (**A**) a schematic view of one of the 25 km^2 grid with (**B**) a schematic representation of the sampling unit. The red circle represents the point count (radius 100 m), the hatched yellow line represent the transect (120 m width) and green light squares represent the sampling units for vegetation sampling. Thin yellow lines in (**B**) are terrain level curves.

grasslands" for the highland grasslands in the Atlantic Forest Biome. The region makes part of the grasslands of southeastern South America (SESA) that extend further to the south and west.

Fifteen areas dominated by natural grasslands were selected for bird sampling throughout the study region; vegetation sampling was conducted in thirteen of those areas. The sampling design followed the Rapeld System (Magnusson *et al.* 2013) that is recommended by the Brazilian Program on Biodiversity Research (PPBIO), with some adaptations. In each area, an imaginary grid of 5 × 5 km was draw, with five horizontal and five vertical lines equally distant 1 km. Per grid, nine out of the total of twenty-five intersections were randomly selected, using a stratified approach that considered three different landscape positions (hilltop, slope, depression) in their approximate importance in each area. All grasslands were under grazing and situated in well-conserved regions with low land cover change (Fig. 2).

Birds sampling

We conducted bird sampling twice in each plots: using point counts of 10 min and 100 m radius (represented by red circle in Fig. 1B) and using transects of 250 × 120 m (60 m each side or observer; yellow hatched area in Fig. 1B). The average time for transect sampling was 9.4 ± 2.2 min. The surveys were conducted under homogeneous weather conditions and at the same time of the day by the same two observers (E.C. and C.B.A.), totalizing 264 points and 258 transects.

Vegetation structure sampling

Physical vegetation structure was quantified to characterize the habitat. In each plot, structure was recorded in 10 sampling units of 1 × 1 m, equally distributed in the center of the 250 m transect used for bird sampling (light green squares in Fig. 1B). We measured vegetation height in five points (four corners and center) in each sampling unit. In addition, inside the sampling units we estimated, in percentage, cover of bare soil, dead vegetation (dead biomass) and total live vegetation (green biomass).

Statistical analysis

We standardized bird data by relativizing abundance and richness data recorded at each point or transect by evaluated area and by the time spent in the respective sampling to eliminate effort bias. We used Wilcoxon signed rank test (for paired samples) to compare the results stemming from application both sampling units, using for abundance only the maximum number of individuals recorded in the two samples of each point and transect. We evaluated the relationship between descriptors of vegetation structure and bird abundance and richness with non-linear regression (for the thirteen areas were vegetation data was available). Analysis were carried out in the R program (R Core Team 2016) and BioEstat (Ayres *et al.* 2007).

RESULTS

We recorded 4753 individuals of 187 species in point counts, and 4436 individuals of 173 species in transects. There were 158 species shared between the two methods, 29 species were recorded only in point counts, and 15 only in transects (Table 1). The two methods did not differ in abundance of birds recorded (Wilcoxon signed rank test: $V = 4623$; $P = 0.31$), but they resulted in a significant difference in richness (Wilcoxon signed rank test: $V = 5028$; $P = 0.01$) (Fig. 3). All relationships between bird community parameters and environmental parameters were very weak ($r^2 < 0.07$). For data from both methods, the relation between bird communities and vegetation height was significant. For the point count method, the relationship among bird richness and cover of bare soil was significant (Table 2).

Figure 2. Examples of grasslands from southern Brazil. Grasslands landscape in Alegrete, Rio Grande do Sul state (Pampa Biome, left); grasslands landscape in Palmas, Paraná state (Atlantic Forest Biome, right). Photo author: Christian B. Andretti.

Table 1. Bird species recorded only by point counts (29 species) or transects (15 species), from a total of 202 registered species in the southern Brazilian grasslands, with the respective number of individuals (*n*) and frequency of occurrence. Between parenthesis is the number of point counts or transects in which the species was recorded from a total of 258 transects and 264 points sampled. Scientific names and species taxonomic sequence follow Piacentini *et al.* (2015). Asterisk indicates grassland specialists (*sensu* Azpiroz *et al.* 2012).

Species	Method	*n*	Frequency
Chauna torquata	Point count	2	0.008 (1)
Dendrocygna autumnalis	Point count	2	0.008 (1)
Dendrocygna bicolor	Transect	2	0.008 (1)
Cygnus melancoryphus	Point count	31	0.008 (1)
Cairina moschata	Point count	1	0.008 (1)
Anas flavirostris	Transect	1	0.008 (1)
Anas georgica	Point count	4	0.015 (2)
Ardea cocoi	Transect	2	0.016 (2)
Egretta thula	Point count	3	0.015 (2)
*Elanus leucurus**	Point count	1	0.008 (1)
*Circus buffoni**	Transect	2	0.008 (1)
*Geranoaetus melanoleucus**	Point count	1	0.008 (1)
Aramides ypecaha	Transect	1	0.008 (1)
Pardirallus maculatus	Point count	1	0.008 (1)
Pardirallus sanguinolentus	Transect	1	0.008 (1)
Himantopus melanurus	Transect	5	0.016 (2)
*Bartramia longicauda**	Transect	11	0.023 (3)
Jacana jacana	Point count	3	0.015 (2)
Cypseloides senex	Point count	4	0.015 (2)
Heliomaster furcifer	Point count	1	0.008 (1)
Chloroceryle americana	Point count	1	0.008 (1)
Nystalus chacuru	Point count	2	0.008 (1)
Picumnus cirratus	Point count	2	0.008 (1)
*Cariama cristata**	Transect	3	0.016 (2)
Psittacara leucophtalma	Point count	6	0.008 (1)
Pionipsitta pileata	Transect	4	0.016 (2)
*Geositta cunicularia**	Transect	4	0.023 (3)
Phacellodomus ruber	Transect	4	0.008 (1)
Phacellodomus ferrugineigula	Point count	2	0.008 (1)
Synallaxis albescens	Transect	2	0.008 (1)
Elaenia flavogaster	Transect	2	0.008 (1)
*Polystictus pectoralis**	Point count	2	0.008 (1)
*Gubernetes yetapa**	Point count	1	0.008 (1)
Cyanocorax caeruleus	Point count	5	0.023 (3)
Riparia riparia	Point count	2	0.008 (1)
Turdus leucomelas	Point count	2	0.008 (1)
Amblyramphus holosericeus	Point count	5	0.008 (1)
Chrysomus ruficapillus	Point count	21	0.023 (3)
Coereba flaveola	Point count	6	0.023 (3)

Species	Method	*n*	Frequency
Pipraeidea melanonota	Point count	2	0.008 (1)
Pipraeidea bonariensis	Point count	10	0.045 (6)
Gubernatrix cristata	Point count	4	0.015 (2)
*Sporophila pileata**	Point count	1	0.008 (1)
*Sporophila palustris**	Transect	2	0.008 (1)

Table 2. Results of non-linear regression (r^2) between environmental variables and parameters recorded in different bird census methods. Significant regressions ($P \leq 0.05$) are in bold and marked with "*".

	Abundance		**Richness**	
	Point count r^2 (P)	**Transect** r^2 (P)	**Point count** r^2 (P)	**Transect** r^2 (P)
Vegetation height (cm)	0.03 (**0.05***)	0.07 (0.**004***)	0.002 (0.65)	0.02 (0.15)
Vegetation cover (%)	0.02 (0.14)	0.01 (0.24)	0.03 (0.09)	0.01 (0.26)
Bare soil (%)	0.01 (0.20)	0.02 (0.16)	0.05 (**0.02***)	0.01 (0.24)
Dead vegetation (%)	0.01 (0.23)	0.01 (0.24)	0.01 (0.31)	0.006 (0.44)

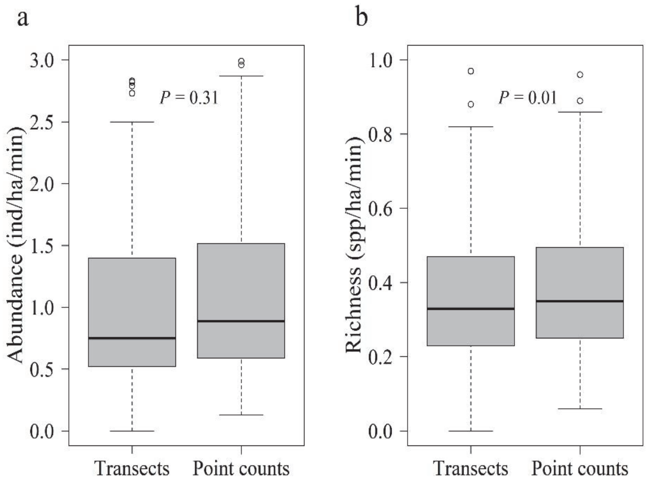

Figure 3. Bird abundance (**A**) and richness (**B**) recorded in transects and point counts in the southern Brazilian grasslands. The line in each box represents the median; top and bottom of each box represent upper and lower quartiles, respectively; whiskers represent maximum and minimum values; circles represent outliers. The *P*-value is based on Wilcoxon signed rank test (for paired samples).

DISCUSSION

There is a considerable body of literature and discussion on gains and losses when using points or transects to survey birds, resulting mostly from studies in the northern hemisphere and in forests (see Emlen 1971, Ralph *et al.* 1995). To date this is the first study that evaluates the effectiveness of the two main bird survey methods (point and transect method) for South American grassland birds. In our study, we standardized all variables that – according to literature – have effects on census results, such as time of the day, survey length, the area covered and the number of observers (*e.g.*, Ralph *et al.* 1993, Ralph *et al.* 1995, Nichols *et al.* 2000). This means that our data contains little sources of bias due to variation of study parameters. We conducted sampling at a large number of strip transects with fixed width and at points with a fixed radius, always in the same period of the year (spring/summer) and at the same time of the day. Additionally, as our study grids covers the whole range of south Brazilian grasslands, an expressive part of SESA grasslands, our results are representative of a large region with a species-rich bird community (more than 200 species).

We found that the point count and the transect method, at least in the way they were conducted in this study, led to similar results regarding bird community structure in SESA grasslands. Point count method has a slight advantage over the transect method when the objective of the study is to evaluate bird species richness. Possibly, standing researchers can pay more attention to songs and movements. Rodrigues & Prado (2018) found that point counts were better than transects to estimate bird species richness in a vegetation gradient in the Brazilian savanna, especially in shrublands and grasslands. This result is especially relevant when we consider that the transect method was one of the most frequently applied method in grasslands of North America between 1985 and 2001 (Diefenbach *et al.* 2003) and is commonly applied in grasslands in South America (*e.g.*, Marone 1991, Isacch *et al.* 2003, Fontana *et al.* 2016). For three North-American grassland bird species, detection probabilities were low for transect distances longer than 25 m for most observers and species, and about 60% of birds were missed by observers at distances longer than 50 m (Diefenbach *et al.* 2003). The increase in visual detections by flushing, considered to be an advantage of transects (Golding & Dreitz 2016), can be reduced because the observer may not detect all individuals that were scared away, were not heard or kept silent (Rodrigues & Prado 2018).

The point method registered almost twice as many exclusive species than the transect method; however, most of these species that were not shared between methods occurred only once or twice. This difference might be a result of stochastic phenomena that should be investigated in further studies, but could also be related to the significantly higher species richness that was recorded using the point count method. Additionally, we registered birds from the border of forests in both methods. This result should be consequence of specific site features, as trees or small forest patches that were present close to some sampling plots. No strong differences were found when analyzing the number of grasslands specialists (*sensu* Azpiroz *et al.* 2012) which totaled only five exclusive species for each method.

Although both survey method showed very low correlation with physical vegetation structure, data obtained with the point count method presented two significant correlations. In contrast, the transect method showed only one significant correlation. If bird communities are to be used as informative for habitat degradation (Mekonen 2017), it is important that the bird data effectively reflects habitat structure. Our data indicates that the point method proved to be slightly better, but of course the correlation values are too low to allow for more detailed interpretation – possibly a consequence of the overall good conservation state of our sampled landscapes. As it is known that many bird species respond to vegetation structure (Derner *et al.* 2009), it seems interesting to conduct comparative studies, with standardized methods as in ours, at sites with contrasting habitat conditions or along stronger environmental gradients. In our study, all grasslands were grazed under similar levels, which means that they were structurally rather uniform. In order to be able to direct land-management, conservation and restoration decisions regarding the role of grassland vegetation structure for bird preservation, it seems especially interesting to compare grasslands with different history of land use (*i.e.* primary *vs.* secondary grasslands, Leidinger *et al.* 2017), or grasslands under different types of management, such as grazing (in different intensities), and fire (*e.g.*, Fedrigo *et al.* 2018, Overbeck *et al.* 2018).

Our study is the first attempt to compare the most used bird surveys methods in grasslands of South America. This will be helpful as a proposal for standardization of sampling methods in the future, in a way that economy of data acquisition and exactness in the estimation of population trends can be best balanced. Such standardization is important for biodiversity monitoring, which should allow for the integration of data (interdisciplinary or not) in order to be employed for land-use management and conservation decisions (Magnusson *et al.* 2013).

Many types of different counting techniques have been previously used to estimate relative abundance and population trends of grassland birds in southern South America. In consequence, comparability of studies is poor and application of results from single studies in conservation at a broader scale difficult (Isacch *et al.* 2014, Azpiroz & Blake 2016, Fontana *et al.* 2016, Dias *et al.* 2017). Despite transects method which at current is more commonly used for recording community of birds in open habitats, we emphasize that point counts with limited radius, as presented in this study, appears to be a very useful technique for future surveys of grassland birds in SESA. We indicate that most questions meriting the effort required to carry out point counts also merit serious attempts to estimate detection probabilities associated with the counts, as already pointed by Nichols *et al.* (2000). Future studies should focus on the discrepancy of probabilities of detection in different methods, including the question if any method favors specific species or functional groups, and what consequences for density estimates stem from this. Additionally, the question of the scale-dependency of the different methods should still be addressed.

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ARTICLE

Bird assemblages from western Sierras Grandes and Traslasierra Valley in central Argentina: an important area for conservation of Chacoan and mountain birds

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ABSTRACT: Between 1970 and 1980, many ornithological prospections were made in central Argentina. With this work we intend to fill some of the existing gaps regarding such knowledge. We conducted bird surveys in the central-western region of Córdoba province. We identified 240 bird species (63% of province's avifauna) belonging to 48 families: 10 of which are considered under some threat category, 37 are migrants, and two are endemic to the region. Throughout a qualitative analysis of ordination, we identified three clusters of environments that share similar bird composition. Among those, the most dissimilar group was composed of aquatic environments, whereas the two other groups included wooded and anthropized environments and high altitude environments, respectively. The high bird richness recorded in a relatively small region, encompassing a variety of environments, place upon this area a high bird conservation value. The inclusion of this area in the system of "Important Bird Areas" (IBAs) may prompt protection actions.

KEY-WORDS: altitudinal gradient, bird diversity, endemic birds, environmental heterogeneity, IBAs, threatened birds.

INTRODUCTION

Located in central Argentina, Córdoba province hosts a large and diverse number of avian species. Approximately 376 native bird species within 51 families have been recorded (Stempelmann & Schulz 1890, Frenzel 1891, Nores & Yzurieta 1975, Nores & Yzurieta 1979, Nores *et al.* 1980, Nores *et al.* 1983, Narosky & Yzurieta 1989, Nores *et al.* 1996). These species are distributed in Córdoba throughout a large variety of habitats, such as grassy highlands, xerophytic woodlands, wetlands and marshes. This is the result of the convergence of several ecological regions: the Great Chaco Ecoregion, the Pampas Ecoregion, and the Espinal Ecoregion (Luti *et al.* 1979, Zak & Cabido 2002, Nori *et al.* 2011). Despite the biodiversity found throughout this province, existing ornithological studies show a clear bias towards a few major areas: Mar Chiquita Lake in the northeast, and the grasslands on the top of Sierras Grandes in central Córdoba (*e.g.* Nores & Yzurieta 1983, Nores 1995, Giraudo *et al.* 2006).

Historically, the high bird abundance and the presence of endemic and threatened species has conferred the province high conservation value. Córdoba avifauna includes eight species endemic to Argentina and nine species globally endangered or threatened (López-Lanús *et al.* 2008). This has sustained the designation of nine Important Bird Areas (IBAs) in Córdoba province (Di Giacomo 2005). However, only fifty percent of those IBAs have effective protection. Furthermore, other regions with potential for avian conservation remain out of consideration due to the lack of information regarding avian species presence and distribution. Some of these regions are still relatively unaffected by anthropic disturbance, as is the case for western Sierras Grandes and Traslasierra Valley.

Sierras Grandes and the adjacent Sierras of Comechingones (Sierras Grandes-Comechingones hereafter) are the highest mountains within Córdoba province (maximum height 2780 m a.s.l.). The western face presents short and steep slopes, where numerous streams run down, some of which shape the basin of Río de los Sauces and Allende Lake, commonly under the denomination "Traslasierra Valley" (Carignano *et al.* 2014, Fig. 1). Río de los Sauces alluvial valley has a plant community typical of Chaco lowland Forest, yet the mountain slopes also comprise a variety of contrasting vegetation units (*i.e.* woodland, shrubland, grassland; see description in study site section) in accordance with the altitudinal gradient (600 to 2700 m a.s.l.). This particular topography allows for the development of a highly heterogeneous landscape in a relatively small area, and the variety of environments hosts a great bird diversity. For example, the mountain tops include birds with an Andean origin, whereas lowland areas have Chacoans species (Nores & Yzurieta 1983, Nores & Cerana 1990). These characteristics confer western Sierras Grandes-Comechingones and Traslasierra Valley a high value for bird conservation.

The main goals of this study were to (1) study avian richness and composition while comparing bird assemblages among different habitats, and to (2) assess the feasibility of including this region into the system of IBAs. Specifically, we seek to know the avian richness and avian community composition at western Sierras Grandes-Comechingones and Traslasierra Valley, and to identify the similarities between bird assemblages among different habitat types. Our study aims to improve the understanding of the distribution of avian species across different habitats in this heterogeneous area, which historically has been understudied by ornithologists, in order to highlight the importance of this area for the conservation of birds in Lowland and Mountain Chaco region.

METHODS

Study area

Surveys were conducted in an area of Sierras Grandes delimited in the north by the rivers Río Chico de Nono and Río de los Sauces and the coast of Allende Lake. In the east, the area was limited by the Sierras Grandes-Comechingones summit. The west and south limits correspond to the meridian 65°03'W and the parallel 32°10'S, respectively, comprising an area of 464.75 km^2 (Fig. 1).

The physiognomy of plant communities and main plant species observed along Traslasierra Valley and western Sierras Grandes-Comechingones system from lowest to the highest altitude (*sensu* Luti *et al.* 1979, Fig. 2) included:

Lowland Chaco woodland (500–800 m a.s.l.): this area is dominated by several tree species such as *Aspidosperma quebracho-blanco*, *Prosopis flexuosa*, *Prosopis chilensis*, *Ziziphus mistol* and *Cercidium australe*. Shrubs commonly found in the area include *Larrea divaricata*, *Mimozyganthus carinatus*, *Maytenus spinosa*, and *Acacia furcatispina* (Cabido *et al.* 1992).

Mountain Chaco woodland (800–1350 m a.s.l.): characterized by the dominating presence of *Lithraea molleoides* and, to a lesser extent, *Celtis ehrenbergiana*, *Bouganvillea stipitata*, *Schinopsis haenkeana*, and *Xanthopylum coco.* Among the shrubs, dominant species include *Flourensia* sp. and *Condalia buxifolia* (Cabido *et al.* 1998).

Mountain shrubland (1350–1700 m a.s.l.): this community is characterized by the lack of trees, the dominant shrub being *Heterothalamus alienus*, and to

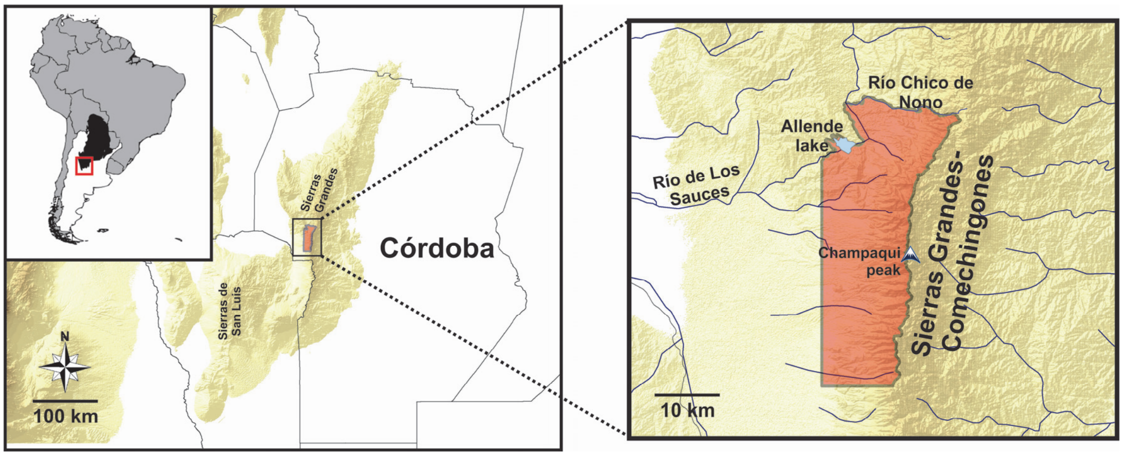

Figure 1. The map represents the location of our study site in Córdoba province, Argentina. The black shading area in the South American map represents the Great Chaco Forest. The red area in the right square indicates the study area, the north edge is delimitated by Río Chico de Nono, Río de los Sauces and the northern coast of Allende artificial lake, the east boundary is the maximal coat of Sierras Grandes-Comechingones, and the west and south limits correspond to the meridian 65°03'W and the parallel 32°10'S respectively. The delimited area goes from 700 m a.s.l. at the west limit to 2780 m a.s.l. (Champaquí peak, the highest altitude in Córdoba province) at the east limit. The area occupies 464.75 km^2.

a lesser extent *Acacia caven*, *Baccharis* sp., and many Poaceae species.

Mountain grassland and *Polylepis* forest (1700–2800 m a.s.l.): consists of a mosaic of *Polylepis australis* woodland (mainly in humid and pronounced ravines), tussock grasslands (dominated by *Poa stuckertii*, *Deyeuxia hieronymi*), grazing lawn (dominated by *Alchemilla-Carex* lawn), granite outcrops, and eroded areas with exposed rock surface (Cingolani *et al.* 2004, 2008).

We assigned surveyed birds to different habitat types considering the following environment classification based on previous descriptions (see Fig. 2): 1 - artificial lake; 2 - river; 3 - stream; 4 - lowland forest; 5 - mountain forest; 6 - mountain shrubland; 7 - mountain grassland; 8 - *Polylepis* forest; 9 - agricola field; and 10 - urban area.

Data collection

Three different survey techniques were used to prevent biases that may be caused by one single technique (Bibby *et al.* 2000): (a) detection of species presence through direct observations with binoculars and aural identification of songs, (b) recording of species presence by means of capture with mist nets and (c) recording of species presence via interviews with local residents. Scientific nomenclature is in accordance with South American Classification Committee (SACC–American Ornithologists' Union, Remsen-Jr. *et al.* 2015). The conservation status of each bird species follows López-Lanús *et al.* (2008).

(a) Between January 2011 and December 2015,

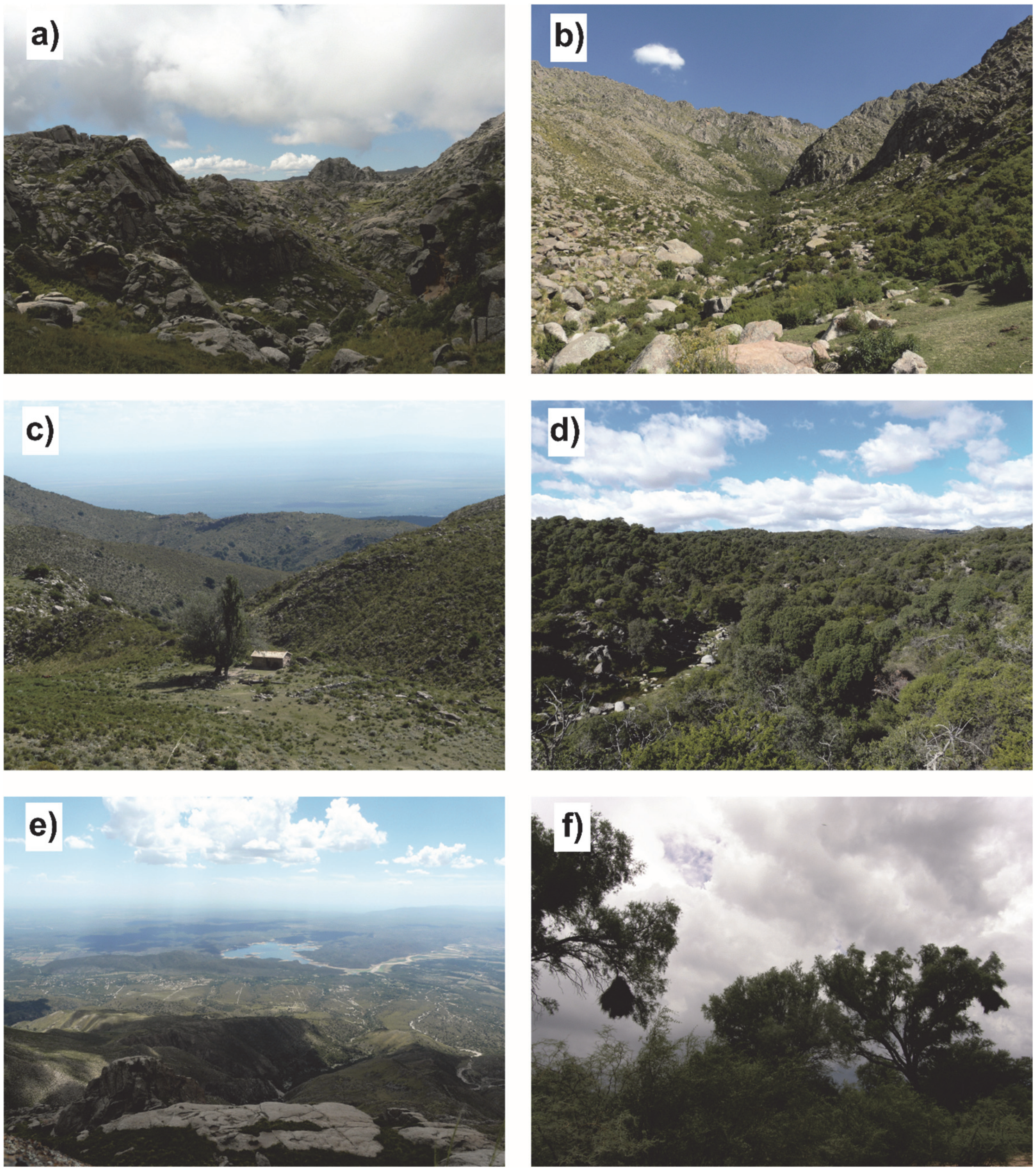

Figure 2. Different environments included in the study area. (**A**) Mountain grassland, (**B**) ravine with a *Polylepis* forest, (**C**) mountain shrubland, (**D**) mountain forest, (**E**) panoramic view of Traslasierra Valley showing Allende artificial lake, and (**F**) lowland forest.

we conducted approximately 80 surveys in the study area and registered bird species visually and aurally. Each survey consisted in walks during time-periods of high bird activity, from sunrise to midday and from 5:00 to sunset. In addition, we conducted nocturnal walks using playback to detect nocturnal species of Caprimulgidae and Strigiformes. Sixty percent of those surveys were conducted in areas corresponding to lowland and mountain Chaco woodland (data from a collateral specific study, Vergara-Tabares 2017), and areas of Allende artificial Lake and Río de los Sauces.

(b) During the autumn-winter 2014, we used mist nets in three sectors of mountain woodland. We also used mist nets during 20–29 April, 10–19 July, and 20–29 September at three sites [Los Hornillos (31°54'5.10''S; 64°58'28.92''W), San Javier (32°1'42.77''S; 65°0'13.34''W) and Luyaba (32°10'4.44''S; 65°0'29.35''W)]. Nets were mounted in sites with intense bird activity and were separated by at least 50 m (*i.e.* near the streams and/or between patches of arboreal vegetation). We opened four 12-m nets from sunrise to 12:00 h and from 16:00 h to sunset during three successive days (approximately 108 h/net per site).

(c) Interviews: some local residents, mostly rural inhabitants, were interviewed and questioned about the bird species they had identified to be in the region. In order to minimize the confusion generated by common bird names (which vary from one region to another), we used photo books of Chacoan birds with their scientific and common names to avoid misleading recognitions. This methodology allowed us to check *in loco* whether the species mentioned in the interviews were expected to occur in this region of study, focusing on those species that may have suffered local extinctions in many sites of their ranges (*e.g. Gubernatrix cristata*, *Strix chacoensis* and *Pheucticus aureoventris*).

Data analysis

We graphically explored the relationship among the different habitats and bird assemblage composition using UPGMA based on Jaccard's qualitative index of similarity. Qualitative indexes were estimated on a presence-absence matrix of birds registered in the different habitats. We used the Vegan package (Oksanen *et al.* 2007) in the free user analysis platform R (R Core Team 2012).

RESULTS

A total of 240 species of birds belonging to 48 families were recorded (Appendix I). The most represented families were Tyrannidae, Furnariidae, and Thraupidae with 35, 24, and 24 species, respectively. For the non-passerines, the most represented families were Accipitridae, Ardeidae, Picidae, and Rallidae with 12, 8, 8, and 8 species respectively. Forty-five species occurred exclusively within one type of environment (Fig. 3A, Appendix I) and two species occurred in seven non-aquatic environments (*i.e. Turdus chiguanco* and *Zonotrichia capensis*). According to López-Lanús *et al.* (2008), we recorded two "Endangered" species (*Gubernatrix cristata* only through interviews and *Buteogallus coronatus*), two threatened species, and six "Vulnerable" species (although *S. chacoensis* only through interviews, Appendix I).

Graphical exploration with UPGMA showed three groups of habitats based on bird assemblage composition (Table 1, Fig. 4). Two similar groups included: 1) mountain shrubland, mountain grassland, and *Polylepis* forest ("highland habitats" hereafter), and 2) lowland forest, mountain forest, agricola field, and urban areas ("lowland habitats" hereafter). The third, less similar, group included the following aquatic habitats: artificial lake, stream, and river ("aquatic habitats" hereafter). We

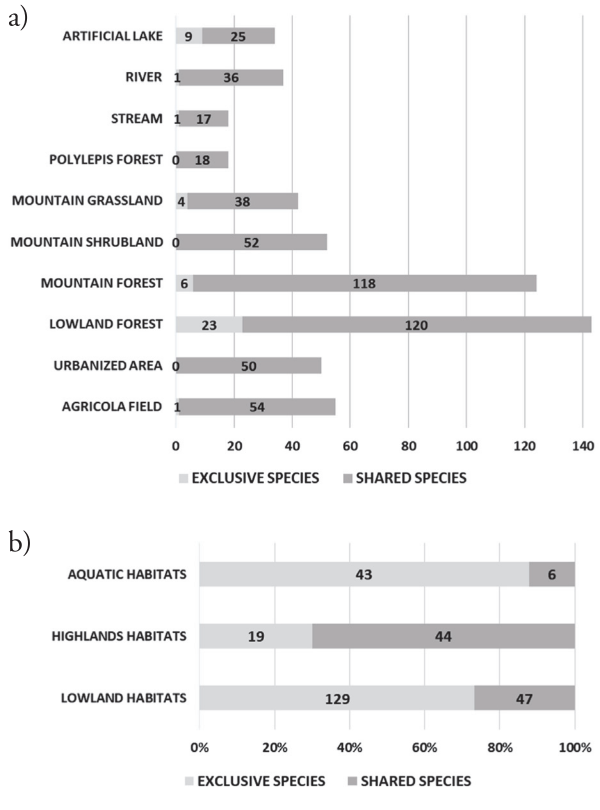

Figure 3. (**A**) Number of bird species recorded at each environment of our study site. The light gray section of the bar indicates the number of species that inhabits exclusively that particular environment and the dark gray section shows the number of species that are found in more than one environment. (**B**) Proportion of exclusive (light gray bars) and shared (dark gray bars) species per group of habitats (number of species in bold numbers). Group of habitats are illustrated in Fig. 4.

Table 1. Similarity matrix of Jaccard index among habitats surveyed in western slopes of Sierras Grandes-Comechingones and Traslasierra Valley, Argentina.

	Lowland forest	**Mountain forest**	**Mountain shrubland**	**Mountain grassland**	***Polylepis* forest**	**Agricola field**	**Urban area**	**Stream**	**River**	**Artificial lake**
Lowland forest	1.00									
Mountain forest	0.59	1.00								
Mountain shrubland	0.14	0.22	1.00							
Mountain grassland	0.05	0.11	0.50	1.00						
Polylepis forest	0.01	0.07	0.29	0.29	1.00					
Agricola field	0.30	0.21	0.17	0.11	0.04	1.00				
Urban area	0.28	0.32	0.24	0.12	0.07	0.47	1.00			
Stream	0.00	0.00	0.00	0.00	0.00	0.04	0.00	1.00		
River	0.00	0.00	0.00	0.02	0.00	0.03	0.01	0.36	1.00	
Artificial lake	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.11	0.60	1.00

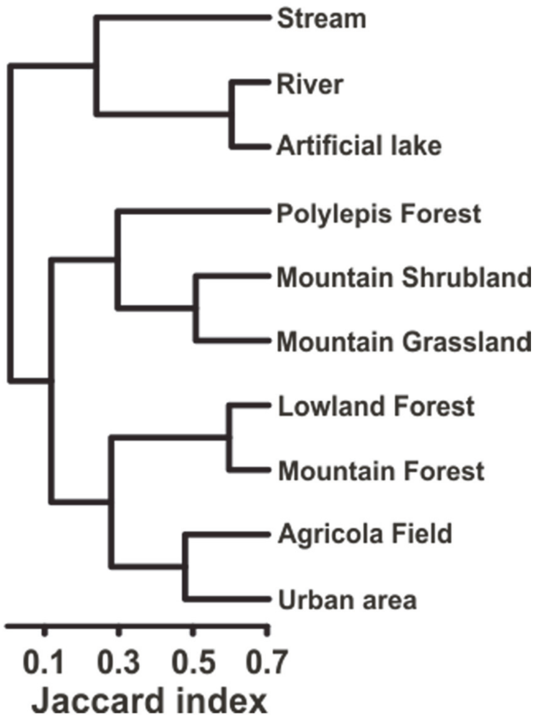

Figure 4. Hierarchical clustering analysis (UPGMA) for avian assemblages in different habitats in western slopes of Sierras Grandes-Comechingones and Traslasierra Valley using Jaccard similarity distances.

regrouped species *a posteriori* to count species exclusively present in each group of habitats. Aquatic habitats showed the highest proportion of exclusive species (but the lowest bird richness) and highland habitats was the group with lowest proportion of exclusive species. Lowland habitats showed intermediate proportions of exclusive species but the highest richness (129 species, see Fig. 3B).

A total of 17 species expected to ocurr in the area were not found (Appendix II).

DISCUSSION

Noteworthy species

Below we present some information and comments about noteworthy birds species registered in the study area, including species threatened by local activities, species included in threat categories, and endemic species. Some of this information may be relevant for conservation purposes (Di Giacomo 2005).

Andean Condor (*Vultur gryphus*): its range formerly stretched along the total length of the Andes mountains, from Venezuela to Tierra del Fuego, including Sierras Centrales of Córdoba and San Luis (Houston *et al.* 2016). We frequently observed this nearly-threatened species in our study site (Fig. 5A, B). In a few opportunities, we observed groups of 40–50 individuals feeding on dead horses or cows in areas above 1400 m a.s.l. Although a population decline has been reported for this species in Ecuador, Peru and Bolivia, the species appears to be common and the population seems to be stable in Argentina (Houston *et al.* 2016). However, in Argentina, lead poisoning (from ammunition used to hunt game) is potentially a new and increasing threat for the species (Saggese *et al.* 2009, Lambertucci *et al.* 2011).

Chaco Eagle (*Buteogallus coronatus*): We recorded two individuals of this eagle during 2011 in the central area of our study region (Fig. 5D) and we found the first active nest for Córdoba province (previous to this study there were only hints but no confirmation that the species would potentially nest in the region, Torres *et al.* 2006). On 03 February 2014, we found one nest in the southern portion of the prospected area with one nestling in advanced state of development (Fig. 5C). We were able to record many feeding events by both parents (see Capdevielle *et al.* 2015). The nest consisted of a platform built on a Molle de Beber (*Lithraea molleoides*) located in the mountain forest (at ~950 m a.s.l.). During the two following years, a pair of *B. coronatus* produced a new nestling in the same nest. Distribution of *B. coronatus* in western and north central Argentina extends south to Río Negro, La Pampa, and southern Buenos Aires (Collar *et al*. 1992, Gonnnet & Blendinger 1998). This eagle occurs in open and semi open habitats consisting of mixed open grassland, bushland, savannah, marsh and open woodland in lowland areas (Maceda 2007). In view of its low population density and the number of threats faced by this species, the IUCN Red List conservation status of the Chaco Eagle is "Endangered" (BirdLife International 2016).

Spot-winged Falconet (*Spiziapteryx circumcincta*): this monotypic species is considered endemic to the Chaco region, but is also present in monte shrubs of Río

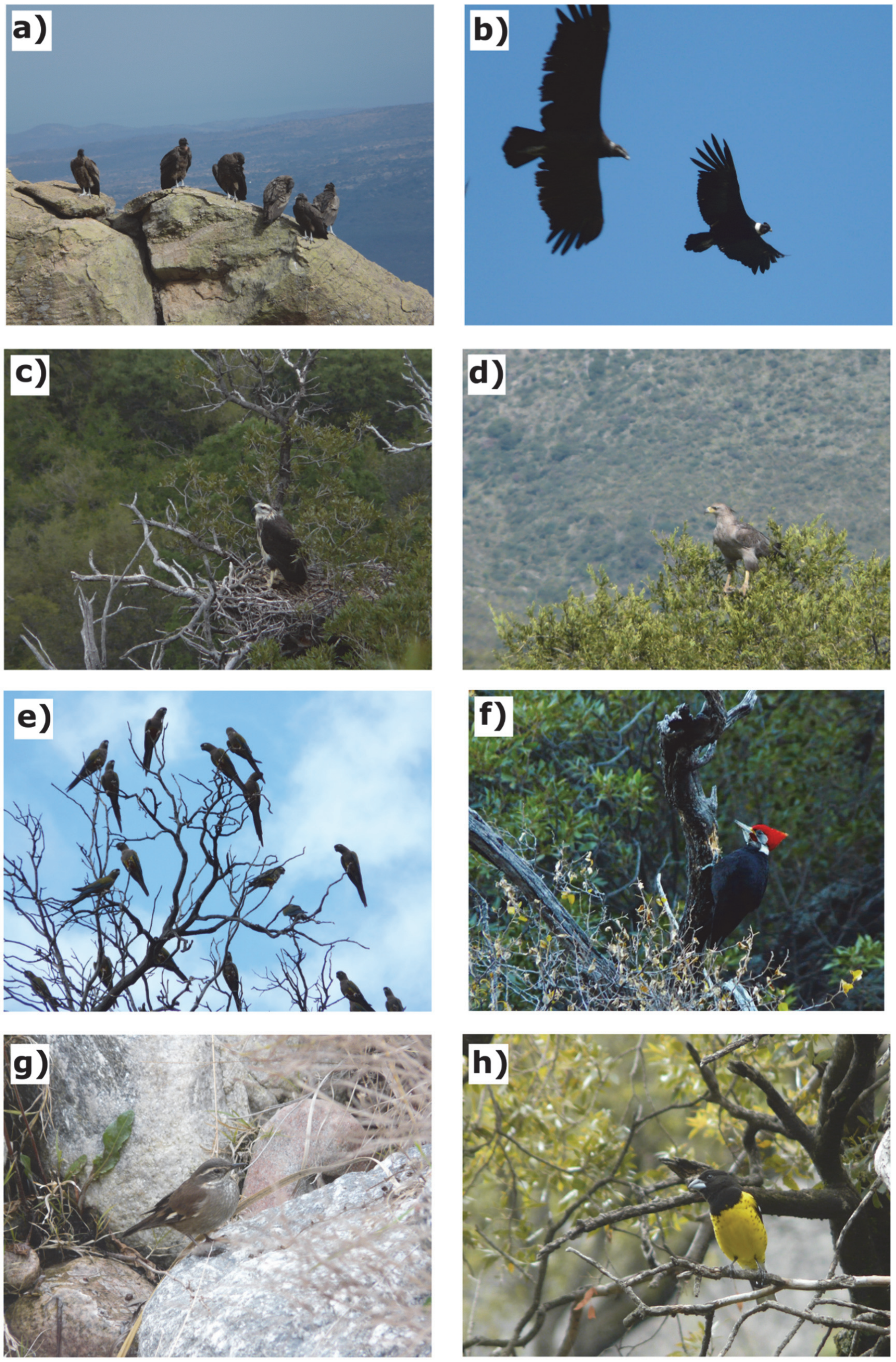

Figure 5. Noteworthy bird species registered at our sturdy area: (**A**) group of juvenile individuals of Andean Condors; (**B**) adults Andean Condors, a female on the left and a male on the right; (**C**) Crowned Eagle fledglings in their nest. First records of a Crowned Eagle nest for Córdoba province; (**D**) one of the Crowned Eagle pair that produced fledglings; (**E**) group of Burrowing Parrots that conform a colony in Los Barrancos Wildlife Refuge; (**F**) male of Black-bodied Woodpecker, the second woodpecker most abundant in mountain forests (Vergara-Tabares, unpub. data); (**G**) Olrog's Cinclodes, one of two endemic species in central mountains of Cordoba province; (**H**) male of Black-backed Grosbeak, a species threatened by illegal captures and traffic for cage birds. Photo author: D.L. Vergara-Tabares.

Negro, Argentina (Bierregaard *et al.* 2016). This species is not globally threatened (Bierregaard-Jr. *et al.* 2016), but López-Lanús *et al.* (2008) categorized this falconet as "Vulnerable" in Argentina. Its status is virtually unknown, although it is considered locally common in Córdoba, where its habitat has been seriously devastated in the region (Zak & Cabido 2002). We recorded this species in lowland forests and, in lower frequencies, in mountain forests mainly during winter.

Burrowing Parrot (*Cyanoliseus patagonus*): this species includes 4 subspecies, where *C. p. conlara* (Nores & Yzurieta 1983) occurs in San Luis and Córdoba provinces. Masello *et al.* (2011) evidenced that this subspecies represents a hybrid population of *C. p. patagonus* and *C. p. andinus*, and this is the most genetically diverse of the four *C. patagonus* taxonomic groups. This population was identified as one of four management units for conservation, being important for their genetic characteristics and low population size (1700 individuals; Masello *et al.* 2015). Due to behavioral attributes, we were able to register four noteworthy colonies of Burrowing Parrots in our study area. The largest colony occurs within the limits of Los Barrancos Wildlife Refuge, and the others (similar in size), occur in burrows at Río de Los Sauces and in ravines at mountain area between 900 and 1000 m a.s.l. However, smaller groups were recorded feeding along all the woody areas in our study region (except in *Polylepis* forests, Fig. 5E).

Chaco Owl (*Strix chacoensis*): the geographic distribution of the Chaco Owl overlaps approximately 90% of the overall Chaco region (Trejo *et al.* 2012). This owl inhabits both dense and semi-open vegetation on hilly and flat areas (Cracraft 1985). Despite its wide distribution, it is listed as "Vulnerable" in Argentina (*e.g.* López-Lanús *et al.* 2008, Trejo *et al.* 2012). López-Lanús *et al.* (2008) consider *S. chacoensis* moderately sensitive to anthropogenic habitat changes. Habitat conversion and fragmentation is probably the main threat to this species (Holt *et al.* 2016). In Córdoba province, the species has been recorded in Chancani Provincial Park and we documented its presence in lowland forest via local interviews. Although we conducted night searches of *S. chacoensis* using playbacks, we were unable to detect this species.

Black-bodied Woodpecker (*Dryocopus schulzi*): this woodpecker (Fig. 5F) is endemic to the Chaco region, and it is considered "Nearly Threatened" (López-Lanúz *et al.* 2008, Lammertink 2014, Winkler & Christie 2016). Despite its wide distribution across the Chaco region, this species is generally rare on a local scale (Madroño & Pearman 1992). However, on a regional scale in the western face of Sierras Grandes-Comechingones, we commonly recorded this woodpecker in mountain forests habitats from Las Chacras to Luyaba − close to their southern limit − (Vergara-Tabares, unpub. data). Madroño & Pearman (1992) suggest the existence of two main populations, one in central Paraguay and the other one in Córdoba province. However, Yzurieta (1995) has stated that this woodpecker is rare in Córdoba, contrary to our observations in the study area. Big woodpeckers, such as *D. schulzi*, are sensitive to logging and deforestation, as trees are required to build their nests (Lammertink 2014). Therefore, urbanization of pristine mountain forests may present a new threat for these locally abundant populations of *D. schulzi*. Human activity may not only threaten the survival of *D. schulzi* populations, but also the presence or persistence of other woodpecker species, including the southernmost populations of *Campephilus leucopogon* (Mikusiński 2006), an uncommon species in Córdoba (Yzurieta 1995).

Cordoba Cinclodes (*Cinclodes comechingonus*): this species breeds only in the isolated Sierras Grandes, occupying mainly streams in mountain grasslands and *Polylepis* forests (Remsen-Jr. 2016a). We recorded this species in all mountain grasslands and *Polylepis* forests. During autumn-winter, we observed individuals at lower altitudes (~900 m a.s.l.). Although this species inhabits a restricted range, it is not considered globally threatened because the habitat occupied by this species is relatively free from human disturbances other than cattle grazing (Cingolani *et al.* 2004).

Olrog's Cinclodes (*Cinclodes olrogi*): this species (Fig. 5G) is restricted to the Sierras Grandes, mirroring the distribution of the Cordoba Cinclodes (Remsen-Jr. 2016b). In winter, we recorded *C. olrogi* in streams at lower elevations. This species is less common than *C. comechingonus*, and it is more strictly associated with streams.

Cinnamon Warbling-finch (*Poospiza ornata*): this is a species endemic to Argentina (Mazar-Barnett & Pearman 2001). In summer, *P. ornata* occur in a strip that extends from northwestern to southeastern Argentina, moving to sites located further north and east of its summer distribution during the winter (Cueto *et al.* 2011). We have obtained scarce records, only in lowland forests, during our surveys. Although this species is a common inhabitant of arid lowland woodlands and shrubs in the Monte Desert, and taller shrubs in xeric Andean foothill ravines, some individuals may arrive at lowland Chaco Forest (Traslasierra Valley) in winter (Jaramillo 2016b). *Poopiza ornata* was classified as "Least Concern" by IUCN (2011). However, López-Lanús *et al.* (2008) have listed this species as "Vulnerable", due to its restricted distribution, the imposing risk by illegal wildlife trade, and the lack of accurate information about its population size and dynamics.

Yellow Cardinal (*Gubernatrix cristata*): this species historically occurred in north and central Argentina, extreme southeastern Brazil and Uruguay. Currently, this species is one of the few Neotropical birds that has suffered a massive and negative effect from the caged bird trade. Consequently, remaining populations of this cardinal are small and fragmented (Jaramillo 2016a). During the 1980's, Miatello *et al.* (1994) registered some individuals in several areas inside and adjacent to our study site. Based on this observation, Nores (1996) considered this species under recovery in Córdoba province. We performed specific searches for this species using playback without success. Contrasting with our negative results, the interviews with rural inhabitants reveal the presence of *G. cristata* until five years ago.

Black-backed Grosbeak (*Pheucticus aureoventris*): this species (Fig. 5H) is distributed in south Peru, south and east Bolivia and northwestern Argentina (Brewer & de Juana 2014). Although most of the populations are sedentary, there is some evidence that suggests a pattern of local movements at the geographical end of its range of distribution that includes our study site (Chebez 2009). In accordance with this evidence, our observational records for this species were obtained only during the breeding season in spring-summer, only in ravines from 900 to 2000 m a.s.l. (*i.e.* mountain woodlands and *Polylepis* forests). In addition, we found two nests during December 2012 near Los Hornillos stream. Although López-Lanús *et al.* (2008) considered *P. aureoventris* a non-threatened species in Argentina, at a local scale its presence is rare, making this species especially valuable to be trapped and caged as a pet. We also directly observed extraction of nestlings for bird trade, activity that would reduce the reproductive success of its wild populations (López-Lanús *et al.* 2008).

Ultramarine Grosbeak (*Cyanocompsa brissonii*): this species has a large range of distribution (Brewer 2016) and is considered a quite common species. In Argentina, it is also considered a quite common and non-threatened species (López-Lanús *et al.* 2008). Although this species is not included in any threat category, the loss and fragmentation of its habitat and the illegal capture and trade of individuals as cage birds represent a conservation problem. In fact, this species is one of the most common illegally traded species (Ferreira & Glock 2004, Alves *et al.* 2010, Richard *et al.* 2010). We observed captive individuals in numerous houses throughout our study area.

Bird assemblages and human threats

In this study, we recorded 240 bird species in several bird assemblages from western Sierras Grandes and Traslasierra Valley in central Argentina. Considering that in Córdoba province there are 376 cited species (Nores *et al.* 1996), it is noteworthy that the study area (0.28% of the provincial territory) hosts 63.6% of the overall avifauna of Córdoba province. Moreover, not only is it remarkable for the rich composition of its avifauna, but also for the presence of some threatened species, such as *B. coronatus* at both regional and global scales. Another important observation is the common presence of the "Near Threatened" *D. schulzi* in mountain forests and endemic and restricted-range species such as *C. comechingonus* and *C. olrogi* that highlight the conservation value of the area for birds.

The great bird richness found in the area is likely due to two main factors. First, the evident altitudinal gradient in the study area (from 600 m a.s.l to 2800 m a.s.l) allows for the existence of several contrasting vegetation units. This heterogeneous landscape is able to host different bird assemblages, such as grassland birds, woody birds, and aquatic birds. Secondly, although in Córdoba province the expansion of the agricultural frontier for the past 30 years is alarming, especially in the north, east and south of the province (Silvetti 2012, Hoyos *et al.* 2013, Cáceres 2015), this process in the west of the province is less evident, leaving large forest areas which still host a rich diversity of birds. Nevertheless, agricultural and urban encroachments are recent threats to this area, particularly the replacement of natural cover by soybean crops under artificial irrigation (Fehlenberg *et al.* 2017).

We identified three groups of habitats based on similarity of bird assemblages. The most dissimilar group corresponded to aquatic habitats (*i.e.* stream, river, and artificial lake). The other two groups were composed of terrestrial habitats: one included wooded and anthropized habitats at low altitude between 600 and 1300 m a.s.l. (*i.e.* lowland forest, mountain forest, agricola field, and urban area) and the other group included highland habitats above 1300 m a.s.l. (*i.e.* mountain shrubland, mountain grassland, and *Polylepis* forest). Aquatic habitats had the greatest proportion of exclusive species, a pattern explained by the presence of aquatic specialized species (see Fig. 3B). Though, notably, this group also presents the lowest richness. Despite the fact that lowland habitats do not show a high proportion of exclusive species, these habitats present the highest richness (see Fig. 3A, B). Given the pattern of habitat aggregation and great number of exclusive species in each group, we considered that these entities might represent discrete units of conservation that would be susceptible to different human threats and worthy of protection.

Each group of habitats and their associated avifauna seem to suffer from different threats. For instance, in the lowland habitats, forests are replaced by agricultural habitats (lowland forest) and urban habitats (lowland and mountain forests). Furthermore, highland habitats experience anthropogenic fires and over-grazing of grasslands that contribute to the increasing erosion rates (Argañaraz *et al.* 2015). Finally, the capture of some species for caged bird trade is a widely distributed and common activity in cities such as Villa Dolores and Mina Clavero (pers. obs.). Because of the high avifauna richness of the region, as well as its numerous threats, it is necessary to conduct educational and awareness campaigns focused on the local community to highlight the importance of the area for forest and bird conservation. The study area represents an important remnant of lowland and mountain Chaco Forest in a province with only 3% of the original forest remaining (Hoyos *et al.* 2013). This area has been identified as one with priority for endemic conservation for the Great Chaco region (Nori *et al.* 2016). The inclusion of the area in the system of Important Bird Areas (IBAs) is imperative to preserve this particular and threatened ecosystem in Córdoba province and its rich and unique bird community. We believe this inclusion would contribute to the development of bird and environment conservation and education programs.

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APPENDIX I

List of bird species recorded at western Sierras Grandes-Comechingones and Traslasierra Valley. We also included the environment type that each species inhabits and the category of conservation. The number of environment represents: 1 - lowland Chaco woodland; 2 - mountain Chaco woodland; 3 - Romerillo shrubland; 4 - mountain grassland; 5 - *Polilepys* forest; 6 - agricola field; 7 - urbanized area; 8 - stream; 9 - river; and 10 - artificial lake. Status abbreviations: LC - "Least Concern"; EN - "Endangered"; VU - "Vulnerable", AM - Threatened. Abundance classification: C - Common; U - Uncommon; R - Rare; and A - Accidental. Seasonal presence: Y - Year-round; S - Summer presence; W - Winter presence; and A - Altitudinal movements.

Taxon	**English Name**	**Environment**	**Status**	**Abundance**	**Seasonal Presence**
Tinamidae					
Nothura darwinii	Darwin's Nothura	1, 6	LC	C	Y
Nothoprocta cinerascens	Brushland Tinamou	1, 2	LC	C	Y
Nothoprocta pentlandii	Andean Tinamou	2, 3, 4	LC	C	Y
Nothura maculosa	Spotted Nothura	1	LC	C	Y
Crypturellus tataupa	Tataupa Tinamou	1, 2	LC	U	Y
Eudromia elegans	Elegant-crested Tinamou	1	VU	R	Y
Podicipedidae					
Tachybaptus dominicus	Least Grebe	10	LC	A	Y
Podiceps major	Great Grebe	10	LC	C	Y
Podilymbus podiceps	Pied-billed Grebe	9, 10	LC	C	Y
Rollandia rolland	White-tufted Grebe	9, 10	LC	C	Y
Phalacrocoracidae					
Phalacrocorax brasilianus	Neotropic Cormorant	9, 10	LC	C	Y
Ardeidae					
Ardea cocoi	White-necked Heron	9, 10	LC	U	Y
Ardea alba	Great Egret	9, 10	LC	C	Y
Egretta thula	Snowy Egret	8, 9	LC	C	Y
Bubulcus ibis	Cattle Egret	6, 8, 9	LC	C	Y
Syrigma sibilatrix	Whistling Heron	6, 8	LC	C	Y
Butorides striata	Striated Heron	8, 9	LC	U	Y
Nycticorax nycticorax	Black-crowned Night-heron	8, 9	LC	C	Y
Ixobrychus involucris	Stripe-backed Bittern	9, 10	LC	R	Y
Threskiornithidae					
Phimosus infuscatus	Bare-faced Ibis	9, 10	LC	U	Y

Taxon	**English Name**	**Environment**	**Status**	**Abundance**	**Seasonal Presence**
Plegadis chihi	White-faced Ibis	9, 10	LC	C	Y
Theristicus caudatus	Buff-necked Ibis	4, 9	LC	U	S
Cathartidae					
Vultur gryphus	Andean Condor	4	VU	C	Y
Cathartes aura	Turkey Vultur	1, 2	LC	C	Y
Coragyps atratus	Black Vultur	1, 2, 3, 4, 6, 7	LC	C	Y
Anatidae					
Anas bahamensis	White-cheeked Pintail	10	LC	C	Y
Anas georgica	Yellow-billed Pintail	8, 9, 10	LC	C	Y
Anas flavirostris	Speckled Teal	8, 9, 10	LC	C	Y
Anas platalea	Red Shoveler	10	LC	C	Y
Oxyura vittata	Lake Duck	9, 10	LC	U	Y
Heteronetta atricapilla	Black-headed Duck	10	LC	R	Y
Netta peposaca	Rosy-billed Pochard	10	LC	C	Y
Accipitridae					
Geranoaetus melanoleucus	Black-chested Buzzard-eagle	2, 3, 4	LC	C	Y
Geranoaetus polyosoma	Red-backed Hawk	2, 3, 4	LC	C	Y
Geranoaetus albicaudatus	White-tailed Hawk	4	LC	U	Y
Elanus leucurus	White-tailed Kite	1	LC	U	S
Buteo magnirostris	Roadside Hawk	1, 2	LC	C	Y
Circus buffoni	Long-winged Harrier	3, 4	LC	C	Y
Circus cinereus	Cinereous Harrier	1, 4	LC	C	Y
Parabuteo unicinctus	Bay-winged Hawk	1	LC	R	Y
Rostrhamus sociabilis	Snail Kite	9, 10	LC	C	Y
Accipiter striatus	Sharp-shinned Hawk	2	LC	C	Y
Accipiter bicolor	Bicolored Hawk	1, 2	LC	U	Y
Buteogallus coronatus	Crowned Eagle	1, 2	EN	R	Y
Falconidae					
Caracara plancus	Southern Crested-caracara	1, 2, 3, 4, 6, 7	LC	C	Y
Milvago chimango	Chimango Caracara	1, 2, 3, 4, 6, 7	LC	C	Y
Spiziapterix circumcinctus	Spot-winged Falconet	1, 2	VU	C	Y
Falco peregrinus	Peregrine Falcon	1, 2, 7	LC	C	Y
Falco femolaris	Aplomado Falcon	1, 6	LC	C	Y
Falco sparverius	American Kestrel	1, 2, 6	LC	C	Y
Rallidae					
Aramides cajaneus	Gray-necked Wood-rail	2, 8	LC	C	Y
Pardirallus sanguinolentus	Plumbeous Rail	8	LC	C	Y
Gallinula galeata	Common Gallinule	8, 9	LC	C	Y
Gallinula melanops	Spot-flanked Gallinule	10	LC	U	Y
Fulica armillata	Red-gartered Coot	9, 10	LC	C	Y
Fulica leucoptera	White-winged Coot	9, 10	LC	C	Y
Fulica rufifrons	Red-fronted Coot	9, 10	LC	C	Y
Fulica ardesiaca		10	LC	A	

Taxon	English Name	Environment	Status	Abundance	Seasonal Presence
Aramidae					
Aramus guarauna	Limpkin	9, 10	LC	U	Y
Cariamidae					
Chugna burmeisteri	Black-legged Seriema	1, 2	LC	U	Y
Jacanidae					
Jacana jacana	Wattled Jacana	10	LC	C	Y
Recurvirostridae					
Himantopus mexicanus	American Stilt	9, 10	LC	C	Y
Charadriidae					
Vanellus chilensis	Southern Lapwing	4, 6, 7, 9, 10	LC	C	Y
Charadrius collaris	Collared Plover	9	LC	U	Y
Scolopacidae					
Tringa melanoleuca	Greater Yellowlegs	9, 10	LC	U	Y
Tringa flaviceps	Lesser Yellowlegs	9, 10	LC	U	Y
Calidris bairdii	Baird's Sandpiper	10	LC	U	S
Gallinago gallinago	Common Snipe	3, 4	LC	U	Y
Columbidae					
Columba livia	Rock Pigeon	6, 7	LC	C	Y
Patagioenas picazuro	Picazuro Pigeon	1, 2, 6	LC	C	Y
Patagioenas maculosa	Spot-winged Pigeon	1, 2, 6, 7	LC	C	Y
Zenaida auriculata	Eared Dove	1, 2, 3, 6, 7	LC	C	Y
Columbina picui	Picui Ground-dove	1, 2, 6, 7	LC	C	Y
Leptotila verreauxi	White-tipped Dove	2, 6, 7	LC	C	Y
Psittacidae					
Thectocercus acuticaudata	Blue-crowned Parakeet	1, 2, 7	LC	C	Y
Cyanoliseus patagonus	Burrowing Parrot	1, 2	LC	U	Y
Myiopsitta monachus	Monk Parakeet	1, 2, 6, 7	LC	C	Y
Psilopsiagon aymara	Gray-hooded Parakeet	2, 3, 4, 5, 7	LC	C	A
Amazona aestiva	Turquoise-fronted Parrot	1, 2	LC	R	Y
Cuculidae					
Coccyzus melacoryphus	Dark-billed Cuckoo	1, 2	LC	U	S
Guira guira	Guira Cuckoo	1, 2, 6, 7	LC	C	Y
Tapera naevia	Striped Cuckoo	1, 2, 6	LC	C	S
Tytonidae					
Tyto alba	Barn Owl	1, 2, 6, 7	LC	U	Y
Strigidae					
Bubo virginianus	Great Horned Owl	2, 3, 4	LC	U	Y
Megascops choliba	Tropical Screech-owl	1, 2	LC	C	Y
Glaucidium brasilianum	Ferruginous Pygmy-owl	1, 2	LC	C	Y
Pseudoscops clamator	Striped Owl	1	LC	R	Y
Athene cunicularia	Burrowing Owl	1, 2, 6, 7	LC	C	Y
Strix chacoensis	Chaco Owl	1	AM	R	Y
Asio flammeus	Short-eared Owl	4, 6	LC	U	Y

Taxon	English Name	Environment	Status	Abundance	Seasonal Presence
Caprimulgidae					
Systellura longirostris	Band-winged Nightjar	1, 2	LC	U	Y
Hydropsalis torquata	Scissor-tailed Nightjar	1, 2	LC	C	Y
Setopagis parvula	Little Nightjar	1	LC	C	Y
Apodidae					
Streptoprogne zonaris	White-collared Swift	2, 3, 4, 5,	LC	U	Y
Aeronautes andecolus	Andean Swift	2, 3, 4, 5	LC	C	Y
Trochilidae					
Heliomaster furcifer	Blue-tufted Starthroat	1, 2	LC	C	Y
Sephanoides sephaniodes	Green-backed Firecrown	2	LC	A	
Chlorostilbon lucidus	Glittering-bellied Emerald	1, 2, 6, 7	LC	C	Y
Sappho sparganurus	Red-tailed Comet	2, 3, 4, 5, 7	LC	C	A
Alcedinidae					
Chloroceryle amazona	Amazon Kingfisher	8, 9, 10	LC	U	Y
Chloroceryle americana	Green Kingfisher	8, 9, 10	LC	U	Y
Megaceryle torquata	Ringed Kingfisher	8, 9, 10	LC	C	Y
Bucconidae					
Nystalus maculatus	Spot-backed Puffbird	1, 2	LC	C	Y
Picidae					
Colaptes campestris	Campo Flicker	1, 2, 3, 6, 7	LC	C	Y
Colaptes melanochloros	Green-barred Woodpecker	1, 2, 3, 7	LC	C	Y
Melanerpes cactorum	White-fronted Woodpecker	1	LC	C	Y
Melanerpes candidus	White Woodpecker	1, 2	LC	U	Y
Veniliornis mixtus	Checkered Woodpecker	1, 2, 7	LC	C	Y
Picumnus cirratus	White-barred Piculet	1, 2	LC	U	Y
Campephilus leucopogon	Cream-backed Woodpecker	1, 2, 7	LC	U	Y
Dryocopus schulzi	Black-bodied Woodpecker	2, 7	AM	C	Y
Furnariidae					
Geositta rufipennis	Rufous-banded Miner	3, 4, 5	LC	U	Y
Upucerthia dumetaria	Scale-throated Earthcreeper	1, 2	LC	U	Y
Tarphonomus certhioides	Chaco Earthcreeper	1, 2	LC	C	Y
Cinclodes atacamensis	White-winged Cinclodes	8, 9	LC	C	A
Cinclodes comechingonus	Cordoba Cinclodes	8, 9	VU	C	A
Cinclodes fuscus	Buff-winged Cinclodes	6, 8, 9	LC	C	W
Cinclodes olrogi	Olrog's Cinclodes	8, 9	VU	C	A
Furnarius rufus	RufousHornero	1, 2, 3, 6, 7	LC	C	Y
Furnarius cristatus	Crested Hornero	1, 6	LC	C	Y
Coryphistera alaudina	Lark-like Brushrunner	1, 2, 6, 7	LC	C	Y
Phleocryptes melanops	Wren-like Rushbird	9, 10	LC	U	Y
Cranioleuca pyrrophia	Stripe-crowned Spinetail	1, 2	LC	C	Y
Asthenes baeri	Short-billed Canastero	1, 2	LC	C	Y
Asthenes pyrrholeuca	Sharp-billed Canastero	1, 2	LC	U	Y
Asthenes modesta	Cordilleran Canastero	3, 4	LC	C	Y

Taxon	**English Name**	**Environment**	**Status**	**Abundance**	**Seasonal Presence**
Asthenes sclateri	Puna Canastero	3, 4	LC	C	Y
Anumbius annumbi	Firewood-gathered	1, 6	LC	C	Y
Synallaxis frontalis	Sooty-fronted Spinetail	1, 2	LC	C	Y
Synallaxis albescens	Pale-breasted Spinetail	1, 2	LC	C	Y
Leptasthenura platensis	Tufted Tit-spinetail	1, 2	LC	C	Y
Leptasthenura fuliginiceps	Brown-capped Tit-spinetail	2, 4, 5	LC	U	Y
Pseudoseisura lophotes	Brown Cacholote	1, 2, 3, 6, 7	LC	C	Y
Lepidocolaptes angustirostris	Narrow-billed Woodcreeper	1, 2	LC	C	Y
Drymornis bridgesii	Scimitar-billed Woodcreeper	1, 2, 3, 7	LC	C	Y
Thamnophilidae					
Thamnophilus caerulescens	Variable Antshrike	1, 2	LC	C	Y
Taraba major	Great Antshrike	1, 2	LC	R	Y
Rhinocryptidae					
Rhinocrypta lanceolata	Crested Gallito	1, 2	LC	U	Y
Melanopareiidae					
Melanopareia maximiliani	Olive-crowned Crescentchest	3, 4, 5	LC	C	Y
Tyrannidae					
Campostoma obsoletum	Southern Beardless-tyrannulent	1, 2, 7	LC	C	Y
Myiophobus fasciatus	Bran-colored Flycatcher	1, 2	LC	C	S
Hemitriccus margaritaceiventer	Pearly-vented Tody-tyrant	1, 2	LC	C	Y
Elaenia albiceps	White-crested Elaenia	1, 2	LC	U	S
Elaenia parvirostris	Small-billed Elaenia	1, 2	LC	C	S
Sublegatus modestus	Southern Scrub-flycatcher	1, 2	LC	U	Y
Suiriri suiriri	Suiriri Flycatcher	1, 2	LC	C	Y
Lessonia rufa	Rufous-backed Negrito	8, 9	LC	U	W
Serpophaga nigricans	Sooty Tyrannulet	9, 10	LC	U	Y
Serpophaga subcristata	White-crested Tyrannulet	1, 2	LC	C	Y
Serpophaga munda	White-bellied Tyranulet	1, 2	LC	C	Y
Pyrocephalus rubinus	Vermilion Flycatcher	1, 6	LC	C	S
Euscarthmus meloryphus	Tawny-crowned Pygmy-tyrant	1, 2	LC	C	Y
Anairetes flavirostris	Yellow-billed Tit-tyrant	2	LC	C	Y
Anairetes parulus	Tufted Tit-tyrant	2, 5	LC	U	A
Stigmatura budytoides	Greater Wagtail-tyrant	1, 2	LC	C	Y
Myiodynastes maculatus	Streaked Flycatcher	2	LC	C	S
Pitangus sulphuratus	Great Kiskadee	1, 6, 7	LC	C	Y
Tyrannus melancholicus	Tropical Kingbird	1, 2, 6, 7	LC	C	S
Machetornis rixosa	Cattle Tyrant	1, 6, 7	LC	C	Y
Myiarchus tyrannulus	Brown-crested Flycatcher	1, 2	LC	R	S
Myiarchus swainsoni	Swainson's Flycatcher		LC	C	S
Hirundinea ferruginea	Cliff Flycatcher	2, 3, 7	LC	C	Y
Knipolegus aterrinus	White-winged Black-tyrant	1	LC	U	S
Knipolegus striaticeps	Cinereous Tyrant	1	LC	U	S

Taxon	**English Name**	**Environment**	**Status**	**Abundance**	**Seasonal Presence**
Hymenops perspicillatus	Spectacled Tyrant	1, 3, 4	LC	C	Y
Empidonomus aurantioatrocristatus	Crowned Slaty-flycatcher	1, 2, 7	LC	C	S
Tyrannus savana	Fork-tailed Flycatcher	1, 7	LC	C	S
Xolmis coronatus	Black-crowned Monjita	1	LC	U	W
Xolmis irupero	White Monjita	1, 6	LC	C	Y
Agriornis micropterus	Gray-bellied Shrike-tyrant	1, 2, 3,	LC	U	W
Agriornis murinus	Lesser Shrike-tyrant	1, 6	LC	U	W
Agriornis montanus	Black-billed Shrike-tyrant	3, 4, 5	LC	C	Y
Muscisaxicola rufivertex	Rufous-naped Ground-tyrant	3, 4	LC	C	Y
Muscisaxicola maclovianus	Dark-faced Ground-tyrant	6	LC	U	W
Tityridae					
Pachyramphus validus	Crested Becard	2	LC	U	S
Pachyramphus polychopterus	White-winged Becard	2	LC	U	S
Cotingidae					
Phytotoma rutila	White-tipped Plantcutter	1, 3, 6	LC	C	Y
Vireonidae					
Vireo olivaceus	Red-eye Vireo	1, 2	LC	C	S
Cyclarhis gujanensis	Rufous-browed Peppershrike	1, 2	LC	C	Y
Hirundinidae					
Progne elegans	Southern Martin	2, 3, 6	LC	C	S
Progne tapera	Brown-chested Martin	2, 3	LC	C	S
Tachycineta leucorrhoa	White-rumped Swallow	1, 2, 7	LC	C	S
Tachycineta leucopyga	Chilean Swallow	1	LC	C	W
Pygochelidon cyanoleuca	Blue-and-White Swallow	1, 2	LC	C	Y
Troglodytidae					
Troglodytes aedon	House Wren	1, 2, 3, 4, 6, 7	LC	C	Y
Cistothorus platensis	Grass Wren	3, 4, 5	LC	C	Y
Polioptilidae					
Polioptila dumicola	Masked Gnatcatcher	1, 2, 3	LC	C	Y
Turdidae					
Catharus ustulatus	Swainson's Thrush	1, 2	LC	R	S
Turdus amaurochalinus	Creamy-bellied Thrush	1, 2, 6, 7	LC	C	Y
Turdus rufiventris	Rufous-bellied Thrush	1, 2, 3, 5, 6, 7	LC	C	Y
Turdus nigriceps	Slaty Thrush	2	LC	U	Y
Turdus chiguanco	Chiguanco Thrush	1, 2, 3, 4, 5, 6, 7	LC	C	Y
Mimidae					
Mimus triurus	White-banded Mockingbird	1, 6	LC	C	W
Mimus patagonicus	Patagonian Mockingbird	1	LC	U	W
Mimus saturninus	Chalk-browed Mockingbird	1, 2, 3, 6, 7	LC	C	Y
Motacillidae					

Taxon	English Name	Environment	Status	Abundance	Seasonal Presence
Anthus furcatus	Short-billed Pipit	3, 5	LC	U	Y
Anthus lutescens	Yellowwish Pipit	3	LC	U	Y
Anthus hellmayri	Hellmayr's Pipit	3	LC	C	Y
Parulidae					
Parula pitiayumi	Tropical Parula	1	LC	U	Y
Geothlypis aequinoctialis	Masked Yellothroat	1, 2	LC	C	Y
Myioborus brunniceps	Brown-capped Redstart	3, 4, 5	LC	C	A
Thraupidae					
Pipraeidea bonariensis	Blue-and-yellow Tanager	1, 2, 3, 7	LC	C	Y
Thraupis sayaca	Sayaca Tanager	1	LC	C	Y
Phrygilus alaudinus	Band-tailed Sierra-finch	3, 4	LC	C	Y
Phrygilus unicolor	Plumbeous Sierra-finch	3, 4, 5	LC	C	Y
Phrygilus carbonarius	Carbonated Sierra-finch	1, 2	LC	R	W
Phrygilus plebejus	Ash-breasted Sierra-finch	3, 4, 5	LC	C	Y
Sicalis flaveola	Saffron Yellow-finch	1, 6, 7	LC	C	Y
Sicalis luteola	Grassland Yellow-finch	1, 6	LC	C	Y
Saltraticula multicolor	Many-colored Chaco-finch	1	LC	C	Y
Poospiza ornata	Cinnamon Warbling-finch	1	VU	C	W
Poospiza hypochondria	Rufous-sided Warbling-finch	3, 5	LC	U	Y
Poospiza nigrorufa	Black-and-rufous Warbling-finch	1, 2	LC	C	Y
Poospiza torquata	Ringed Warbling-finch	1	LC	C	Y
Poospiza melanoleuca	Black-capped Warbling-finch	1, 2	LC	C	Y
Lophospingus pusillus	Black-crested Finch	1	LC	U	Y
Gubernatrix cristata	Yellow Cardinal	1, 2	EN	R	
Paroaria coronata	Red-crested Cardinal	1	LC	U	Y
Coryphospingus cucullatus	Red-crested Finch	1	LC	U	Y
Sporophila caerulescens	Double-collared Seedeater	1, 2	LC	C	S
Catamenia analis	Band-tailed Seedeater	2, 3, 4	LC	C	Y
Catamenia inornata	Plain-colored Seedeater	3, 4, 5	LC	C	Y
Diuca diuca	Common Diuca-finch	1	LC	C	S
Embernagra platensis	Great Pampa-finch	1, 3	LC	C	Y
Saltator aurantiirostris	Golden-billed Saltator	1, 2, 3, 6, 7	LC	C	Y
Emberizidae					
Zonotrichia capensis	Rufous-collared Sparrow	1, 2, 3, 4, 5, 6, 7	LC	C	Y
Rhynchospiza strigiceps	Stripe-capped Sparrow	1	LC	C	Y
Ammodramus humeralis	Grassland Sparrow	1, 3	LC	C	Y
Cardinalidae					
Pheucticus aureoventris	Black-backed Grosbeak	2, 3, 5	LC	U	S
Piranga flava	Hepatic Tanager	1, 2	LC	C	Y
Cyanocompsa brissonii	Ultramarine Grosbeak	1, 2	LC	U	Y

Taxon	English Name	Environment	Status	Abundance	Seasonal Presence
Icteridae					
Icterus cayanensis	Epaulet Oriole	1, 2, 7	LC	C	Y
Molothrus rufoaxillaris	Screaming Cowbird	1, 2, 6, 7	LC	C	Y
Molothrus bonariensis	Shiny Cowbird	1, 2, 6, 7	LC	C	Y
Agelaioides badius	Bay-winged Cowbird	1, 2, 6, 7	LC	C	Y
Sturnella loyca	Long-tailed Meadowlark	3, 4	LC	C	Y
Sturnella superciliaris	White-browed Blackbird	1, 6	LC	C	Y
Fringillidae					
Euphonia chlorotica	Purple-throated Euphonia	1, 2	LC	U	Y
Sporagra magellanica	Hooded Siskin	1, 3, 4, 6, 7	LC	C	Y
Passeridae					
Passer domesticus	House Sparrow	6, 7	LC	C	Y

APPENDIX II

Bird species predicted to occur at our study area and including probable habitat (see references in Appendix I). It includes species known from nearby areas, based on Nores (1996) and unpublished data.

Species	English name	Environment
Annas cyanoptera	Cinnamon Teal	10
Buteo swainsoni	Swainson's Hawk	1, 6
Pandion haliaetus	Osprey	10
Cariama cristata	Red-legged Seriema	1
Nyctibius griseus	Common Potoo	1
Chordeiles minor	Common Nighthawk	1
Chaetura meridionalis	Sick's Swift	1
Upucerthia validirostris	Buff-breasted Earthcreeper	4
Leptasthenura aegithaloides	Tufted Tit-Spinetail	1
Phacellodomus sibilatrix	Little Thornbird	1
Lathrotriccus euleri	Euler's Flycatcher	1
Pseudocolopteryx acutipennis	Subtropical Doradito	3, 4
Pseudocolopteryx flaviventris	Warbling Doradito	9, 10
Tachuris rubrigastra	Many-colored Rush-tyrant	9, 10
Knipolegus hudsoni	Hudson's Black-tyrant	1, 6
Muscisaxicola capistratus	Cinnamon-bellied Ground-tyrant	4, 6
Phrygilus gayi	Gray-hooded Sierra-Finch	1, 3, 4

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ARTICLE

Bird molting and breeding in an area undergoing re-vegetation in the Atlantic Forest of southeastern Brazil

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ABSTRACT: Molting and breeding cycles are high-energetic costs events, and usually synchronized and temporally well defined in tropical avian communities. However, in degraded and/or undergoing restoration areas, environmental stresses, such as forest fragmentation and restriction of food resources, could locally change these patterns. This study aims to analyze molting and breeding in a bird assembly in an undergoing re-vegetation area in the Atlantic Forest of southeastern Brazil. By mist netting, we searched for evidence of molting of flight feathers and presence of brood patch in captured birds. We also recorded three environmental variables (temperature, rainfall, and photoperiod) to test whether they affect those events. We sampled 85 individuals from 36 species. The breeding cycle started in July and peaked in November and December. The molting period was between July and April of the next year and peaked in January and February. Molting and breeding events were related to temperature. The overlap between these events was of 11% ($n = 9$). Our data suggest that molt and breeding times are in accordance to other studies where the climate is more seasonal, yet more studies are necessary to investigate those biological cycles and their possible alterations due to environmental degradation.

KEY-WORDS: fragmentation, mist nets, overlap, reproduction, restoration.

INTRODUCTION

Migration, molting, and reproduction are the life cycle events of birds that demand the highest energy expenditure (Foster 1974, Marini & Durães 2001), and an evolutionary strategy to reduce these costs would be to reduce their temporal overlap (Clark 2004, Newton 2009, Jahn *et al.* 2017). Yet, individuals of many tropical species undergo molting and breeding events with some overlap (Marini & Durães 2001, Piratelli 2012). This may be related, in comparison to their temperate counterparts, to reduced physiological demands (Foster 1974, Wingfield 2005), such as fewer eggs (Martin *et al.* 2000), gonad size reduction (Hau *et al.* 2010), and an extended molting period (Ryder & Wolfe 2009; but see Silveira & Marini 2012).

Many abiotic factors are thought to influence the timing of molting and breeding in the Neotropical region. Minor changes in photoperiod (*e.g.* increasing the duration of daytime) may cause shifts in behavior, and trigger the development of brood patch and gonads, and an increase in brain activities of areas related to song (Dawson *et al.* 2001, Chandola-Saklani *et al.* 2004, Dawson 2013). Another influence is the availability of food resources, which is needed to supply energy intake (Hemborg & Lundberg 1998) and, in some cases, may be closely related to local precipitation and temperature (*e.g.* Repenning & Fontana 2011). Seasonal forests have a marked climatic seasonality, with a rainy season in a larger food supply (Pennington *et al.* 2009), and a dry season with more limited resources (Araújo-Filho 2009), which may affect bird behavior and physiology (*e.g.* Ryder & Wolfe 2009).

Forest degradation and fragmentation are changes that may cause stress in birds (Lens *et al.* 1999), mainly due to restrictions in food supply and suitable breeding sites (Ford *et al.* 2001). Animals respond to stress with endocrine changes, affecting physiological processes that, if they persist for a long time, can negatively affect survival, reproduction, and resistance to diseases (Boonstra 2004, Romero 2004, Lundberg 2005). Thus, nutritionally deficient birds could have their breeding affected by lack of nutrients for their maintenance and for egg production (Mauget *et al.* 1994).

Many areas are globally undergoing forest restoration as an alternative to minimize the impacts of forest fragmentation (Crouzeilles *et al.* 2016), aiming to recover the original structure and functionality of the ecosystems (SER 2004). Although there are several studies on bird molting and breeding in Brazil (*e.g.* Piratelli *et al.* 2000, Mallet-Rodrigues 2005, Silveira & Marini 2012, Araujo *et al.* 2017), to our knowledge, there are no molting studies that have been done in areas undergoing forest restoration. Such studies may help elucidate periods related to molting and breeding cycles in relation to environmental factors that may interfere with these processes in sites under severe forest fragmentation (Laurance *et al.* 2002, Gastauer *et al.* 2015).

Here we aimed to determine bird molting and breeding periods and whether these events overlap in an area under a restoration program in the Atlantic Forest of southeastern Brazil. We expect little or no overlap between those events, by the patterns already described in assemblages of birds in the Atlantic Forest (*e.g.* Marini & Durães 2001, Maia-Gouvêa *et al.* 2005) and by the high energy demand requirements involved. We predicted that these events are related to such environmental variables as photoperiod, rainfall and temperature.

METHODS

Study area

This research was carried out at Fazenda São Luiz in the region of Itu, state of São Paulo, Brazil (23°14'15.18''S; 47°24'3.29''W; Fig. 1), with an area of 526 ha. The land use in the past was defined by intensive coffee crops from 1940 to 1980, then by pasturelands until 2007, when the restoration program began, resulting in small isolated fragments of native vegetation. The restored area has 386 ha, which planting age ranges from 4 to 11 years. The planting was carried out randomly in alternating lines composed of pioneer and secondary species, with spacing of 2 × 3 m between the lines. Some of the most common tree species are *Schinus terebinthifolius* Raddi, *Cytharexyllum myrianthum* Cham., *Guazuma ulmifolia* Lam., *Machaerium nyctitans* (Vell.) Benth and *Cedrela fissilis* Vell (Gagetti *et al.* 2016). The predominant vegetation is Semideciduous Seasonal Forest with a transition to Cerrado (Brazilian savanna). It is characterized by marked climatic seasonality in rainfall, and trees may lose 20 to 50% of their leaves in the dry season (Araújo-Filho 2009). The climate is humid temperate of the Cwa type, according to Köppen system, being characterized by dry winters and hot summer, with average rainfall of 56 mm and 160 mm, respectively (Alvares *et al.* 2013). The rainy season occurs from October to March, followed by the dry season, from April to September (Cepagri 2017).

Molting and breeding periods

We mist-netted birds from May 2016 to April 2017 to detect the periods of molting and breeding. We used seven to nine mist nets (36 mm, 12 × 3 m) placed 5 m from the edge of two restored areas, the first with 6 (4.22 ha), and the second with 8 years (8.39 ha) after initial restoration process. The total capture effort was 45,631 (h/m^2), with an average of 30 h in 3 days of capture per month, mostly in the second fortnight. The nets were open at dawn, closed in the hottest part of the day (noon), and then reopened until dusk.

We investigated only the flight feathers molting, by the presence of sheathed feathers and by the difference in length compared to other feathers (Fig. 2). We recognized individuals in active molt as those simultaneously replacing at least one feather on both sides of the tail and on both wings (Marini & Durães 2001).

We considered an individual as being in breeding condition by the presence of a brood patch, defined by loss of contour feathers in the ventral region or by hypervascularization in this area (Jones 1971). We used a ranking system varying from stages 1 to 5 to verify the degree of brood patch development (IBAMA 1994, Fig. 3). Despite the breeding period is not restricted to the egg laying period, we used this event as evidence of

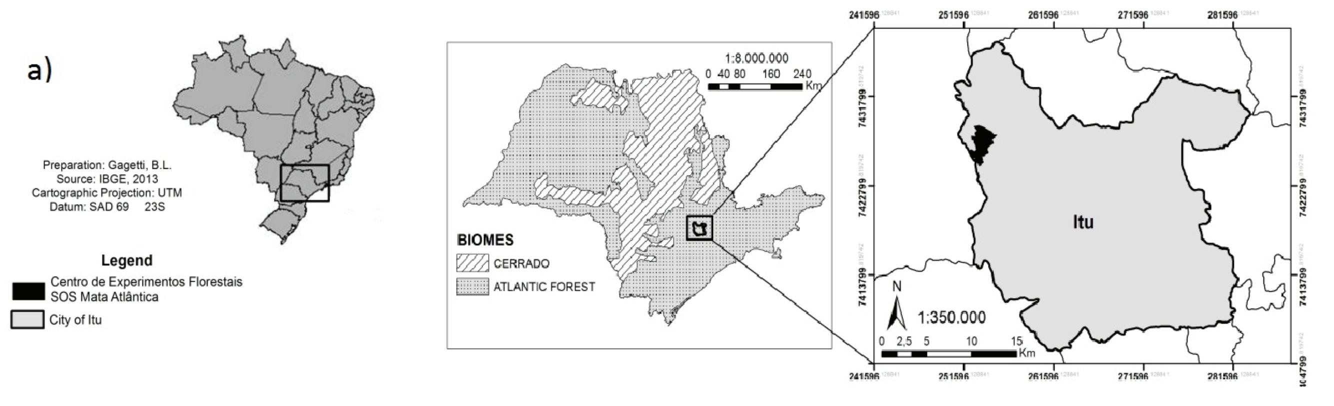

Figure 1. Location of *Centro de Experimentos Florestais SOS Mata Atlântica* in the region of Itu, state of São Paulo, southeastern Brazil. (Modified from Gagetti *et al.* 2016 with permission from the authors).

breeding. Sexual maturity of each individual was checked by plumage characteristics and/or color of the gape. All individuals considered as young were excluded from the analyses.

The overlap of molting and breeding was defined by evidence of both events in the same individual, *e.g.* if a bird had brood patch at any stage of development (stages 1–5) and was in molting, we considered it to be overlapping breeding and molt.

Environmental variables

We retrieved regional data on monthly means of temperature and rainfall from *Centro Integrado de Informações Agrometeorológicas* (Ciiagro 2017), and values of photoperiod through the website Golden Hour Calculator (http://www.b-roll.net/goldenhour/generate.php). We collected information on time of sunrise and sunset for each day of each month of sampling. Thus, we

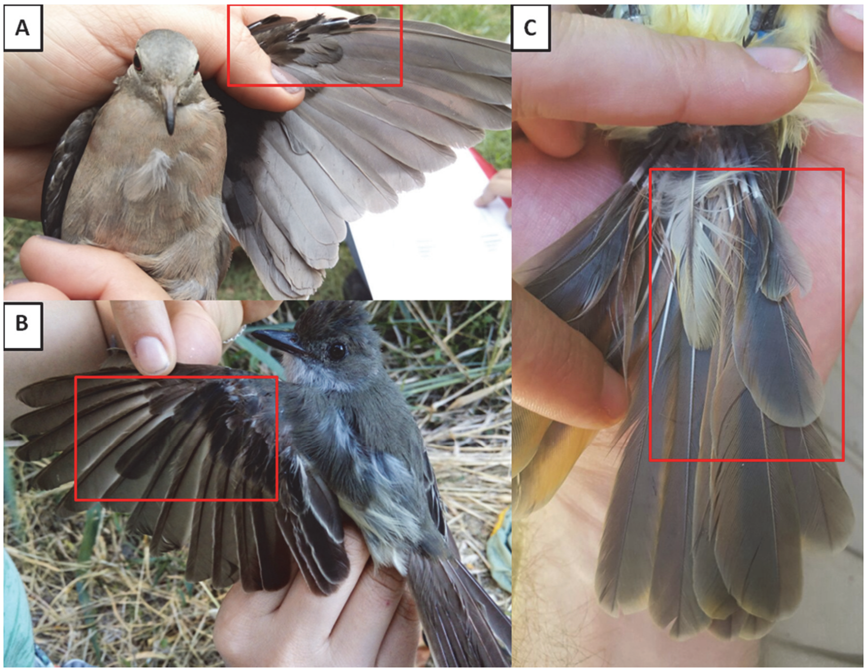

Figure 2. Captured individuals with flight feather molt from May 2016 to April 2017 in the region of Itu, state of São Paulo, southeastern Brazil. (**A**) *Columbina talpacoti*, left wing; (**B**) *Myiarchus swainsoni*, left wing; (**C**) *Myiarchus tyrannulus*, tail. Photo author: Paulo Andrade.

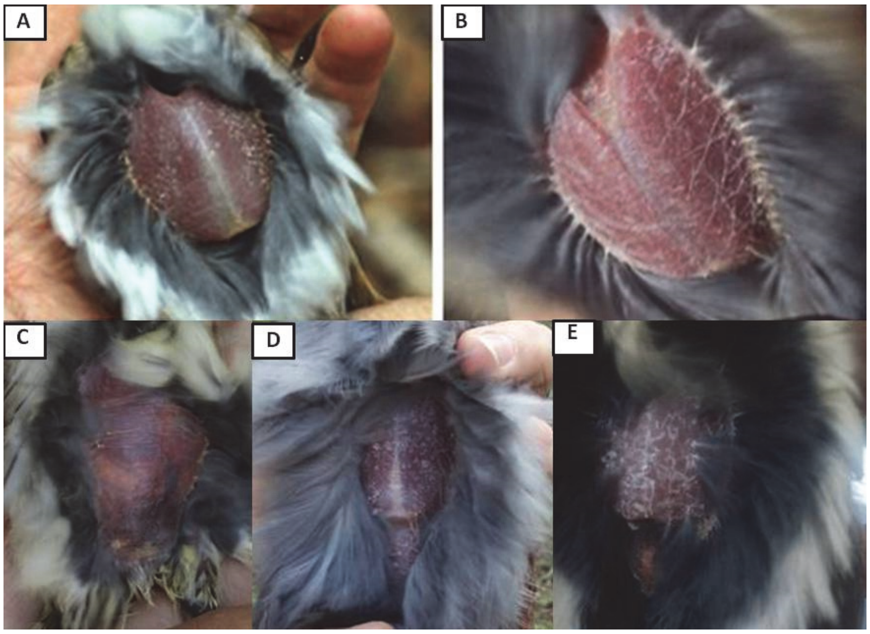

Figure 3. Stages (scores) of brood patch development of captured birds. (**A**) Score 1; (**B**) Score 2; (**C**) Score 3; (**D**) Score 4; (**E**) Score 5. Photo authors: Daniele Moreno and Paulo Andrade.

calculated the total number of minutes per day and the monthly average, with the sum of the minutes per day divided by the number of days in the month.

Data analysis

We determine the molting and breeding periods using percentage of the number of individuals in molting and breeding condition recorded in each month of sampling, and we tested for molt-breeding overlap using a Chi-square test.

We tested the collinearity of predictor variables (photoperiod, temperature, and rainfall) by VIF (Variance Inflation Factor). We used VIF = 3 to find a set of explanatory variables without collinearity, taking one variable at a time and recalculating FV values, repeating the process until FV values were less than 3. As temperature and photoperiod were collinear, we excluded photoperiod from the analyses. Then, we used binomial Generalized Linear Models - GLM to check for any relation of temperature and rainfall with molt and breeding. All analyses were run in the software R 3.4.1 (R Core Team 2017).

RESULTS

We captured 85 birds, 8 of which were recaptured. These individuals represent 36 species and 14 families (Table 1), mostly passerines (*n* = 28; 77.7%). July and August had the largest number of captured birds (*n* = 26; 33.7%). The most-captured species were *Turdus leucomelas* Vieillot, 1818 (*n* = 7; 9.1%), *Tachyphonus coronatus* (Vieillot, 1822) (*n* = 6; 7.8%) and *Tiaris fuliginosus* (Wied, 1830) (*n* = 6; 7.8%).

Breeding, molting and overlap

We captured 59 individuals in breeding condition. The breeding period lasted from July to February, and the highest number of individuals with a brood patch (*n* = 19; 32.2%) was sampled in September and October, most in early stages of development. Individuals with fully-developed brood patches were more common from November to December (*n* = 6, Fig. 4).

We sampled 9 birds with flight feathers molting, from July to April, with a higher incidence in January and February (*n* = 5; 55.5%, Fig. 5). From those, 6 were molting wings, one its tail feathers and 2, both wings and tail. All 9 individuals exhibited molt-breeding overlap (about 11%; see Table 1). Overlap was more common from January to April (*n* = 7; 77.7%). Therefore, some birds may present reproductive activities regardless they are also molting ($\chi^2 = 3.94$, $df = 1$, $P = 0.05$).

Environmental variables

We found that both molt and breeding are related to temperature ($P < 0.001$ for both). While none of these two response variables (*i.e.* molt or reproduction) were influenced by rainfall ($P = 0.84$ and $P = 0.34$, respectively).

DISCUSSION

Breeding, molting and overlap

Our findings are in accordance to previous studies carried out in the Atlantic Forest, that breeding period lasts from August to April, peaking in November (Marini & Durães 2001, Mallet-Rodrigues 2005, Piratelli 2012). The molting season in our study was similar to others in the same biome, from September to May, peaking

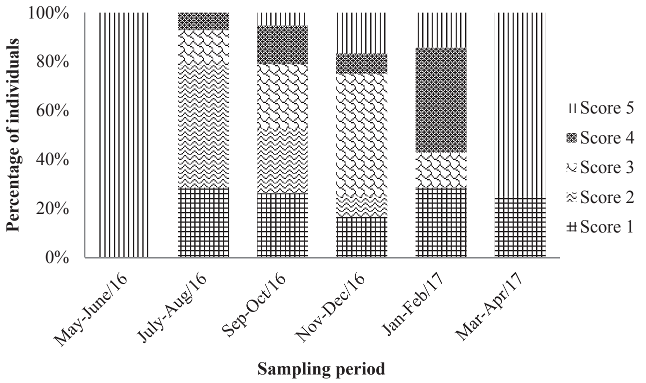

Figure 4. Percentage of individual birds captured with different scores of brood patch development from May 2016 to April 2017 in the region of Itu, state of São Paulo, southeastern Brazil. Score 0: nonexistent brood patch; Score 1: developing brood patch; Scores 2 and 3: brood platch in maximum development, active; Scores 4 and 5: reduction and disappearance of the brood patch (IBAMA 1994).

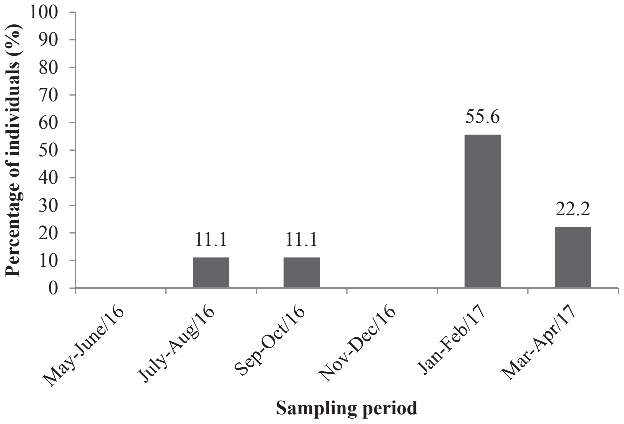

Figure 5. Percentage of individual birds molting flight feathers from May 2016 to April 2017 in the region of Itu, state of São Paulo, southeastern Brazil.

Table 1. Bird families and species captured (nomenclature follows Piacentini *et al.* 2015). Columns represent number of total captures, number of individuals captured molting flight feathers or with a brood patch and number of individuals with both events, from May 2016 to April 2017 in the region of Itu, state of São Paulo, southeastern Brazil.

Taxon	Captures	Molting	Brood patch	Overlap
Columbidae Leach, 1820				
Columbina talpacoti (Temminck, 1810)	2	1	2	1
Leptotila verreauxi Bonaparte, 1855	6	2	4	1
Leptotila rufaxilla (Richard & Bernard, 1792)	1	1	1	1
Cuculidae Leach, 1820				
Piaya cayana (Linnaeus, 1766)	2	1	2	0
Tapera naevia (Linnaeus, 1766)	1	0	1	0
Bucconidae Horsfield, 1821				
Malacoptila striata (Spix, 1824)	1	1	1	1
Picidae Leach, 1820				
Picumnus temminckii Lafresnaye, 1845	1	0	0	0
Veniliornis spilogaster (Wagler, 1827)	1	0	1	0
Thamnophilidae Swainson, 1824				
Thamnophilus doliatus (Linnaeus, 1764)	1	0	1	0
Thamnophilus caerulescens Vieillot, 1816	2	1	2	1
Furnariidae Gray, 1840				
Synallaxis frontalis Pelzeln, 1859	2	1	2	0
Rhynchocyclidae Berlepsch, 1907				
Leptopogon amaurocephalus Tschudi, 1846	3	0	2	0
Tolmomyias sulphurescens (Spix, 1825)	1	0	1	0
Tyrannidae Vigors, 1825				
Myiopagis viridicata (Vieillot, 1817)	1	0	1	0
Myiarchus swainsoni (Cabanis & Heine, 1859)	1	1	1	1
Myiarchus ferox (Gmelin, 1789)	3	0	3	0
Myiarchus tyrannulus (Statius Muller, 1776)	2	1	1	1
Pitangus sulphuratus (Linnaeus, 1766)	2	0	0	0
Myiodynastes maculatus (Statius Muller, 1776)	3	0	3	0
Megarynchus pitangua (Linnaeus, 1766)	1	0	1	0
Cnemotriccus fuscatus (Wied, 1831)	1	0	1	0
Lathrotriccus euleri (Cabanis, 1868)	1	0	1	0
Vireonidae Swainson, 1837				
Cyclarhis gujanensis (Gmelin, 1789)	2	0	2	0
Turdidae Rafinesque, 1815				
Turdus leucomelas Vieillot, 1818	7	0	6	0
Turdus amaurochalinus Cabanis, 1850	1	0	0	0
Passerellidae Cabanis & Heine, 1850				
Zonotrichia capensis (Statius Muller, 1776)	1	0	1	0
Parulidae Wetmore, Friedmann, Lincoln, Miller, Peters, van Rossem, Van Tyne & Zimmer 1947				
Basileuterus culicivorus hypoleucus Bonaparte, 1850	3	0	2	0
Myiothlypis flaveola Baird, 1865	2	2	2	0

Taxon	Captures	Molting	Brood patch	Overlap
Thraupidae Cabanis, 1847				
Tangara sayaca (Linnaeus, 1766)	4	1	3	1
Tangara cayana (Linnaeus, 1766)	1	0	0	0
Volatinia jacarina (Linnaeus, 1766)	2	1	1	1
Coryphospingus cucullatus (Statius Muller, 1776)	2	0	2	0
Tachyphonus coronatus (Vieillot, 1822)	4	0	3	0
Tiaris fuliginosus (Wied, 1830)	6	0	1	0
Thlypopsis sordida (d'Orbigny & Lafresnaye, 1837)	2	0	1	0
Cardinalidae Ridgway, 1901				
Cyanoloxia glaucocaerulea (d'Orbigny & Lafresnaye, 1837)	1	0	0	0

from January to April (Bugoni *et al.* 2002, Repenning & Fontana 2011, Piratelli 2012). Following previously described patterns (*e.g.* Poulin *et al.* 1992, Silveira & Marini 2012) the incidence of molting was higher right after the breeding season.

There are some general patterns about molt-breeding overlap that can be identified across studies. It is widespread in the Neotropics (Foster 1975, Piratelli *et al.* 2000, Marini & Durães 2001, Rohwer *et al.* 2009, Piratelli 2012, Silveira & Marini 2012, Jahn *et al.* 2017) and can occur in tropical regions around the world (Payne 1969, Ralph & Fancy 1994, Verea *et al.* 2009, Moreno-Palacios *et al.* 2013, Pyle *et al.* 2016). We found that molting and breeding events had a higher overlap than in other studies in the Atlantic Forest in south, southeastern and central regions of Brazil (*e.g.* Marini & Durães 2001, Repenning & Fontana 2011, Piratelli 2012). However, considering that the number of overlapping individuals that we captured was lower, which prevents us from generalizing our findings, but this is the first step with results on bird phenology in restoration areas of the Atlantic Forest.

All individuals earlier described as having overlap were passerines (Marini & Durães 2001, Piratelli 2012, Araujo *et al.* 2017), while here we also sample four non-passerine birds (three doves and one puffbird; Table 1). We also sampled bird families reported in previous studies (*e.g.* Thraupidae, Thamnophilidae and Tyrannidae - Marini & Durães 2001, Araujo *et al.* 2017). However, only one species was the same reported in previous similar studies (*Thamnophilus caerulescens* Vieillot, 1816) (Marini & Durães 2001) molting in temperate regions takes about 40–70 days to complete, while tropical birds have a slower metabolism, taking an average of 120 days to complete molting, increasing energy demand when overlapping with breeding (Silveira & Marini 2012). The replacement of feathers demands time, energy and nutrients (Lindström *et al.* 1993), thus, overlapping molt and breeding may only occur in periods of high resource availability (Poulin *et al.* 1992). Although many birds can overlap molt and breeding (Payne 1969, Marini & Durães 2001, Piratelli 2012), the energy costs involved can be translated into tradeoffs. A feather growth rate of up to 40% slower has already been described, with more than twice the time spent in feeding, reducing by half the time for feathers care, and feathers quality and flight speed as well, increasing risks of predation (Echeverry-Galvis & Hau 2013).

The longer the duration of molting, the greater the frequency of overlap with breeding (Johnson *et al.* 2012). A slower molt reduces the gaps between flight feathers and the risk of predation, ensuring an improvement in feathers quality and allowing more energy to be directed towards immunological resistance (Hedenström & Sunada 1999). Foster (1974) suggests that molt-breeding overlap in tropical regions may occur due to extended breeding periods and more potential re-nesting; this may maximize birds' reproductive output in areas where nesting success is low, as fragmented landscapes (Rodrigues *et al.* 2018), which is the case of our study area.

Environmental variables

We found relationship between temperature and patterns of molting and breeding. It is known that both temperature and rainfall define the period of molting worldwide (Poulin *et al.* 1992, Piratelli *et al.* 2000, Tyson & Preston-Whyte 2000, Repenning & Fontana 2011, Piratelli 2012, Ndlovu *et al.* 2017). Data relating temperature and rainfall to reproduction are conflicting (*e.g.* Poulin *et al.* 1992, Piratelli *et al.* 2000, Repenning & Fontana 2011, Piratelli 2012, Araujo *et al.* 2017), since there is no agreement between them.

We observed some overlap between molting and breeding. We recommend long-term studies to evaluate how reforestation programs can be optimized to provide suitable habitats for birds, enabling them to perform their biological cycles and reducing the environmental stress inherent in degraded areas. If one of the main goals of ecological restoration is to rescue ecosystem functions, providing bird habitat quality may reflect well-defined biological rhythms, increasing the success of recolonization by those species.

ACKNOWLEDGEMENTS

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SHORT-COMMUNICATION

Do Fork-tailed Flycatchers (*Tyrannus s. savana*) stop to molt during fall migration?

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ABSTRACT: Fork-tailed Flycatchers (*Tyrannus s. savana*) breed from central to southern South America, then migrate to northern South America, where they undergo a winter molt. However, exactly when this winter molt begins is not known. Previous research showed that some Fork-tailed Flycatchers stopover for an extended period in Mato Grosso do Sul in late January/early February, during fall migration. We hypothesized that these flycatchers are suspending fall migration to initiate flight feather molt, as do congeners in North America. In February 2016, we located a roost of >100 migratory flycatchers in Mato Grosso do Sul state and captured two adults and two juveniles, one of which was an adult female that was symmetrically molting the first primary feather. This is the furthest south that this species has been found molting flight feathers and suggests that some Fork-tailed Flycatchers undertake fall molt-migration to Mato Grosso do Sul. Further research on the relationship between timing of molt and migration of this and other birds that migrate within South America will be essential to evaluate the evolution of their life history strategies, seasonal interactions, and limitations they face throughout the year.

KEY-WORDS: intra-tropical migration, Mato Grosso do Sul, post-reproductive, remiges.

The timing of feather molt in migratory birds is a topic of increasingly growing interest, given the recognition in recent years that molt is a key event in their annual cycle (*e.g.*, Leu & Thompson 2002, Carlisle *et al.* 2005), which must be carefully timed so as to not conflict with other important but energetically costly activities such as breeding and migration (*e.g.*, Echeverry-Galvis & Hau 2013).

Fork-tailed Flycatchers (*Tyrannus s. savana*) that migrate within South America (*i.e.*, the nominate subspecies) breed from central Brazil to south-temperate latitudes of South America (Fitzpatrick *et al.* 2004). They have one annual remex molt in the basic flight molt sequence (*i.e.* proceeding distally in the primaries, Jenni & Winkler 1994), which occurs from March to June on the wintering grounds in northern South America (Jahn *et al.* 2016a). Although the body molt of this migratory subspecies occurs throughout the year, including during winter and while breeding, the molt of the remiges is currently only known to occur on the wintering grounds (Jahn *et al.* 2016a). Previous research based on light-level geolocator data shows that Fork-tailed Flycatchers breeding at Estação Ecológica de Itirapina, São Paulo state, Brazil, have two fall migration strategies (Jahn *et al.* 2016b). Some migrate directly to the wintering grounds after breeding, whereas others first move west after breeding to southwestern Brazil (Mato Grosso do Sul state), where they remain for several weeks in January and February (Jahn *et al.* 2016b). Nevertheless, why some flycatchers make this westward movement and prolonged stopover is still unknown and precludes understanding the relationship between timing of molt and migration in this widespread Neotropical species.

With the goal of identifying when migratory Fork-tailed Flycatchers (hereafter, "flycatchers") initiate their winter molt, we measured feather molt of flycatchers during early fall migration in southwestern Brazil. We test the hypothesis that some flycatchers stopover in southwestern Brazil for several weeks after breeding to begin feather molt.

We banded migrating flycatchers at Fazenda Ribalta, Mato Grosso do Sul state, Brazil (22.5°S; 49.8°W). This property used to be a cattle ranch, but is now mostly used to grow Soybeans (*Glycine max*). We captured migratory flycatchers at this place on 10 February 2016. Flycatchers roosted in a bamboo grove (Poaceae) located behind the ranch buildings. We caught flycatchers with four 3 × 12 or 3 × 18 m polyester or nylon nets (38 mm mesh size), placed 2–6 m from the bamboo grove used by flycatchers to roost. Nets were raised up to 8 m high and stacked, using bamboo poles. Captured flycatchers were banded with an individually numbered metal band or Darvic color bands and processed using techniques described in Ralph *et al.* (1993) before being released.

We aged and sexed flycatchers following Pyle (1997) and determined reproductive condition, subcutaneous fat content, primary feather wear, body molt intensity and body and flight feather molt following Ralph *et al.* (1993).

We captured and measured two adults (one male and one female) and two juveniles; none had a smooth or vascularized brood patch, nor exhibited a swollen cloacal protuberance. Of these, the two adults had no body molt, one juvenile had light preformative molt, and the other juvenile exhibited heavy preformative molt. None of the flycatchers captured were molting flight feathers, except for the adult female, which was symmetrically molting the first primary feather (*i.e.* molting the first primary feather on both wings, Fig. 1), representing the definitive prebasic molt. The two juveniles had light primary feather wear and the two adults exhibited moderate primary feather wear.

The two juvenile flycatchers had a subcutaneous fat score of 3 and 4. The adult male had a subcutaneous fat score of 5, as did the female that was symmetrically molting the first primary feather.

These results represent the furthest south that Fork-tailed Flycatchers have been found molting flight feathers, and provides preliminary evidence that some flycatchers move to southwestern Brazil to begin flight molt. The subcutaneous fat score (slightly bulging fat) of the female was much higher than that observed in breeding flycatchers (A.E.J., unpub. data), suggesting that it was stopping over or migrating through our study site in Mato Grosso do Sul. Notably, the two juveniles were molting body feathers, whereas the adults had no body molt. Although the sample size is low, these results suggest that age-dependent timing of feather molt exists in this species just after the breeding season, as has been found later in winter (Jahn *et al.* 2016a).

Figure 1. Picture of the right wing of a female Fork-tailed Flycatcher *Tyrannus s. savana*. Note primary 1, which is actively molting (arrow). Note that the tertials are less worn than the primary and secondary feathers, suggesting that the tertials represent an alternate molt.

Future research on molt strategies of birds that migrate in the Neotropics promises not only a better understanding of their evolutionary history, it will also provide the necessary information to tailor specific conservation plans for migratory species with different life history and molt strategies.

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ARTICLE

Breeding biology of Neotropical Accipitriformes: current knowledge and research priorities

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ABSTRACT: Despite the key role that knowledge on breeding biology of Accipitriformes plays in their management and conservation, survey of the state-of-the-art and of information gaps spanning the entire Neotropics has not been done since 1995. We provide an updated classification of current knowledge about breeding biology of Neotropical Accipitridae and define the taxa that should be prioritized by future studies. We analyzed 440 publications produced since 1995 that reported breeding of 56 species. There is a persistent scarcity, or complete absence, of information about the nests of eight species, and about breeding behavior of another ten. Among these species, the largest gap of breeding data refers to the former "*Leucopternis*" hawks. Although 66% of the 56 evaluated species had some improvement on knowledge about their breeding traits, research still focus disproportionately on a few regions and species, and the scarcity of breeding data on many South American Accipitridae persists. We noted that analysis of records from both a citizen science digital database and museum egg collections significantly increased breeding information on some species, relative to recent literature. We created four groups of priority species for breeding biology studies, based on knowledge gaps and threat categories at global level. Group I (great scarcity of information, plus higher categories of threat): *Leptodon forbesi*, *Cryptoleucopteryx plumbea*, and *Buteogallus lacernulatus*; Group II (breeding data have recently increased, but threat categories are high): *Spizaetus isidori*, *Accipiter gundlachi*, *Buteogallus coronatus*, *Pseudastur occidentalis*, and *Buteo ventralis*; Group III ("Near Threatened" species with still scarce breeding information): *Accipiter poliogaster*, *Accipiter collaris*, *Buteogallus aequinoctialis*, and *Pseudastur polionotus*; and Group IV (other priority cases): *Buteo ridgwayi*, *Buteo galapagoensis*, four eagles (*Morphnus guianensis*, *Harpia harpyja*, *Spizaetus ornatus* and *Buteogallus solitarius*), *Leptodon cayanensis*, *Accipiter superciliosus*, *Buteogallus schistaceus*, and the three *Leucopternis* hawks (*L. semiplumbeus*, *L. melanops* and *L. kuhli*). We also discuss the way that novel breeding data can show in what manners different species and populations are responding to environmental changes.

KEY-WORDS: eagles, hawks, information gaps, life history, raptors, reproduction.

INTRODUCTION

Accipitriformes (osprey, kites, hawks, and eagles; families Pandionidae and Accipitridae) is an extremely diversified and successful clade of diurnal raptors (Ferguson-Lees & Christie 2001, Márquez *et al.* 2005, Amaral *et al.* 2009, Dickinson & Remsen-Jr. 2013). These predators have a noteworthy participation in trophic webs, being able to mediate the whole structure and diversity of a community (Bierregaard-Jr. 1995, Touchton *et al.* 2002), and are also relevant indicators of environmental quality (Jullien & Thiollay 1996, Blendinger *et al.* 2004, Thiollay 2007) and providers of important environmental services (Estes *et al.* 2011). Breeding biology of this clade is widely varied (Newton 2010, Whitacre & Burnham 2012), and knowledge about the breeding patterns of each species and subspecies plays a central role in their effective conservation (de Labra *et al.* 2013).

Many breeding aspects of Accipitriformes are in fact important parameters for management and conservation programs. For instance, clutch size is directly related to population size, and this is related with extinction risk of species (Krüger & Radford 2008). Conversely, their reproductive rates are related to population density (Krüger 2000). Also, nest site choices reveal habitat selection by these raptors (Ferguson-Lees & Christie 2001), and therefore make evident their sensitivity to environmental changes (Trejo 2007a).

According to the latest classification adopted by the American Ornithologists' Union (NACC 2017, Remsen-Jr. *et al.* 2018 – therefore, AOU), there are 28 genera and 67 species of Accipitriformes occurring in the Neotropical region. Nonetheless, most Neotropical breeding data presented in some key references on diurnal raptors (*e.g.*, Ferguson-Lees & Christie 2001, del Hoyo *et al.* 2016) have important limitations. Information often consist of no more than anecdotal breeding records coming from scattered studies, or are generalizations based other tropical regions of the world (*e.g.*, Newton 2010), largely unverified to occur in the Neotropics (Whitacre & Burnham 2012).

Bierregaard-Jr. (1995) reviewed the state of the knowledge available addressing various aspects of the biology of 81 diurnal raptors that breed mainly in Central and South America. Regarding the breeding biology, the author showed that nests of 11 species of Accipitriformes and breeding behavior of 15 were not described. Moreover, most research concentrated on a few regions, such as further north of the Neotropics (*e.g.*, southern part of North America, and Guatemala). He also mentions that breeding data on most of South American species and subspecies of raptors is lacking (Bierregaard-Jr. 1995).

More recently, similar reviews were done only on a few South American countries (Pardiñas & Cirignoli 2002, Trejo *et al.* 2006, Trejo 2007a, b, Raimilla *et al.* 2012, Cortés *et al.* 2013). These studies assessed from four to 28 species, and just two reviews (Trejo 2007a, b) dealt with a larger amount (55 species). All these analyses comprised only studies conducted in the specific country (ies) (*i.e.*, Argentina, Chile and Uruguay), and so none included raptors that occur north of the Southern Cone of South America. Consequently, these surveys left out the Amazon Basin, one of the world's most deficient areas on bird breeding data, and around 20 species of Accipitriformes (Whitacre & Burnham 2012, del Hoyo *et al.* 2016, Xiao *et al.* 2016).

Countries that produce most scientific publications on breeding biology of Neotropical birds do not have english as their native language (Heming *et al.* 2013, Freile *et al.* 2014). For instance, all recent reviews on South American raptor research were written in Spanish (save their abstracts), with the exception of Trejo *et al.* (2006). Yet, there is still a visibility bias affecting science made in such countries (Cabot & de Vries 2004, Lortie *et al.* 2007), making such publications not easily accessible for researchers that do not read spanish or portuguese (see Bierregaard-Jr. 1995).

Moreover, many information on the natural history of Neotropical raptors come from studies not specifically designed for this aim (Cortés *et al.* 2013). Such studies often are published at small, local journals or bulletins (Figueroa, *in litt.*). Thus, important advances in knowledge are hardly visible to ornithologists from other countries. Indeed, Bierregaard-Jr. (1995) mentioned that "inaccessibility" of certain Latin American journals may have prevented him from collecting information from them. However, since then, internet access to many of these journals greatly improved (*e.g.*, *Hornero*, from Argentina; http://digital.bl.fcen.uba.ar), allowing more complete reviews to be made. Also, during the last two decades, the ornithological community of South America increased considerably, boosting the number of publications (Vuilleumier 2004, Freile 2005, Freile *et al.* 2014).

Scrutiny of oological (egg) collections from museums could also be useful for avian breeding biology research (McNair 1987). Yet, very few researchers in the Neotropics used museum eggs for analyzing breeding traits of diurnal raptors (*e.g.*, Denis *et al.* 2013, Hayes 2014), the most frequent approach being the presentation of revised summaries of some specific collections (*e.g.*, Román & Wiley 2012). Also, Bierregaard-Jr. (1995) did not provide information on museum eggs when evaluating knowledge on breeding biology of diurnal raptors, although such data is to some extent included in past literature (*e.g.*, Belcher & Smooker 1934). The amount of information (unpub. data) that we and other authors (Murphy 1989, Olsen & Marples 1993) obtained from museum egg sets strongly suggests that such sources could provide data not easily obtainable from other sources.

Considering the above, there is a need for a new comprehensive survey to access the state of the knowledge on the breeding biology of Neotropical Accipitriformes, and an update on research priorities. So, our main objective was to make a comprehensive analysis of the literature on breeding biology of Neotropical Accipitriformes produced after Bierregaard-Jr.'s (1995) review, and thus, to define the taxa that should be prioritized by future studies. We created an updated classification of current levels of knowledge of the breeding biology of these raptors, evaluating the progress made in the last decades. We also discuss the information gaps, ponder on their possible causes, implications, and potential solutions to the lack of breeding data, and present additional information obtained from alternative sources such as a citizen science database and museum collections. To conclude, we briefly exemplify how breeding data can show the ways that different species and populations are responding to environmental changes.

METHODS

Taxa

We follow Bierregaard-Jr.'s (1995) criteria by not including species with centers of distribution outside the Neotropics (see below), and Nearctic taxa that do not breed in there (which excluded the family Pandionidae from the analysis). Thus, we perform a comprehensive recent review of Neotropical raptors, including 56 species. Our subspecies division follows Dickinson & Remsen-Jr. (2013).

Categories and scoring criteria, and major changes in classification

We used two categories concerning reproduction, largely based on Bierregaard-Jr. (1995) and Trejo (2007a). Under "nest", the information that we analyzed includes the physical description of the nest, as well as its seasonality and location, clutch size, and description of eggs. That is, all aspects, mostly "physical", related to the early nesting stage. Under "breeding behavior", we included breeding displays of adult birds; descriptions of copulating and parental behaviors; incubation and fledging times; development of the young (both morphological and behavioral); the period of dependence of juvenile(s) after its first flights (post-fledging dependency period); and more detailed information – provided by relatively few studies – such as spatial distribution of breeding pairs, rate of reproductive success, nest productivity, and subsequent dispersal and survival of juveniles.

The numerical scores assigned in the classificatory scale of knowledge also follow the criteria of Bierregaard-Jr. (1995) and Trejo (2007a): (0) no information; (1) only anecdotal/scattered reports; (2) detailed study of one breeding pair or event; (3) study of more than one pair in the same population, and/or a substantial amount of anecdotal reports of representative areas of the species range; (4) detailed studies of separate populations in different portions of the species range; and (5) detailed information from the entire range of the species.

Besides producing an updated classification of current levels of knowledge about the breeding biology of these raptors, these scores act as an intuitive measuring scale to signal whether some reproductive aspects and taxa still need more studies (see also "Research recommendations and conservation relevance"). More importantly, they allowed a comparison between our scores and those reported by Bierregaard-Jr. (1995), to assess whether levels of knowledge changed in the last decades, and thus identify persistent gaps.

Classification had to be evaluated and updated, due to changes since 1995. Two of these changes were the recent splits of the "Gray Hawk" complex (*Buteo nitidus*/*Buteo plagiatus*; Millsap *et al.* 2011), and of Cuban Black Hawk *Buteogallus gundlachii* and Common Black Hawk *Buteogallus anthracinus* (Wiley & Garrido 2005). On the first case, the split of the taxon into southern and northern forms facilitates the evaluation of its case, and we chose to consider the scores attributed to "*Buteo nitidus*" by Bierregaard-Jr. (1995), as default for both *B. nitidus* and *B. plagiatus*. For the Black Hawks, Bierregaard-Jr. did not report a separate score for the then subspecies *gundlachii*, what prevented us from making a comparison of levels of knowledge about this taxon then and now. Nevertheless, we briefly discuss the status of Cuban Black Hawk on Appendix III.

Bierregaard-Jr. (1995) reported different scores for the taxa *Accipiter ventralis*, *Accipiter chionogaster* and *Accipiter erythronemius*, but these are currently classified as subspecies of the Sharp-shinned Hawk *Accipiter striatus* (Remsen-Jr. *et al.* 2018). In turn, Sharp-shinned Hawk was not included in Bierregaard-Jr.'s review, for having a center of distribution outside Central and South America. Ferguson-Lees & Christie (2001) already argued that this so-called "Central and South American group" of Sharp-shinned Hawk's subspecies (that is, *A. s. ventralis*, *A. s. chionogaster* and *A. s. erythronemius*) is so divergent, that treatment at species level should be considered for at least some of these, but not for other groups of subspecies such as the Caribbean. Since Remsen-Jr. *et al.* (2018) acknowledge that the taxonomic status of *A. striatus* still needs clarification, we comment on the knowledge on those three subspecies on Appendix III.

Other hawk species with some breeding populations in the Neotropics (mostly in the Caribbean) but centers of distribution in the Nearctic were excluded from our analysis. We based such decision not only because comparing scores of knowledge then and now was impossible, since Bierregaard-Jr. (1995) also excluded those from his assessment. Most importantly, we rely on evidence of little divergence between some of such disjunct populations and its Nearctic counterparts, on respect of phenotypic traits (Ferguson-Lees & Christie 2001), especially most breeding aspects (*e.g.*, Santana & Temple 1988). Likewise, such findings are being further supported by an ongoing meta-analysis of geographical variation on these species breeding patterns (author's unpub. data).

Other splits adopted by Bierregaard-Jr. (1995), but not maintained on current classification, are "*Accipiter chilensis*" (subspecies of Bicolored Hawk *A. bicolor*), "*Buteogallus subtilis*" (included three subspecies of Common Black Hawk) and "*Buteo poecilochrous*" (subspecies of Variable Hawk *Geranoaetus* [*Buteo*] *polyosoma*). We ignored the scores that Bierregaard-Jr. separately assigned to each of these taxa, and analyzed only those ascribed to the currently recognized species. Yet, we commented on the status of some of these subspecies when relevant.

Literature search methods and sources

We screened the Global Raptor Information Network (GRIN; http://www.globalraptors.org/grin/indexAlt.asp) until October 2016. This database focus only on raptors, concentrating information on diurnal species from around the world and includes bibliography of other renowned databases on raptors such as The Peregrine Fund and Raptor Information System. We analyzed the literature on reproduction of the 56 species after 1994, indicated in the section "Breeding" in the species accounts. We also searched for other studies whose titles refer to reproductive aspects, mainly the bibliography contained in the topic "Breeding biology". In some isolated cases, we considered in this review breeding data not published in other sources and made available by researchers in the GRIN database.

We chose to use Google Scholar (http://scholar.

google.com/) as the main tool to complement GRIN reference search because we noted it was able to locate the same references found with Scopus and Searchable Ornithological Research Archive (SORA; http://elibrary.unm.edu/sora), search tools also chosen by almost all recent revisions (Trejo 2007a, b, Raimilla *et al.* 2012, Cortés *et al.* 2013). The search terms we used were all possible scientific names recently assigned for these species (except for those variables only in the suffix, which were already supplied by the search heuristic), combined with each of the following terms: nest, ninho, nido, nidificação, anidamiento, anidación, reprodução, reproducción, breeding, and biologia reprodutiva. The great redundancy of results when using somewhat similar terms indicated the effectiveness of the choices, and terms like "nesting" and "biología reproductiva" were discarded.

We searched for all kinds of references, from articles in any category of scientific journal, through monographs, conference abstracts and posters, to technical reports and unpublished manuscripts. We reviewed citations contained in the references, even though most were already found in key word searches. Yet, we could not retrieve 19 (4.1%) of the 459 references produced between 1995–2016 (Appendix IV), neither through requesting directly from their authors nor from databases such as The Peregrine Fund.

We also screened and retrieved information from a bibliographical review of Brazilian birds (Oniki & Willis 2002), and the following books: Bird *et al.* (1996), Sick (1997), Machado *et al.* (1998), Arballo & Cravino (1999), Naka & Rodrigues (2000), Höfling & Camargo (2002), Fontana *et al.* (2003), Reichle *et al.* (2003), Wheeler (2003), Willis & Oniki (2003), Antas (2004), Mikich & Bérnils (2004), de la Peña (2005), Márquez *et al.* (2005), Angehr (2006), Sigrist (2006), Eisermann & Avendaño (2007), Gussoni & Guaraldo (2008), Whitacre (2012), Santos (2014), Straube *et al.* (2014), and Alvarado *et al.* (2015).

Exclusion and inclusion search criteria

As previously mentioned, Bierregaard-Jr. (1995) claimed that antiquity or "obscurity" of certain journals, particularly Latin American's, prevented him from gathering information from them. Yet, he did include some of these studies that were cited in more broadly distributed journals. We verified that some of these Latin American journals (*e.g.*, *Hornero*) were already scrutinized by recent reviews (Trejo 2007a, b, Raimilla *et al.* 2012). Notwithstanding, we could not determine with certainty which studies prior to 1995 were not included by Bierregaard-Jr., given that his study lacks a complete list of references. So, we opted to consider only papers published from 1995 on, to avoid repeating data already collected. After all, one of our aims was to get a clear picture of the amount of research done in the last decades, and not previously.

We also assume that papers from 1995 would not have been included by Bierregaard-Jr. Depending on the date of completion of his search (not stated in the paper), the author could have included at least some of these studies, but information contained in such papers is not consistent with certain scores assigned by him [*e.g.*, the Gray-backed Hawk *Pseudastur occidentalis*, studied by Vargas (1995)]. This fact suggests that in most cases the inclusion of these papers in that review may not have occurred. Nevertheless, only a few studies from 1995 were found in our review, suggesting that the influence of possible duplicate data on the different species would be irrelevant.

Some books contain secondary information often without direct citation of the original data (*e.g.*, Ferguson-Lees & Christie 2001, Márquez *et al.* 2005, Sigrist 2006). Because of lack of clear indication of each of their sources in the text, we could not retrieve the original studies year or sometimes even the geographic region. Thus, we also chose to not include such breeding reports, except when it was clearly indicated in the text that it was an original data.

Research recommendations and conservation relevance

We created a four-group classification of research priorities on species breeding aspects, based mostly on knowledge gaps (by means of the assigned numerical scores), but also considering current threat categories at the global level (IUCN 2017). Group I includes species with great scarcity of available information about their reproduction, combined with higher categories of threat. Group II comprises species whose studies have advanced, although very little since Bierregaard's (1995) review, but which are at some higher threat category. Group III includes species whose knowledge is still scarce and are currently "Near Threatened" according to IUCN. Finally, Group IV represents species framed in three possible situations: *i*) the knowledge about their breeding has not increased (although it was already very high, *i.e.* scores of 4 or 5) and also are in some greater category of threat; *ii*) the remaining species considered "Near Threatened"; or *iii*) species not threatened, but of which nothing or practically nothing is known about their reproduction and/or have at least one of the topics of breeding aspects classified as 1 (see "Categories and scoring criteria, and major changes in classification").

Screening of the Handbook of Birds of the World and WikiAves

The Handbook of Birds of the World (HBW) was the baseline for Bierregaard-Jr.'s (1995) gap analysis and until today is considered a reference for current knowledge about biology of bird species (*e.g.*, Trejo *et al.* 2006, Xiao *et al.* 2016). Thus, we opted to review information in the online version "HBW Alive" (http://www.hbw.com). Our purpose was to determine if data available regarding reproductive aspects (topic "Breeding", in each species account) were commensurate with the actual state of knowledge about these subjects.

The online database WikiAves (www.wikiaves.com) is a collaborative tool launched in 2008 that allows posting of photographic records of bird species that occur in Brazil. This initiative has a great advantage over other popular citizen science platforms, such as eBird (ebird.org), by working with digital records and not lists. Also, we are not aware of initiatives from other Neotropical countries (*e.g.*, http://www.wikiaves.com.ar/inicio.php) that are equally reliable and allow similar content-based searches of their records.

Considering the enduring scarcity of avian breeding records from South American mid-latitudes (Baker 1938, Heming *et al.* 2013), the fact that WikiAves focus on Brazil is particularly convenient. We searched for breeding records of 25 species in this database. The low number of species was due primarily to the scope of WikiAves, which only contains species recorded in Brazil. In addition, we chose to review only species that obtained scores less than 3 in at least one of the categories, or those with values equal to or greater than that, but for which there was a marked relative scarcity of South American data. In the "Advanced Search" tool for photos, we used (separately) the filters: egg, nest, juvenile, copulating, incubating, courting, caring/feeding its chick(s), and making nest. The search was made in October 2016 and we included only records whose identification was considered secure – both at specific level and, in the case of breeding behaviors and/or stages that were clearly illustrated in the photographic records. Records already present in papers located in the survey were discarded.

Museum egg records

Eggs and labels were photographed in the following egg collections between 2014–2017 at Western Foundation of Vertebrate Zoology - WFVZ (Camarillo, USA), Natural History Museum - NHMUK (Tring, UK), National Museum of Scotland - NMS (Edinburgh, UK), Muséum national d'Histoire Naturelle - MNHN (Paris, France), Naturhistoriches Museum - NMW (Wien, Austria), Instituto de Investigación de los Recursos Biológicos "Alexander von Humboldt" - IAVH (Villa de Leyva, Colombia), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" - MACN (Buenos Aires, Argentina), Museo de Ciencias Naturales de La Plata - MLP (La Plata, Argentina) and in Brazil, Museu de Zoologia da Universidade de São Paulo - MZUSP (São Paulo), Museu Nacional do Rio de Janeiro - MN (Rio de Janeiro), Museu Paraense "Emilio Goeldi" - MPEG (Belém), and Coleção Ornitológica "Marcelo Bagno" - COMB (Brasília). We also visited the online egg collections of the Field Museum of Natural History - FMNH (Chicago, USA), and the Arctos Collaborative Collection Management Solution (arctos.database.museum), and had access to data of the egg collection of the Smithsonian Institution (USNM, Washington, D.C., USA), and the American Museum of Natural History (AMNH, New York, USA). Finally, we consulted the catalog of the Cris-Rivers Region Museum (CRRM, Oradea, Romania; Béczy 1971).

These author's previous experience suggests that diurnal raptor's eggs collected in the United States can outnumber those from all other new world countries together, on a ratio of roughly nine to one (authors' unpub. data). Also, Bierregaard-Jr. (1995) verified that when the distribution of a species reaches the southern part of North America, it tends to be much more studied there than in the rest of its range. Considering the above, we opted to not include museum data from eggs collected in the USA in this analysis. Breeding information from that country certainly is already overly represented in literature, and augmenting it with museum records would only exacerbate this bias.

Museum egg sets are a proven reliable source (McNair 1987), but a few inconsistencies in the records of certain collectors have been reported (Hellmayr & Conover 1949, Thorstrom & Kiff 1999). Thus, we carefully validated species identification based on our own experience, on remarks from other researchers, and also resorting on other references that provide clutch sizes, egg measurements and descriptions (*e.g.*, the GRIN database). A few species suffer from faulty information about their eggs and clutches in the literature, and these cases are still being validated by us. Such egg sets are not assigned to any species here but are included in the total number of sets we found from the Neotropics. In the process of validating eggs' identification, measurements were standardized using the software ImageJ (Bridge *et al.* 2007, Troscianko 2014).

RESULTS

Bierregaard-Jr.'s (1995) review found 431 references of 81 species and included information about various aspects of Neotropical raptor biology. Meanwhile, our research found 440 references exclusively about breeding biology of 54 species (out of 56 studied taxa – as we did not find any published records for two species).

Such results are presented in Appendix I, with complete reference list on Appendix II. This represents an increase in the number of published references since Bierregaard-Jr.'s review, especially since he covered many other aspects of biology, included also Falconidae, and had no date limitation (unlike our scope of 22 years). We found 11 references and citations referring to data from captive birds, but these were not included in our review given the uncertainty involving raptor's breeding aspects in unnatural conditions (Cabot-Nieves *et al.* 2013).

Much of the breeding data we found came from inventories that provide a list of species for one or more localities, often highlighting new occurrences or noteworthy records (*e.g.*, Bodrati *et al.* 2010), or research addressing ecological aspects of bird communities of a given region (*e.g.*, Cintra & Naka 2012). Observations on the breeding activity of some species are frequently included in such studies (*e.g.*, Hennessey *et al.* 2003), and it is common for raptors to receive some prominence (*e.g.*, Greeney & Nunnery 2006). However, such reports still remain mostly anecdotal (*e.g.*, Ruvalcaba-Ortega & González-Rojas 2009). For instance, nest records often do not provide any information on nest content or stage (*e.g.*, Bodrati *et al.* 2010), frequently because the nest was presumably inaccessible to the researchers (*e.g.*, Bellatti 2000). Many times all that can be concluded is that the species was "nesting" in a given locality, during a quite long period of time (*e.g.*, Cavicchia & García 2012).

Of the 11 species of Neotropical accipitrids for which the nest had not been described prior to 1995, six remain undescribed and two present only anecdotal/scattered reports (Table 1). Of 15 species with no information about their breeding behavior (*e.g.*, *Leptodon cayanensis*, *Cryptoleucopteryx plumbea, Leucopternis melanops*) in 1995, little or no additional information is still not available for 10. Also, in 1995 only anecdotal descriptions were available for the nests of 15 species, and breeding behaviors of another 14 species. This case remains the same for the Tiny Hawk *Accipiter superciliosus* and Rufous Crab Hawk *Buteogallus aequinoctialis*, which have no recent published information. Yet, 66% of the analyzed species ($n = 37$) showed an increase in knowledge, of these, nearly half ($n = 19$) showed an increase in only one of the categories, and the remaining in both.

Probably the most significant increases in knowledge were for Barred Hawk *Morphnarchus princeps* and White-throated Hawk *Buteo albigula,* followed by Gray-bellied Hawk *Accipiter poliogaster*, Chaco Eagle *Buteogallus coronatus*, Gray-backed Hawk and Rufous-tailed Hawk *Buteo ventralis*, and also Rufous-thighed Kite *Harpagus diodon.* The following species also had a significant increase in knowledge about the two breeding categories: Black-and-white Hawk-Eagle *Spizaetus melanoleucus*, Black-collared Hawk *Busarellus nigricollis*, Long-winged Harrier *Circus buffoni*, Crane Hawk *Geranospiza caerulescens*, Solitary Eagle *Buteogallus solitarius* and Short-tailed Hawk *Buteo brachyurus*. On the other hand, very scant information was found for the former "*Leucopternis*" hawks, currently classified in five genera. Even the best-known species in this polyphyletic group of 10 species (Amaral *et al.* 2009), the Barred Hawk and the White Hawk *Pseudastur albicollis*, either have only anecdotal reports in distinct areas of the species distribution range, or detailed studies of nests from just one population (*e.g.*, Muela & Valdez 2003, Cisneros-Heredia 2006, Gelis & Greeney 2007, Draheim 2012).

As Bierregaard-Jr. (1995) also noted, we found a longstanding concentration of studies further north of the Neotropics (*i.e.*, southern United States), as well as in the northern portion of this region. For instance, Guatemala still stood out due to the quantity and quality of research developed by the Peregrine Fund's Maya Project, which resulted in a large number of published studies on raptor biology (*e.g.*, Seavy & Gerhardt 1998, Seavy *et al.* 1998, Thorstrom & Quixchán 2000, Sutter *et al.* 2001, Panasci & Whitacre 2002), ultimately leading to the publication of a book (Whitacre 2012). The Southern Cone of South America also have a large amount of research developed in Chile, already emphasized by Bierregaard-Jr. (1995), and Argentina (*e.g.*, Jiménez 1995, Trejo *et al.* 2001, Ojeda *et al.* 2003, Medel-Hidalgo *et al.* 2015, Pérez 2015, Rivas-Fuenzalida *et al.* 2015).

Even for species considered already relatively well known, with both categories scoring 3 or 4, there is a lasting shortage of research on South American populations or subspecies. This was the case for the White-tailed Kite *Elanus leucurus*, the Swallow-tailed Kite *Elanoides forficatus*, and the Zone-tailed Hawk *Buteo albonotatus*, among others. We also found little or no information about the breeding biology of some subspecies of some polytypic species, including the Cuban Kite (*Chondrohierax uncinatus wilsonii*), considered a full species and "Critically Endangered" by IUCN (2017); Mangrove Black Hawk (*Buteogallus anthracinus subtilis*), included in a separate species by Bierregaard-Jr. (1995); Pearl Kite (*Gampsonyx swainsoni magnus*); and Snail Kite (*Rostrhamus sociabilis major*). Additional comments in Table 1 are given to indicate taxa and/or regions in which research is critically needed.

Although incomplete, some sets of new studies revealed both similarities and divergences in breeding behavior between different populations. For instance, the cooperative behavior of Harris's Hawks *Parabuteo unicinctus,* well known for the subspecies *P. u. harrisi* in the United States, at the time of Bierregaard-Jr.'s (1995) review was not reported anywhere else in the species range. There is now good evidence that cooperative breeding also occurs in at least one population of the nominate subspecies in southeastern Brazil (Silva & Olmos 1997), hence this behavior is not restricted to North America.

Table 1. Assessment of current knowledge on the breeding biology of 56 species of Neotropical Accipitriformes.

Species	Bierr. Nest	Bierr. Behav	Nest	Breeding behavior	Research priority	Comments
Elanus leucurus	4	4	4	4	No	Lack of more detailed data from most regions, mainly South America.
Gampsonyx swainsonii	3	3	3	3	No	Still a lack of behavioral data from most regions, particularly later stages.
Chondrohierax uncinatus	4	3	4	4	No	Most data missing from South America; nothing from subspecies *wilsonii.*
Leptodon cayanensis	1	0	3	1	IV	Detailed data from only two areas; very few behavioral data, particularly later stages.
Leptodon forbesi	0	0	0	1	I	Only breeding displays.
Elanoides forficatus	3	3	4	4	No	Many detailed studies, but there is still a lack of detailed data from other areas.
Morphnus guianensis	2	2	3	3	IV	Some detailed studies, but still a lack of behavioral data in many regions.
Harpia harpyja	4	3	4	4	IV	Still a lack of detailed data from some portions of the range (*e.g.*, Atlantic Forest).
Spizaetus tyrannus	3	3	3	4	No	Still a lack of detailed data from many regions.
Spizaetus melanoleucus	1	1	3	3	No	Isolated cases and incomplete observations.
Spizaetus ornatus	4	4	4	4	IV	New data did not change status.
Spizaetus isidori	3	2	3	3	II	Still a lack of detailed data from many regions.
Busarellus nigricollis	1	1	3	3	No	Still a lack of detailed data from many regions.
Rostrhamus sociabilis	4	4	4	4	No	Many detailed studies, but still missing data from most regions/subspecies.
Helicolestes hamatus	3	3	3	3	No	New data did not change status; only one population studied in detail.
Harpagus bidentatus	3	1	3	3	No	Only one population studied in detail; still a lack of behavioral data.
Harpagus diodon	1	0	3	3	No	Isolated cases and incomplete observations; still a lack of behavioral data.
Ictinia plumbea	3	3	4	3	No	Still a lack of more behavioral data from many regions.
Circus cinereus	3	1	3	3	No	Lack of more detailed data from many regions.
Circus buffoni	1	1	3	3	No	Lack of more detailed data from many regions.
Accipiter poliogaster	0	0	2	3	III	Basically, just one or two pairs studied in detail.
Accipiter superciliosus	1	1	1	1	IV	Still very little information.
Accipiter collaris	0	0	0	1	III	Only information of specimens on breeding condition.
Accipiter gundlachi	3	1	3	3	II	Some detailed studies, but coming from a few areas.
Accipiter bicolor	3	3	3	3	No	Most data missing for two subspecies; new data but several old ones discarded.
Geranospiza caerulescens	1	1	3	3	No	Only one population studied in detail.
Cryptoleucopteryx plumbea	0	0	0	0	I	No new data.
Buteogallus schistaceus	0	0	0	0	IV	No new data.
Buteogallus anthracinus	4	4	4	4	No	Still a lack of South American data, especially from subspecies *subtilis.*
Buteogallus aequinoctialis	1	1	1	1	III	Still very little information.
Buteogallus meridionalis	4	3	4	3	No	New data did not change status; still a lack of detailed data from many regions.
Buteogallus lacernulatus	0	0	0	1	I	Only displays.
Buteogallus urubitinga	3	3	4	3	No	Still a lack of more behavioral data from most regions.
Buteogallus solitarius	1	1	3	3	IV	Data on nests or late stages (nothing in between); lack of data from most regions.
Buteogallus coronatus	1	1	4	3	II	Many detailed studies, but there is still a lack of more behavioral data.

Species	Bierr. Nest	Bierr. Behav	Nest	Breeding behavior	Research priority	Comments
Morphnarchus princeps	0	0	3	3	No	Most data missing from many regions.
Rupornis magnirostris	3	3	4	3	No	Some detailed studies, but still a lack of behavioral data from most regions/subsp.
Parabuteo unicinctus	4	4	4	4	No	New data did not change status; but evidence of cooperative behavior in Brazil.
Parabuteo leucorrhous	1	1	2	3	No	Isolated cases and incomplete observations.
Geranoaetus albicaudatus	3	3	3	3	No	Detailed data only of two subspecies; lack of detailed data from many regions.
Geranoaetus polyosoma	3	3	4	3	No	Still a lack of more behavioral data.
Geranoaetus melanoleucus	3	3	4	3	No	Some detailed studies, but still a lack of more behavioral data from many regions.
Pseudastur polionotus	0	0	1	1	III	Very little information.
Pseudastur albicollis	3	3	3	3	No	New data did not change status; only one population studied in detail.
Pseudastur occidentalis	0	1	3	3	II	Only one population studied in detail.
Leucopternis semiplumbeus	1	0	1	1	IV	No significant advances.
Leucopternis melanops	0	0	?	?	IV	No real advances.
Leucopternis kuhli	0	0	1	0	IV	Only one nest.
Buteo plagiatus	3	3	4	3	No	Still a lack of detailed data from most regions.
Buteo nitidus	3	3	3	3	No	New data did not change status; many missing data, incl. more egg descriptions.
Buteo ridgwayi	5	4	5	4	IV	New data did not change status; still a lack of more behavioral data.
Buteo albigula	1	0	4	3	No	Breeding status in northern range still uncertain; many missing data, incl. on eggs.
Buteo brachyurus	1	1	3	3	No	Lack of more detailed data from most regions, mainly South America.
Buteo galapagoensis	5	5	5	5	IV	-
Buteo albonotatus	3	2	3	3	No	Still limited to the northern range.
Buteo ventralis	1	0	3	3	II	Still limited to Chile; many missing data, including more egg descriptions.

Bierr. Nest and Bierr. Behav = scores assigned by Bierregaard-Jr. (1995), on Nest and Breeding behavior respectively; Nest and Breeding behavior = scores assigned by this study. Scores: (0) no information; (1) only anecdotal/scattered reports; (2) detailed study of one breeding pair or event; (3) study of more than one pair in the same population, and/or substantial amount of anecdotal reports of representative areas of the range; (4) detailed studies of separate populations in different portions of the range; and (5) detailed information from the entire range. Shaded cells denote improvements on knowledge in the last decades. Research priority = whether species should be prioritized by future studies on breeding biology, and for those that should, the priority group (I-IV) to which it was assigned; names of such species are also given in bold letters. Further explanations on the main text. Taxonomic ordering follows AOU (2018).

On the other hand, Short-tailed Hawk's breeding traits such as duration of the post-fledging dependency period and nest defense behaviors diverge not only among the different subspecies but even within the same country (Monsalvo 2012).

The species formerly called the Gray Hawk was separated into two species by Millsap *et al.* (2011), amendment accepted by the AOU (Remsen-Jr. *et al.* 2018). However, most recent studies of *Buteo nitidus*, all published prior to this split (*e.g.*, Patrikeev 2007, Ruvalcaba-Ortega & González-Rojas 2009), focused on the current northern species (Gray Hawk, *B. plagiatus*). Thus, the status of the Gray-lined Hawk (*B. nitidus sensu* AOU) remains the same. Although the number of references found was similar (ten and seven, respectively; Appendix I), information about Gray Hawks comes from almost 100 breeding events, at about ten different locations. Whereas for Gray-lined Hawks, only six records were found, and some of these informations could not have their localities confirmed. Such lack of detail prevented us from determining if data on the eggs of the latter species provided in recent literature (Sick 1997, Reichle *et al.* 2003) do not, in fact, refer to the northern species eggs.

Based on the criteria put forward before (see "Categories and scoring criteria, and major changes in classification" in the Methods), the highest priority species for research on their breeding aspects are, as follow: White-collared Kite *Leptodon forbesi*, Plumbeous Hawk *Cryptoleucopteryx plumbea*, and the White-necked Hawk *Buteogallus lacernulatus* (Group I); Black-and-chestnut Eagle *Spizaetus isidori*, Gundlach's Hawk *Accipiter gundlachi*, Chaco Eagle, Gray-backed Hawk, and Rufous-tailed Hawk (Group II); Gray-bellied Hawk, Semicollared Hawk *Accipiter collaris*, Rufous Crab Hawk and Mantled Hawk *Pseudastur polionotus* (Group III); and the two island species of *Buteo* hawks (Ridgway's *B. ridgwayi* and Galapagos *B. galapagoensis*), four eagles (Crested *Morphnus guianensis*, Harpy *Harpia harpyja,* Ornate Hawk-Eagle *Spizaetus ornatus* and Solitary Eagle), Gray-headed Kite *Leptodon cayanensis*, Tiny Hawk, Slate-colored Hawk *Buteogallus schistaceus*, and the three *Leucopternis* hawks (Group IV).

Despite recent reviews considered HBW as informative of the state-of-the-art (Trejo *et al.* 2006, Xiao *et al.* 2016), we concluded that information provided in the "Breeding" topic in this reference is outdated for at least 18 of the 56 species that we analyzed. In the WikiAves database, we compiled a total of 174 photographic records representing breeding aspects, for 18 of the 25 species surveyed (Appendix V). No reliable records were available for the remainder of the species. For one of these 18 species, Gray-bellied Goshawk, which had detailed literature records of only one or two breeding pairs (de Vries & Melo 2000, Thorstrom 2002, Boesing *et al.* 2012), inclusion of data from WikiAves augmented its assessment score (Table 2).

Another species for which WikiAves allowed a change in the assigned score was the White-collared Kite, whose only nesting record (Brito 2013, also quoted by HBW) is posted on that platform. It is also noteworthy the case of the Rufous-thighed Kite, for which WikiAves provides 42 records of at least 15 distinct breeding events in six different states of Brazil, including pairs with nesting accompanied throughout, and even in consecutive years. In addition to these three species, another five showed a significant increase in breeding records from South America, although these not have allowed an effective change in their scores (Table 2).

We located 729 egg sets from the Neotropical

Table 2. Results of the search for photographic breeding records from the WikiAves database, for 25 species of Neotropical Accipitriformes.

Species	Change in score(s)	Comments
Elanus leucurus	No	Many records of different stages and populations, but did not change status.
Chondrohierax uncinatus	No	Only three or four breeding pairs; always more southernly records.
Leptodon cayanensis	No	Only one nest, not monitored.
Leptodon forbesi	Nest = 1	The first nest of the species, also cited in HBW.
Spizaetus melanoleucus	No	Little informative and poorly distributed records.
Rostrhamus sociabilis	No	Many records of different stages and populations, but did not change status.
Helicolestes hamatus	No	Only two breeding localities, records of later breeding stages.
Harpagus bidentatus	No	Three records from the same locality, presumably of the same pair.
Harpagus diodon	No	Some breeding events monitored thoroughly, including same pair in different years.
Accipiter poliogaster	Nest = 3	Little informative and always more southernly records.
Accipiter superciliosus	No	Nothing.
Accipiter bicolor	No	Only three records, with no new information on subspecies.
Geranospiza caerulescens	No	Very diverse breeding stages, especially of the subspecies *flexipes*.
Buteogallus schistaceus	No	Nothing.
Buteogallus anthracinus	No	Only one nest, no new information.

Species	Change in score(s)	Comments
Buteogallus aequinoctialis	No	One copulation record.
Buteogallus lacernulatus	No	No reliable records.
Parabuteo leucorrhous	No	Nothing.
Pseudastur polionotus	No	Only one nest, not monitored.
Pseudastur albicollis	No	Only two nests, no new information.
Leucopternis melanops	No	Nothing.
Leucopternis kuhli	No	Nothing.
Buteo nitidus	No	Some poorly distributed records.
Buteo brachyurus	No	Many records of different stages and populations, but did not change status.
Buteo albonotatus	No	No reliable records.

Change in score(s) = whether scores assigned previously in our review, for the two categories concerning reproduction ("Nest" and "Breeding Behavior", see Table 1) augmented with inclusion of data from WikiAves. Shaded cells denote any substantial addition of new information, relative to recent literature.

region in egg collections, besides six records of eggs laid in captivity in this same region. Of these 729, 706 could be soundly assigned to some species (Table 3), from which 58% pertain to only four species: White-tailed Kite, Common Black Hawk, Roadside Hawk *Rupornis magnirostris*, and Gray Hawk. Around 88% of the total of clutches of these four species were collected in Mexico. This country is also the origin of almost two-thirds of the egg sets of all 31 species reliably identified in museum collections. Argentina and Chile are respectively the second and third countries with more collected clutches, but each represents less than 10% of the total.

We propose a correction in the identification of four clutches, all in the WFVZ collection and all previously recognized as misidentified by L. Kiff (Appendix VI). From our analyses, we conclude that their correct identifications probably agree with those tentatively suggested by him in the data slips accompanying these egg sets. We highlight the relevance of the egg sets assigned to White-rumped and Gray-lined Hawks, as they almost doubled the number of breeding reports for each of these species. Overall appearance and dimensions from the former's eggs are similar to those reported by Zilio & Mendonça-Lima (2012), the only other clutch known for the White-rumped Hawk, but museum eggs are slightly larger.

Unfortunately, the clutches of Gray-lined Hawk that we located are essentially the same widely used as reference for this species (Belcher & Smooker 1934), yet their measurements are within the range described for the allospecies Gray Hawk *B. plagiatus* (del Hoyo *et al.* 2016).

Also relevant are egg sets from the subspecies *Gampsonyx swainsoni magnus* (*n* = 1) and *Rostrhamus sociabilis major* (*n* = 7), both largely absent in recent literature. We also located five clutches of the Mangrove Black Hawk (former *Buteogallus subtilis*), for which Bierregaard-Jr. (1995) found no breeding information in literature (but see Wetmore 1965). Likewise, in our literature review we located only poorly detailed, scattered reports of nesting in a few localities of its range (Barrantes 1998, Pérez-León 2007, Alava *et al.* 2011). Relative to recent literature, museum eggs allowed a substantial increase in breeding information for a total of six species.

DISCUSSION

Breeding knowledge is not yet uniformly distributed across different regions for most species of Neotropical Accipitridae, with many areas lacking more studies about their populations or subspecies. The main evidence of this poor distribution of breeding data is the fact that we have not assigned any new score of 5 (*i.e.*, detailed information coming from the entire range). Information on many South American Accipitridae is still scant, even after two decades (Bierregaard-Jr. 1995). With exception of a few restricted-range subspecies, most of the least-studied populations occur in mid-latitudes of South America or in the Amazon Basin, a situation that barely improved in the last eight decades (Baker 1938, Xiao *et al.* 2016).

The regions where most quality-research are still concentrated are near the limits of many species ranges.

Table 3. Results of the search for museum egg records of Neotropical Accipitriformes.

Species	No. of sets	Comments
Elanus leucurus	65	Mostly from Mexico; also southern South America.
Gampsonyx swainsonii	2	From Colombia and Peru; the latter of subspecies *G. s. magnus*.
Chondrohierax uncinatus	8	All from Mexico; eggs from Trinidad were misidentified.
Leptodon cayanensis	5	Three of these were misidentified as other species.
Elanoides forficatus	4	From Brazil and Venezuela.
Morphnus guianensis	1	From Panama; presumably from the wild but no further details known.
Harpia harpyja	1	From Amazon Basin; plus 6 clutches laid in captivity.
Spizaetus ornatus	1	From Guatemala, at the same site of Peregrine Fund's Maya Project.
Busarellus nigricollis	4	All sets but one from Paraguay.
Rostrhamus sociabilis	34	Most from South American countries; seven clutches of *R. s. major.*
Ictinia plumbea	18	Records from throughout the species' range.
Circus cinereus	7	All sets from Chile.
Circus buffoni	6	All sets but one from Argentina.
Accipiter bicolor	3	One misidentified clutch was discarded (Lloyd & Kiff 1999).
Geranospiza caerulescens	5	All sets from Mexico.
Buteogallus anthracinus	100	90% from Mexico; five clutches of "Mangrove Black Hawk".
Buteogallus meridionalis	25	Around half from Mexico and the other half from South America.
Buteogallus urubitinga	14	Mostly from Mexico; also northern South America.
Buteogallus solitarius	1	From Mexico.
Rupornis magnirostris	142	Mostly from Mexico; others scattered throughout the species' range.
Parabuteo unicinctus	43	Mostly from Mexico.
Parabuteo leucorrhous	4	Largely increased the total number of breeding reports.
Geranoaetus albicaudatus	10	Records scattered through the species' range.
Geranoaetus polyosoma	43	Only one set from its northern range; 11 from the Falkland Islands.
Geranoaetus melanoleucus	23	All sets from its southern range.
Pseudastur albicollis	1	From Trinidad.
Buteo plagiatus	104	All sets but one from Mexico.
Buteo nitidus	3	All from Trinidad; seemingly no other eggs of the species are known.
Buteo brachyurus	13	All sets but one from Mexico.
Buteo galapagoensis	5	No new information added.
Buteo albonotatus	10	From its northern range.

No. of sets = number of soundly identified egg sets. Shaded cells denote any substantial addition of information, relative to recent literature. Further explanations on the main text.

Some aspects of the behavior of a species could be geographically restricted (Thiollay 1989), and its breeding aspects can be distinct at extreme limits of its geographical distribution (Kennedy *et al.* 1995). Thus, generalizations about the breeding biology of raptors become highly susceptible to errors (Bierregaard-Jr. 1995, Trejo 2007a).

Albeit results show that the informative potential of geographically isolated data and anecdotal descriptions may be important contributions to our knowledge on raptors breeding ecology (Whitacre & Burnham 2012), we emphasize the importance of conducting detailed studies with different populations.

Most recent studies that provide some new information on breeding aspects of Neotropical Accipitriformes are generalist in nature. The lack of detail of anecdotal reports may be due to logistical limitations during field work and to the studies scope, but it is also likely that it is often due to unawareness by local researchers of the relevance of the material. Whichever the reason, an emblematic outcome of this, is one occasional report of "breeding" that, if well described, would be the first description on any reproductive aspect of the Black- faced Hawk *Leucopternis melanops* (Cintra & Naka 2012). Because of the lack of detailed information, this report could not be properly attributed by us to any of the categories assessed (Table 1). Additionally, it is possible that such lack of detail may be caused by imperfections in the peer-review system (Figueroa, *in litt.*), or in publication policies of the journals, that does not give the opportunity to the publishing of complete information on natural history, or disregard the value of local breeding data.

A few of the less abundant and restricted-range species still attract most of the attention of field ornithologists. Bierregaard-Jr. (1995) already remarked on the oddness of a scarcity of breeding information for some common species, while a few, and not necessarily common ones (*e.g.*, Harpy Eagle), are increasingly well studied. For example, knowledge about the breeding behavior of the Gray-headed Kite, a conspicuous and widespread species (Thorstrom *et al.* 2012), is still mostly anecdotal (Table 1, Appendix I). Figueroa (2015) stated that among potential causes for these information gaps of common raptors, may be the species own "commonness", associated with a number of other biases of research focus in ornithology. On the other hand, knowledge of all the former "*Leucopternis*" species still can be considered the largest gap of breeding data among Neotropical Accipitridae, from Bierregaard-Jr.'s 1995 review up to date.

We noted that records posted in the WikiAves database could attenuate gaps in knowledge about some raptors in middle latitudes of South America. However, possibly the weakest point of this database is precisely its geographical limitation to Brazil. We believe that the development of similar initiatives in other Neotropical countries should be helpful as a complementary measure to elucidate diverse information on the biology of this region's avifauna (Lees & Martin 2014). We also stress the importance of the use of digital records in such citizen science tools, making possible for the researchers the correction of misidentifications. It is particularly relevant when it comes to diurnal raptors, a group renowned for having problematic identification in the field (Griffiths & Bates 2002, Seipke *et al.* 2006, 2011), leading to errors in citizen science records (Bailey 2015) and even in published peer-reviewed studies (de Vries & Melo 2002, Alves *et al.* 2017).

We also reinforce the importance of "conventional" records in museums (McNair 1987), as they offer the same benefits as exposed above. They make possible to verify previous identifications (*e.g.*, Griffiths & Bates 2002, Appendix VI) and therefore prevent the perpetuation of cascading errors. By using museum egg sets, this study and others (Murphy 1989, Olsen & Marples 1993, Hayes 2014) also gathered breeding data that could not be obtained from other sources, such as literature. Such fact is clearly illustrated in the cases of taxa with substantial increases in number of breeding records after the scrutiny of oological collections (see Table 3).

Museum data on some diurnal raptors can yet be very limited. For instance, we stress the need for collecting additional information on eggs of both White-rumped and Gray-lined Hawks, since our validation of the identification of their museum sets must be seen as conditional. In fact, sometimes the very same egg sets we analyzed are the only (or at least the major) source for egg measurements of a species provided by any reference. In such cases, only by carefully scrutinizing all references ever produced on a given species, and also by examining closely-related species, it is possible to avoid circular reasoning in validating the identification of these eggs. Perhaps some species' eggs still are unknown, if literature information are based in sets with questionable identification.

We also verified that oological collections undergo the same geographic bias found in both recent and former (Bierregaard-Jr. 1995) literature breeding records. Essentially the same regions (*i.e.*, northernmost and southernmost Neotropical countries, and the United States) predominate with respect to amount of breeding data. Trinidad and Tobago is an exception to this pattern, because the work of egg collectors (*e.g.*, Belcher & Smooker 1934) seems to be the ultimate source of almost all reproductive information on its raptors (Herklotts 1961, Ffrench 1991). In fact, no recent literature reference was found for this country.

Adequate knowledge of breeding parameters is necessary to better understand how different species and populations respond to environmental changes (Marini *et al.* 2010, D'Elia *et al.* 2015). Such information is particularly relevant for diurnal raptors, as they: provide important environmental services, preying upon potential pests and invasive species (Estes *et al.* 2011, Speziale & Lambertucci 2013, Martins & Donatelli 2014); act as flagship species (Sergio *et al.* 2008, Donázar *et al.* 2016); and as indicators of environmental quality (Jullien & Thiollay 1996, Blendinger *et al.* 2004, Thiollay 2007). Recent studies (*e.g.*, Alexandrino *et al.* 2016) are putting in check traditional classifications of sensitivity to disturbance, widely used for Neotropical avifauna, such as the landmark database by Stotz *et al.* (1996). In fact, despite some valuable efforts (*e.g.*, Jullien & Thiollay 1996, Thiollay 2007), little is actually known about the extent to which each species of Neotropical raptor fits in the sensitivity gradient (Bierregaard-Jr. 1995, Touchton *et al.* 2002, Roda & Pereira 2006).

As mentioned before, nest site choices of Accipitridae demonstrate habitat use (Ferguson-Lees & Christie 2001), and so highlight their sensitivity to environmental changes (Trejo 2007a). Then again, recent studies indicate a need to update classifications of sensitivity to habitat change of some Accipitridae. For example, Harpy Eagles and Short-tailed Hawks have an alleged need for nest sites in relatively pristine native forest (Albuquerque 1995). Yet, such allegation does not match a series of recent breeding records that demonstrate a much greater degree of tolerance, with successful nesting reported at human-altered habitats (Silva 2007, Monsalvo 2012, and references therein). These recent reports also showed that both prey delivery rates and fledgling success in such situations are similar or higher than those on more pristine habitats. Nonetheless, nesting in such modified conditions might lead to still undetected impacts, like higher nest predation risks (Newton 2010). Thus, further studies are necessary, to verify the occurrence of possible negative effects.

Open-country raptors are generally considered to be less threatened than forest species (*e.g.*, Piana & Marsden 2014), as mentioned by Bierregaard-Jr. (1995). In fact, recent research shows that suitable habitats for species such as the Roadside Hawk might increase with anthropogenic changes (Carrete *et al.* 2009), and lead to a substantial rise in nest productivity, in human-modified habitats (Panasci & Whitacre 2002). On the other hand, we also retrieved studies that claim that other raptors of open habitats may be negatively impacted by changes in land use. Throughout the Americas, species such as Cinereous Harriers (*Circus cinereus*) (Camilotti *et al.* 2008), Chaco Eagles (Albuquerque *et al.* 2006), and even White-tailed Hawks (Brown & Glinski 2009) are apparently losing breeding areas. In any case, there is a shortage of data about how environmental changes affect the breeding of different species and populations. So, for proper management of such potentially affected populations, additional research on reproductive rates is essential.

The relevance of studying generalist and abundant species should not be disregarded, given the extremely significant participation of raptors in trophic webs (Estes *et al.* 2011). Breeding range expansions have been reported recently for some generalist species, such as some *Buteo* hawks (Williams-III *et al.* 2007, Sandoval 2009). These expansions result in insertion of these raptors into new food webs, interacting with populations of prey species with which they had no previous contact. Some Accipitriformes can prey upon introduced or invasive species (Wheeler 2003, Pineda-López *et al.* 2012, Martins & Donatelli 2014), and the effects of the latter on breeding parameters of native predators still require further research (Speziale & Lambertucci 2013). For instance, in Snail Kite breeding areas the introduction of an alien novel prey increased reproductive success (Cattau *et al.* 2016), highlighting the ecological relevance of raptor species.

This assessment of current knowledge of the breeding biology of Neotropical Accipitriformes indicated that, albeit 66% of the evaluated species had some improvement on levels of knowledge, the scarcity of breeding data on many South American Accipitridae persists. Yet, we noted that records from both a citizen science digital database and oological collections resulted in a significant increase in breeding information for a total of 13 species, relative to recent literature. There is a persistent need for research to be conducted north of the Southern Cone of South America, and we recommend that breeding biology studies should focus on the 24 species selected as research priorities. Knowledge of the breeding biology of Accipitridae not only plays a key role in enabling proper management and conservation of their populations. It also will point the way for more efficient studies in the future, generating better data about the biology of these predators and, in the final analysis, on the functioning of ecosystems as a whole (Bierregaard-Jr. 1995, Trejo 2007a).

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Associate Editor: Gustavo S. Cabanne

APPENDIX I

Literature references with breeding data of 56 species of Neotropical Accipitriformes, produced between 1995–2016.

Species	Located references
Elanus leucurus	Erichsen *et al.* 1996; McMillian & Pranty 1997; Pranty & McMillian 1997; Sick 1997; Arballo & Cravino 1999; Carvalho *et al.* 2001b; Maceda & Kin 2001; Wheeler 2003; Antas 2004; Leveau *et al.* 2004; Chatellenaz 2005; de la Peña 2005; Di Giacomo 2005; Joppert 2007; Niemela 2007; Pérez-León 2007; Scheibler 2007; Carvalho-Filho *et al.* 2008; Gussoni & Guaraldo 2008; González-Acuña *et al.* 2009; Chatellenaz *et al.* 2010; Furman & Bastías 2012; Montalvo *et al.* 2014; Alvarado *et al.* 2015; Camacho-Varela & Acosta-Chaves 2015; Romano *et al.* 2015; Marsden *et al.* 2016.
Gampsonyx swainsonii	Martínez 1998; Reichle *et al.* 2003; Di Giacomo 2005; Jones 2005; Strewe *et al.* 2009; Sandoval *et al.* 2010.
Chondrohierax uncinatus	Ericson & Amarilla 1997; Di Giacomo 2000; Thorstrom *et al.* 2001; Clark 2002; 2003; Krügel 2003; Reichle *et al.* 2003; Clark 2004; Rappole *et al.* 2007; Carvalho-Filho *et al.* 2008; Thorstrom & McQueen 2008; Canuto 2009; Whitacre 2012; Sampaio *et al.* 2013; Phillips *et al.* 2015.
Leptodon cayanensis	Thorstrom 1997; Bornschein & Reinert 2000; Carvalho-Filho *et al.* 2002; Cabanne 2005; Carvalho-Filho *et al.* 2005; Olmos *et al.* 2006; Carvalho-Filho *et al.* 2008; Canuto 2009; Bodrati *et al.* 2010; Ghizoni-Jr. & Azevedo 2010; Whitacre 2012.
Leptodon forbesi	Pereira *et al.* 2006; Dénes 2009; Dénes *et al.* 2011.
Elanoides forficatus	Meyer & Collopy 1995; Brown *et al.* 1997; Gerhardt *et al.* 1997; Sykes-Jr. *et al.* 1999; Naka & Rodrigues 2000; Coulson 2001; Blihovde 2002; Coulson 2002; Naka *et al.* 2002; Willis & Oniki 2002; Reichle *et al.* 2003; Gerhardt *et al.* 2004; Meyer *et al.* 2004; Soehren 2004; Zimmerman 2004; Azevedo & Di Bernardo 2005; Carvalho-Filho *et al.* 2008; Coulson *et al.* 2008; Crease 2009; Gruber 2009; Lopes *et al.* 2009; Whitehead & Jones 2009; Bodrati *et al.* 2010; Chiavacci *et al.* 2011; Whitacre 2012; Carpenter & Allen 2013; Kjeldsen 2103; Enge *et al.* 2014.
Morphnus guianensis	Whitacre *et al.* 2002; Mikich & Bérnils 2004; Vargas-González *et al.* 2006a; Raine 2007; Cintra & Naka 2012; Whitacre 2012; Crease & Tepedino 2013; Gomes 2014; Gomes & Sanaiotti 2015; Sanaiotti *et al.* 2015.

Species	**Located references**
Harpia harpyja	Chebez 1995; Alvarez *et al.* 1996; Alvarez-Cordero 1996; de Lucca 1996; Sick 1997; Machado *et al.* 1998; Galetti & Carvalho 2000; Ibáñez *et al.* 2002; Piana 2002; Rettig 2002; Sanaiotti 2002; Hennessey *et al.* 2003; Peterson *et al.* 2003; Willis & Oniki 2003; Mikich & Bérnils 2004; Suárez *et al.* 2004; Luz 2005; Muñiz-López 2005; Silveira *et al.* 2005; Olmos *et al.* 2006; Pereira & Salzo 2006; Vargas-González *et al.* 2006a; b; Giudice *et al.* 2007; Pacheco *et al.* 2007; Piana 2007; Silva 2007; Anfuso *et al.* 2008; Trinca *et al.* 2008; Pinheiro & Dornas 2009; May 2010; Seymour *et al.* 2010; Sánchez-Lalinde *et al.* 2011; Ubaid *et al.* 2011; Vargas-González & Vargas 2011; Aguiar-Silva *et al.* 2012; Cintra & Naka 2012; Muñiz-López *et al.* 2012; O'Shea & Ramcharan 2012; Rotemberg *et al.* 2012; Aguiar-Silva *et al.* 2014; Vargas-González *et al.* 2014; Aguiar-Silva *et al.* 2015; Kuniy *et al.* 2015; Sanaiotti *et al.* 2015; Sousa *et al.* 2015; Watson *et al.* 2016.
Spizaetus tyrannus	Sick 1997; Olmos *et al.* 2006; Sigrist 2006; Lopes & Braz 2007; Canuto 2008; Carvalho-Filho *et al.* 2008; Jones & Komar 2008a; Phillips 2009; Pimentel & Olmos 2011; Canuto *et al.* 2012; Cintra & Naka 2012; Whitacre 2012; Straube *et al.* 2014; Meyer 2016.
Spizaetus melanoleucus	Andrade *et al.* 1996; Sick 1997; Reichle *et al.* 2003; Anderson *et al.* 2004; Eisermann 2007; Canuto 2008; Carvalho-Filho *et al.* 2008; Canuto 2009; Phillips 2009; Phillips & Seminario 2009; Bodrati *et al.* 2010; Canuto *et al.* 2012; Whitacre 2012; Kohler & Rezini 2013.
Spizaetus ornatus	Sick 1997; Thorstrom 1997; Andrade & Andrade 1998; Machado *et al.* 1998; Naveda-Rodríguez 2002; Seipke & Cabanne 2002; Reichle *et al.* 2003; Greeney *et al.* 2004; Mikich & Bérnils 2004; Naveda-Rodríguez 2004; Mendonça-Lima *et al.* 2006; Giudice 2007; Canuto 2008; Carvalho-Filho *et al.* 2008; Canuto 2009; Kirwan 2009; Phillips 2009; Joenck *et al.* 2011; Canuto *et al.* 2012; Cintra & Naka 2012; Whitacre 2012; Joenck *et al.* 2013; Kjeldsen 2013; Phillips & Hatten 2013; Harvey *et al.* 2014.
Spizaetus isidori	Valdez & Osborn 2002; Strewe & Navarro 2003; Valdez & Osborn 2004; Roesler *et al.* 2008; Greeney *et al.* 2011; Castañeda 2012; Araóz & Alvedaño 2013; Zuluaga & Echeverry-Galvis 2016.
Busarellus nigricollis	Sick 1997; Di Giacomo 2000; Reichle *et al.* 2003; Willis & Oniki 2003; Antas 2004; Chatellenaz 2005; de la Peña 2005; Di Giacomo 2005; Márquez *et al.* 2005; Chatellenaz *et al.* 2010; Knight 2010; Bertassoni *et al.* 2012; Evangelista *et al.* 2012.
Rostrhamus sociabilis	Alvarez-López & Kattan 1995; Rodgers-Jr. 1996; Sick 1997; Valentine-Darby *et al.* 1997; Bennetts *et al.* 1998; Palmer 1998; Valentine-Darby *et al.* 1998; Angehr 1999; Arballo & Cravino 1999; Bennetts & Kitchens 1999; Dreitz *et al.* 1999; Bennetts & Kitchens 2000; Dreitz 2000; Dreitz & Duberstein 2001; Dreitz *et al.* 2001; Rodgers-Jr. *et al.* 2001; Welch & Kitchens 2001; Beissinger & Snyder 2002; Bennetts *et al.* 2002; Dreitz *et al.* 2002a; b; Petracci & Basanta 2002; Reichle *et al.* 2003; Rodgers-Jr. & Schwikert 2003; Wheeler 2003; Antas 2004; Dreitz *et al.* 2004; Chatellenaz 2005; de la Peña 2005; Angehr 2006; Jiménez & Zook 2007; Rodgers-Jr. 2007; Carvalho-Filho *et al.* 2008; Jones & Komar 2008a; Reichert 2009; Chatellenaz *et al.* 2010; Palmer 2011; Bowling *et al.* 2012; Posso *et al.* 2012; Reichert *et al.* 2012; Román & Wiley 2012; Fortes & Denis 2013; Hernández-Vázquez *et al.* 2013; Bencke & Pereira 2014; Machado *et al.* 2015; Cattau *et al.* 2016.
Helicolestes hamatus	Greeney *et al.* 2004.
Harpagus bidentatus	Schulze *et al.* 2000; Walther 2003; Greeney *et al.* 2004; Carvalho-Filho *et al.* 2008; Greeney & Gelis 2008; Cintra & Naka 2012; Whitacre 2012.
Harpagus diodon	Naka & Rodrigues 2000; Azevedo *et al.* 2003; Cabanne 2005; Azevedo *et al.* 2006; Sigrist 2006; Cabanne & Roesler 2007; Carvalho-Filho *et al.* 2008; Canuto 2009; Bodrati *et al.* 2010; Lees & Martin 2014.

Species	**Located references**
Ictinia plumbea	Seavy *et al.* 1997; Sick 1997; Seavy *et al.* 1998; Reichle *et al.* 2003; Antas 2004; Cabanne 2005; Chatellenaz 2005; de la Peña 2005; Di Giacomo 2005; Angehr 2006; Carvalho & Bohórquez 2007; Pérez-León 2007; Carvalho-Filho *et al.* 2008; Gussoni & Guaraldo 2008; Salvador-Jr. & Silva 2009; Bodrati *et al.* 2010; Chatellenaz *et al.* 2010; Jacomassa 2011; Whitacre 2012; Kjeldsen 2013; Pinto-Ledezma & Justiniano 2013; Chatellenaz 2015; Maciel *et al.* 2016.
Circus cinereus	Saggese & de Lucca 1995; Donázar *et al.* 1996; Maurício & Dias 1996; Sick 1997; Arballo & Cravino 1999; Bó *et al.* 2000; Jaksic *et al.* 2002; Bó *et al.* 2004; de la Peña 2005; Baladrón *et al.* 2007; Camilotti *et al.* 2008; Capllonch *et al.* 2011; Alvarado *et al.* 2015.
Circus buffoni	Bó *et al.* 1996; Sick 1997; Arballo & Cravino 1999; Bó *et al.* 2004; Chatellenaz 2005; Carvalho-Filho *et al.* 2008; Kirwan & Shirihai 2008; Chatellenaz *et al.* 2010; Alvarado *et al.* 2015.
Accipiter poliogaster	de Vries & Melo 2000; 2002; Thorstrom 2002a; Bodrati *et al.* 2010; Lima & Ribeiro 2011; Boesing *et al.* 2012.
Accipiter superciliosus	Hennessey *et al.* 2003; Thiollay 2007; Carvalho-Filho *et al.* 2008; Bodrati *et al.* 2010.
Accipiter collaris	Cuervo *et al.* 2008.
Accipiter gundlachi	Rompré *et al.* 1999; Wallace *et al.* 1999; Peña *et al.* 2012; Ferrer-Sánchez & Rodríguez-Estrella 2014; Ferrer-Sánchez 2015; Ferrer-Sánchez & Rodríguez-Estrella 2016.
Accipiter bicolor	Pavez & González 1998; Thorstrom & Kiff 1999; Thorstrom & Quixchán 2000; Reid *et al.* 2002; Figueroa *et al.* 2004a; b; Mikich & Bérnils 2004; Ojeda *et al.* 2004; Carvalho-Filho *et al.* 2005; Figueroa *et al.* 2007; Marini *et al.* 2007; Azpiroz & Menéndez 2008; Carvalho-Filho *et al.* 2008; Canuto 2009; Bodrati *et al.* 2010; Zorzin 2011; Whitacre 2012; Hayes 2014; Alvarado *et al.* 2015; Medel-Hidalgo *et al.* 2015; Rivas-Fuenzalida 2015b; Rivas-Fuenzalida *et al.* 2015c.
Geranospiza caerulescens	Sick 1997; Arballo & Cravino 1999; Sutter *et al.* 2001; del Ángel 2002; Reichle *et al.* 2003; Chatellenaz 2005; Sigrist 2006; Carvalho-Filho *et al.* 2008; Canuto 2009; Whitacre 2012.
Buteogallus anthracinus	Barrantes 1998; Boal 2001; Barradas-García *et al.* 2004; Márquez *et al.* 2005; Barradas-García & Morales-Mávil 2007; Clark 2007b; Pérez-León 2007; Flesch 2008; Sadoti 2008; Troy & Stahlecker 2008; Flesch 2009; Ruvalcaba-Ortega & González-Rojas 2009; Alava *et al.* 2011; Sadoti 2012; Uribe-Hernández *et al.* 2012; Etzel *et al.* 2014; Smith & Finch 2014; Licence & McCarty 2015.
Buteogallus aequinoctialis	Mikich & Bérnils 2004.
Buteogallus meridionalis	Narozky & Martelli 1995; Best *et al.* 1996; Sick 1997; Andrade & Andrade 1998; Arballo & Cravino 1999; Reichle *et al.* 2003; Antas 2004; Chatellenaz 2005; de la Peña 2005; Di Giacomo 2005; Navarro *et al.* 2007; Carvalho-Filho *et al.* 2008; Strewe *et al.* 2009; Chatellenaz *et al.* 2010; Marini *et al.* 2012; Maurício *et al.* 2013; Camacho-Varela *et al.* 2015; Silva & Machado 2015.
Buteogallus lacernulatus	Carvalho-Filho *et al.* 2008; Canuto 2009.
Buteogallus urubitinga	Best *et al.* 1996; Seavy & Gerhardt 1998; Arballo & Cravino 1999; Di Giacomo 2000; Naveda-Rodríguez 2002; Reichle *et al.* 2003; Antas 2004; Naveda-Rodríguez 2004; Chatellenaz 2005; de la Peña 2005; Di Giacomo 2005; Carvalho-Filho *et al.* 2006; Carvalho-Filho *et al.* 2008; Canuto 2009; Chatellenaz *et al.* 2010; Whitacre 2012; Kjeldsen 2013.
Buteogallus solitarius	Mee *et al.* 2002; Strewe & Navarro 2003; Jones 2005; Clark 2007a; Seminario *et al.* 2011; Phillips 2012; Phillips & Martinez 2013; Phillips *et al.* 2014.

Species	**Located references**
Buteogallus coronatus	Sick 1997; Bellocq *et al.* 1998; Machado *et al.* 1998; Carvalho *et al.* 2002; Maceda *et al.* 2003; Mikich & Bérnils 2004; de la Peña 2005; Di Giacomo 2005; Albuquerque *et al.* 2006; Barcellos & Accordi 2006; Granzinolli *et al.* 2006; Torres *et al.* 2006; Bragagnolo *et al.* 2007; Lobos *et al.* 2007; Maceda 2007; Maceda *et al.* 2007; Carvalho-Filho *et al.* 2008; Tizianel 2008; Chiaravalloti *et al.* 2009; Sarasola *et al.* 2010; Banhos & Sanaiotti 2011; Lobos *et al.* 2011; Berkunsky *et al.* 2012; Fandiño & Pautasso 2013; Urios *et al.* 2014; Kilpp 2015; Montalvo *et al.* 2015; Barbar *et al.* 2016.
Morphnarchus princeps	Sánchez & Sánchez-M. 2002; Muela & Valdez 2003; Márquez *et al.* 2005; Greeney & Nunnery 2006; Gelis & Greeney 2007; Greeney *et al.* 2008.
Rupornis magnirostris	Best *et al.* 1996; Capllonch 1997; Maragliano & Montalti 1997; Arballo & Cravino 1999; Naka & Rodrigues 2000; Panasci & Whitacre 2000; Carvalho *et al.* 2001a; Höfling & Camargo 2002; Naka *et al.* 2002; Panasci & Whitacre 2002; Reichle *et al.* 2003; Antas 2004; Bó *et al.* 2004; Chatellenaz 2005; de la Peña 2005; Di Giacomo 2005; Marini *et al.* 2007; Navarro *et al.* 2007; Carvalho-Filho *et al.* 2008; Gussoni & Guaraldo 2008; Salvador-Jr. & Silva 2009; Santos & Rosado 2009; Santos *et al.* 2009; Verea *et al.* 2009; Bodrati *et al.* 2010; Chatellenaz *et al.* 2010; Cavicchia & García 2012; Cintra & Naka 2012; Mojica 2012; Panasci 2012; Panasci unpub. data *apud* GRIN 2012; Uribe-Hernández *et al.* 2012; Romano *et al.* 2015.
Parabuteo unicinctus	Blue 1996; Silva & Olmos 1997; Arballo & Cravino 1999; Gerstell & Bednarz 1999; Patten & Erickson 2000; Maceda & Kin 2001; Willis & Oniki 2003; de la Peña 2005; Márquez *et al.* 2005; Dwyer 2006; Figueroa & González-Acuña 2006; Jenner *et al.* 2007; Pérez-León 2007; Dwyer & Mannan 2009; Ellis *et al.* 2009; Cavicchia & García 2012; Furman & Bastías 2012; Alvarado *et al.* 2015.
Parabuteo leucorrhous	Freile & Chaves 2000; Mikich & Bérnils 2004; Greeney & Nunnery 2006; Tobias & Seddon 2007; Zilio & Mendonça-Lima 2012.
Geranoaetus albicaudatus	Sick 1997; Bellatti 2000; Granzinolli 2003; Reichle *et al.* 2003; Di Giacomo 2005; Granzinolli & Motta-Junior 2006; Granzinolli *et al.* 2006; Actkinson *et al.* 2007; Granzinolli & Motta-Junior 2007; Rappole *et al.* 2007; Carvalho-Filho *et al.* 2008; Haralson 2008; Actkinson *et al.* 2009; Brown & Glinski 2009; Salvador-Jr. & Silva 2009; Motta-Junior *et al.* 2010; Greeney *et al.* 2011; Maurício *et al.* 2013.
Geranoaetus polyosoma	Jiménez 1995; Donázar *et al.* 1996; Jaksic & Lazo 1999; Bó *et al.* 2004; de la Peña 2005; Alvarado & Figueroa 2006a; Cabot & de Vries 2009; Cabot *et al.* 2010a; b; Greeney *et al.* 2011; Hahn *et al.* 2011; Lüthi 2011; Alvarado *et al.* 2015; Shirihai *et al.* 2015.
Geranoaetus melanoleucus	de Lucca & Saggese 1995; Hiraldo *et al.* 1995; Narozky & Martelli 1995; Best *et al.* 1996; Donázar *et al.* 1996; Sick 1997; Arballo & Cravino 1999; Jaksic & Lazo 1999; Sousa 1999; Bellatti 2000; Pavez 2001; Saggese & de Lucca 2001; Bencke *et al.* 2003; de la Peña 2005; Trejo *et al.* 2006b; Zorzin *et al.* 2007; Salvador-Jr. *et al.* 2008; Chatellenaz *et al.* 2010; Arriagada *et al.* 2011; Lüthi 2011; de Lucca & Saggese 2012; Alvarado *et al.* 2015; Ignazi 2015; Pérez 2015; Raimilla *et al.* 2015; Lemos 2016.
Pseudastur polionotus	Willis & Oniki 2002; Bencke *et al.* 2003; Corrêa *et al.* 2008; Canuto 2009.
Pseudastur albicollis	Draheim 1995; Cisneros-Heredia 2006; Cintra & Naka 2012; Whitacre 2012.
Pseudastur occidentalis	Vargas 1995; Best *et al.* 1996.
Leucopternis semiplumbeus	Ferguson-Lees & Christie 2001.
Leucopternis melanops	Ferguson-Lees & Christie 2001; Cintra & Naka 2012.
Leucopternis kuhli	Kirwan 2009.
Buteo plagiatus	Bibles & Mannan 2004; Werner 2004; Patrikeev 2007; Rappole *et al.* 2007; Flesch 2008; Flesch & Saavedra 2008; Flesch 2009; Ruvalcaba-Ortega & González-Rojas 2009; Sandoval 2009; Vargas-Masís & Ramírez 2012.

Species	**Located references**
Buteo nitidus	Sick 1997; Reichle *et al.* 2003; Navarro *et al.* 2007; Sandoval 2009; Strewe *et al.* 2009; Cintra & Naka 2012.
Buteo ridgwayi	Thorstrom 2002b; Thorstrom *et al.* 2005; 2007; Woolaver 2011; Woolaver *et al.* 2013a, b, c, Woolaver *et al.* 2015.
Buteo albigula	Gelain *et al.* 2001; Trejo *et al.* 2001; Ojeda *et al.* 2003; Pavez *et al.* 2004; Trejo *et al.* 2004; Trejo *et al.* 2006a; Silva-Rodríguez *et al.* 2008; Henry & Aznar 2009; Rivas-Fuenzalida *et al.* 2013; Alvarado *et al.* 2015; Rivas-Fuenzalida *et al.* 2015b.
Buteo brachyurus	Naka & Rodrigues 2000; Carvalho *et al.* 2001a; Jones 2002; Wheeler 2003; Meyer 2004, 2005; Meyer & Zimmerman 2007; Rappole *et al.* 2007; Williams-III *et al.* 2007; Brush 2008; Carvalho-Filho *et al.* 2008; Flesch 2008; Rizkalla *et al.* 2009; Salvador-Jr. & Silva 2009; Howell 2010; Snyder *et al.* 2010; Monsalvo 2012; Enge *et al.* 2014; Straube *et al.* 2014; Oliveira *et al.* 2015; FWC [s.d.].
Buteo galapagoensis	Faaborg *et al.* 1995; DeLay *et al.* 1996; Bollmer *et al.* 2003; Whiteman & Parker 2004a; b; Bollmer *et al.* 2005; Jaramillo & Vargas 2010; Rivera *et al.* 2011; Muñoz 2012.
Buteo albonotatus	Kennedy *et al.* 1995; Sick 1997; Pérez-León 2007; Carvalho-Filho *et al.* 2008; Flesch 2008; Howell 2010; Olmos & Albano 2012.
Buteo ventralis	Figueroa *et al.* 2000; Imberti 2003; Rivas-Fuenzalida *et al.* 2009, 2011; Norambuena *et al.* 2012; Medel-Hidalgo *et al.* 2013; Norambuena *et al.* 2013; Raimilla *et al.* 2013; Rivas-Fuenzalida & Asciones-Contreras 2013; Figueroa unpub. data *apud* GRIN 2015; Rivas-Fuenzalida 2015a; Rivas-Fuenzalida & Asciones-Contreras 2015; Rivas-Fuenzalida *et al.* 2015a, 2016.

APPENDIX II

Complete list of references retrieved in this review and cited in Appendix I.

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APPENDIX III

Results of the search for literature breeding data of two species of Accipitriformes not presented on Bierregaard-Jr.'s (1995) review.

Sharp-shinned Hawk *Accipiter striatus* – the vast majority of breeding records of the so-called "Central and South American group" of subspecies (*sensu* Ferguson-Lees & Christie 2001) refer to *A. s. erythronemius*, whose breeding traits were classified as entirely unknown by Bierregaard-Jr. (1995; but see comments by Di Giacomo 2005). Different populations of this subspecies' range were studied in detail, but most other breeding reports are anecdotal. Central American *A. s. chionogaster* (also labeled as having unknown breeding biology by 1995) now at least had one of its populations studied in detail. Finally, the Andean form *A. s. ventralis* have no new breeding data; its nest remains undescribed, and knowledge on breeding behavior is based solely on older scattered information (Bierregaard-Jr. 1995).

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Cuban Black Hawk *Buteogallus gundlachii* – apparently there is still little breeding data, as we located very few reports, and just two of these studies provide more detailed descriptions of breeding events.

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APPENDIX IV

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APPENDIX V

Results of the search for photographic breeding records of Neotropical Accipitriformes on the WikiAves database.

Species	**Records' reference numbers**
Elanus leucurus	WA1251178; WA1253853; WA1263279; WA1272398; WA1272409; WA1279861; WA1281964; WA1288071; WA1290781; WA1293418; WA1300395; WA1376684; WA1499798; WA1720428; WA1721934; WA1770437; WA1835635; WA1835637; WA1837761; WA1841067; WA1904171; WA2037143; WA2071064; WA2090188; WA21325; WA21537; WA2271383; WA250965; WA466357; WA661980; WA698506; WA719423; WA729366; WA732823; WA915133; WA915840; WA915852; WA936035.
Chondrohierax uncinatus	WA1160532; WA1688095; WA1937776; WA1968066; WA1981003.
Leptodon cayanensis	WA723947; WA723948.
Leptodon forbesi	WA938449.
Spizaetus melanoleucus	WA1140737; WA1140739; WA1370302; WA1378059; WA1438023; WA195643; WA2206395; WA2242350; WA2249207; WA2322423.
Rostrhamus sociabilis	WA1214147; WA1218422; WA1280372; WA147627; WA1493450; WA1588325; WA1771055; WA2021254; WA2021256; WA2108507; WA226747; WA24193; WA36753; WA474247; WA484024; WA64884; WA696195; WA696196; WA81214; WA819399.
Helicolestes hamatus	WA1589021; WA1966794; WA953944.
Harpagus bidentatus	WA2198552; WA2240795; WA668871.
Harpagus diodon	WA1156861; WA1200479; WA1228366; WA123732; WA1237599; WA14961; WA14962; WA1966820; WA1966889; WA206624; WA209513; WA219297; WA219978; WA222095; WA222762; WA244381; WA250110; WA251551; WA252886; WA255778; WA255779; WA255914; WA257012; WA275906; WA280598; WA507006; WA73820; WA76435; WA76436; WA76815; WA785304; WA819506; WA82627; WA860802; WA861618; WA884512; WA887671; WA887710; WA889684; WA897892; WA900167; WA98349.
Accipiter poliogaster	WA1920902; WA1985763; WA1989199; WA1992309; WA1994808; WA2005934; WA2034929; WA2047459; WA2132296; WA2319849; WA779787.
Accipiter bicolor	WA106136; WA1744297; WA89938.
Geranospiza caerulescens	WA140630; WA141005; WA1444043; WA1565980; WA1649149.
Buteogallus anthracinus	WA950092.
Buteogallus aequinoctialis	WA1503515.
Pseudastur polionotus	WA1570081; WA1570097; WA1581106.
Pseudastur albicollis	WA215803; WA722126.
Buteo nitidus	WA1184610; WA1392108; WA2187978; WA2187993; WA388429; WA476978; WA506191.
Buteo brachyurus	WA1116480; WA1356894; WA1356902; WA176090; WA176091; WA2033914; WA225567; WA33877; WA513759; WA513770; WA513777; WA513781; WA513790; WA513819; WA513828; WA819112; WA819113.

APPENDIX VI

Proposed corrections to four misidentified museum egg sets of Neotropical Accipitriformes. Arguments referring to geographical distribution are not presented since all species involved are sympatric at these collection localities (del Hoyo *et al.* 2016).

Set WFVZ 15561 - formerly assigned to Lined Forest-Falcon *Micrastur gilvicollis.* Seemingly, no information exists on Lined Forest-Falcon's eggs (Bierregaard-Jr. 1995, GRIN 2009, del Hoyo *et al.* 2016). This one-egg set was obtained by G. D. Smooker, whose identifications have already been questioned (Thorstrom & Kiff 1999). More importantly, the egg is much larger than those of another similar-sized, closely-related *Micrastur* falcon (Whitacre 2012). Thus, we doubt it could be properly atributed to Lined Forest-Falcon.
Measurements, clutch-size and overall appearance are suitable with known clutches of the Gray-headed Kite measured by us and to other data presented by Whitacre (2012). Thus, it almost certainly belongs to this species.
We recommend the treatment of this set as cfr. *Leptodon cayanensis*.

Set WFVZ 15951 - previously assigned to Black-collared Hawk *Busarellus nigricollis.* Also from Smooker's collection. Measurements of theses two eggs are much smaller than Black-collared Hawk's eggs (GRIN 2010), but consistent with those of Zone-tailed Hawk *Buteo albonotatus* (del Hoyo *et al.* 2016), as suggested by L. Kiff on the data slip of this set. Yet, contrary to the previous and next cases, these species overall appearances and "field jizzes" are quite different (J.A.B.M., pers. obs.) to justify such a misidentification by the collector. Also, dimensions, clutch-size and general appearance of the eggs did not allow a rigorous identification. We do not discard that the clutch refers to Zone-tailed Hawk, but evidence is not conclusive as they may refer to other hawks as well.
We recommend that this set should not be treated as *Busarellus nigricollis*, and tentatively identify as cfr. *Buteo albonotatus*.

Sets WFVZ 16312 and 16313 - both formerly assigned to Hook-billed Kite *Chondrohierax uncinatus.*
These three eggs are very distinct from, and much larger than, Hook-billed Kite's (J.A.B.M., pers. obs., Di Giácomo 2000, Whitacre 2012). Both dimensions, clutch-sizes and overall appearance fits with Gray-headed Kite's clutches. Albeit measurements of the two-egg clutch (WFVZ 16312) are slightly smaller than most Gray-headed Kite's, they fit with those of another two egg-clutch of this species, provided by Carvalho-Filho *et al.* (2005).
We assign these sets to *Leptodon cayanensis*.

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