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**Cover:** Adult male Yellow Cardinal (*Gubernatrix cristata*) at the Espinilho State Park, Rio Grande do Sul state, southern Brazil. Beier *et al.* (in this volume) provides information on social organization and breeding parameters of this threatened species. Photo author: Márcio Repenning.

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# Important tools for Amazon Parrot reintroduction programs

Cristiano Schetini de Azevedo<sup>1,3</sup>, Livia Soares Furtado Rodrigues<sup>2</sup> & Julio Cesar Rodrigues Fontenelle<sup>1,2</sup>

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**ABSTRACT:** Anti-predator behavior and personality have important consequences for the survival of captive-bred animals after reintroduction in the wild. The personality of an animal can be defined as low within-individual variation in behavior relative to between-individual variation in behavior. Mortality caused by predation is the main reason for reintroduction failure, and training captive-born animals to avoid predators can solve this problem. However, how anti-predator training affects the personality of animals is uncertain. The objective of this study was to test the behavioral responses of captive Amazon Parrots (*Amazona aestiva*, Psittacidae) submitted to an anti-predator conditioning protocol, and to evaluate if anti-predator training affects parrot personalities. Twenty-six parrots were trained against predators using taxidermized models; their personalities were evaluated by calculating boldness scores before and after anti-predator training sessions. Parrots increased the expression of anti-predator behaviors when tested with all models; control groups behaved in a more relaxed way. The anti-predator responses persisted for 60 days after the end of the training sessions. Boldness scores increased in 50% of cases after anti-predator training sessions, and in only 33% of cases did parrots become shyer after anti-predator training. The tendency of parrots to exhibit bold behaviors in the personality tests, even after the training sessions, may be explained by their early experiences, low behavioral plasticity or high cognitive ability. Training naïve parrots was an effective tool to enhance behavioral responses against predators before reintroduction. The study of personality is of great importance in reintroduction and translocation programs to determine the position of each individual in the shy-bold continuum and to help select individuals more suited for reintroduction.

**KEY-WORDS:** anti-predator training, captivity, conservation, personality, Psittacidae.

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## INTRODUCTION

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Predation is one of the most important factors that affect species distribution and abundance (McLean *et al.* 1999, Begon *et al.* 2006). Anti-predatory behavior has important consequences for the survival and population dynamics of prey, and in the stability of predator-prey interactions (Stankowich & Blumstein 2005). Anti-predator behavior has been studied mostly in fish, birds and mammals (Griffin *et al.* 2000), and the most commonly performed strategies by animals include hiding, escaping, freezing or fighting (Sanz & Grajal 1998, Eilam 2005, Rosier & Langkilde 2011, Yorzinski & Platt 2012, Miles *et al.* 2013). Captive-born animals or animals reared in predator-free territories may lose their anti-predator skills (Curio 1988), and because it is energetically costly to maintain these behaviors, they tend to disappear over time (Ryer & Olla 1998).

Mortality caused by predation has been critical in some reintroduction/translocation attempts (Beck *et al.*

1991, Short *et al.* 1992, Miller *et al.* 1994). Death of captive-born animals soon after reintroduction can be minimized by releasing the animals in predator-free areas, by building fences to avoid the entrance of predators, by eliminating the local predators by translocations or hunting, or by training naïve animals to recognize and to avoid predators (Griffin *et al.* 2000). The use of anti-predator conditioning has increased in the last decade (Miller *et al.* 1994, Maloney & McLean 1995, McLean 1996, Richards 1998, McLean *et al.* 1999, Azevedo & Young 2006, Specht 2007, Miles *et al.* 2013).

Many species, from humans to arthropods, differ individually in how they respond to environmental stimuli such as novelty, risk, and sociability (Lendvai *et al.* 2011). These differences are determined by behavioral and physiological traits, and can be described by their personalities (Groothuis & Carere 2005). The personality of an animal can be defined as the low within-individual variation in behavior relative to between-individual variation in behavior (Carter & Feeney 2012), *i.e.*

individual behaviors can consistently differ across situations or contexts, and these differences tend to be stable over time (Sih *et al.* 2004, Bell & Stamps 2004, Dingemanse & Réale 2005, McDougall *et al.* 2006, Stamps & Groothuis 2010, Wolf & Weissing 2012).

Personality traits, such as the shy-bold continuum (Wilson *et al.* 1994, Kurvers *et al.* 2010), can be used to describe and measure behavioral variation in humans and other species (Wilson *et al.* 1994, Watters & Powell 2012). A bold animal is one inclined to take risks, especially in novel situations, and a shy animal is one not inclined to take risks (Toms *et al.* 2010). Personality traits can be partly heritable (10–50%, van Oers *et al.* 2004, 2005, Taylor *et al.* 2012), and the topic of how personality is maintained in animal populations across time (evolutionary patterns) and had been subject of recent under study (Wolf & Weissing 2012).

The assessment of animal personality traits has some practical applications, especially for captive animals, since it can help keepers in the selection of the most suitable animals for exhibition, reproduction and handling, for instance (Carlstead 1999). Behavioral assessment can also be a tool for the selection of the best animals to reintroduce into the wild in conservation programs (Azevedo & Young 2006), since the reintroduction of captive-bred animals is an alternative approach to species conservation (Foose 1986, Cade 1988). For instance, bold individuals should not be reintroduced since they may suffer a high-risk of death due to their propensity to take risks (Bremner-Harrison *et al.* 2004). Alternatively, shy individuals should not be reintroduced since they may show reduction in foraging and growth rates (Biro & Stamps 2008). The ideal scenario would be the reproduction of individuals occupying intermediate positions in the shy-bold continuum, *i.e.* neither too bold or too shy; this would enable the correct response when individuals are exposed to a threat, such as a predator, or when searching for food or partners (Azevedo & Young 2006).

The Turquoise-fronted Parrot [*Amazona aestiva* (Linnaeus, 1758); hereafter Amazon parrot] is one of the most common Brazilian parrots (Béjcek & Stastný 2002), occurring in all biomes, except the Pampas (Schunk *et al.* 2011). Although *A. aestiva* are not considered threatened by extinction (IUCN 2015 – “Least Concern”; MMA 2014 – not threatened), chicks are frequently captured in the wild and traded illegally (Beissinger & Bucher 1992, Seixas & Mourão 2002, Schunk *et al.* 2011), mainly due to their capacity to imitate the human voice (Ribeiro & Silva 2007). Many specimens are rescued annually by governmental agencies and are sent to rehabilitation centres for future reintroduction (Beissinger & Bucher 1992, Seixas & Mourão 2002). Consequently, testing an anti-predator conditioning protocol for this species is important because this could increase the chances

of establishment of viable parrot populations after reintroductions.

Despite the importance of reintroduction as a tool for species conservation (Foose 1986, Cade 1988), without behavioral interventions in captivity, such as anti-predator conditioning, individuals can show high mortality rates after release in the wild, especially due to predation (Macias *et al.* 2003, White-Jr. *et al.* 2005, Valle *et al.* 2010, Veloso-Júnior *et al.* 2010, Alonso *et al.* 2011). Psittacines, as an example, were preyed by snakes, hawks and ocelots in reintroduction programs with no pre-release anti-predator conditioning (Macias *et al.* 2003, Valle *et al.* 2010, Veloso-Júnior *et al.* 2010). Anti-predator conditioning for an Amazon parrot species is only known for *Amazona vittata* (Boddaert, 1783), reintroduced in Puerto Rico by the Puerto Rican Parrot Recovery Program, which reports a strong positive response of the parrots to the predator-aversion training (White-Jr. *et al.* 2005).

Few studies have evaluated if anti-predator training can change personality traits. Among these, the results are ambiguous, with some studies showing that personality was altered after anti-predator training sessions (Azevedo & Young 2006, Specht 2007), with bolder animals becoming less bold, and other showing that personality was not altered after anti-predator training sessions (Smith & Blumstein 2012).

The aim of this study was to test behavioral responses to an anti-predator conditioning program for captive Amazon Parrots, using *A. aestiva* as a model. We hypothesized that the predator-aversion behaviors would be enhanced after consecutive training sessions, helping the naive parrots (those living for longer periods in captivity that had no previous experiences with predators) to recognize and avoid predators. This study also intended to evaluate the personality of captive-bred *A. aestiva* individuals and tested the hypothesis that individuals become shyer after being trained against predators, due to increased fearfulness caused by predator visualization.

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## METHODS

### Animals

We randomly selected thirty adult *Amazona aestiva* individuals spontaneously returned to the Brazilian Environmental Agency (*Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis - IBAMA*) at a 1:1 sex ratio (parrots were sexed through DNA analysis). All parrots had lived for at least 5 years in captivity. The study was conducted in the IBAMA facilities, at Belo Horizonte, Minas Gerais state, southeastern Brazil. Parrots were held in two enclosures measuring 7.10 m length × 1.8 m width



× 2.45 m height (15 parrots in each enclosure), placed 2 m apart, away from human interferences and surrounded by natural habitat. Two parrots died during the study due to injuries caused by fights inside the aviaries, thus data from only 28 individuals were included in the study. All experiments were approved by IBAMA's Animal Ethics Committee.

The birds were fed twice daily, in the morning (around 08:00 h) with Psittacidae feed (Evicanto Papagaios<sup>®</sup>) and in the afternoon (around 14:00 h) with fruits and seeds. Water was provided *ad libitum*. Birds were marked with colored rings on their legs to facilitate individual recognition.

### Anti-predator training ethogram

An ethogram for the Turquoise-fronted parrots (Table 1) was compiled based on 20 h of *ad libitum* sampling during 20 days of preliminary observations (Altmann 1974) and previous studies (Prestes 2000, Andrade & Azevedo 2011). Behaviors were classified into aversion (anti-predator behaviors) and relaxing behavior (those

not displayed in predatory situations) categories, based on the preliminary observations and in the studies of Andrade & Azevedo (2011).

### Anti-predator training protocol

Anti-predator training was done using two taxidermized models of potential predators – an Ocelot [*Leopardus pardalis* (Linnaeus, 1758)] and a Harris's Hawk [*Parabuteo unicinctus* (Temminck, 1824)] – and an adult human; a chair was used as a control model. The presentation of models was followed by an aversive stimulus (chasing by an unfamiliar human). All training sessions were done in groups of three parrots each (except two groups with two parrots; the parrots remained in the same group during the entire experiment): two groups were trained against the three predator types (mixed group); two groups were trained against the ocelot model (ocelot group); two groups were trained against the hawk model (hawk group); two groups were trained against the human (human group), totaling six groups (two groups per predator type); and two groups received no training (control) (Table 2).

**Table 1.** Behavioural ethogram of *Amazona aestiva* individuals kept at IBAMA/BH with behavior description used during anti-predator training sessions and classification used to calculate boldness scores.

Behavior	Acronym	Description	Category	Classification
Self or Allopreening	PREE	Parrot preens own feathers or feathers of other individuals.	Relax	Boldness
Nodding head	ND	Parrot nods its head.	Anti-predator	-
Aggression	AGR	Parrot pecks conspecifics aggressively.	Relax	Boldness
Yawning	YA	Parrot yawns.	Relax	-
Walking on perch	WP	Parrot walks on the perch.	Relax	Boldness
Walking on the floor	WF	Parrot walks on the floor.	Relax	Shyness
Walking on wire	WW	Parrot walks on the enclosure's wiremesh.	Relax	Shyness
Inactive	IN	Parrot remains inactive or sleeping.	Relax	Boldness
Inactive on wire	IW	Parrot remains inactive on the wiremesh.	Relax	Shyness
Alert	AL	Parrot adopts an alert posture (head up, looking fixedly towards something).	Anti-predator	Shyness
Hiding behind the shrub	HID	Parrot hides behind the shrub, avoiding the predator models.	Anti-predator	Shyness
Sleeping	SLEE	Parrot sleeps.	Relax	-
Pacing	PAC	Parrots walks from one side to another on the perch, on the wiremesh or on the floor, using the same route for no apparent reason.	Abnormal	Shyness
Flying	FLY	Parrot flies away from the predator models.	Anti-predator	Shyness
Vocalizing	VOC	Parrot emits social vocalizations.	Relax	Shyness
Pecking on feather/leaf	PF	Parrot pecks on free feathers or tree leaves on the ground.	Relax	Boldness
Head scratching	HS	Parrot scratches its head with its feet.	Relax	Boldness
Wing/leg stretching	WS	Parrot stretches its wings or legs.	Relax	Boldness
Pecking on plastic markings or on perch		Parrot pecks plastic markings of the perches or the perches inside the enclosure.	-	Boldness
Pecking on the platform		Parrot pecks the wooden platform of the novel objects.	-	Boldness
Playing with object		Parrot plays with the novel object.	-	Boldness
Cleaning the beak		Parrot scratches its beak on the perch to clean it.	-	Boldness
Not visible	NV	Parrot is not visible.	-	-

Some behaviors were observed only during anti-predator training sessions and others only during personality tests.

**Table 2.** Identification number and sex of parrots submitted to anti-predator training sessions and to the personality tests before and after the application of the anti-predator training sessions, and the predator stimuli used.

Anti-predator training sections				
Hawk	Ocelot	Human	Mixed (Hawk/Ocelot/Human)	Control
7♀	13♀	19♀	1♂	24♀
8♂	14♀	20♀	2♀	25♀
9♂	15♂	21♂	3♂	26♂
10♀	16♀	22♀	4♀	27♀
11♂	17♀	23♂	5♂	28♀
12♂	18♂	29♂†	6♂	30♂†

† Parrots that died during anti-predator training sessions.

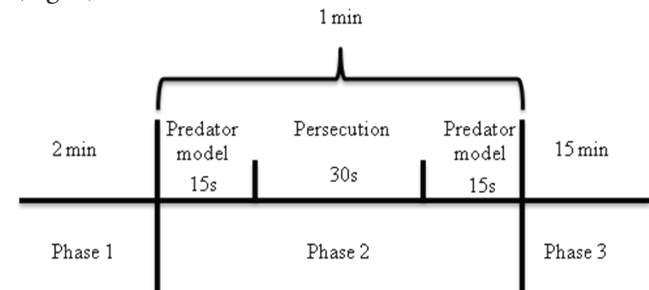
Training sessions were run in an enclosure similar to the maintenance aviary (50 m from the maintenance aviaries), but with its laterals covered by an opaque black plastic to prevent birds from seeing outside surroundings. The roof of the aviary was not covered by a black plastic. A circular opening of 0.3 m in diameter in the black plastic in the front of the enclosure allowed the researcher to video record all training sessions using a webcam COMPAQ. The enclosure's door was also covered with the black plastic and during the experiment was opened to show the models to the parrots inside. A bush at the end of the enclosure provided the parrots with shelter.

Each parrot group received three training sessions, except the mixed group, who received nine training sessions (three with each predator model); control groups, although not trained with predator models, also received three sessions with a chair. Training sessions were run in four consecutive days of February 2012, always between 08:00–09:00 h and 16:00–17:00 h, since these birds are diurnal and inactive in the hottest periods of day (Collar 1997, Pitter & Christiansen 1997, Gilardi & Munn 1998).

Parrots were captured in the maintenance enclosure and then transferred to the test enclosure each day, and a 15-min period was adopted for birds' acclimation and relaxing. All captures were done quietly, with minimal interference to avoid stressing the parrots and no influences of this procedure were detected during data analysis. When in the test enclosure, parrots in the maintenance enclosures could not see or hear the test groups. Each trial lasted 18 min, which consisted of 2 min filming before the presentation of the predator (phase 1), 1-min of conditioning (phase 2), and 15 min of filming after the end of conditioning (phase 3), thus, more than one group received anti-predator training in the same day, but not simultaneously.

The 1-min of conditioning was adapted from Griffin *et al.* (2001): the stimulus (predator) was shown to the animals for 15 s before a human dressing a costume (see below) and carrying a net entered the enclosure and began a 30 s simulated capture procedure (aversive experience;

birds were never caught). After the capture simulation, the predator appeared again to the parrots for more 15 s (Fig. 1).

**Figure 1.** Protocol used in the anti-predator training of the Amazon parrots.

The ocelot, human and chair stimuli appeared to the parrots through the frontal enclosure's door; the hawk appeared to the parrots through the enclosure's roof. The costume used by the man had the objective to camouflage his silhouette, *i.e.* for the parrots, the chaser was not a human. Control groups received the same training protocol used for the other groups, but the human persecution never occurred. Data were collected using focal sampling with instantaneous recordings in 15 s intervals (Altmann 1974).

### Memory tests

Memory tests were performed 30 and 60 days after the anti-predator training session. These tests consisted in showing the predator models to all groups of parrots (trained and controls) similar to that of the anti-predator training sessions, except that the chasing simulation did not occur.

### Personality tests

Behaviors recorded in the ethogram representing boldness and shyness were identified (Table 1). Risk-taking behaviors, normally expressed during encounters with predators or in stressful situations, were considered shy behaviors (van Oers & Naguib 2013), and

aggression, exploratory and maintenance behaviors, exhibited during calm, non-stressful events, were selected as bold (Smith & Blumstein 2013). A boldness score was calculated for each individual following Bremner-Harrison *et al.* (2004). Boldness scores were calculated per individual before and after anti-predator training sessions, during the novel object trials (personality tests; see below). The number of occurrences for shyness and boldness behaviors was counted to calculate the score. The number of shyness behaviors were multiplied by 1 and the number of boldness behaviors were multiplied by 2, and the higher the score, the bolder the individual was considered (Bremner-Harrison *et al.* 2004, Kurvers *et al.* 2010).

Personality tests consisted in presenting two unknown objects to the parrots: a traffic cone and a pot of potato chips connected to a bottle of milk; one object was shown to the birds before the anti-predator training sessions and the other object was shown to the birds after the anti-predator training sessions. The objects were presented to the birds on a platform at the centre of the enclosure. Four perches, with markings indicating the distances to the object (less than 1.3 m and more than 1.3 m), were connected to the platform.

The tests were conducted in the maintenance aviaries at 08:00 h and each group of parrots participated in only one test before and only one test after anti-predator training sessions. The behaviors and the distance of the birds to the objects (approach distance) immediately after its presentation were recorded for 60 min for each object, using the instantaneous focal-animal sampling method with 1-min intervals (Martin & Bateson 2007). The tests were filmed using the webcam of a COMPAQ notebook. Personality tests after anti-predator training sessions occurred before the memory tests, in the day following the end of the anti-predator training sessions.

### Data analysis of anti-predator tests

Data normality was evaluated using the Anderson-Darling test. Since the data did not meet the requirements for normality, we used Friedman's non-parametrical ANOVA test, with Dunn's *post-hoc*, to evaluate differences between parrots' responses to the different predator models (control, ocelot, hawk, mixed, mixed hawk, mixed ocelot, mixed human, and human), between phases (before, during and after the appearance of the predator model). Wilcoxon's test was used to compare the parrots' behaviors between 30 and 60 days after training (memory tests). The results for the mixed group were evaluated pooled (data from the tests with all predator models together) and separated (with only the responses showed for each predator model; hawk, ocelot and human). For all statistical analyses, the confidence level was 95% ( $\alpha = 0.05$ ) (Zar 1998).

### Data analysis of personality tests

Using an Anderson-Darling test we determined that our data did not meet the requirements for parametric statistics, so the data were square-root transformed and parametrical statistical tests were used throughout.

A paired *t*-test was used to test whether boldness scores differed significantly between treatments (before and after anti-predator training) and to test if displayed behaviors differed between distances (less than 1.3 m and more than 1.3 m) (Zar 1998). One-way ANOVA was used to test for differences in boldness score variation between treatments [Boldness Score after anti-predator training minus Boldness Score before anti-predator training (BSa - BSb)] (Zar 1998).

The correlation between mean percentage of predator aversion behaviors (= average of 30-day and 60-day shy behaviors  $\times 100$  / total recorded behaviors) and personality was tested using non-linear correlation analysis with quadratic function. Cluster analysis was used to determine the similarity in personality between individuals before and after anti-predator training sessions. The distance measure used was the difference between boldness scores and amalgamation rule was UPGMA (Zar 1998). Statistical tests were run using Minitab 12, Mynstat 12 and Past. For all statistical analyses, the confidence level was 95% ( $\alpha = 0.05$ ).

## RESULTS

### Anti-predator training

Parrots behaved similarly during the conditioning phase 2 of the anti-predator training sessions, only differing in the expression of inactivity, with the parrots of the control group more inactive than the parrots of the hawk and ocelot groups (Fig. 2). Parrots trained with the ocelot hid more than the control group, and parrots trained against all predators (mixed group) flew more than the parrots of the control group (Fig. 2). Parrots of the control group paced and slept more than the other groups; parrots of the mixed group nodded their heads more than the parrots of the hawk group (Fig. 2). Relaxing behaviors, like yawning, self and allopreening, were not exhibited during the conditioning phase.

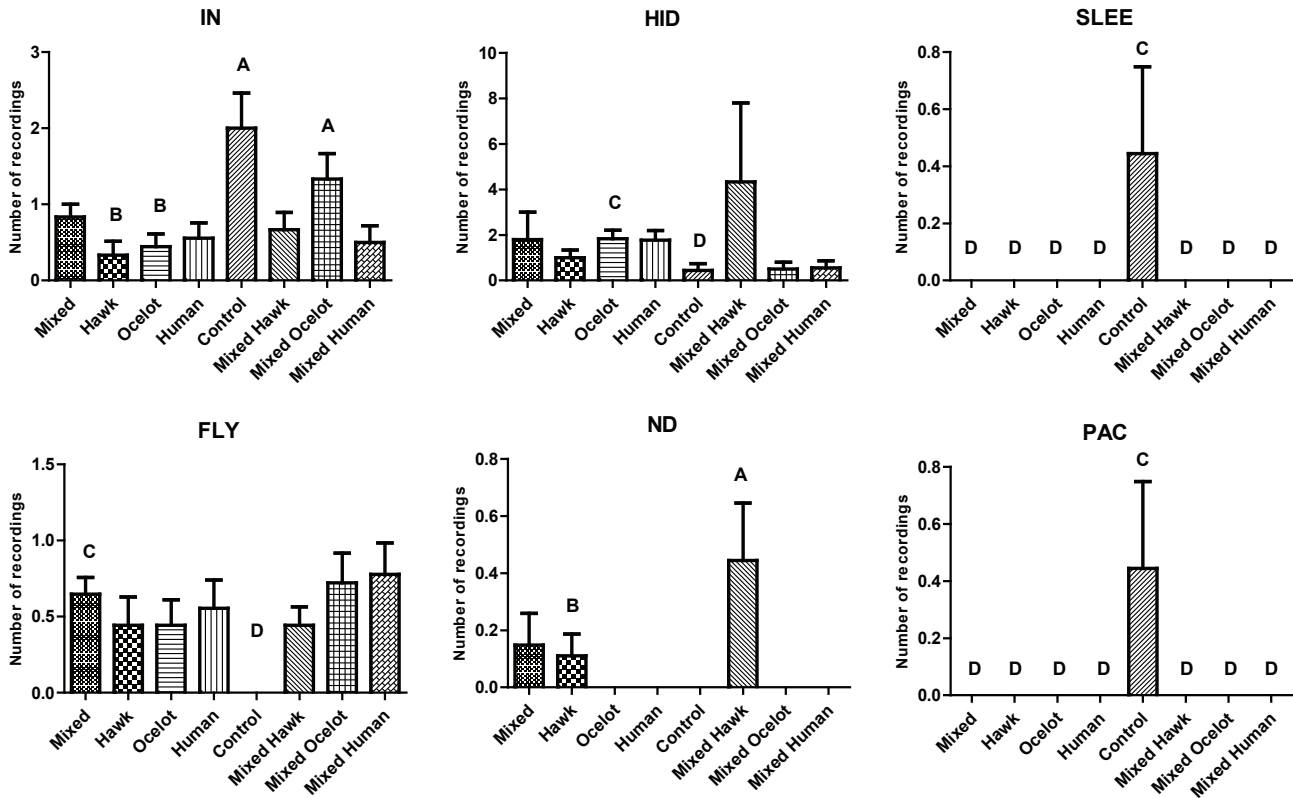
Parrots expressed more anti-predatory behaviors with all predator models during phase 3 (hiding behind the shrub, and flying). The control group behaved in a more relaxed way, expressing more behaviors like walking on the perch, inactivity, and sleeping (Fig. 3).

Aversion behaviors increased significantly after the presentation of the predator models, including with the human model (Fig. 3). Relaxing behaviors decreased

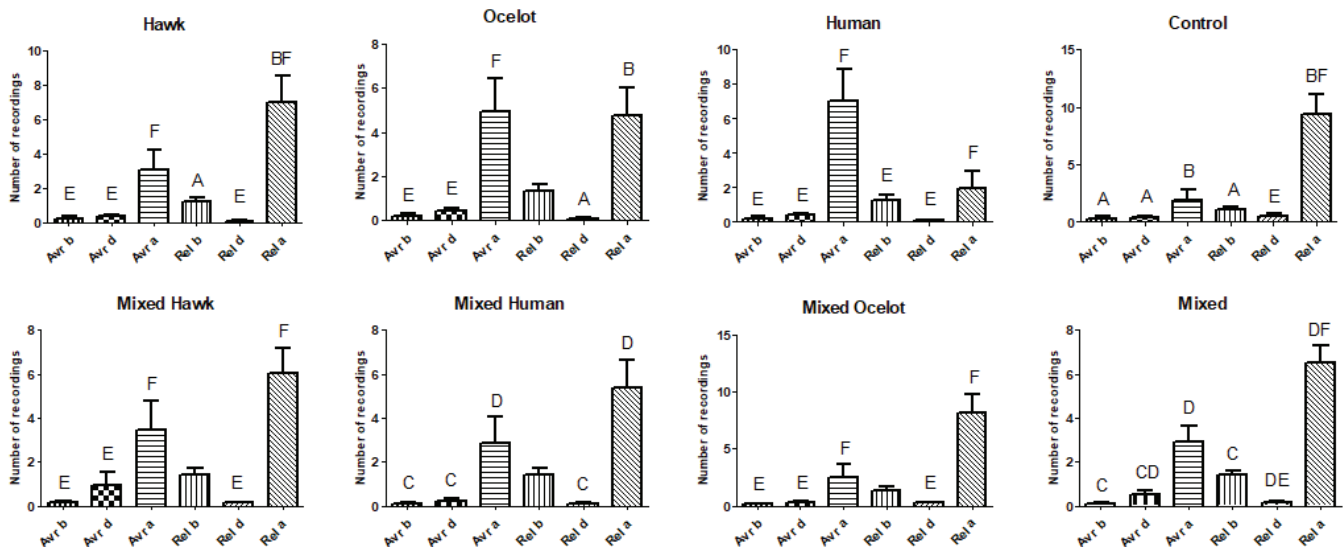
during the presentation of the predator models, but increased significantly during phase 3, especially during the last 5 min of phase 3 (Fig. 3). Although aversion behaviors increased in phase 3 in the control group, it showed the lowest increase when compared to the predator models (Fig. 3).

No differences in the behaviors of the parrots were observed 30 and 60 days after the anti-predator training for all predator models, except for the behaviors inactive

in the hawk group, and walking on perch in the mixed group. Parrots trained against the hawk were more inactive 30 days after the end of the anti-predator training sessions (mean  $\pm$  SE: 30 days:  $25.22 \pm 6.14$ ; 60 days:  $9.39 \pm 4.11$ ;  $Z = 2.29$ ,  $P = 0.01$ ,  $n = 18$ ;  $df = 1$ ). Parrots trained in the mixed group walked more on the perch 30 days after the end of the anti-predator training sessions (mean  $\pm$  SE: 30 days:  $1.94 \pm 0.57$  records; 60 days:  $0.83 \pm 0.35$ ;  $Z = 2.37$ ,  $P < 0.01$   $n = 18$ ;  $df = 1$ ).



**Figure 2.** Behaviors displayed by Amazon Parrots during phase 2 of the anti-predator training sessions. IN = inactive; HID = hiding behind tree; FLY = flying; ND = nodding head; PAC = pacing; SLEE = sleeping; Superscript letters: CD =  $P < 0.05$ ; AB =  $P < 0.01$ .

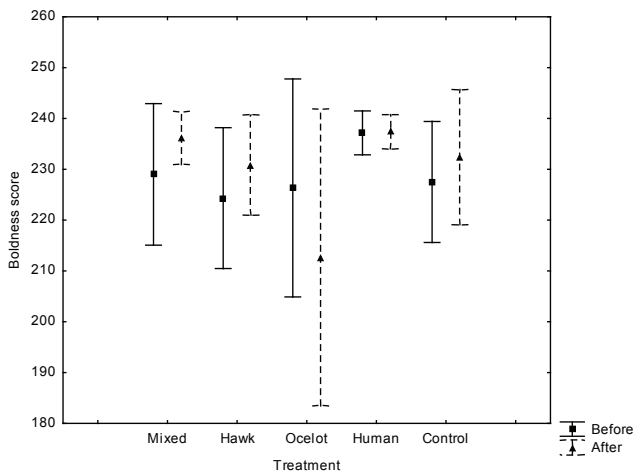


**Figure 3.** Behaviors displayed by the Amazon Parrots during phases 1, 2 and 3 of the anti-predator training sessions. Avr = aversion behaviors; Rel = relaxing behaviors; b = before the appearance of the predator model (phase 1); d = during the appearance of the predator model (phase 2); a = after the appearance of the predator model (phase 3); AB  $P < 0.05$ ; CD  $P < 0.01$ ; EF  $P < 0.001$ .

### Personality tests

Boldness scores of parrots ranged between 178 and 240. The personality of most individuals changed after the treatments. The scores increased significantly in 50% of cases ( $t = -4.47, n = 16, df = 15, P < 0.001$ ) and decreased significantly in 33% of cases ( $t = 2.35, n = 16, df = 15, P = 0.02$ ).

The most fearful individuals before training based on boldness scores were those that were trained against the Harris's Hawk (boldness score's mean: 224; Fig. 4), and the most fearful individuals after training were those that were trained against the Ocelot (boldness score's mean: 212; Fig. 4). In general, there was a tendency of increased boldness after training, except in parrots trained against ocelots, where the boldness score decreased (Fig. 4).



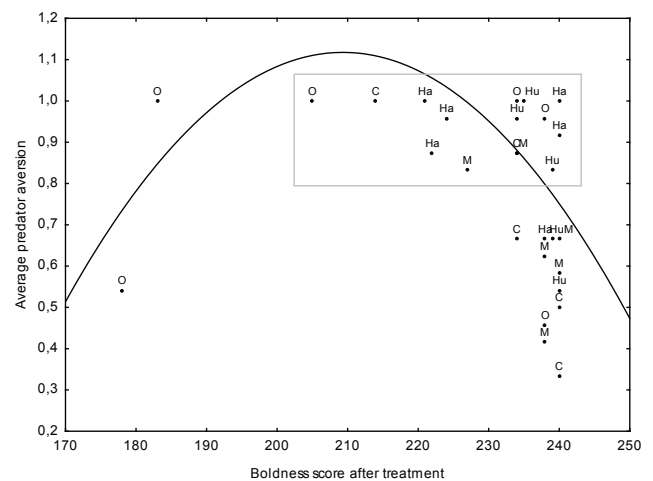
**Figure 4.** Means and confidence intervals (95%) of Blue-fronted Parrot boldness scores before and after anti-predator training sessions. All individuals underwent anti-predator training (except control ones), either against all models (mixed) or one predator only (hawk, ocelot, and human).

There were no significant differences in the personality of parrots that underwent different training and controls ( $F = 1.7, n = 28, df = 4, P = 0.177$ ), before and after treatment ( $F = 0.1, n = 28, df = 4, P = 0.814$ ), and no significant interaction between these factors was observed ( $F = 1.7, n = 28, df = 4, P = 0.186$ ). Additionally, there were no significant differences in mean differences of boldness scores ( $BSa - BSb$ ) between treatments ( $F = 1.7, P = 0.186$ ). However, parrots displayed behaviors more frequently in the distances greater than 1.30 m from the objects ( $t = -6.45, P < 0.001, n = 56, df = 1$ ).

Cluster analysis did not group parrots from different treatments or separate control parrots from individuals who underwent anti-predator training. For instance, before the treatment, bird 18 was separated from the other individuals and had a boldness score indicative of shyness ( $BSb = 188$ ). After the treatment, the same individual was grouped with other parrots (27, 4, 9, 11,

and 12), and exhibited a higher boldness score ( $BSa = 205$ ). Parrots that exhibited intermediate boldness scores after training belonged mostly to the group trained with the Harris's Hawk (9, 11, and 12), but also to the control (25), ocelot (18), and mixed groups (4).

Boldness scores after training had a significant quadratic relationship with mean percentage of predator aversion, measured 30 and 60 days after the treatments ( $Aversion = -16.0 + 0.16 \times BSa - 0.0004 \times BSa^2$ ) (Fig. 5), which means that parrots with intermediary boldness scores showed higher aversion to the predators.



**Figure 5.** Relationship between boldness scores after anti-predator training and average aversion to three predator types 30 and 60 days after training. Bolder individuals only exhibited lower aversion values. The box indicates the region of the graph with intermediate and bold individuals that exhibited high aversion to predators and that would be good candidates for release. The letters indicate the different training regimes: C – control, Ha – trained against Harris's Hawk, O – trained against ocelot, Hu – trained against human, and M – mixed training against all predator models.

### DISCUSSION

Anti-predator training modified the behaviors of the parrots, increasing their awareness about their predators and diminishing relaxing behaviors. Additionally, the anti-predatory behaviors persisted for at least 60 days after the end of the anti-predator training sessions. Anti-predator behaviors have to be effective in the very first time a prey encounters its predator, but these responses can be improved with experience (McLean & Rhodes 1991, Griffin *et al.* 2000). Although the parrots of this study responded to the predators in the first session, they exhibited stronger responses after two training sessions; a similar result was observed for the Noisy Friarbird *Philemon corniculatus* (Latham, 1790) trained by Curio *et al.* (1978).

Relaxing behaviors were more frequent in the parrots of the control group during phase 2 (predator model appearance), and this response reflects the fact that the parrots were able to recognize that the model of a chair

was not a threatening stimulus. New Zealand Robins [*Petroica australis* (Sparrman, 1788)], Greater Rheas [*Rhea americana* (Linnaeus, 1758)] and Tropical Screech-owls [*Megascops choliba* (Vieillot, 1817)] also responded to a control stimulus expressing relaxing behaviors (Maloney & McLean 1995, Azevedo & Young 2006, Specht 2007). The abnormal behavior pacing was exhibited by one parrot of the control group (number 26); this individual displayed such behavior in all phases of the study, and should be eliminated from the group of parrots destined to be reintroduced.

The behavior hiding behind the shrub was more frequently exhibited in response to the mixed hawk group. This response was also observed in a study with Hispaniolan Amazon Parrots [*Amazona ventralis* (Müller, 1776)] trained against falcons (White-Jr. *et al.* 2005), and when training owls against hawks (Alonso *et al.* 2011). Nodding head was exhibited mainly against the hawk model. The most frequent anti-predator response of Rock Partridges [*Alectoris graeca* Meisner, 1804)] to a hawk model was to crouch (Zaccaroni *et al.* 2007) which, according to the authors, is a cryptic behavior, very effective against predatory birds. Maybe this behavior, associated to the green plumage of the parrots (they become cryptic immerse in the vegetation), constitute a good way to avoid being located by flying predators (Alcock 2013).

Inactive and flying were the most recorded behaviors displayed by parrots in association with Ocelot and human models. Possibly, the best tactic against terrestrial predators, which use a silent and furtive approach toward prey, is to remain inactive in order to monitor and evaluate the behavior of the predator (Zaccaroni *et al.* 2007). This strategy allows prey to save energy, since it will only exhibit escape behaviors if necessary (risk-disturbance hypothesis; Frid & Dill 2002). The Ocelot and the human models elicited both behaviors, but for the human model, these responses were stronger than for the Ocelot, where parrots flew away in almost all sessions. Perhaps this stronger response to the human model could be a result of the perception of a greater risk of predation by the parrots, which corroborates the risk-disturbance hypothesis of Frid & Dill (2002).

Memory tests showed that the responses of parrots to the predators lasted for at least 60 days after the end of the training sessions. Similar results were found in a study of Greater Rheas (Azevedo & Young 2006). Predator encounters probably occur within a period of two months in the wild, and the persistence of the proper anti-predatory responses is important, since it can increase the survival rate of the parrots when reintroduced.

It is difficult to establish the exact number of training sessions necessary to elicit the right anti-predatory behaviors and to avoid habituation, but it is suggested that the least number of training sessions is best to avoid

habituation (Griffin *et al.* 2000, Hemmi & Merkle 2009). For example, Houbara Bustards [*Chlamydotis undulata* (Jacquin, 1784)] habituated to a fox model after two training sessions (van Heezik *et al.* 1999), and Greater Rheas habituated to predator models after five training sessions (Azevedo & Young 2006). Parrots in this study did not show signs of habituation since the responses to the predator models were consistent over all trials; in fact, in the first two trials they were already responding strongly to the predators.

Anti-predator training changed the personality of Blue-fronted Amazon Parrots, and in most cases it promoted an increase in the boldness scores. A study with Greater Rheas, a study with tropical Screech-owls, and a study with Trinidadian Guppies [*Poecilia reticulata* (Peters, 1859)] found significant decreases in the boldness scores of the individuals after anti-predator training sessions (Azevedo & Young 2006, Specht 2007, Smith & Blumstein 2012). In the present study, boldness scores decreased after anti-predator training sessions in only 33% of sampled parrots.

It is known that fear responses can vary according to the personality of the individuals (Verbeek *et al.* 1994, Wilson 1998, Carere *et al.* 2005), and according to the individual's life history (early experiences) (Levine *et al.* 1993, Fox & Millam 2004). For instance, bolder Rainbow Trout [*Onchorhynchus mykiss* (Walbaum, 1792)] became shyer after watching shy individuals being presented to novel objects (Frost *et al.* 2007). In the current study, the early experiences of the parrots could not be determined, since all individuals were recovered from traffic. Although interviews were conducted with the parrot owners, they did not provide any information about the origins of the birds, fearing legal punishment. The only information about the early experiences of parrots was that all individuals studied had lived in captivity for at least five years. The boldness of the parrots trained against humans achieved the highest mean-scores and the minimum treatment variation (236 before training to 237 after training; corroborating the hypothesis that they may be hand-reared. This result indicates that these individuals may not be ideal for reintroduction, since the chance of being recaptured by humans may be great or that training against humans should be more intense. Feenders *et al.* (2011) showed that hand-reared Starlings [*Sturnus vulgaris* (Linnaeus, 1758)] had greater latency time to move in novel environments than wild-caught ones, but found no difference in the behavioral responses between both groups of birds in a novel object experiment.

The later experiences of the parrots, however, could be determined since the parrots stayed in the IBAMA facilities for at least four months prior to experiments. All parrots received a routine of environmental enrichment, and it has been shown that environmental enrichment

diminishes neophobia in Amazon Parrots (Meehan *et al.* 2003, Fox & Millam 2007). The consistency of lack of variation in responses of parrots to the novel objects before-after-anti-predator training may be reflecting this routine.

The tendency of parrots to exhibit bold behaviors in the personality test even after the training sessions may be explained by their remarkable cognitive ability (Emery 2006). The ability to differentiate non-predators from predators ensures that animals do not generalize their responses to non-predators (Griffin *et al.* 2000, Azevedo *et al.* 2012), as the objects used in the tests. Probably parrots perceived that the objects presented did not pose danger because their shape differed from that of their predators (Bremner-Harrison *et al.* 2004, Kurvers *et al.* 2010, Lendvai *et al.* 2011). Parrots in the control group exhibited a similar response, remaining calm and showing bold behaviors during training, in which a harmless object (a chair) was presented to them. This corroborates the idea that the parrots were able to discriminate between the objects used during the personality tests and the predators used during the anti-predator training.

In conclusion, anti-predator (aversion) behaviors increased significantly with the training sessions showing that the parrots adjusted their responses according to the new situation. Additionally, the adequate anti-predatory response persisted for 60 days, showing that the conditioning technique was successful. The anti-predator conditioning program also affected the personalities of the parrots, making parrots bolder or shyer. The anti-predator training protocol should be included in all conservation programs dealing with parrots, since this can enhance the survival skills of the birds after reintroduction. Personality tests combined with anti-predator training may help to select accurately the individuals more suited for release, and intermediate individuals or bold ones that recognize potential predators and exhibit aversive behaviors toward predators should be preferred.

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# Cooperative breeding and demography of Yellow Cardinal *Gubernatrix cristata* in Brazil

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**ABSTRACT:** We studied demography, territoriality and social/mate system of the Brazilian population of Yellow Cardinal (*Gubernatrix cristata*). The study was conducted in the municipality of Barra do Quaraí, western Rio Grande do Sul, Brazil, during two breeding seasons (October to February, 2013–2015). We ringed 35 (seven females, 14 males and 14 young) out of 53 individuals found, and by September 2015, the Brazilian population of Yellow Cardinal had 38 remaining individuals. Adult sex ratio was 1.5:1 and the lifespan was at least 8 years. Pairs are socially monogamous and territorial, with male-biased philopatry and female-biased dispersal. The mean territory size was 18 ha, and mean home range was 27.7 ha. Some pairs and nests (23%) were attended by one or two nest helpers, which contributed on nest and territory defense, and provisioning of nestlings and fledglings. Presence of helpers is a key new finding for this species. Parental care was biparental or cooperative, and the pair had high frequency of visits to the nest than helpers. Mean nest productivity was two fledglings/successful nest attended by helpers, and one fledgling/successful nest not attended by helpers. We recorded second broods after a successful attempt, only when helpers were present. Overall Mayfield nesting success was 18%, 40% for nests with and 13% without helpers. We recorded a case of inbreeding, between father and daughter. The species need for large home ranges and factors that may adversely affect the breeding success such as inbreeding, predation, and parasitism can exacerbate the status of the threatened Brazilian population and the species. It reinforces the importance of autecology studies and their contribution to the conservation schemes.

**KEY-WORDS:** breeding territory, home range, nest helpers, small population, threatened species.

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## INTRODUCTION

The Yellow Cardinal, *Gubernatrix cristata*, is a passerine of temperate South America and its natural history is relatively unknown. It occurs in the savannas of Argentina, Uruguay and southern Brazil (Jaramillo 2011). Due to their color and song, they are often captured for illegal trade in wildlife (Martins-Ferreira *et al.* 2013). Illegal trapping and wildlife trade, along with habitat loss, were the main causes of the great population decline for this species, now considered as globally “Endangered” and regionally threatened (BirdLife International 2015), “Endangered” in Argentina and Uruguay (López-Lanús *et al.* 2008, Azpiroz *et al.* 2012), and “Critically Endangered” in Brazil (Martins-Ferreira *et al.* 2013).

Home range is an area where an individual restricts its activities during the year or period (Odum & Kuenzler 1955). When part of or all home range is defended against other conspecifics it is defined as a territory (Nice 1941, Odum & Kuenzler 1955). Home range is a cognitive map of resources that individuals keep up-to-date to fulfil their requirements (Powell & Mitchell 2012). Social and

breeding behavior affect the territorial and home range dynamics, such as their sizes, boundaries, acquisition, dispersal, among others. Because natural habitats are usually fragmented to some degree, small patches may not have sufficient area for home ranges and also increase predation and parasitism near edges (Beier *et al.* 2002), as well as the patch isolation may have negative effects on dispersal (Pavlacky-Jr. *et al.* 2012).

Cooperative breeding is a social system characterized by a breeding pair and one or more individuals that did not breed, but collaborate to rear a brood (Woolfenden & Fitzpatrick 1984, Burt *et al.* 2007). These individuals are called nest helpers (hereafter, helpers). Why some individuals tend to postpone their own reproduction and help to rear a brood from others has intrigued scientists for decades. Studies have tried to explain how the cooperative breeding evolved (Poiani & Jermiin 1994, Du Plessis *et al.* 1995, Arnold & Owens 1998, Heinsohn & Legge 1999, Doerr & Doerr 2006, Russell *et al.* 2007, Hatchwell 2009, Cockburn & Russell 2011, Jetz & Rubenstein 2011, Feeney *et al.* 2013, Downing *et al.* 2015, Drobniak *et al.* 2015), but life-histories differ

considerably between species and there is not a one-size-fits-all hypothesis (Cockburn 1998, Berg *et al.* 2012, Gamero *et al.* 2014). There are more than 10,000 extant bird species in the world, and 9% are estimated to present cooperative breeding (Cockburn 2006), and among the oscines 18.5% (Cockburn 2003). The Neotropics is the region with highest biodiversity on Earth, but it is the relatively less studied in terms of bird behavior (Stutchbury & Morton 2001). It is estimated that 6% (218 species) of all Neotropical birds have cooperative breeding (Jetz & Rubenstein 2011), but the effective number of species that breed cooperatively may be slightly higher as the breeding systems and natural histories of more birds are being described.

Here, we describe cooperative breeding in the Yellow Cardinal for the first time. We compare breeding and success between pairs with and without helpers to determine the potential benefits of cooperation. We also examine demography of the Brazilian population of the cardinal, and place cooperation in terms of social system and breeding territories. We then interpret these new findings in the context of conservation of this threatened species.

## METHODS

### Study area

The study was carried out in Barra do Quaraí, state of Rio Grande do Sul. From four study sites, three are located at Espinilho State Park (ESP; 30°12'S; 57°30'W), and one at São Marcos Ranch (SMR), adjacent to the ESP. Only one site at ESP was not grazed by livestock. The mean annual rainfall is 1300 mm and it is highly variable between years. Mean annual temperature is 24.3°C, with occurrence of < 0°C in winter, and occasionally > 40°C in summer. The vegetation is a savanna dominated by *Prosopis affinis* and *Vachellia caven* (Fabaceae) and is the largest among the last remnants of that type of savanna in southern Brazil (Marchiori & Alves 2011).

### Data collection

We began with a pilot study from November 2012 until January 2013. We then carried out observations from October to February, during two breeding seasons (2013–2015) of the only known population of Yellow Cardinal in Brazil. Population size, sex ratio, and longevity were estimated using banded birds, and unmarked individuals when it was possible to identify them by unique marks on plumage. We searched for Yellow Cardinals at the beginning of each breeding season (October) and captured adults using mist nets and marked with an aluminum

ring (standard CEMAVE/ICMBio; the Brazilian Banding Agency) and a unique combination of colored plastic rings. Ten days old nestlings or chicks that just fledged were also marked. We measured birds following Eck *et al.* (2011): wing chord, tail length, tarsus length, bill and culmen length, nostril to bill tip, and total length, using a precision caliper (0.1 mm) and a ruler (1.0 mm). Body mass was measured using a precision dynamometer (0.5 g) of kind Pesola® Swiss Micro 20060. Plumage categorization follows Wolfe *et al.* (2010).

Individual behavior was recorded *ad libitum* while monitoring nests and when away from the nest (Altmann 1974). Observations of parental care were mainly in the morning, from sunrise until 11:00 h, or afternoon, from 17:00 h until sunset, using binoculars (12 × 50 mm) and spotting telescope (25–60×). We used a camcorder at one nest, with mean recording time of 72 ± 21.7 min (50–100 min; *n* = 5) every 2–3 days. We divided nestling stage in two nestling phases: initial (1–8 days) and final (9–16 days), and calculated the visit rate for each individual and phase.

We considered breeding territory as the maximum area that a male defended and where it nested (Nice 1941, Welty & Baptista 1988) and home range as the area frequently used but not necessarily defended (Odum & Kuenzler 1955, Powell & Mitchell 2012). When found, we noted the coordinates of family groups or individuals using a handheld GPS. Encounters that ended without chasing or fight and individuals gone on opposing directions, we considered as territory boundaries. We estimated the area of breeding territories using Minimum Convex Polygon at 95% confidence (MCP 95%) (Odum & Kuenzler 1955). We estimated home range size using Fixed Kernel Density Estimation at 95% probability of occurrence (KDE 95%), and kernel bandwidth calculated by Least Squares Cross Validation (LSCV) (Seaman *et al.* 1999, Jacob & Rudran 2006). We used only data from individuals with more than 25 locations due to minimum sample size limitations of KDE (Seaman *et al.* 1999). Breeding territory and home range estimations were calculated using package *adehabitatHR* (Calenge 2006) in R (R Core Team 2015).

Productivity was calculated as the mean number of fledglings by all successful nests. We calculated the apparent success (Marini *et al.* 2010), as the ratio between the number of successful nests and all monitored nests. Complementarily, we calculated Mayfield nesting success (Mayfield 1975), with modifications to compare nests with and without helpers (Hensler & Nichols 1981).

### Statistical analysis

To assess differences on morphometric measurements between sexes and parental care between nestling phases

we used the non-parametric Mann-Whitney *U*-test (Wilcoxon rank-sum test). Comparison of the frequency of visits to the nest of each group member (male, female and helper) were run with Kruskal-Wallis *H* tests, followed by post-hoc pairwise Mann-Whitney *U*-tests. Values are presented as mean  $\pm$  SD and considered statistically significant when  $P < 0.05$ .

## RESULTS

### Capture, morphometric and demographic data

We captured and marked 35 birds (7 adult females, 14 adult males, and 14 young). We also recognized 18 unmarked individuals (seven females, four males, and seven young). Of the 53 birds found in this study, 15 disappeared, and the remaining 38 were the known population of Yellow Cardinal in Brazil at that time. We found a secondary sex ratio of 1.5:1 (21/14). A male captured as adult in 2008 was last seen in February 2015 and so was at least 8 years old. There was no difference in body mass between sexes (males:  $47.8 \pm 2.8$  g,  $n = 9$ ; females:  $47.9 \pm 3.5$  g,  $n = 4$ ), and we found sexual dimorphism only in wing chord (males:  $94.9 \pm 2.9$  mm,  $n = 9$ ; females:  $89.9 \pm 2.5$  mm,  $n = 4$ ;  $U = 2.5$ ,  $P = 0.02$ ) and tarsus length (males:  $27.0 \pm 0.8$  mm,  $n = 9$ ; females:  $25.4 \pm 1.0$  mm,  $n = 4$ ;  $U = 4.5$ ,  $P = 0.04$ ) (Table 1).

**Table 1.** Morphometric measurements of marked adults Yellow Cardinal (*Gubernatrix cristata*) grouped by sex. Values presented as mean  $\pm$  1 SD ( $n$ ).

Measurement	Male	Female
Body mass (g)	$47.8 \pm 2.8$ (9)	$47.9 \pm 3.5$ (4)
Total length (mm)	$200.5 \pm 4.8$ (8)	$195.3 \pm 6.0$ (3)
Wing cord (mm)	$95.0 \pm 2.9$ (9)	$89.9 \pm 2.5$ (4)
Tail length (mm)	$89.0 \pm 3.9$ (9)	$87.4 \pm 2.7$ (4)
Tarsus length (mm)	$27.0 \pm 0.8$ (9)	$25.4 \pm 1.0$ (4)
Bill length (mm)	$18.2 \pm 1.1$ (9)	$19.2 \pm 0.6$ (4)
Culmen length (mm)	$15.6 \pm 2.1$ (7)	$16.1 \pm 0.1$ (2)
Nostril to bill tip (mm)	$11.5 \pm 0.4$ (9)	$11.5 \pm 0.3$ (4)

### Social/mate system

The Yellow Cardinal is socially monogamous and the mated pairs may stay together for more than one breeding season, and only two divorces were observed. Additionally, two males lost their mates and mated again. In 2013, from nine mating pairs, one female disappeared and one divorced. After a successful nest, the divorced female and her two offspring disappeared in December 2013, but all three were seen again in October 2014. At that time, the female had found another male, and the two offspring became helpers. In 2014, one female at a

nest was lost to predation and a second female divorced. All other pairs remained together. The divorced female of 2014 was later found paired in a neighboring territory in 2015. On a territory where both individuals of the pair were marked, we ringed a nestling at the nest in January 2013. In May 2013, the female disappeared, but the young was observed with the male. In October 2013, we found father and daughter on their territory and apparently paired, which was confirmed in December 2013 when we found a nest with nestlings. This male remained alone during the second breeding season. It is the first record of inbreeding in the Yellow Cardinal. A fledgling from this pair was ringed, but all young and the female were not seen since January 2014.

### Nest helpers

In 2012, we found a group with an adult male, an adult female and a male helper in formative plumage with some grey patches. We observed three pairs accompanied by male helpers from December 2012 to January 2013. We found 30 nests in two breeding seasons (2013–2015), of which helpers attended seven. A female helper attended one mating pair in the first season (2013). Two male helpers attended a mating pair in the second season (2014–2015), but apparently, only one of them fed the nestlings.

Helpers were observed contributing in territory and nest defense, feeding nestlings and caring of fledglings. In the latter case, a mating pair had a successful nesting attempt in December 2012 and re-nested in January 2013. The helper attended the first nest but not the re-nesting attempt, as it was taking care of fledglings.

Fledglings may stay in the natal territory for up to 10 months ( $n = 1$  female). Apparently, helpers are offspring of the mating pair, and it was confirmed in one case where helpers were marked as nestlings. In other cases, helpers were in formative plumage, which we assume that they were offspring of the previous breeding season of the breeding pair.

A male was found in October 2013 defending a small territory. It budded off part of its natal territory, where it was helper in the previous breeding season (2012–2013). This male did not mate, and then it returned to its natal territory as helper, where it stayed at least until February 2014. In October 2014, this male was found alone on its previous territory. Later in the season (November 2014), we found it in another territory and paired with an unmarked female, where it had two breeding attempts.

### Productivity and nesting success

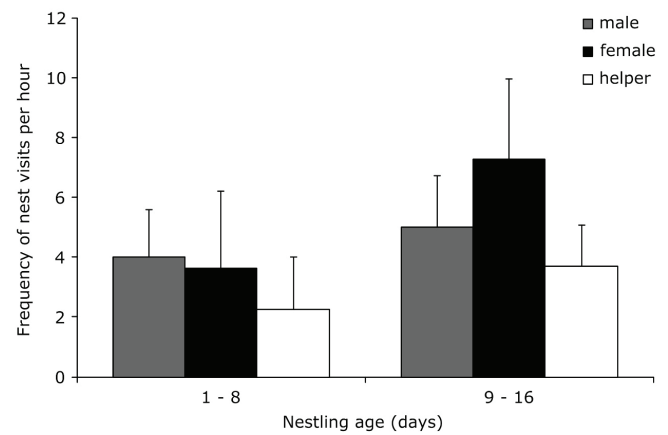
Mean productivity per successful nest was  $1.6 \pm 0.74$  fledglings ( $n = 8$ ). Successful nests without helpers fledged

a mean of one chick (4 fledglings/4 nests), and with helpers fledged two (8 fledglings/4 nests). The apparent success of nests with and without helpers was 57% (4/7) and 31% (4/13), respectively. The Mayfield Nesting Success was 40% and 13% for nests with and without helpers, respectively (18% for all nests pooled). There was no difference between nests with and without helpers in probability of survival for incubation ( $0.544 \pm 0.239$  vs.  $0.403 \pm 0.117$ ;  $Z = 0.53$ ;  $P = 0.60$ ), nor nestling stage ( $0.732 \pm 0.231$  vs.  $0.318 \pm 0.125$ ;  $Z = 1.58$ ;  $P = 0.11$ ).

### Parental care

We observed about 12 h of parental care at three nests and recorded 6 h at one nest. The total frequency of visits to the nest was  $12.28 \pm 5.26$  visits/h and we found a significant difference between initial and final nestling phases ( $9.91 \pm 3.88$  vs.  $16.0 \pm 5.16$  visits/h;  $U = 14$ ,  $P = 0.03$ ,  $n = 18$ ). Males made  $4.39 \pm 1.69$  visits/h, females  $5.06 \pm 3.13$  visits/h and helpers  $2.83 \pm 1.72$  visits/h (Figure 1). There was a significant difference on visit rate between family members during the complete nestling period ( $H_2 = 7.92$ ;  $P = 0.02$ ), especially between helpers and females ( $2.83 \pm 1.72$  vs.  $5.06 \pm 3.13$  visits/h;  $U = 89.5$ ;  $P = 0.02$ ), and helpers and males ( $2.83 \pm 1.72$  vs.  $4.39 \pm 1.69$  visits/h;  $U = 84$ ;  $P = 0.01$ ). Only females increased significantly their visit rate from initial to final nestling phase ( $3.64 \pm 2.58$  vs.  $7.29 \pm 2.69$  visits/h;  $U = 12.5$ ;  $P = 0.02$ ). There was no difference between frequency of visits per group member on initial phase ( $H_2 = 4.32$ ;  $P = 0.12$ ), but there was significant difference on final phase ( $H_2 = 7.75$ ;  $P =$

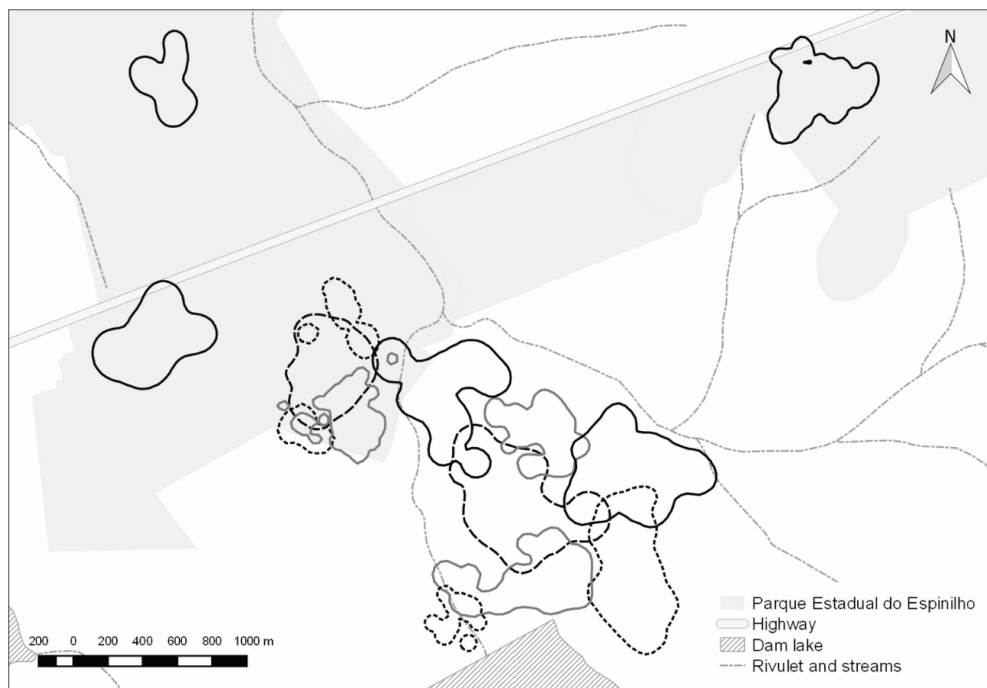
$0.02$ ) between helpers and females ( $3.71 \pm 1.38$  vs.  $7.29 \pm 2.69$  visits/h;  $U = 5$ ;  $P = 0.01$ ).



**Figure 1.** Frequency of visits to the nest of male (grey bars), female (black bars), and helper (white bars) on nestling age of the Yellow Cardinal (*Gubernatrix cristata*). Bars represent mean  $\pm$  1 SD.

### Breeding territories

Mean estimated breeding territory size was  $17.9 \pm 5.6$  ha (11.9–28.4 ha;  $n = 9$ ). Mean home range size was  $27.7 \pm 9.1$  ha (14.5–41.9 ha;  $n = 9$ ; Figure 2). Breeding territories were relatively stable and defended year-round. A yearling female was marked in October 2013 and found later paired with a male two territories away from her natal territory in November 2013. The mean distance between simultaneous nests of different breeding pairs/territories was  $443 \pm 155$  m (215–628 m;  $n = 6$ ).



**Figure 2.** Distribution of home ranges (polygons) of 13 breeding pairs of Yellow Cardinal (*Gubernatrix cristata*), in the municipality of Barra do Quaraí, state of Rio Grande do Sul, Brazil. Shaded area represents the protected area of Espinilho State Park. Polygon lines (grey, continuous black, dotted, dashed) are only for visual differentiation purposes.

Birds were territorial, with both sexes defending the territory. Encounters between individuals of different territories were noted ( $n = 8$ ), where at least 50% ( $n = 4$ ) resulted on agonistic interactions and chasing. In one case (January 2012), two males stepped into another pair's territory, where it had an active nest, and they were readily chased and expelled by the breeding pair. In another case, a mating pair with two juveniles came into a neighbor territory. Agonistic interactions occurred inside the invaded territory, where only adults engaged in fight, accompanied by juveniles from safe distance. Three days later, we found these two pairs fighting in the same site.

Breeding territories increased from nine during the first season to 12 in the second season. The main cause was males that were helpers or were alone on the first season, but that found females to mate on the second season. Two of these males were alone on isolated territories and moved into larger available areas. Other two males were helpers on a prior season, moved to other areas (a territory far from natal ground) by territorial budding and paired with unmarked females (November 2014).

We noted some movements outside territories for some individuals. One case was in winter (July 2015), when a pair was found alongside a vicinal dirty road, where they gone about 700 m far from their territory. The pair was apparently foraging on rice seeds of a harvested field, with other bird species, as Red-crested Cardinal (*Paroaria coronata*), Saffron Finch (*Sicalis flaveola*), Shiny Cowbird (*Molothrus bonariensis*) and Grayish Baywing (*Agelaioides badius*). Other case was noted during the second breeding season at a stream between two territories (about 200 m from both territorial boundaries). There was a tree with dark purple and ellipsoid fruits (*Chrysophyllum marginatum*, Sapotaceae) at the stream bank. In 12 November 2014, we observed a widowed male feeding on those fruits, and the tree was east of its territory. In 15 November 2014, we encountered two males of a territory south of the tree. In both situations, the individuals did not show any territorial behavior.

## DISCUSSION

We present here the first study about the Brazilian population of the Yellow Cardinal. We report that the remaining population is very small in Brazil and we confirmed a case of inbreeding, the first in the wild. We also found that the Yellow Cardinal defends large territories, fledglings show delayed dispersal and with male-biased philopatry. Moreover, we show that the species may breed cooperatively with nest helpers.

We are confident that the entire Brazilian population of Yellow Cardinal from Espinilho savanna was monitored by searching all potential areas of

occurrence of the species. Small populations are likely to have genetic and demographic problems through time, such as inbreeding (Lande 1988, Stacey & Taper 1992, Pimm *et al.* 1993), which we observed in this population. Unmarked individuals that appear in definitive basic plumage may be immigrants from Argentina (about 4 km) or Uruguay.

The small bias towards males on adult sex ratio (1.5:1) that we found, despite the small sample and not being significant, may be caused by the tendency for males to become helpers (Doerr & Doerr 2006) and female-biased adult mortality (Székely *et al.* 2014). For White-banded Tanager, *Neothraupis fasciata*, a close-related species, the primary sex ratio was 1:1, including all nestlings of all clutches (Gressler *et al.* 2014). Apparently, Yellow Cardinal is a species with female-biased dispersal, and males tend to be philopatric. Dispersal is a critical event in the life of an individual, with high inherent risks that tend to reduce the survival of dispersing birds. In addition, the opposite is true for philopatric individuals, which tend to have higher survival rates. White-banded Tanager have female-biased dispersal (Soares 2007) with slightly lower survival rates for females when fledglings (less than 2 months old) and small biases on sex ratio towards males as a result of higher survival rates of the philopatric sex, being 15% higher for subadult males than for subadult females (Gressler 2012). Female-biased adult sex ratios are also associated to higher divorce rates (Liker *et al.* 2014). We found a relatively low divorce rate (14%), which corroborates this proposition.

Mortality rates are unknown for the Yellow Cardinal, and in our study, it was not possible to estimate adult survival rates due to difficulties to distinguish between mortality and dispersal, and the short-term monitoring. However, adult survival seems to be high in the Brazilian population, whereas all nine adults marked in the first breeding season were found and monitored in the second season. We estimated the age for a male (about 8 years old) based on ringing data and plumage, but this individual may be older as we do not know how old it was when it was marked. A wild female of Northern Cardinal (*Cardinalis cardinalis*), a passerine with similar body size, was reported to survive more than 15 years old (Klimkiewicz & Fitcher 1987). Birds marked as nestlings are excellent opportunities to obtain precise data on lifespan, as for other life-history traits, by means of continuous monitoring.

While there was no sexual dimorphism with respect to body mass (as in Argentina, Domínguez *et al.* 2015), we did find differences in wing and tarsus measurements. In Thraupidae, most species exhibit slight or no sexual dimorphism in body mass (Hilty 2011). Sexual size dimorphism is reported more frequently for species with monomorphic plumage (Faria *et al.* 2007, Chiarani &

Fontana 2015). Székely *et al.* (2007) suggests that wing and tarsus lengths may be related to mating competition, where larger individuals have an advantage.

Parental care is unknown in nearly half (4313 species) of the 9456 species of birds for which parental care was summarized (Cockburn 2006). This is the case for the Yellow Cardinal, which we can now say is an occasional cooperative breeder. Phylogeny may play a role alongside environmental conditions on cooperative breeding occurrence (Edwards & Naem 1993), and it could emerge or disappear within a lineage (Berg *et al.* 2012). Recent molecular phylogenies found that *Gubernatrix*, *Hedyglossa* (*Diuca*) and *Neothraupis* compose a monophyletic clade (Barker *et al.* 2013, Burns *et al.* 2014), and cooperative breeding was already reported for *Neothraupis* (Alves 1990, Manica & Marini 2012).

We noted that individuals could begin the season alone on their own territory and become helpers later in the same season. Nests with helpers had twice the productivity as those with only the pair. Since we do not have data for parental care in nests without helpers, we were not able to identify the cause of increase in productivity by helper presence. The White-banded Tanager had similar productivity with and without helpers, but with helpers, parental effort by the adult male decreased (Manica & Marini 2012). Load lightening hypothesis predicts that one or both parents could reduce their contribution to the nest due to the extra food delivered by helpers, increasing parent survival (Manica & Marini 2012). Other possible effects of helper presence are reduced maternal allocation of resources on eggs (Paquet *et al.* 2013), and reduced rates of nest predation (Schaub *et al.* 1992) and brood parasitism (Canestrari *et al.* 2009). We observed post-fledging care by helpers, which allows breeders to perform more breeding attempts, as well as it might increase their survival (Langen 2000). More data on parental care for Yellow Cardinal is needed to understand how helpers affect productivity and survival.

We found that breeding territories were close together on park-like vegetation, with almost no unoccupied area between them, which may indicate habitat saturation. High adult survival rates and habitat saturation are potential causes of cooperative breeding (Arnold & Owens 1998), as it is for White-banded Tanager (Alves 1990, Manica & Marini 2012). Also, the presence of helpers may reduce nest parasitism (Feeney *et al.* 2013). Nevertheless, the Brazilian population of Yellow Cardinal is suffering with high rates of brood parasitism by Shiny Cowbird, including nests with helpers (CB, MR and CSF, pers. obs.).

Breeding territory and home range sizes may be considered large for a passerine of its size (~47 g). However, our estimations could be biased due to small sampling effort, and may be considered with caution,

especially for home ranges estimates. Other grassland birds have smaller territories and home ranges. It was estimated that mean territory size for Lesser Grass-finch (*Emberizoides ypiranganus*, 20 g) is 1.1 ha (maximum 2.4 ha) (Chiarani & Fontana 2015), 3.7 ha for White-banded Tanager (Soares 2007). Chiarani & Fontana (2015) found that 83% of Lesser Grass-finch territories had the same males defending it in both breeding seasons. Pereira (2015) found a density of one territory/100 ha for Yellow Cardinal in the same study site, reflecting its large territories. Dardanelli *et al.* (2006) studied the minimum area requirements of a bird community in Argentina, and they found that, from 54 woodland species, 80% needed no more than 3 ha. However, they also found that nine species needed fragments of 80 ha or more, six of which also occur in our study site: Sharp-shinned Hawk (*Accipiter striatus*), White-fronted Woodpecker (*Melanerpes cactorum*), Tufted Tit-Spinetail (*Leptasthenura platensis*), Scimitar-billed Woodcreeper (*Drymornis bridgesii*), Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), and Suiriri Flycatcher (*Suiriri suiriri*).

Delayed and female biased dispersal is reported for other cooperatively breeding birds (*e.g.* Florida Scrub-jay *Aphelocoma coerulescens*, Woolfenden & Fitzpatrick 1984 and White-banded Tanager Soares 2007). Delayed dispersal is also commonly associated with cooperative breeding (Koenig *et al.* 1992), but some species delay dispersal without helpers (*e.g.* Siberian Jay *Perisoreus infaustus*, Ekman & Griesser 2016). Some cooperatively breeding species are able to expand and defend larger territories due to increased group size. Consequently, groups with larger territories increase the chances of territory budding by helpers (Woolfenden & Fitzpatrick 1984).

### Conservation actions

Some findings of our study are of conservation concern for this species: small population size, inbreeding, relatively large breeding territories, and saturated habitat. A captive-breeding program of Yellow Cardinal is underway in Brazil, with planned releases of captive-bred individuals in sites with historical occurrence of the species (Martins-Ferreira *et al.* 2013). Habitat loss and fragmentation due to land use conversion (*e.g.* from livestock to monocultures and forestry) and bird trapping still being main conservation problems for the Yellow Cardinal in some regions. Demographic parameters, such as adequate home range needs, must be considered when defining how and where to release captive-bred Yellow Cardinals. We highly recommend further studies on habitat selection by Yellow Cardinal, as well as studies to understand the role of helpers and the continuous monitoring of the Brazilian population.

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# Breeding observations on Buff-bellied Puffbird *Notharchus swainsoni* (Piciformes: Bucconidae) at Rancho Laguna Blanca, San Pedro Department, Paraguay

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**ABSTRACT:** Aside from evidence of the Buff-bellied Puffbird *Notharchus swainsoni* nesting in arboreal termitaria, no breeding data is available. Here we present 100 days of observation of an active nest of the species in eastern Paraguay. The nest was active from late September to early December, and the two clutches observed were of three and four white eggs. After the first clutch failed a second one was laid. The incubation period was between 14–21 days and the fledgling period 30 days. The nest structure was cavity/with-inclined-tunnel/simple/unlined. Parent birds fed the chicks an insectivorous diet and fiercely defended the nest. This is the first detailed breeding data published for the species.

**KEY-WORDS:** behaviour, breeding season, eggs, re-nesting, reproduction.

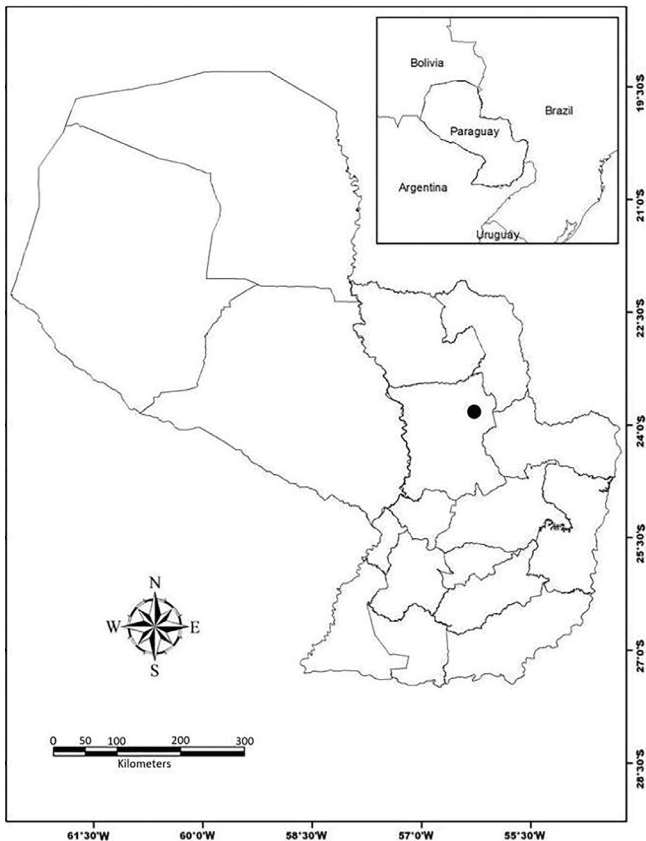
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The Bucconidae or puffbirds are a Neotropical family distributed from Mexico to Argentina, comprising 36 species in 10 genera (Clements *et al.* 2016). The breeding habits of the family are poorly known, though most species are monogamous, territorial, and cavity or hole nesters (Rasmussen & Collar 2002). The genus *Notharchus* consists of five large, distinctive, mainly black-and-white plumaged species that are typical of forest and forest edge habitats. Little has been reported about breeding habits in this genus, but all known species are generally, though not obligate, cavity nesters in arboreal termitaria (Skutch 1948, Sick 1993, Rasmussen & Collar 2002, Mazzoni *et al.* 2013, Vasconcelos *et al.* 2015).

Four species of puffbird occur in Paraguay, including the Atlantic Forest endemic Buff-bellied Puffbird *Notharchus swainsoni* (Gray, 1846) (Guyra Paraguay 2004), which is distributed from southern Bahia to Santa Catarina in Brazil, and inland to eastern Paraguay and Misiones Province in extreme northeastern Argentina (Alvarenga *et al.* 2002). In Paraguay, it is an uncommon inhabitant of humid forests and their interface with Cerrado, east of the Rio Paraguay (Guyra Paraguay 2005). The distribution approximates to the area once covered by the Upper Paraná Atlantic Forest (Guyra Paraguay 2005).

The breeding behaviour of Bucconids has attracted little attention from researchers. Like other members of the genus, Buff-bellied Puffbird have been observed to excavate nests in arboreal termitaria, but no further data on breeding in the species is available (Rasmussen & Collar 2002). Here we provide the first breeding data for this species from an area of interface between Atlantic Forest and Cerrado at Rancho Laguna Blanca, San Pedro Department, eastern Paraguay, based on observations of a breeding pair from September to December 2015.

Rancho Laguna Blanca (23°48'43.6"S; 56°17'41.3"W; 200 m above sea level) in northern eastern Paraguay (Fig. 1) is an 804 ha private property consisting of over 400 ha of near pristine Cerrado, a patch of degraded Atlantic Forest and areas of transitional semideciduous, semihumid gallery forest. The four main Cerrado ecotopes are present and grow on a predominately sandy substrate (Eiten 1972, 1978). The study area is based around an eponymously-named freshwater lake of 157 ha, which is possibly the only geologically true lake in Paraguay (Guyra Paraguay 2008). The property was designated as a *Reserva Natural* in 2010 for a period of five years, but this official protected status ended in January 2015.



**Figure 1.** Location of Rancho Laguna Blanca, San Pedro Department, eastern Paraguay.

### Nest building

The observation period was from 20 September to 22 December 2015 (method *ad libitum*, Altmann 1974). Observations began when tapping and scraping noises indicative of construction were audible from within the nest, these continuing throughout the following five days. The nest was in an active arboreal *Nasutitermes* sp. (Blattodea, Termitidae) termitarium situated in a *Copaifera langsdorfii* tree (Fabaceae) (Fig. 2A). It was

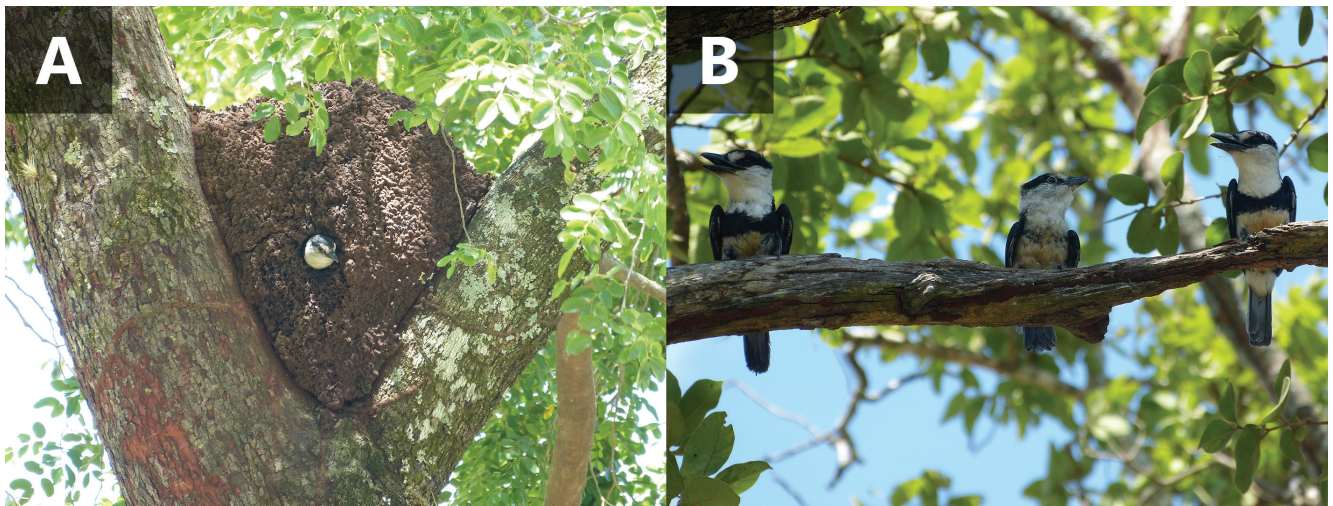
positioned in a fork created by the trunk splitting into two main branches of 93 and 66 cm girths. The entrance tunnel was at a height of 3.9 m above ground. The maximum exterior dimensions of the termitarium were 53 cm high, 32 cm between supporting branches and 51 cm between entrance and rearmost surface. The nest type can be classified as cavity/with-inclined-tunnel/simple/unlined (*sensu* Simon & Pacheco 2005).

Due to only minor differences in plumage between the adults, sexual identification was not attempted, although both birds were seen frequenting the termitarium and transporting small fragments of it away from the nest. During construction, termites could be observed within the nest cavity due to disruption of the structure by the birds. Repair work by the insects later maintained a nesting chamber separate from areas of insect activity.

### Eggs, incubation and nest period

To avoid disturbance during the early stages of nesting, the cavity was not examined until 4 October. The narrow, approximately circular entrance tunnel was used for inspection of the nest chamber, using a mirror attached to a piece of strong wire. One egg was present at this stage and a second was observed at a nest inspection four days later (8 October). The two ovular eggs were both brilliant white in colouration. Egg biometrics could not be obtained as the eggs could not be safely removed from the cavity without damage.

Both eggs were found broken (either predated or evicted) at the base of the nest tree on the morning of 14 October. An examination of the nest chamber at this time revealed another egg inside the nest that had not been present during a nest examination two days earlier. However, this third egg was also found broken 3.6 m from the base of the tree on 23 October. No eggs were



**Figure 2.** *Notharchus swainsoni* chick at nest entrance on 22 December 2015 (A). Author: A. Mathews. Fledgling *Notharchus swainsoni* (center) with parents on 18 December 2015 showing ontogenetic differences such as beak proportions, lack of clear breast band, pale orbital ring, and shorter tail (B). Photos: A. Mathews.

observed in the nest chamber between this point and 28 October, though the adults were frequently seen to visit the nest. However, four new eggs were found during a nest inspection on 4 November.

A hatchling was observed on 18 November, indicating an incubation period of somewhere between 14–21 days (based on minimum and maximum estimates). A second hatchling was recorded on 20 November, and a third on 22 November, suggesting approximately two day intervals between hatching dates. A fourth egg either failed to hatch or the chick was predated, as no remains were found during nest inspection after fledging.

A gaping nestling approached the nest entrance on 27 November. At this point adults were becoming increasingly aggressive towards observers. The adult birds perched on branches close to the nest and swooped directly at the observer's head, principally during insertion of the mirror but also upon approach or retreat. On occasion, the birds would emit a short and inquisitive squawk whilst tilting their head before swooping from branches approximately 2 m from the nest. On two instances, the bird collided with the observer's head during one of these defensive manoeuvres and at this point nest examination was suspended to avoid undue stress.

Nestling vocalisations first became audible on 29 November and were recorded on 1 December. These vocalisations continued past the fledging stage and can be described as repetitive sequences of high-pitched squeaks, varying slightly in pitch and frequency (recording XC302843 at [www.xeno-canto.org](http://www.xeno-canto.org)). Hourly monitoring periods were undertaken intermittently during the mid-developmental period to identify prey selection. The observed diet of the nestlings was entirely insectivorous, and the following insect orders were recorded (number of observations in parentheses): adult (2) and larval (6) Lepidoptera, Coleoptera (4), Hymenoptera, mostly Vespoidea (11), Odonata (3), Orthoptera - grasshoppers, katydids (2), Blattodea - cockroaches (2), Auchenorrhyncha, predominantly Cicadidae (11) and Mantodea (2). The frequency of larger prey items, particularly cicadas, increased during the final stages of development.

Adults captured arthropods primarily by foliage gleaning and sally-gleaning from a fixed perch. Birds detected stationary prey and captured them on the substrate, then returned either to a favoured perch or flew directly to the nest cavity to feed the nestlings. Favoured foraging perches were used repeatedly, although foraging was not always restricted to the proximity of the nest, as the adults would sometimes be absent from the area during the observation period. Neither adult fully entered the cavity to feed the nestlings during the later stages of nesting, instead clinging to the entrance and awaiting the approach of the nestlings.

## Fledging

Fledging occurred on 18 December, giving a fledging period of between 26 and 30 days. The first fledgling flew directly from the nest entrance to a nearby branch where adults were perched. Similar begging vocalisations induced feeding by the adults. At this stage the diet consisted almost exclusively of cicadas (perhaps because of their abundance at this time of year). A second chick fledged four days later, on 22 December, leaving the termitarium when neither adult was present and flying directly towards the observer, enabling it to be captured by hand. The morphometrics of the chick, taken using a 30-cm ruler and 100-g Pesola® balance are as follows: mass = 74 g; Rtail = 53 mm; wing chord = 90 mm; tarsus length = 20 mm; culmen = 20 mm; bill gape to tip = 33 mm; bill nare to tip = 18 mm. The fate of the third chick is unknown as it was not observed to leave the nest, yet neither were any remains found during the later nest inspection.

Fledglings generally resembled the adults but differed in the clearly shorter bill and tail, the lack of a dark breast band, and presence of a clear white orbital ring. The bill lacked the obvious hooked tip of adults and had an indistinctly paler tip (Fig. 2B).

## Nest structure

The termitarium was abandoned following fledging and was not used for roosting or refuge even during periods of bad weather. On 28 December, the nest was dissected to obtain internal measurements of the nest chamber and tunnel. The roughly hemispherical nest dimensions were collected using a 30-cm ruler, spirit level, and protractor for tunnel incline. Its dimensions were as follows: entrance tunnel diameter = 60 × 60 mm; upward incline of entrance tunnel = 50°; length of entrance tunnel = 160 mm; distance from entrance to rear of chamber = 320 mm; length of nest chamber = 160 mm; width of nest chamber = 240 mm; height of nest chamber (range) = 60–110 mm. The interior of the nest chamber contained a large quantity of faecal matter. Arthropod remains were limited to small fragments of chitin from Coleopteran elytra; a fragment of a cicada head; three unidentified pupae that were unlikely to be related to diet and some termites that fell into the chamber during dissection of the nest.

Due to the habit of nesting in conspicuous arboreal termitaria, nests of this species are not infrequently encountered in Paraguay, but detailed nest descriptions have never been provided and no accompanying breeding data exists. Previous Paraguayan nests have been reported during September and October at heights of between 3.5 m and 12 m (Brooks *et al.* 1993, de la Peña 2010), but no further information is available.

Excavation of this nest was already underway in late September, later than the only previous reported data for Paraguay where excavation was reported to occur during July and August (de la Peña 2010). Rasmussen & Collar (2002) note that breeding takes place during September and October, but do not provide a locality for the data. However, the nest reported here was active for a much longer period, with the first brood corresponding to this season, but the resultant re-nesting following the loss of the first clutch extending the dates by several months. This suggests that, at least in Paraguay, the breeding season may be much less restricted.

Skutch (1948) observed a 10-day interval between nest completion and egg laying in Black-breasted Puffbirds *Notharchus pectoralis* (Gray, 1846) and the species was noted to lay three eggs at two day intervals in Panama, this being consistent with our observations. The only other species for which clutch size has been published in this genus is Pied Puffbird *N. tectus* (Boddaert, 1783) which is reported to lay two eggs (Rasmussen & Collar 2002). Consequently the clutch of 3 and 4 eggs reported here is apparently larger than that reported for other species, though caution is needed before drawing any firm conclusions because of the limited data available. Anecdotal data suggests that a large nest volume and the presence of a healthy termite population are important selection criteria for nesting birds (Brightsmith 2004). The presence of the insects is an undoubted advantage due to their constant nest maintenance which preserves the structural integrity of the nest chamber (Brightsmith 2004, Mazzoni *et al.* 2013). The ecological role of termitarium cavity nesting birds, particularly in secondary forest where large trees with natural cavities are rare, is an emerging area of study (Vasconcelos *et al.* 2015). The construction of such nests and their subsequent abandonment after use has been proven to provide secondary hollows for a diverse fauna of other cavity-nesting species including amongst many others owls, certain hirundines and psittacids, and even provides roosting opportunities for bats and small mammals (Sick 1993, Jullien & Cariveau 2001, Faria *et al.* 2006, Vasconcelos *et al.* 2015). The potential role of excavators such as puffbirds as keystone species in fragmented secondary forest environments is thus worthy of additional study.

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# Distribution and abundance of Pectoral Antwren (*Herpsilochmus pectoralis*) and Caatinga Antwren (*Herpsilochmus sellowi*) in the Atlantic Rainforest of northeast Brazil

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**ABSTRACT:** The Pectoral Antwren (*Herpsilochmus pectoralis*) and Caatinga Antwren (*H. sellowi*) are thamnophilids endemic to northeastern Brazil. The Pectoral Antwren is considered an “Endangered” species by the IUCN. The present study aimed at providing data on the distribution, abundance, habitat, and conservation status of these species in Rio Grande do Norte state (RN), Brazil, in order to help define conservation strategies for the species. Thirty-three sites in the Atlantic Forest domain were sampled between November 2005 and March 2008, for a total sampling effort of 414 h. Observations took place mainly between 5:30 h and 12:00 h, and records were based on visual and/or auditory detections. Standardized censuses were conducted in four different phytophysognomies to determine abundance and density. *Herpsilochmus pectoralis* was found in 73% ( $n = 24$ ) of the sampled areas, mean density was estimated at 89.1 individuals.km<sup>2</sup> and population size was approximately 13,921 individuals for the state. Available area of occupancy was 156.25 km<sup>2</sup>. *Herpsilochmus sellowi* was present in 39% ( $n = 13$ ) of the areas, with mean density of 60.4 individuals.km<sup>2</sup>, estimated population of 7202 and area of occupancy of 119.25 km<sup>2</sup>. The population estimate found in this study for *H. pectoralis* is high for a small geographical area, thus demonstrate that BirdLife International information is underestimated. These data widen knowledge of the species at local and national levels, in addition to confirming the importance of *H. pectoralis* in RN state. The low number of protected areas in the region is alarming, given that privately-owned areas face fragmentation, selective deforesting, burnings and significant real estate development.

**KEY-WORDS:** conservation, density, habitat, population, threatened bird.

## INTRODUCTION

The genus *Herpsilochmus* Cabanis, 1847 is exclusively Neotropical and contains 17 species, with the highest diversity in the Amazon Basin (Zimmer & Isler 2003, Remsen-Jr. *et al.* 2014). Twelve species are found in Brazil (Piacentini *et al.* 2015), five of which are endemic to the country: Caatinga Antwren *Herpsilochmus sellowi*, Bahia Antwren *H. pileatus*, Predicted Antwren *H. praedictus*, Aripuana Antwren *H. stotzi* and Pectoral Antwren *H. pectoralis*. Since they are predominantly forest species, they have been threatened by fragmentation and loss of habitat. As a result, some are globally “Endangered” (BirdLife International 2000, 2017). The Pectoral Antwren *H. pectoralis* is a threatened species (IUCN 2004, BirdLife International 2017) distributed locally in semideciduous

forest, deciduous forest, and wooded *restinga* (coastal tropical and subtropical moist broadleaf forest) from northeastern Maranhão, east to Rio Grande do Norte and south to Bahia (Cory & Hellmayr 1924, Pinto 1978, Ridgely & Tudor 1994, Sick 1997, Zimmer & Isler 2003, Silva *et al.* 2008, Silveira 2008, BirdLife International 2017). The Caatinga Antwren *Herpsilochmus sellowi* is distributed from the state of Maranhão to Bahia and Minas Gerais with a disjoint population (Whitney *et al.* 2000). Although it has been associated to the Caatinga, it also occurs in the *restinga*, open savannas, as well as in deciduous and nondeciduous forests (Olmos 1993, Whitney *et al.* 2000, Zimmer & Isler 2003, Silva *et al.* 2008). Because information about distribution, ecology and population parameters of these species is scarce, systematic studies are needed to establish conservationist

measures (Zimmer & Isler 2003). Accordingly, this study aims to broaden knowledge on geographic distribution, viable habitat, and estimated regional population of *H. pectoralis* and *H. sellowi* in northeastern Brazil.

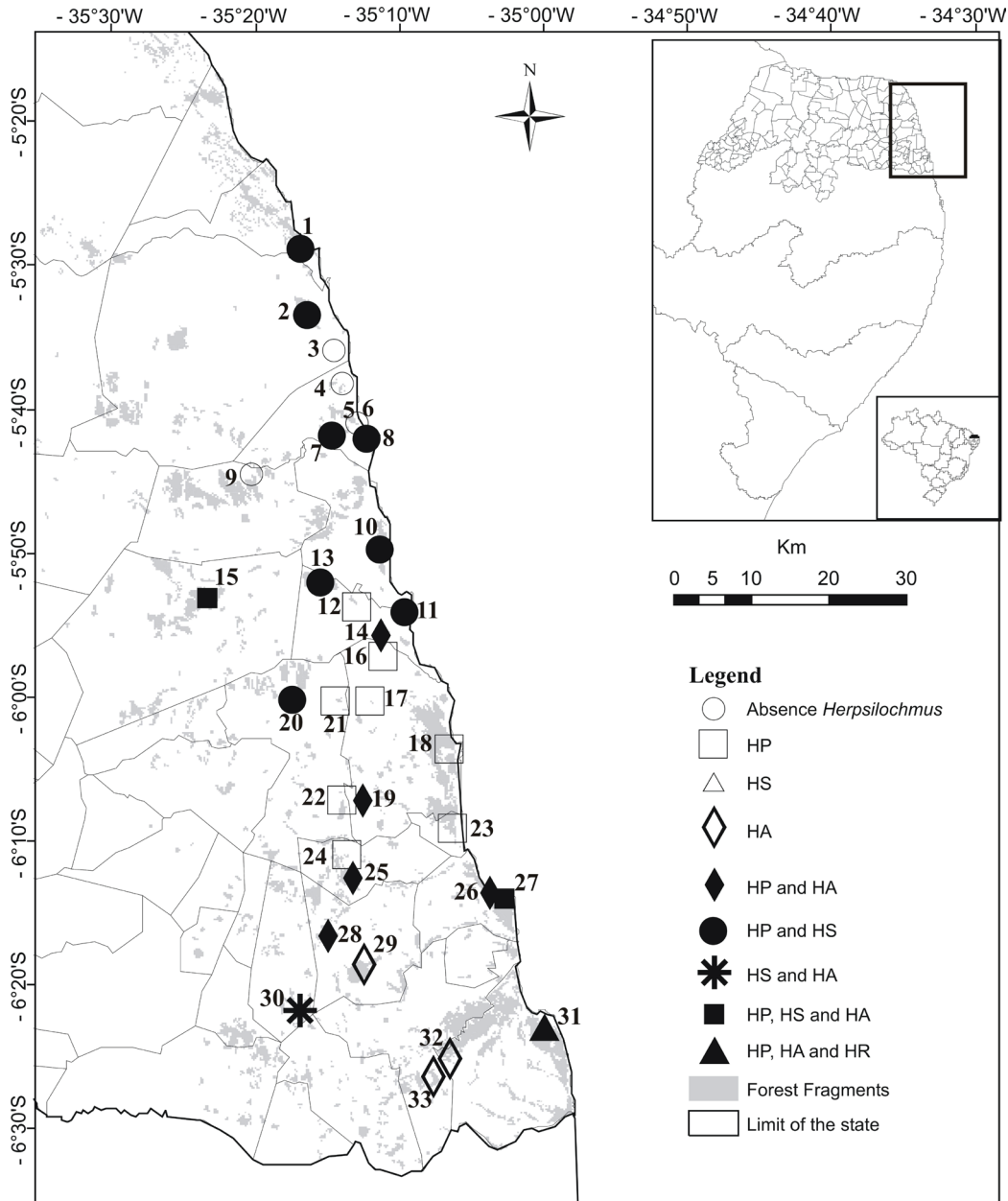
## METHODS

Thirty-three sites in 16 municipalities located in the Atlantic Forest of Rio Grande do Norte (RN), northeastern Brazil, were sampled between November

2005 and March 2008 (sampling effort of 414 man.h) (Table 1). The study areas are situated on the east coast, between the towns of Maxaranguape and Baía Formosa (Fig. 1). The eastern portion of RN has mean annual rainfall of 1400 mm, and its climate is defined as type "A" according to Köppen's classification system (rain concentrated between February and July) (IDEMA 2002). Sampling locations were chosen based on plant cover identified on satellite images. Forest fragments in the domain of Atlantic Forest in the state which had 50 or more ha were sampled.

**Table 1.** Locations sampled in the Atlantic Forest domain in Rio Grande do Norte state, northeast Brazil, with respective geographic coordinates, area size, sampling effort and number of contacts with *Herpsilochmus pectoralis* and *Herpsilochmus sellowi*.

Location and Municipality	Geographic Coordinates and Altitude (in m a.s.l.)	Area (km <sup>2</sup> )	Effort (h)	Number of detections	
				<i>H. pectoralis</i>	<i>H. sellowi</i>
1. Lagoa do Pacheco, Maxaranguape	05°29'35"S; 35°16'25"W, 34 m	0.88	5	8	10
2. Muriu Militar Area, Ceará Mirim	05°32'44"S; 35°16'38"W, 32 m	6.16	6	14	16
3. Caiana, Ceará Mirim	05°37'08"S; 35°14'04"W, 48 m	3.80	10	0	4
4. Cachoeirinha de Pitangui, Extremoz	05°36'10"S; 35°14'20"W, 15 m	2.00	4	0	0
5. Imbiribeira, Extremoz	05°38'38"S; 35°15'00"W, 38 m	2.90	12	0	11
6. Contenda, Extremoz	05°39'44"S; 35°13'36"W, 34 m	0.90	12	0	0
7. Estivas, Extremoz	05°40'56"S; 35°15'40"W, 34 m	5.28	50	145	126
8. APA Jenipabu, Extremoz	05°42'05"S; 35°12'25"W, 34 m	18.18	22	24	14
9. Guajiru, São Gonçalo do Amarante	05°44'26"S; 35°18'32"W, 45 m	0.60	4	0	0
10. Dunas State Park of Natal, Natal	05°50'12"S; 35°11'40"W, 70 m	11.72	30	203	91
11. Morro do Careca, Natal/Barreira do Inferno Parnamirim	05°53'02"S; 35°09'34"W, 30 m	11.00	12	5	4
12. Mata do Catre Military Area, Parnamirim	05°53'01"S; 35°13'36"W, 49 m	2.15	5	2	0
13. Industrial Park, Parnamirim	05°52'41"S; 35°14'36"W, 28 m	0.88	40	177	17
14. Mata do Jiqui, Parnamirim	05°55'45"S; 35°11'21"W, 39 m	0.79	20	60	0
15. Mata de Jundiá, Macaíba	05°53'21"S; 35°23'07"W, 56 m	2.70	30	13	48
16. Pium, Nizia Floresta	05°57'30"S; 35°10'23"W, 51 m	0.50	3	2	0
17. Lagoa do Bonfim, Nizia Floresta	06°01'44"S; 35°13'12"W, 37 m	1.10	3	2	0
18. Campo de Santana, Nizia Floresta	06°04'42"S; 35°06'30"W, 30 m	10.80	3	28	0
19. Golani, Nizia Floresta	06°07'44"S; 35°13'40"W, 90 m	1.10	6	34	0
20. Mendezinho I, São Jose de Mipibu	06°01'52"S; 35°16'10"W, 70 m	1.00	3	6	0
21. Mendezinho II, São Jose de Mipibu	06°01'39"S; 35°16'32"W, 53 m	0.76	5	2	1
22. Manimbu, São Jose de Mipibu	06°07'54"S; 35°13'44"W, 90 m	1.70	2	24	0
23. Areal, Senador Georgino Avelino	06°08'27"S; 35°06'13"W, 26 m	1.70	2	3	0
24. Urucará, Ares	06°09'50"S; 35°13'30"W, 52 m	2.90	16	2	0
25. Baldum, Ares	06°11'12"S; 35°13'09"W, 40 m	4.70	4	4	0
26. Mata do Bastião, Tibau do Sul	06°13'46"S; 35°04'08"W, 21 m	0.50	5	2	0
27. Ecological Sanctuary of Pipa, Tibau do Sul	06°13'35"S; 35°03'56"W, 60 m	0.80	20	52	2
28. Limoal, Goianinha	06°14'16"S; 35°13'19"W, 21 m	11.40	3	4	0
29. Fazenda Bom Jardim, Goianinha	06°18'25"S; 35°14'03"W, 90 m	6.46	5	0	0
30. APA Piquiri-Una, Timbó, Espírito Santo	06°22'30"S; 35°17'17"W, 44 m	10.50	12	0	20
31. RPPN Mata Estrela, Baía Formosa	06°22'25"S; 35°01'24"W, 64 m	20.39	36	40	0
32. Mata da Bela, Baía Formosa	06°25'12"S; 35°07'04"W, 21 m	1.00	15	0	0
33. Mata da Paraíba, Canguaretama	06°26'47"S; 35°07'26"W, 71 m	1.70	9	0	0



**Figure 1.** Geographic distribution of *Herpsilochmus* spp. in the Atlantic Forest of Rio Grande do Norte state, northeast Brazil. White circle means absence of *Herpsilochmus*; black circle indicates syntopy between *H. pectoralis* (HP) and *H. sellowi* (HS); white triangle indicates records of *H. sellowi*; black triangle indicates sympatry between *H. pectoralis*, *H. atricapillus* (HA) and *H. rufimarginatus* (HR); black square indicates syntopy between *H. pectoralis*, *H. sellowi* and *H. atricapillus*; white square indicates the presence of *H. pectoralis*; white diamond indicates the presence of *H. atricapillus*; black diamond indicates syntopy between *H. pectoralis* and *H. atricapillus*; asterisk indicates syntopy between *H. sellowi* and *H. atricapillus*. Areas: 1. Lagoa do Pacheco, 2. Muriu Militar Area, 3. Caiana, 4. Cachoeirinha de Pitanguí, 5. Imbiribeira, 6. Contenda, 7. Estivas, 8. APA Jenipabu, 9. Guajiru, 10. Dunas State Park of Natal, 11. Morro do Careca, 12. Mata do Catre Military Area, 13. Industrial Park, 14. Mata do Jiqui, 15. Mata de Jundiá, 16. Pium, 17. Lagoa do Bonfim, 18. Campo de Santana, 19. Golani, 20. Mendezinho I, 21. Mendezinho II, 22. Manimbu, 23. Areal, 24. Urucará, 25. Baldum, 26. Mata do Bastião, 27. Ecological Sanctuary of Pipa, 28. Limoal, 29. Fazenda Bom Jardim, 30. APA Piquiri-Una, 31. RPPN Mata Estrela, 32. Mata da Bela and 33. Mata da Paraíba.

We searched for the species along trails and/or roads in the study areas, mainly between 5:30 h and 12:00 h and sometimes between 14:00 h and 17:00 h. Records were based on visual (aided by 8 × 21 binoculars) and auditory detections. The following information was recorded at each observation: species observed, number of individuals, habitat, and presence of congener species. The following tape recorders were used to document information: Sony (DAT) TCD-D8 equipped with a

Sennheiser-ME-66 microphone, which were archived at Wikiaves digital repository. Geographic coordinates and altitudes were obtained with Magellan 315 or Garmin 12 GPS.

At Mata de Jundiá, Industrial Park, Estivas and Dunas Park, areas which represent different vegetation types, anthropic impacts and/or are conservation units under integral protection, we defined 1-km transects to estimate abundance and density of *H. pectoralis* and *H.*



*sellowi*. A 1-h standardized census was conducted at dawn on each sampling day (onset at 5:30 h). We recorded the number of individuals observed, taking care not to attribute more than one detection to the same individual during the same sampling effort. Mean abundance was obtained by dividing the number of detections per species by the number of observation days at each location. In order to estimate population density of the *H. pectoralis* and *H. sellowi* in areas, we used the linear transect method (Buckland *et al.* 1993, Thomas *et al.* 2002). This requires following the premises of decreasing order of importance: animals directly on the line are always detected, animals are detected in their initial position, before any movement caused by the presence of the observer, perpendicular distances are measured correctly, and detections are independent events (Buckland *et al.* 1993, Thomas *et al.* 2002). Density was calculated using the Distance 6.0 software and models were selected according to Akaike's Information Criterion (AIC). The selected model to estimate density was half-normal with cosine adjustment. The density and effective width were represented by coefficient of variation (%CV) and confidence interval 95% (CI). Density was estimated using the formula  $D = N/(2*EW*L)$ , where:  $D$  = density (individuals/km<sup>2</sup>),  $N$  = number of sightings,  $EW$  = effective width of the sample area (in km) and  $L$  = total number of km surveyed (Buckland *et al.* 1993).

Viable habitat was estimated for populations of *H. pectoralis* and *H. sellowi*, based primarily on similar plant cover. In order to accomplish this we compared satellite images of potential species distribution areas. To estimate viable areas we disregarded any cultivated area, those in the process of regeneration or subjected to strong anthropic pressure. We used Landsat images from 2002 (INPE 2007) and Ortofoto images from 2006 of the Rio Grande do Norte coast (IDEMA 2007). Areas with adequate habitat were divided into quadrants of 500 × 500 m to verify which quadrants were occupied by each of the species. The analyzes of adequate habitats and area of occupancy by species was performed in ArcGIS 9.0 software.

To estimate population size of *H. pectoralis* and *H. sellowi* on the east coast of RN, occupancy area was multiplied by the means of density between the different plant physiognomies and an estimate of density, considering the whole study area. The first population estimate is a more conservative estimate, where we multiplied the mean density between the physiognomies by the occupancy area by each species. The second population estimate multiplied the density found throughout the study area by the occupancy area by each species.

Descriptive statistical analyses (mean, standard deviation, minimum and maximum values) are reported.

Non-parametric analysis of variance (Kruskal-Wallis test) was performed to test for abundance differences of both species among the habitats. The significance level was set at 5% for all analyses.

## RESULTS

*Herpsilochmus pectoralis* was recorded in 24 (73%) of the 33 locations sampled. Distribution limits in the state were north (Lagoa do Pacheco, Maxaranguape), south (private reserve - RPPN Mata Estrela, Baía Formosa) and west (Mata de Jundiá, Macaíba) (Fig. 1). *Herpsilochmus sellowi* occurred in 13 (39%) of the 33 locations studied (Fig. 1). The distribution limit of *H. sellowi* in the north coincided with that of the previous species (Fig. 1). Syntopy between *H. pectoralis* and *H. atricapillus* occurred in six fragments, and between *H. atricapillus* and *H. sellowi* in a single area (Fig. 1). These three species only occurred together in Mata de Jundiá, Ecological Sanctuary of Pipa and RPPN Mata Estrela. *Herpsilochmus pectoralis*, *H. atricapillus* and *H. rufimarginatus* were found jointly in the southernmost part of the state (RPPN Mata Estrela) (Fig. 1). There were several observations of mixed-species flocks containing *H. pectoralis* and *H. atricapillus*, and rare observations of flocks containing *H. pectoralis* and *H. sellowi*. Other species often observed in mixed-species flocks with *Herpsilochmus* were Planalto Slaty-Antshrike *Thamnophilus pelzelni*, White-fringed Antwren *Formicivora grisea*, Pearly-vented Tody-tyrant *Hemitriccus margaritaceiventer*, Chivi Vireo *Vireo chivi* and Gray-eyed Greenlet *Hylophilus amaurocephalus*.

Between 2005 and 2008, a total of 856 detections of *H. pectoralis* and 364 of *H. sellowi* were recorded (Table 1). Abundance of *H. pectoralis* were different among habitats. They were higher in semideciduous forest (Industrial Park = 35.4 individuals.day) and lower for deciduous forest (Mata de Jundiá = 2.6 individuals.day) ( $H = 19.3$ ,  $df = 3$ ,  $P < 0.001$ ) (Table 2). There were also varying abundance in the different plant physiognomies for *H. sellowi* ( $H = 15.1$ ,  $df = 3$ ,  $P < 0.001$ ) (Table 2). The total number of contacts with *H. pectoralis* and *H. sellowi* in linear transects was 68 and 46, respectively, where a total of 80 km were covered. The density varied between the plant physiognomies from 53.03 to 142.12 individuals.km<sup>2</sup> for *H. pectoralis* and from 40.49 to 76.57 individuals.km<sup>2</sup> for *H. sellowi* (Table 2). The estimates for all study areas were 103.51 individuals.km<sup>2</sup> for *H. pectoralis* and 57.28 individuals.km<sup>2</sup> for *H. sellowi*.

Estimated suitable habitat for *H. pectoralis* on the eastern coast of RN was 504.7 km<sup>2</sup>. The most representative plant formations were semideciduous forest (216.5 km<sup>2</sup>), *restinga* (114.3 km<sup>2</sup>), deciduous

forest (98.1 km<sup>2</sup>) and open savannas (75.8 km<sup>2</sup>). The only full-protection conservation area in the study region is the Dunas State Park of Natal, which contains 9.55 km<sup>2</sup> suitable for the species, corresponding to 2% of the total area considered likely to be inhabited. There are also sustainable-use conservation areas accounting for 10% (49.07 km<sup>2</sup>) of the estimated area. These environmental protection areas (APA Jenipabu and APA Piquiri-Una,  $n = 2$ ) represent 6% (28.68 km<sup>2</sup>) and RPPN Mata Estrela 4% (20.39 km<sup>2</sup>) of the estimated area. We also underscore the importance of military areas (Muriu Military Area and Mata do Catre Military Area,  $n = 2$ ), which are well preserved and represent 2% (8.31 km<sup>2</sup>) of the estimated

area. The area of occupancy was 156.25 km<sup>2</sup> ( $n = 625$  quadrants) and 119.25 km<sup>2</sup> ( $n = 477$  quadrants) for *H. pectoralis* and *H. sellowi*, respectively.

Based on the combination of area of occupancy (156.25 km<sup>2</sup>) and mean density per plant physiognomy (mean density 89.1 individuals.km<sup>2</sup>) (Table 3), the population was estimated at 13,921 *H. pectoralis* in Rio Grande do Norte and estimate for the area of study was 16,173 individuals. Estimated area of occupancy for *H. sellowi* in Atlantic Forest was 119.25 km<sup>2</sup>, resulting in a population of 7202 individuals (mean density 60.4 individuals.km<sup>2</sup>) (Table 3) and estimate for the area of study was 6830 individuals.

**Table 2.** Abundance and density of *Herpsilochmus pectoralis* and *Herpsilochmus sellowi* at Mata de Jundiá, Industrial Park, Estivas and Dunas State Park of Natal, Rio Grande do Norte, northeast of Brazil. Abundance and mean number of individuals obtained by census and population density based on calculations (individuals.km<sup>2</sup>). CV = Coefficient of Variation and CI = Confidence Interval).

Location	<i>Herpsilochmus pectoralis</i>		<i>Herpsilochmus sellowi</i>	
	Abundance Mean ± SD (Min – Max)	Density (% CV; CI 95%)	Abundance Mean ± SD (Min – Max)	Density (% CV; CI 95%)
Mata Jundiá	2.6 ± 1.3 (1 – 4)	67.84 (25.57; 39.50 – 116.52)	9.6 ± 1.5 (8 – 11)	57.83 (20.51; 37.69 – 88.74)
Industrial Park	35.4 ± 12.7 (20 – 46)	142.12 (18.32; 98.03 – 206.05)	3.4 ± 1.9 (1 – 6)	76.57 (30.18; 39.77 – 147.42)
Estivas	14.5 ± 5.0 (8 – 24)	53.03 (22.81; 32.98 – 85.28)	12.6 ± 3.4 (8 – 16)	66.73 (34.51; 32.16 – 138.46)
Dunas Park	20.3 ± 5.9 (10 – 28)	93.39 (19.25; 62.98 – 138.48)	9.1 ± 2.8 (5 – 14)	40.49 (24.84; 24.11 – 68.01)
Mean Density ± SD		89.1 ± 39.1		60.4 ± 15.3
Whole study area		103.51 (21.11; 61.96 – 172.95)		57.28 (11.58; 45.33 – 72.39)

**Table 3.** Population estimate of *Herpsilochmus pectoralis* and *Herpsilochmus sellowi* in Rio Grande do Norte state, northeast of Brazil.

Physiognomy	<i>Herpsilochmus pectoralis</i>	<i>Herpsilochmus sellowi</i>
	Suitable habitat (km <sup>2</sup> )	Viable habitat (km <sup>2</sup> )
Semideciduous forest	216.5	95.6
Deciduous forest	98.1	98.1
Restinga	114.3	37.7
Open savanna	75.8	80.6
Total area	504.7	312
Occupation area (km <sup>2</sup> )	156.25	119.25
Mean density (individuals.km <sup>2</sup> )	89.1	60.4
Population estimate (individuals)	13,921	7202

## DISCUSSION

*Herpsilochmus pectoralis* and *H. sellowi* are widely distributed on the eastern coast of the state of Rio Grande do Norte, occurring in *restingas*, open savannas, deciduous and semideciduous forests. Data obtained

contribute to knowledge of the geographic distribution of these species. The scant information available for *H. pectoralis* in RN was restricted to three regions in the south of the state, and to *restingas* of Baía Formosa and Tibau do Sul (Teixeira *et al.* 1993, Whitney *et al.* 2000, Olmos 2003). *Herpsilochmus sellowi* was known only in

the Ecological Sanctuary of Pipa in the municipality of Tibau do Sul (Whitney *et al.* 2000).

In RN *H. pectoralis* was found in plant formations similar to those mentioned for other Brazilian states (Wege & Long 1995, Parrini *et al.* 1999, Kirwan *et al.* 2001). However, it was cited in areas with good conservation status (Whitney *et al.* 2000). Our observations show that *H. pectoralis* is common even in fragmented and anthropized areas. *Herpsilochmus sellowi* is much more widely distributed on the east coast of the state, but not found inland in the moist forest enclave of Martins, in contrast to those in Pernambuco, where it occurs (Roda 2002, Roda & Carlos 2004). This species, which is closely associated to the Caatinga (Whitney *et al.* 2000), has been considered endemic to this biome (Parker-III *et al.* 1996). However, all our records of this species are in the Atlantic Forest domain. In studies conducted in other areas of Caatinga this species is registered (Santos 2004, Olmos *et al.* 2005), but in the RN state, recorded only had been made in *restingas*, open savannas, deciduous and semideciduous forests.

The few data available on *H. pectoralis* were only qualitative, classifying the species as locally common or rare (Teixeira *et al.* 1993, Ridgely & Tudor 1994, Silveira 2008), but Teixeira *et al.* (2016) estimated the density of this species in 85 individuals.km<sup>2</sup> in a forest fragment in Rio Grande do Norte. Densities found for *H. pectoralis* and *H. sellowi*, despite using different methods, are similar to those obtained for other common (*e.g.* Variable Antshrike *Thamnophilus caeruleus*, Plain Antwren *Dysithamnus mentalis* and White-backed Fire-eye *Pyriglena leucoptera*) and threatened thamnophilids (*e.g.* Rio Branco Antbird *Cercomacra carbonaria* and Restinga Antwren *Formicivora littoralis*) (Duca *et al.* 2006, Vale *et al.* 2007, Mattos *et al.* 2009). The estimated population of *H. pectoralis* in RN state reached 13,920 individuals or a more optimistic estimate of about 16,170 individuals. This number exceeds the estimates of 3500 to 15,000 individuals in an 860,000 km<sup>2</sup> of distribution size (BirdLife International 2017), but this estimates take into account a density of 2.6–9.6 individuals.km<sup>2</sup>. The density found for species in forest fragments are much larger and similar to that found for other species of the thamnophilidae family. Based on this new species density information, BirdLife International (2017) information seems to be underestimated. We found the species occurring in small fragments of forest and well altered, showing that the species tolerates altered areas. But this species had lost suitable areas with the expansion of sugar cane cultivation and the growth of cities, and today it continues to have its habitat destroyed for infrastructure activities along the coast of Rio Grande do Norte and popular houses.

The large number of unprotected private areas where

*H. pectoralis* occurs reinforces the need for establishing new protected areas, as suggested by Zimmer & Isler (2003). It is also important to correctly manage these units through better control of anthropic influences such as the introduction of new species, invasion, access of domestic animals and people. There is a clear need to establish corridors between the best forest fragments due to the existence of isolated populations such as those found in Dunas State Park of Natal. Due to their extent, number of records and estimated size of population, the following areas are important for the conservation of *H. pectoralis*: RPPN Mata Estrela, as reported by Bencke & Maurício (2006), Muriu Military Area in Ceará Mirim, APA Jenipabu in Extremoz, Dunas State Park of Natal in Natal, Morro do Careca in Natal/Barreira do Inferno in Parnamirim, Mata do Jiqui in Parnamirim, Industrial Park in Parnamirim, Campo de Santana in Nisia Floresta and Limoal in Goianinha. We recommend that government authorities pay more attention to the conservation of these areas. We also underscore the importance of military areas for protecting habitats and threatened species.

Despite the representative populations of *H. pectoralis* and *H. sellowi* in the state, they face short-term threats due to fragmentation and loss of habitat. In some areas we observed deforestation for real estate development, formation of pastures, and monocultures. Real estate speculation in the coastal areas of the state is worrisome, since several large scale projects are being implemented along nearly the entire coast. Some of these were approved without considering the presence of remnant populations of these species. Unplanned development, mainly in the city of Natal, also threatens important areas for populations of *H. pectoralis*. Finally, sugar cane burning has serious impacts on nearby forest fragments. We suggest that these threats could reduce the suitable habitats of *H. pectoralis* by at least 50% in the next decade if current trends are not reversed. For these reason we emphasize the need to define conservation plans for these species, as both occur in highly fragmented areas that are subject to anthropic pressures. In addition, it is also recommended to conduct long-term studies on these populations to address questions about ecological and behavioral aspects such as reproduction, home range, territory, and environmental requirements.

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# Effects of urbanization on the avian community in a southern Brazilian city

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**ABSTRACT:** This paper compares the proportion of urban tolerant birds in the urban avian community and the amount of built-up areas, mostly impervious surface, as indicators of urbanization on patterns of bird species richness in a southern Brazilian city. From September to December 2013 (breeding season), bird surveys were conducted in 120 squares of 100 ha randomly select within Curitiba, Paraná, Brazil. All bird species seen or heard during the sample timeframe were recorded. The extent of urban modification and disturbance was estimated directly from urban landscape data analyses through a geographic information system. Linear regressions were graphed and Spearman rank correlations were calculated to assess the relationship of overall species richness and the percentage of urban tolerant birds against the percentage of built-up areas as the predictor variable. Kruskal-Wallis non-parametric analyses of variance were performed to test if the total richness or the percentage of urban tolerant birds on the assemblages differed between categories of urbanization (low, intermediate and high). We recorded 102 bird species, including 13 urban tolerant species. As expected, urbanization significantly reduced species richness, but urban tolerant species were less affected to changes on land modifications associated to urban growth. The increase in representativeness of “urban-adaptable” species on the bird assemblages of intermediate and high-urbanized areas in Curitiba was probably favored by their broad environmental tolerance. Most urban tolerant species registered are ground foraging resident birds, use a diverse array of anthropogenic resources, and can be found occupying various types of habitat in several human-modified ecosystems.

**KEY-WORDS:** avian community, nonnatives, synanthropic, urban exploiters, urban landscape.

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## INTRODUCTION

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Urban development exerts negative impacts on biodiversity because of habitat loss and ecosystems fragmentation (McKinney 2002). In urban landscapes, the disruption of ecosystem processes (Thom *et al.* 2001), predator proliferation (Baker *et al.* 2008, Fischer *et al.* 2012), elevated noise levels (Proppe *et al.* 2013), and the fragmentation of remaining forests (Zipperer *et al.* 2012) significantly impact the richness (Marzluff 2001) and consequently the composition and functional structure of bird communities (*e.g.* Blair 1996, Marzluff 2001, Lim & Sodhi 2004, Ferenc *et al.* 2013).

The composition and distribution of urban birds are influenced by habitat structure and urban development in Australia (Garden *et al.* 2006), Europe (Ferenc *et al.* 2013), Asia (Sodhi *et al.* 1999), North America (Donnelly & Marzluff 2006), South Africa (van Rensburg *et al.* 2009) and Neotropics (Leveau & Leveau 2005, 2012, Pauchard *et al.* 2006, Fontana *et al.* 2011, Reis *et al.* 2012, Toledo *et al.* 2012, Silva *et al.* 2015). The lowest

values of species richness are usually registered in the most intensively built-up areas, such as the city center (Blair 1996). While there is general consensus in the literature regarding the point of lowest diversity, usually urban core areas (Seress & Liker 2015), species richness is higher in areas of intermediate levels of urbanization (Marzluff 2001, Chace & Walsh 2006).

Patterns of avian community composition within the urban landscape are mediated by species tolerance and ability to exploit urbanized areas. Species sensitive to habitat disturbances have been categorized as “urban avoiders” (McKinney 2002) or “urban-sensitive” (Garden *et al.* 2007), while species that are common in urbanized areas have been categorized as “urban exploiters” (McKinney 2002) or “synanthropes” (Marzluff *et al.* 2001). Birds in urban ecosystems are usually opportunistic species with wide dispersal ability, whereas species with poor dispersal ability, slow reproduction or specialized diets disappear from urban assemblages as urbanization increases (McKinney & Lockwood 1999). The increase in the “urban-adaptable” species and the formation of

similar urban communities in many regions all over the world has been promoting the biotic homogenization process (McKinney 2006).

Several studies examined the composition of urban avian communities and stated that these communities comprise native and nonnatives species, well adapted to human-dominated landscapes, which are tolerant to urban constraints and able to maintain populations in urbanized areas (Manhães & Loures-Ribeiro 2005, Pinheiro *et al.* 2008, Shochat 2010, Fontana *et al.* 2011). Lower levels of urbanization seem to increase richness because of the coexistence of species associated with original and new habitat, whereas higher levels would lead to lower species richness (Blair 1996, Marzluff 2001).

This study aims to assess changes in the species richness and also in the representativeness of urban tolerant birds across a range of sample areas embedded in a southern Brazilian city. We hypothesized that the overall species richness, as opposed to the representativeness of urban tolerant birds, will decline with increasing urbanization. As urban tolerant species generally thrive in urban ecosystems, their richness and presence should be less affected to changes on land modifications associated to urban growth.

## METHODS

### Study area

Curitiba (25°25'S; 49°16'W), a 324-year-old city occupies 432.2 km<sup>2</sup> and is located in the Subtropical Zone of southern Brazil. The average altitude is 934 m a.s.l., ranging between 900 and 1000 m. The city has a subtropical highland climate where the temperature ranges from 21 to 32°C during the rainy summer and from 0 to 13°C in the winter, when rainfall is less abundant. The average annual precipitation is 1413 mm with little variation throughout the year. The population has grown exponentially over the last decades, and reach almost 1.8 million people and an average density of 4062 inhabitants km<sup>-2</sup>, becoming the eighth most populous city in the country in 2014 (ICLEI 2008, Curitiba 2016).

The City's territory has 77,786,020.60 m<sup>2</sup> of forests remnants (20% of the city surface), comprising nowadays more than 50 conservation units, mostly municipal parks. The arborisation of streets, recreational parks and private green areas are dominated by nonnative species, such as the Crape Myrtle (*Lagerstroemia indica*), Chinese Privet (*Ligustrum lucidum*), Rosewood (*Tipuana tipu*), Box Elder (*Acer negundo*), Vilca (*Anadenanthera colubrina*) and the Brazilian Firetree (*Schizolobium parahyba*).

Historical bird records identified 387 native species in Curitiba, along with 30 species considered introduced,

exotic or accidental (Straube *et al.* 2014). The urban resident avian community comprises more than 100 aquatic and terrestrial species, as well as migratory birds. The most common native species found in the city are Rufous Hornero (*Furnarius rufus*), Eared Dove (*Zenaidura auriculata*), Rufous-collared Sparrow (*Zonotrichia capensis*), House Wren (*Troglodytes aedon*), and Great Kiskadee (*Pitangus sulphuratus*), along with the nonnatives House Sparrow (*Passer domesticus*), Rock Dove (*Columba livia*) and the Common Waxbill (*Estrilda astrild*).

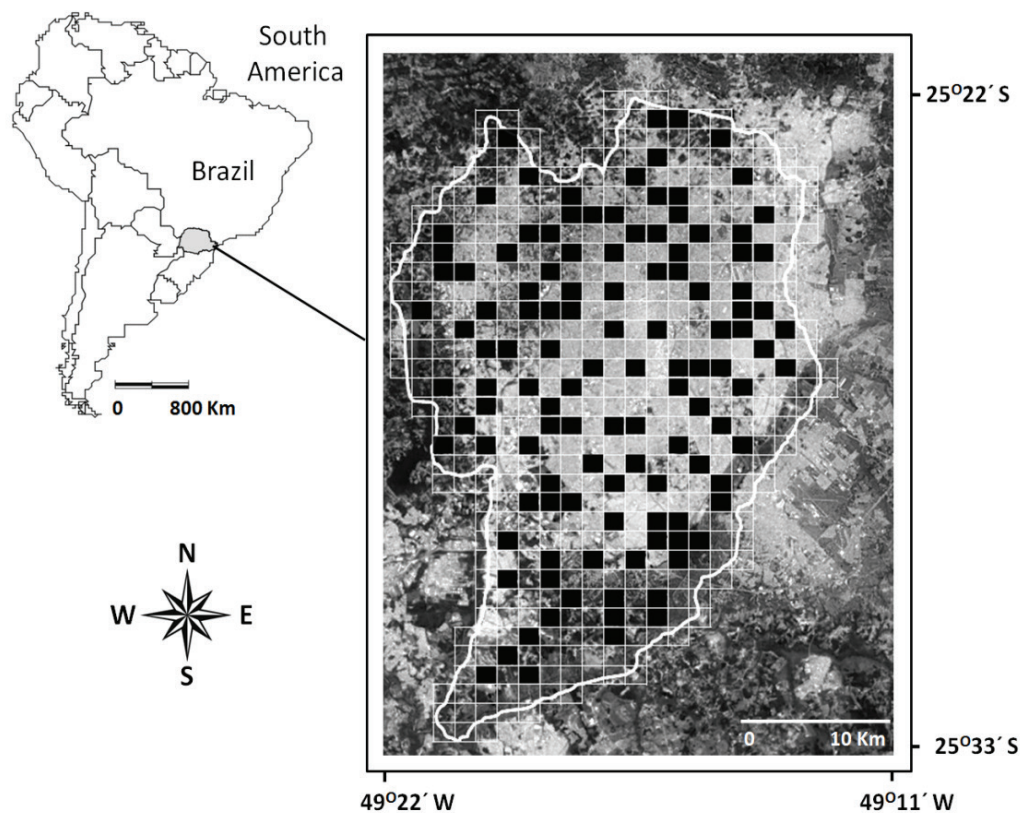
### Sampling and data analysis

Curitiba's territory was divided into 490 equal squares of 100 ha (1000 × 1000 m) to standardize samples and to ensure independence from urban form. At the periphery of the study area, there were 85 irregularly bounded squares that were eliminated due to their irregular size and smaller areas, yielding 405 squares (Fig. 1). For the bird survey, we randomly selected sample sites (squares) within Curitiba using 'sample' function in R software (R Development Core Team 2013). Such random selection ensured that sites with different levels of urbanization (amount of built-up areas) were surveyed. Sample-based rarefaction method was performed to evaluate the adequate sampling effort (number of squares surveyed) (Colwell *et al.* 2004). This measuring of species richness preserves the spatial structure of the data, reflecting processes such as spatial aggregation or segregation of species (Gotelli & Colwell 2011). Sample-base rarefaction curves were calculated (*Mao Tau* estimator, 500 randomizations) in the software EcoSim, version 7.72 (Gotelli & Entsminger 2000).

Fieldwork was carried out during the breeding season (spring), between September and early December of 2013, when most birds establish breeding territories and exhibit strong site fidelity (Sogge 2000). Choosing this period of the year also avoid the temporal fluctuation caused by the presence of migratory birds. Each square was surveyed by walking along public rights-of-way (*e.g.* streets, unpaved roads, grasslands with scattered trees and shrubs, ornamental gardens, parks, non-municipal green spaces, built-up areas) in the period with maximum bird activity (between 6:30 and 10:00 h) on sunny or scattered clouds days. No surveys were performed during periods of rain or high wind. One hour was spent in each 100 ha square, thereby standardizing sampling effort across all sites. This period of time was considered satisfactory for sampling two non-adjointing squares for each day. Adjacent squares were not surveyed during the same day in order to avoid overlapping observations of birds. Birds were detected visually and/or by vocalizations, and all species were assumed to have equal detection probabilities due to the large-scale

urban landscape. This assumption is common to studies of urban bird communities (Chapa-Vargas & Robinson 2006, Donnelly & Marzluff 2006). We recorded the presence of all bird species seen or heard during the

sample timeframe in the surroundings at unlimited distances, excluding high-flying individuals and night-active species. Bird taxonomy and nomenclature follow Piacentini *et al.* (2015).



**Figure 1.** Map of the Curitiba municipality in southern Brazil, showing the distribution of the 120 sample sites (black squares). The small South America map depicts the location of the state of Paraná (shaded) and the city of Curitiba.

We divided the community registered into two groups based upon their life history characteristics and ability to thrive and exploit urbanized ecosystems (Blair 1996). Thirteen species were assigned to the synanthropic guild according to Litteral & Wu (2012), and were therefore considered urban tolerant birds. Besides urban invaders (*i.e.* House Sparrow, Rock Dove, and Common Waxbill), most species that thrive in urban environments are remnant native species, some of which are synanthropic generalists, urban commensals and/or urban-resource dependent (Marzluff 2001).

The extent of urban modification and disturbance was estimated directly from urban landscape data analysis rather than indirect inference or *a priori* assignment. A geographic information system (GIS) was used, built by means of ArcView GIS 3.2 software and geographical databases of the city of Curitiba, provided by Curitiba's Institute of Research and Public Planning (IPPUC). For each sample point (100 ha square), the amount of built-up areas (*e.g.* buildings, roads, industrial areas, paved-over soil, compacted/near-impervious open spaces) was measured. We used the amount of built-up areas as a proxy to evaluate the proportion of impervious surface. Land-surface impermeabilization is one of the most important

landscape modification produced by urbanization, and such anthropogenic habitat fragmentation and disturbance are known to influence avian community (Marzluff *et al.* 2001). Modification of land cover in urban areas has also been shown to cause the urban heat island effect, which leads to higher temperature in urbanized areas than surroundings (*e.g.* Streutker 2003), causing differences in timing of arrival of migratory birds in cities (Tryjanowski *et al.* 2013).

Linear regressions were graphed and Spearman rank correlations were calculated on the total number of species and the percentage of urban tolerant birds as the dependent variables against the percentage of built-up areas as the predictor variable. Non-parametric rank correlations were used because species richness and the proportion of urban tolerant birds could not be successfully normalized to meet assumptions of parametric tests. We used the proportion of impervious surface to indicate the level of urbanization and to determine whether this important modification on the urban landscape affected species richness and the percentage of urban tolerant birds on the assemblages.

To summarize the relative influence of the level of urbanization on bird species richness and composition,

sample units (squares) were categorized into one of the following classes (levels) of urbanization: low (<50% of built-up areas), intermediate (50–75% of built-up areas), and high (>75% of built-up areas). We examined the effect of the urbanization level on avian composition through Kruskal-Wallis non-parametric analyses of variance, as initial examination of the data revealed they do not meet assumptions of parametric tests (Zar 1999). Kruskal-Wallis tests were performed to evaluate if the number of overall species or the percentage of urban tolerant birds on the assemblages differed between different levels of urbanization. Boxplots on both assemblages were constructed.

## RESULTS

A total of 102 bird species, representing 43 families of 29 orders were observed. Species richness estimated using the sample-based rarefaction technique tended to stabilize after 120 squares were sampled. The greatest recorded richness concerned Thraupidae (11 species), Tyrannidae (9 species), and Columbidae (6 species). The families Icteridae and Picidae can also be highlighted because of their representativeness (5 species each) in the surveys. Among the 102 birds identified, 13 were considered urban tolerant species, including three nonnatives (Rock Dove, Common Waxbill, and House Sparrow) (Table 1).

**Table 1.** Common names, scientific names, families, origin (native or exotic), and tolerance to exploit urbanized areas (according to Litteral & Wu 2012) of birds observed during the study period in Curitiba city, southern Brazil.

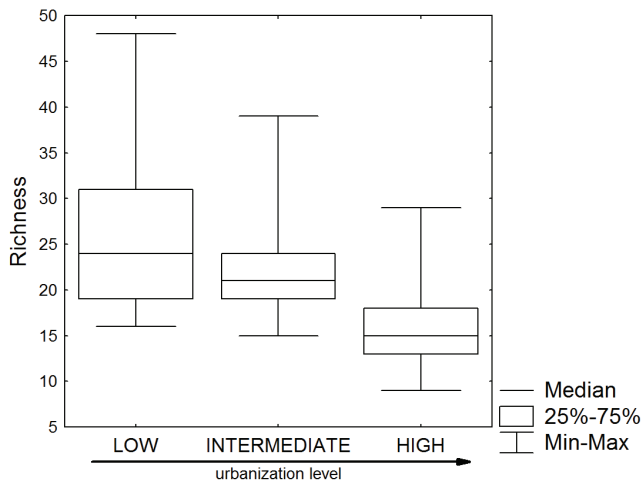
Common name	Species	Family	Origin	Urban tolerant
Brown Tinamou	<i>Crypturellus obsoletus</i>	Tinamidae	Native	No
White-faced Whistling-Duck	<i>Dendrocygna viduata</i>	Anatidae	Native	No
Brazilian Teal	<i>Amazonetta brasiliensis</i>	Anatidae	Native	No
White-cheeked Pintail	<i>Anas bahamensis</i>	Anatidae	Native	No
Dusky-legged Guan	<i>Penelope obscura</i>	Cracidae	Native	No
Neotropic Cormorant	<i>Nannopterum brasilianus</i>	Phalacrocoracidae	Native	No
Black-crowned Night-Heron	<i>Nycticorax nycticorax</i>	Ardeidae	Native	No
Striated Heron	<i>Butorides striata</i>	Ardeidae	Native	No
Great Egret	<i>Ardea alba</i>	Ardeidae	Native	No
Whistling Heron	<i>Syrigma sibilatrix</i>	Ardeidae	Native	No
Buff-necked Ibis	<i>Theristicus caudatus</i>	Threskiornithidae	Native	No
Black Vulture	<i>Coragyps atratus</i>	Cathartidae	Native	No
White-tailed Kite	<i>Elanus leucurus</i>	Accipitridae	Native	No
Roadside Hawk	<i>Rupornis magnirostris</i>	Accipitridae	Native	No
Slaty-breasted Wood-Rail	<i>Aramides saracura</i>	Rallidae	Native	No
Common Gallinule	<i>Gallinula galeata</i>	Rallidae	Native	No
Southern Lapwing	<i>Vanellus chilensis</i>	Charadriidae	Native	Yes
White-backed Stilt	<i>Himantopus melanurus</i>	Recurvirostridae	Native	No
Solitary Sandpiper	<i>Tringa solitaria</i>	Scolopacidae	Native	No
Wattled Jacana	<i>Jacana jacana</i>	Jacaniidae	Native	No
Ruddy Ground Dove	<i>Columbina talpacoti</i>	Columbidae	Native	Yes
Rock Pigeon	<i>Columba livia</i>	Columbidae	Exotic	Yes
Picazuro Pigeon	<i>Patagioenas picazuro</i>	Columbidae	Native	No
Eared Dove	<i>Zenaida auriculata</i>	Columbidae	Native	Yes
White-tipped Dove	<i>Leptotila verreauxi</i>	Columbidae	Native	No
Gray-fronted Dove	<i>Leptotila rufaxilla</i>	Columbidae	Native	No
Squirrel Cuckoo	<i>Piaya cayana</i>	Cuculidae	Native	No
Smooth-billed Ani	<i>Crotophaga ani</i>	Cuculidae	Native	No
Guira Cuckoo	<i>Guira guira</i>	Cuculidae	Native	No
Burrowing Owl	<i>Athene cunicularia</i>	Strigidae	Native	No
White-collared Swift	<i>Streptoprocne zonaris</i>	Apodidae	Native	No
Swallow-tailed Hummingbird	<i>Eupetomena macroura</i>	Trochilidae	Native	No
White-vented Violetear	<i>Colibri serrirostris</i>	Trochilidae	Native	No
Glittering-bellied Emerald	<i>Chlorostilbon lucidus</i>	Trochilidae	Native	No
White-throated Hummingbird	<i>Leucochloris albicollis</i>	Trochilidae	Native	No
Surucua Trogon	<i>Trogon surrucura</i>	Trogonidae	Native	No
Ringed Kingfisher	<i>Megaceryle torquata</i>	Alcedinidae	Native	No
Red-breasted Toucan	<i>Ramphastos dicolorus</i>	Ramphastidae	Native	No
White Woodpecker	<i>Melanerpes candidus</i>	Picidae	Native	No
Yellow-fronted Woodpecker	<i>Melanerpes flavifrons</i>	Picidae	Native	No
White-spotted Woodpecker	<i>Veniliornis spilogaster</i>	Picidae	Native	No
Green-barred Woodpecker	<i>Colaptes melanochlorus</i>	Picidae	Native	No



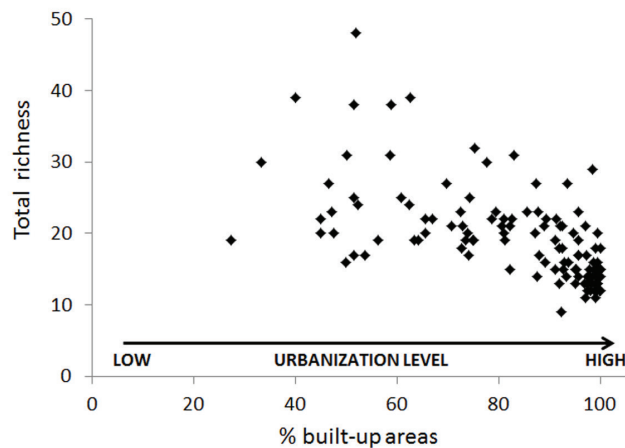
Common name	Species	Family	Origin	Urban tolerant
Campo Flicker	<i>Colaptes campestris</i>	Picidae	Native	No
Southern Caracara	<i>Caracara plancus</i>	Falconidae	Native	No
Yellow-headed Caracara	<i>Milvago chimachima</i>	Falconidae	Native	No
American Kestrel	<i>Falco sparverius</i>	Falconidae	Native	No
Aplomado Falcon	<i>Falco femoralis</i>	Falconidae	Native	No
Plain Parakeet	<i>Brotogeris tirica</i>	Psittacidae	Native	Yes
Pileated Parrot	<i>Pionopsitta pileata</i>	Psittacidae	Native	No
Scaly-headed Parrot	<i>Pionus maximiliani</i>	Psittacidae	Native	No
VARIABLE Antshrike	<i>Thamnophilus caerulescens</i>	Thamnophilidae	Native	No
Olivaceous Woodcreeper	<i>Sittasomus griseicapillus</i>	Dendrocolaptidae	Native	No
Planalto Woodcreeper	<i>Dendrocolaptes platyrostris</i>	Dendrocolaptidae	Native	No
Rufous Hornero	<i>Furnarius rufus</i>	Furnariidae	Native	Yes
Araucaria Tit-Spintail	<i>Leptasthenura setaria</i>	Furnariidae	Native	No
Spix's Spintail	<i>Synallaxis spixi</i>	Furnariidae	Native	No
Swallow-tailed Manakin	<i>Chiroxiphia caudata</i>	Pipridae	Native	No
Southern Beardless-Tyrannulet	<i>Camptostoma obsoletum</i>	Tyrannidae	Native	No
Yellow-bellied Elaenia	<i>Elaenia flavogaster</i>	Tyrannidae	Native	No
White-crested Tyrannulet	<i>Serpophaga subcristata</i>	Tyrannidae	Native	No
Great Kiskadee	<i>Pitangus sulphuratus</i>	Tyrannidae	Native	Yes
Cattle Tyrant	<i>Machetornis rixosa</i>	Tyrannidae	Native	No
Tropical Kingbird	<i>Tyrannus melancholicus</i>	Tyrannidae	Native	No
Fork-tailed Flycatcher	<i>Tyrannus savana</i>	Tyrannidae	Native	No
Long-tailed Tyrant	<i>Colonia colonus</i>	Tyrannidae	Native	No
Euler's Flycatcher	<i>Lathrotriccus euleri</i>	Tyrannidae	Native	No
Rufous-browed Peppershrike	<i>Cyclarhis gujanensis</i>	Vireonidae	Native	No
Chivi Vireo	<i>Vireo chivi</i>	Vireonidae	Native	No
Plush-crested Jay	<i>Cyanocorax chrysops</i>	Corvidae	Native	No
Blue-and-white Swallow	<i>Pygochelidon cyanoleuca</i>	Hirundinidae	Native	Yes
Brown-chested Martin	<i>Progne tapera</i>	Hirundinidae	Native	No
Gray-breasted Martin	<i>Progne chalybea</i>	Hirundinidae	Native	No
Southern House Wren	<i>Troglodytes musculus</i>	Troglodytidae	Native	Yes
Rufous-bellied Thrush	<i>Turdus rufigularis</i>	Turdidae	Native	Yes
Creamy-bellied Thrush	<i>Turdus amaurochalinus</i>	Turdidae	Native	No
White-necked Thrush	<i>Turdus albicollis</i>	Turdidae	Native	No
Chalk-browed Mockingbird	<i>Mimus saturninus</i>	Mimidae	Native	No
Rufous-collared Sparrow	<i>Zonotrichia capensis</i>	Passerellidae	Native	No
Tropical Parula	<i>Setophaga pitaiayumi</i>	Parulidae	Native	No
Masked Yellowthroat	<i>Geothlypis aequinoctialis</i>	Parulidae	Native	No
Golden-crowned Warbler	<i>Basileuterus culicivorus</i>	Parulidae	Native	No
White-browed Warbler	<i>Myiothlypis leucoblepharus</i>	Parulidae	Native	No
Red-rumped Cacique	<i>Cacicus haemorrhous</i>	Icteridae	Native	No
Chopi Blackbird	<i>Gnorimopsar chopi</i>	Icteridae	Native	No
Chestnut-capped Blackbird	<i>Chrysomus ruficapillus</i>	Icteridae	Native	No
Yellow-rumped Marshbird	<i>Pseudoleistes guirahuro</i>	Icteridae	Native	No
Shiny Cowbird	<i>Molothrus bonariensis</i>	Icteridae	Native	Yes
Fawn-breasted Tanager	<i>Pipraeidea melanonota</i>	Thraupidae	Native	No
Blue-and-yellow Tanager	<i>Pipraeidea bonariensis</i>	Thraupidae	Native	No
Diademed Tanager	<i>Stephanophorus diadematus</i>	Thraupidae	Native	No
Sayaca Tanager	<i>Tangara sayaca</i>	Thraupidae	Native	Yes
Saffron Finch	<i>Sicalis flaveola</i>	Thraupidae	Native	Yes
Blue-black Grassquit	<i>Volatinia jacarina</i>	Thraupidae	Native	No
Black-goggled Tanager	<i>Trichothraupis melanops</i>	Thraupidae	Native	No
Red-crested Finch	<i>Coryphospingus cucullatus</i>	Thraupidae	Native	No
Swallow Tanager	<i>Tersina viridis</i>	Thraupidae	Native	No
Double-collared Seedeater	<i>Sporophila caerulescens</i>	Thraupidae	Native	No
Green-winged Saltator	<i>Saltator similis</i>	Thraupidae	Native	No
Hooded Siskin	<i>Spinus magellanicus</i>	Fringillidae	Native	No
Violaceous Euphonia	<i>Euphonia violacea</i>	Fringillidae	Native	No
Common Waxbill	<i>Estrilda astrild</i>	Estrildidae	Exotic	Yes
House Sparrow	<i>Passer domesticus</i>	Passeridae	Exotic	Yes

The most common and widespread species of birds, with a frequency of occurrence of more than 80% in the surveys, were the natives Rufous Hornero, Eared Dove, Great Kiskadee, and Rufous-bellied Thrush (*Turdus rufiventris*), along with the nonnative House Sparrow. Rock Dove and House Sparrow were registered in all sites assessed in high urbanized areas, whereas the Eared Dove and the House Sparrow were the most persistent species in the low to intermediate urbanized sites.

The effect of the urbanization level on avian richness was significant (Kruskal-Wallis  $H_{2,120} = 47.817$ ,  $P = 0.001$ , Fig. 2), however the avian richness was



**Figure 2.** Box-plot on avian total richness of Curitiba, southern Brazil, considering the effect of the proportion of built-up areas (urbanization levels). Low (<50% of built-up areas), intermediate (50–75% of built-up areas), and high (>75% of built-up areas).



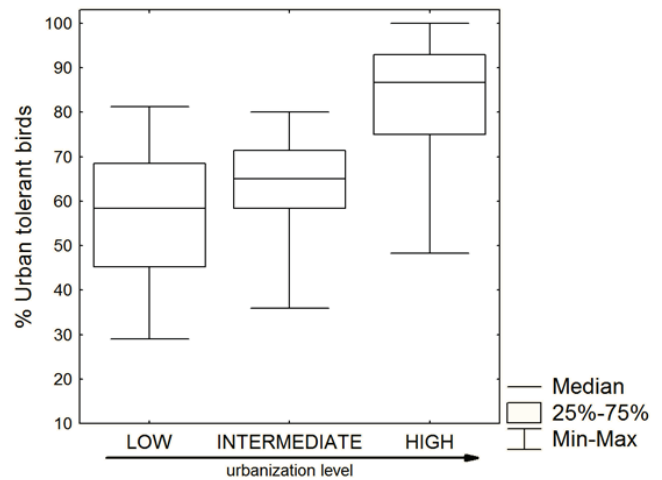
**Figure 3.** Regression on avian total richness in Curitiba, southern Brazil, considering the effect of the proportion of built-up areas (urbanization levels).

## DISCUSSION

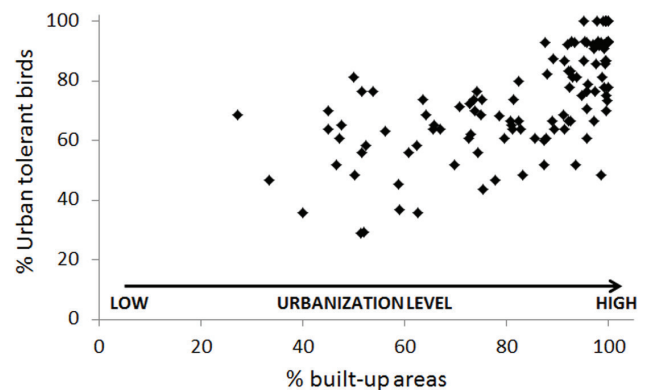
This study examined trends in bird richness and the representativeness of urban tolerant birds across a range of sampled areas embedded in a southern Brazilian city. The assemblage recorded consisted of a high frequency of a relatively few species of birds, including both natives

not statistical different between low and intermediate urbanized sites ( $P > 0.05$ ). Despite the high-variability in data, total richness was lower in sites where the amount of built-up areas was higher (Spearman  $r_s = -0.69$ ,  $P = 0.01$ , Fig. 3).

The effect of the urbanization level on the amount of urban tolerant birds on avian composition was also significant (Kruskal-Wallis  $H_{2,120} = 50.065$ ,  $P = 0.001$ , Fig. 4), except between low and intermediate urbanized sites ( $P > 0.05$ ). The proportion of urban tolerant birds on avian composition was higher in high urbanized sites (Spearman  $r = 0.71$ ,  $P = 0.001$ , Fig. 5).



**Figure 4.** Box-plot on the amount of tolerant birds in avian assemblages of Curitiba, southern Brazil, considering the effect of the proportion of built-up areas (urbanization levels). Low (<50% of built-up areas), intermediate (50–75% of built-up areas), and high (>75% of built-up areas).



**Figure 5.** Regression on the amount of tolerant birds in avian assemblages of Curitiba, southern Brazil, considering the effect of the proportion of built-up areas (urbanization levels).

species (e.g. Ruddy Ground Dove *Columbina talpacoti*, Eared Dove, Great Kiskadee, Rufous-bellied Thrush, Rufous Hornero) and nonnatives (Rock Dove, Common Waxbill, and House Sparrow). The bird assemblages detected are typical of others South American's urban landscapes (e.g. Reynaud & Thioulouse 2000, Leveau & Leveau 2005, 2012, Manhães *et al.* 2005, Pauchard *et al.*

2006, Pinheiro *et al.* 2008, Fontana *et al.* 2011, Reis *et al.* 2012, Toledo *et al.* 2012).

As expected, we found that urbanization plays an important role in shaping spatial distribution of urban bird assemblages. Our analysis supported recent reviews of Hansen *et al.* (2005) and Faeth *et al.* (2011), which have found that for the overall bird community, species richness declines with increasing urban development, and also that the representativeness of species that are ecologically associated with humans increase in sites with high amounts of built-up areas (Sandström *et al.* 2006, DeVictor *et al.* 2007, Kark *et al.* 2007, Conole & Kirkpatrick 2011).

The number of species recorded in areas with high urbanization levels was significantly lower than at the low and intermediate urbanized areas. High (>75% of built-up areas) urbanized sites were found not only in central districts of Curitiba, but also in the surroundings of the urban core. In such sites, the urbanization process decreased the taxonomic and functional characteristics of avian communities through the loss of rare and specialist species, and by the increase of generalist urban birds, a biological phenomenon called biotic homogenization (McKinney & Lockwood 1999). Our results indicated that urbanization changes bird species richness, both by decreasing native species diversity and by the addition of widely distributed synanthropic species, such as Ruddy Ground Dove, Eared Dove, Great Kiskadee, Rufous-bellied Thrush, Rufous Hornero, Rock Dove, Common Waxbill, and House Sparrow. These species appear to benefit from the greater availability of resources that occur in urban areas.

According to Kark *et al.* (2007) and Møller (2009), urban birds share certain life history traits, including being resident (as opposed to migrant), nesting above ground (*i.e.* cavity and canopy nesters), and having a behavioral plasticity that allows a species to have a broad environmental tolerance. The 12 urban tolerant birds identified in Curitiba shared these traits, and they included both native and nonnative species. Even though urbanization and associated modifications negatively affect native species (Blair 1996, Hodgson *et al.* 2007, Kark *et al.* 2007, Evans *et al.* 2011), leading to an increase in invasive ones usually exotics (Blair 2001, Sol *et al.* 2012), Curitiba's highly urbanized environments were not dominated by exotic species. The most widespread and commonly registered species were the natives Rufous Hornero, Eared Dove, Great Kiskadee, and Rufous-bellied Thrush, along with the nonnative House Sparrow. However, our personal observations indicate that the abundance of individuals of exotic species seems to outnumbered native ones. Factors like the higher temperature in urban environments (Roth *et al.* 1989), the greater availability of nest sites (Murgui 2009), and

the greater availability of anthropogenic food (Suhonen & Jokimäki 1988, Leveau & Leveau 2005) may contribute to the higher densities of these exotic species in urban areas (DeVictor *et al.* 2007).

The ground foraging birds was by far the most abundant in terms of the number of species observed, and were represented by granivorous, omnivorous, and insectivorous birds. The dominant trophic guild (granivorous) were represented by Ruddy Ground Dove, Rock Pigeon, Eared Dove, Saffron Finch (*Sicalis flaveola*), and Common Waxbill. Omnivorous were represented by Plain Parakeet (*Brotogeris tirica*), Great Kiskadee, Rufous-bellied Thrush, and House Sparrow, and insectivorous species, represented by Rufous Hornero, Southern Lapwing and Blue-and-white Swallow (*Pygochelidon cyanoleuca*). Such trophic guilds are usually benefited from habitat modification (Willis 1979) and from an increase in built-up areas (Jokimäki & Suhonen 1998).

Our results show that most avian species were negatively affected by urban disturbance, except urban tolerant birds. These observations were consistent with other studies which have found that certain functional groups tend to thrive in urban communities (Blair 1996, Kark *et al.* 2007, Conole & Kirkpatrick 2011), such as sedentary species (Crocini *et al.* 2008) and birds with larger ranges and broader environmental tolerances (Blackburn *et al.* 2009). On the other hand, the exact ecological mechanisms driving urban bird composition according to different levels of anthropogenic disturbances still need further investigation. Most urban tolerant species registered in Curitiba are ground foraging resident birds, which use a diverse array of anthropogenic resources and can be found occupying various types of habitat in the city. The ability to exploit a wide variety of resources, which is useful when resources are scarce or when individuals colonize new environments, contribute to urban bird's ecological flexibility, predisposing them to succeed in human-disturbed habitats (Bonier *et al.* 2007).

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# The abundance of Red-bellied Macaws (*Orthopsittaca manilata*) and Orange-winged Parrots (*Amazona amazonica*) in relation to fruiting Moriche Palms (*Mauritia flexuosa*) at the Aripo Savannas, Trinidad

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**ABSTRACT:** The largest remaining savanna ecosystem on the island of Trinidad is the Aripo Savannas Environmentally Sensitive Area (ASESA). It has been historically fragmented due to a number of anthropogenic activities. This study focused on the densities of the Red-bellied Macaw (*Orthopsittaca manilata*) and Orange-winged Parrot (*Amazona amazonica*), which are known to rely on palms for roosting, nesting and feeding at the ASESA, in relation to the distribution of the fruiting Moriche Palms (*Mauritia flexuosa*) at the ASESA. There was a significant correlation between the total number of birds and number of fruiting Moriche Palms on transects for macaws ( $r_s = 0.708$ ,  $P = 0.022$ ) but not for parrots ( $r_s = 0.421$ ,  $P = 0.225$ ). Average group size increased significantly from the late rainy to the early dry season in macaws, but not in parrots. Point count surveys estimated higher densities than line transects for both macaws (129 vs. 87/km<sup>2</sup>) and parrots (193 vs. 103/km<sup>2</sup>). The use of peripheral areas showed that fragmentation had no effect on the foraging behavior of macaws or parrots. Nevertheless, if the savannas become increasingly modified, human-parrot conflicts may increase and so food resources should be integrated into management plans for this protected area.

**KEY-WORDS:** feeding ecology, fragmentation, population density, Psittacidae, seed dispersal.

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## INTRODUCTION

Thirty percent of Neotropical psittacid species face some threat of extinction and 70% have decreasing population sizes (Collar 2000). The two main drivers of psittacid population decline are habitat loss and the wildlife trade (Juniper & Parr, 1998, Snyder *et al.* 2000, Wiley *et al.* 2004, Deem *et al.* 2008). Bennett & Owens (1997) attribute the high vulnerability of psittacids to their frugivorous diet, large body sizes and small clutch sizes.

Psittacids usually make substantial foraging movements between roosting and feeding sites, exploiting a variety of vegetation types (Ragusa-Netto 2004). Some species switch their diets in response to resource scarcity (Renton 2001, Moegenburg & Levey 2003). Other species move across patchy habitats in relation to the seasonal availability of food resources (Ortiz-Maciél *et al.* 2010). These studies have primarily focused on the feeding behavior of psittacids in forests. Nevertheless, psittacids inhabit a wide range of habitats from semi-open country to savannas (Ragusa-Netto 2004), and avian resource use

within Neotropical savannas remains poorly understood (Maruyama *et al.* 2013). Furthermore, little is known about the interaction between frugivores such as psittacids and the Moriche Palm (*Mauritia flexuosa*) (Villalobos & Bagno 2012), a characteristic species of Neotropical savanna ecosystems including those in Trinidad. Knowledge of how populations respond to the variation in distribution of resources is essential for understanding how species function in their environments (Matuzak *et al.* 2008) and identifying key resources, habitats and areas to be conserved (Renton 2001).

The Aripo Savannas Environmentally Sensitive Area (ASESA) is one of only two remaining natural savanna ecosystems in Trinidad. It supports highly diverse floral and faunal communities. A total of 132 species of birds have been recorded of which three; Lilac-tailed Parrotlet (*Touit batavicus*), Orange-winged Parrot (*Amazona amazonica*), and Red-bellied Macaw (*Orthopsittaca manilata*) are psittacids. Some of these birds are highly associated with the Moriche Palm, such as the rare Moriche Oriole (*Icterus cayanensis chrysocephalus*), the

Sulphury Flycatcher (*Tyrannopsis sulphurea*) and the Fork-tailed Palm-swift (*Tachornis squamata*) (EMA 2007). During World War II the United States Army used the ASESAs as a base during which time roads and bunkers were built. The roads divided the savannas subsequently facilitating quarrying, illegal logging and hunting, which continue today. After the army abandoned the base in 1956 settlements were established around the ASESAs (EMA 2007). Historic fragmentation may have had an impact on the Moriche Palms and consequently its seed dispersers such as the Red-bellied Macaw (Federman *et al.* 2013). Moriche Palms are long lived diploid dioecious plants, and are the dominant palm species bordering the seasonally inundated savannas, in bands 3–20 m wide (Federman *et al.* 2013). In these areas where monodominant stands exist, the presence of other fruiting species is minimal, allowing researchers to directly explore the relationship between avian frugivores and fruit availability (Moegenburg & Levey 2003).

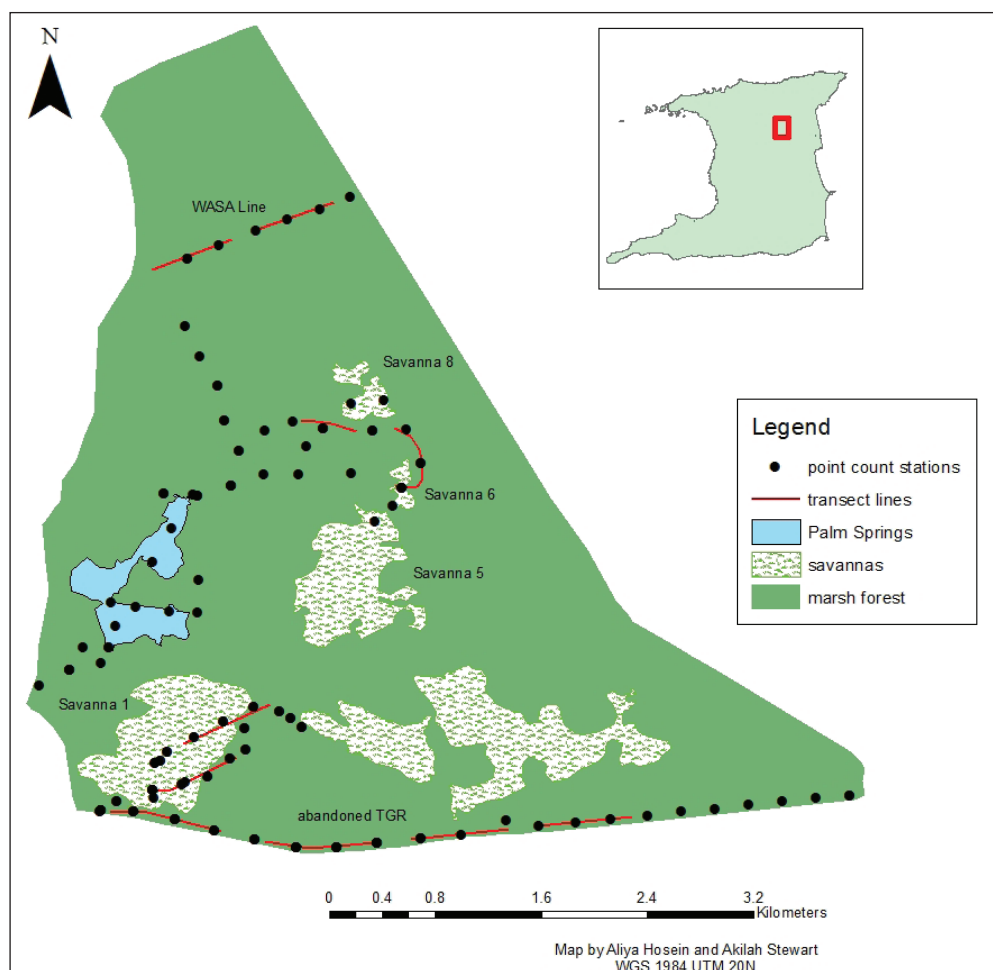
Red-bellied Macaws usually form flocks of up to 100 individuals, as they are highly social and have been reported to be fairly common in the ASESAs (Forshaw 2010). Orange-winged Parrots also form flocks of up to 100 individuals, but are mostly seen flying in pairs

(Forshaw 2010). These psittacids are non-threatened but are dependent upon palm swamp for roosting, feeding and nesting, which makes them vulnerable to threats against this habitat (Bonadie & Bacon 2000, Renton 2004, Brightsmith 2005). The objective of this study is to describe the feeding ecology of the Red-bellied Macaws and Orange-winged Parrots at the ASESAs with particular interest in the relationship between the distribution of fruiting Moriche Palms and psittacid abundance and feeding behavior.

## METHODS

### Study area

The ASESAs (10°35'N; 61°12'W) is a triangular area located south of the Northern Range on the island of Trinidad of the Republic of Trinidad and Tobago (Fig. 1). Its borders are the Valencia River (west); the Aripo River and the Eastern Main Road (east); and the abandoned Trinidad Government Railway Reserve (TGR, south). The ASESAs covers 18.8 km<sup>2</sup> of land surface (EMA 2007).



**Figure 1.** Location of transect lines and point count stations in the Aripo Savannas Environmentally Sensitive Area (ASESA). The ASESA's location in Trinidad is indicated by the red box in the inset map of the island (top right hand corner).

Beard (1946) described the Aripo Savannas as an edaphic marsh savanna formation comprising three vegetative communities: marsh forest, savanna and palm marsh. The land area is mostly marsh forest dominated by the palms; Palma Real (*Oenocarpus bataua*), Manac (*Euterpe precatoria* and *E. oleracea*), Timite (*Manicaria saccifera*), Royal Palm (*Roystonea oleracea*) and Cocorite (*Attalea maripa*) and associated plants. Wild Calabash (*Tabebuia stenocalyx*), Agalie (*Ficus* sp.), Matapal (*Clusia palmicida*), Biscuit Wood (*Ilex arimensis*), and Bois Charbon (*Diospyros ierensis*), are found in the lower stratum. Galba (*Calophyllum lucidum*), Wild Kaimit (*Pouteria* sp.), Yellow Mangue (*Symphonia globulifera*), Bois Bande (*Parinari campestris*), Cajuca (*Virola surinamensis*) and Wild Pine (*Podocarpus coriaceus*) comprise the upper stratum (Young 2006).

The savannas occur as 10 open areas of grass-sedge vegetation amidst the marsh forest (Richardson 1963). Trinidad and Tobago experiences a rainy season which lasts from May to December and a dry season from January to April. In the rainy season the hardpan layer in the savannas prevents percolation of water and the soil becomes waterlogged. In the dry season precipitation is low and the soil becomes extremely hard. These conditions prevent woody plants from colonizing savannas. Savannas are dominated by sedges and grasses such as the endemic *Rhynchospora aripoensis* and *Xyris grisebachii* (Beard 1946). The sedge *Lagenocarpus rigidus* is the most widespread species found throughout the savannas (Cooper *et al.* unpub. data). Among the grasses and sedges there are also bladderworts, ground orchids (*Cyrtopodium parviflorum*), carnivorous sundews (*Drosera capillaris*), Savanna Roseau (*Bactris campestris*) and the occasional tangle of parasitic vine (*Cassytha americana*) (Young 2006).

The palm marsh forms an intermediate between the savannas and marsh forest. It is found either fringing the savannas or in isolated islands (palm islands) within the savannas (Beard 1946) with Fat Pork (*Chrysobalanus icaco*) and Savanna Serrette (*Byrsonima crassifolia*) in the lower stratum and Moriche Palms (*Mauritia flexuosa*) in the upper stratum (Young 2006).

### Abundance

To sample macaw and parrot abundance the variable distance line transect survey method was used (Casagrande & Beissinger 1997, Buckland 2006, Thomas *et al.* 2010) from October 2014 to March 2015, and point counts from January to November 2014 and in January, July and November 2015. A total of 10 transects on existing access trails (Buckland *et al.* 2010), each 1 km long, were dispersed at least 300 m apart (Matuzak *et al.* 2008) throughout the study area to get a representative sample of resource availability (Renton 2001). The transect lines

traversed a variety of habitat types: pine/palm marsh ecotone (TGR1 and 2); palm marsh (TGR3); palm marsh/marsh forest (TGR4, BT, S82); savanna (HR); palm marsh/savanna ecotone (S81); and marsh forest/savanna ecotone (WASA1 and 2). Each transect was sampled once in both the late rainy season (October to December) and the early dry season (January to March) from 06:00 to 09:00 h (EST). Sunrise varied from 05:45 to 06:30 h in this period.

Existing trails were used because the area is inundated during the rainy season, which would make some of the area inaccessible, and the ASES is protected and new trails cannot be cleared. Point count stations, about 250 m apart, were randomly positioned along and within the general area of the designated trails (Fig. 1).

Point counts were conducted from 06:00 to 11:00 h and at each station observation lasted for 10 min. When one or more macaws or parrots were encountered, date, time, location, vegetation type, number of individuals, if perched, and initial perpendicular distances from the observer were recorded. When a macaw was heard but not seen it was recorded as one individual (Pizo *et al.* 1995, Galetti 1997). Care was taken to avoid multiple counts of the same bird, and birds flying over the area were recorded separately from perched birds. A Nikon Forestry Pro laser rangefinder was used to measure distances, and Eagle Optics Ranger 8 × 42 Roof Prism Binoculars RGR-4208 to correctly locate and count psittacids. Species identification was confirmed using Forshaw (2010).

### Diet

The feeding behavior of the psittacids were recorded simultaneously during line transect surveys. One feeding bout was recorded whenever one or more macaws or parrots were found feeding on a plant species. If the bird(s) moved to another plant to feed during the same observation period, a new feeding bout was recorded (Galetti 1993, Galetti & Pizo 1996). For each feeding bout the date, time, location, number of birds foraging, the plant species consumed and part eaten (flowers, pulp or seeds), and vegetation type, were recorded (Galetti 1997, Renton 2001). Specific attention was paid to the location of birds so that groups could be separated and length of visit could be calculated (Moegenburg & Levey 2003, Ragusa-Netto 2004). A feeding bout ended when macaws or parrots finished foraging and moved away (Contreras-González *et al.* 2009).

### Fruiting Moriche Palms

The numbers of female Moriche Palms already bearing immature (exocarp green-brown with green flesh) and ripe (exocarp red-brown with yellow flesh) fruits on both



sides of each transect were counted (Bonadie & Bacon 2000) in the late rainy season. This number did not change during the early dry season.

### Data analysis

Spearman's rank correlation analysis was used to examine the relationship between the number of fruiting palm trees and total numbers of parrots and macaws detected in each transect in the two sampling periods combined (Galetti 1997, Bonadie & Bacon 2000, Ragusa-Netto 2004). The Mann Whitney *U*-test was used for pairwise comparisons, such as group sizes of species and their distribution in relation to seasons, since data followed a non-normal distribution. Statistical analyses were performed using the R software, v. 3.1.2 (R Core Team 2014), for statistical computing and graphing. All statistical tests used  $\alpha = 0.05$ .

All distances for parrots and macaws were pooled across survey months to increase the number of detections for calculating density estimates from point count and line transect surveys using the conventional distance sampling (CDS) engine in Distance 6.2 (Buckland *et al.* 2001, Thomas *et al.* 2010). The outermost distances at which detections were low were excluded from the analysis to get a better fit of detection models. Additionally, all detections of parrots and macaws were treated as clusters. All detection functions were considered and model selection was based on minimum difference in Akaike's Information Criterion  $AIC_c$  (values < 2 considered similarly parsimonious; Rivera-Milán *et al.* 2005).

## RESULTS

### Red-bellied Macaw and Orange-winged Parrot density

Red-bellied Macaws and Orange-winged Parrots were seen on each visit to the ASES. Mean  $\pm$  1 standard deviation of macaw group size in the late rainy season was  $3.47 \pm 4.53$  individuals (range = 1–15,  $n = 34$ ), whereas group size was  $5.87 \pm 9.18$  individuals (range = 2–50,  $n = 39$ ) in the early dry season. Red-bellied Macaw group sizes were

significantly different between the two study periods ( $U = 420$ ,  $P = 0.006$ ). The Red-bellied Macaws were mostly observed in the southwestern half of the ASES along the abandoned TGR, in Savanna 1 and Palm Springs. They were least abundant at the northern and north western end in the marsh forest and palm marsh, and were mostly flight records in these areas (Hosein 2015).

Regarding the Orange-winged Parrot, mean  $\pm$  1 standard deviation of group size in the late rainy season was  $2.69 \pm 3.65$  individuals (range = 1–25,  $n = 91$ ) individuals compared to  $2.14 \pm 1.89$  individuals (range 1–18,  $n = 137$ ) in the early dry season. Orange-winged Parrot group sizes did not differ significantly between the two study periods ( $U = 6218.5$ ,  $P = 0.970$ ). Parrots were observed along all transect lines and at all point count stations. They were consistently found perched in the palm fringes of savannas 1 and 8, as well as in the marsh forest at the northern end of the ASES.

Macaws were detected at a maximum distance of 155.4 m from the line transect. The uniform key function with cosine adjustment term ( $\chi_1 = 3.82$ ,  $P = 0.05$ ;  $AIC_c = 1.62$ ) provided the best fit to the data. Parrots were detected at a maximum distance of 170 m, but in order to remove outliers, perpendicular distances were truncated at 150 m. The uniform key function with cosine adjustment term ( $\chi_1 = 5.07$ ,  $P = 0.02$ ;  $AIC_c = 0.49$ ) provided the best fit to the data.

Point count surveys produced higher density estimates for both species (Table 1). Maximum detection distance for the macaws and parrots were 220 and 200 m, respectively. The half-normal key function with cosine adjustment term provided the best fit to the data for both macaws ( $\chi_2 = 11.02$ ,  $P < 0.05$ ;  $AIC_c = 0.21$ ) and parrots ( $\chi_4 = 8.57$ ,  $P < 0.05$ ;  $AIC_c = 0.49$ ).

### Fruiting Moriche Palms

A total of 1946 mature canopy-sized Moriche Palms were recorded, of which 110 were fruiting. Transect TGR3 had the highest total number of Moriche Palms per km (333), and transect TGR2 had the highest number of fruiting palms (29). There were no Moriche Palms in WASA2. Neither male nor female palms were flowering during the transect study period.

**Table 1.** Mean  $\pm$  1 standard deviation (SD) of the density (Number/km<sup>2</sup>) and coefficient of variation (CV) of Red-bellied Macaws and Orange-winged Parrots from line transect (October 2014 to March 2015) and point count (2014 to 2015 in consecutive months) surveys in the ASES, Trinidad.  $n$  = Number of observations.

	Red-bellied Macaw			Orange-winged Parrot		
	<i>n</i>	Mean $\pm$ SD Number/km <sup>2</sup>	CV (%)	<i>n</i>	Mean $\pm$ SD Number/km <sup>2</sup>	CV (%)
Line transect	31	87.4 $\pm$ 47.7	54.6	90	102.9 $\pm$ 24.4	23.7
Point count	39	129.2 $\pm$ 40.5	31.3	157	192.5 $\pm$ 37.3	19.5

### Red-bellied Macaw and Orange-winged Parrot diet

Orange-winged Parrots were not observed feeding on the palm fruits or fruits of any other available plant species, such as Manac (*Calyptrornis rivalis*), Gri Gri (*Acrocomia aculeate*), Pois Doux (*Inga ingoides*) or Cajuca during survey periods. However, they were seen with a feeding flock of macaws on two occasions along the abandoned TGR. The Red-bellied Macaws were observed feeding on Moriche Palm fruits. Out of 11 feeding observations, eight were made along TGR2 during both survey periods. Single feeding observations were made in Hedgerow, Bunker Trail and WASA 1 during the late rainy season. A positive correlation was found between the total number of birds in the two sampling periods and number of fruiting Moriche Palms on the 10 transects for macaws ( $r_s = 0.708$ ,  $P = 0.022$ ) but not for parrots ( $r_s = 0.421$ ,  $P = 0.225$ ). The feeding macaw flock sizes ranged from 15 to 30 individuals. They generally divided into smaller groups of 2 to 5 around the feeding palm tree. Macaws vocalized during feeding and occasionally switched between individual fruiting Moriche Palms. Feeding took place between 7:00 h and 8:30 h, and lasted between 10 and 30 min. At the end of the feeding bout about half of the flock would circle around the feeding area and return to the feeding palm, at which point the other half of the flock would join before flying off together. They only fed on ripe palm fruits with the exception of one pair that were seen feeding on immature fruits. Some macaws perched on the bunch and used their beaks to remove the scales of the exocarp, after which they would eat the exposed pulp. The fruits were partially eaten and left attached to the bunch with the pulp exposed. Other macaws removed the fruit from the bunch and perched on the palm frond of the same tree, or flew to the nearest palm with the fruit in their beaks. They would then manipulate the fruit with their feet by rolling the fruit while removing the scales of the exocarp. Macaws usually ate all the pulp from fruits that were removed from the bunch. They then dropped the clean endocarp to the base of the palm on which they were perched. Neither intraspecific antagonistic nor sentinel behaviors were observed during feeding.

### DISCUSSION

Macaws and parrots are still abundant in the ASESAs, although widespread fragmentation and human encroachment has occurred in the area (EMA 2007). Density estimates from point count surveys exceeded line transect counts, similar to findings reported for Green-rumped Parrotlets (*Forpus passerines*) in the Llanos of Venezuela (Casagrande & Beissinger 1997). Orange-winged Parrot density was higher than Red-bellied

Macaw, but in other studies Red-bellied Macaw density was higher than other psittacid species at sites containing *Mauritia*-dominated palm swamps (Karubian *et al.* 2005, Rodrigues *et al.* 2012). Both behaviors and the different habitat types surveyed in this study could explain the higher density of Orange-winged Parrot reported. Our results indicate that the ASESAs at present are able to sustain large psittacid populations because of its palm species which supply fruits throughout the year with peak ripe fruit availability during the driest months (Villalobos & Bagno 2012) and other flowering and fruiting tree species. However, due to their low reproductive output, sustained fragmentation of reserves can also cause low psittacid species diversity and densities, as seen in Brazil and Argentina (Marsden *et al.* 2000, Marsden & Pilgrim 2003, Rivera-Milán *et al.* 2005).

Despite their conspicuous vocalizations and size, lower number of sightings and smaller average group sizes were recorded for the macaws in the late rainy season compared to the early dry season. The increase in Red-bellied Macaw flock size from rainy to dry season was also recorded at the palm swamps of the Brazilian Cerrado. Sightings become difficult during the mating period when pairs are formed and they are less vocal. They also cover a larger area when searching for suitable nesting sites, thereby resulting in a decrease in density of individuals (Rodrigues *et al.* 2012). Weather is also known to bring about significant changes in psittacid behavior: rain and lower temperatures reduce song, flying and communal roosting (Brightsmith 2004).

The Red-bellied Macaw prefers palm marsh habitats (Bonadie & Bacon 2000, Oehler *et al.* 2001, Renton 2004, Brightsmith 2005, Rodrigues *et al.* 2012) whereas Orange-winged Parrots can be found in a variety of habitats, such as mangroves, gallery forests and also drier woodlands (Forshaw 2010). The diets of both species contain mostly palm fruits (Bonadie & Bacon 2000) but according to Roth (1984) Red-bellied Macaw is specialized on the Moriche Palm fruit and, therefore, remains close to these palms. This would explain its high abundance in the palm marshes at the ASESAs. The distributions of fruiting Moriche Palms and Red-bellied Macaws were correlated in the ASESAs, and a close association with the Moriche Palm has also been observed in the palm swamps of the Nariva Swamp and Brazilian cerrados (Bonadie & Bacon 2000, Villalobos & Bagnos 2012, Rodrigues *et al.* 2012).

Interestingly, most macaw sightings and feeding observations were made along the abandoned TGR, at the edge of the ASESAs adjoining a residential area, and in the palm marsh fringing Savanna 1, where fruiting Moriche Palms were most abundant, suggesting that their behavior may not be affected thus far by habitat fragmentation. Savanna 1 is located near Cumuto village and Forestry Division buildings and is the designated

tourism and education zone. Psittacids demonstrate the ability to track food resources thereby changing habitat use on both spatial and temporal scales (Renton 2001). It is possible that psittacids compare suitable foraging sites. Moegenburg and Levey (2003) have shown that relative abundance of fruits and not absolute abundance affects foraging choices in frugivores. The high number of macaws present in the south western end of the ASESAs may be in relation to the availability of the Moriche Palm fruits. This implies the need to study its fruit tracking behavior across the entire landscape (Moegenburg & Levey 2003) including the nearby villages and palm swamp in the Arena Forest.

Macaws and parrots foraging in developed areas can result in increased conflicts between humans and psittacids as savannas become increasingly modified (Matuzak *et al.* 2008). Oehler *et al.* (2001) predict that a decrease in palm fruit availability may intensify the use of substitute food resources such as cacao and other cultivated crops by psittacids, thereby creating competition for food resources between local farmers and psittacids. This particularly applies to the Orange-winged Parrot that already exhibits this behavior and is classified as vermin under the Conservation of Wild Life Act of Trinidad and Tobago. Its depredation of crops can be lethally controlled on privately owned land, but could be prevented by augmenting food species in protected areas.

It is known that Red-bellied Macaws function as seed dispersers since they can transport and eat the Moriche Palm fruits without damaging seeds. On a small spatial scale this is critical for gene flow for the Moriche Palm population. Federman *et al.* (2013) reported high levels of nearest-neighbour mating in a collection area of 10 km<sup>2</sup> at the ASESAs. They suggest this may be related to fragmentation and uncontrolled hunting of other seed dispersers such as the Red Brocket Deer (*Mazama americana*). The macaws sometimes left the fruit attached to the bunch while feeding. Other studies from central Brazil have shown that, as a result, the exposed pulp was made available in the canopy layer to other bird species including Palm Tanager (*Thraupis palmarum*), Sayaca Tanager (*Thraupis sayaca*), Black-faced Tanager (*Schistochlamis melanopis*), Chopi Blackbird (*Gnorimopsar chopi*) and Curl-crested Jay (*Cyanocorax cristatellus*) (Tubelis 2009, Villalobos & Bagno 2012). In a study by Tubelis (2009) an Ash-throated Crake's (*Porzana albicollis*) stomach was found to contain solely Moriche Palm pulp, indicating that fruits opened by psittacids were also eaten by other bird species while on the ground. Both Palm Tanager and Ash-throated Crake can be found at the Aripo Savannas.

Results from this study highlight the importance of palm marshes within the ASESAs to Red-bellied Macaw and Orange-winged Parrot populations as habitats in

which food resources are obtained. It is also a site in which the public can see large numbers of free-living parrots and macaws to foster a culture of responsibility for protecting the environment.

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# Seasonal variation of understory insectivorous birds and arthropods in an area of secondary Atlantic Forest, southeast Brazil

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**ABSTRACT:** Seasonal variation of understory insectivorous birds and arthropods was investigated in an area of secondary Atlantic Forest, in southeast Brazil. Birds were captured with mist-nets and arthropods collected on the ground and foliage. A total of 348 captures of 243 individuals belonging to 15 bird species were obtained. Among 3416 arthropods, 1782 were collected on the ground and 1634 on the foliage. There was no significant variation in numbers of captures, individuals and bird species between dry and rainy seasons. However, arthropods were more abundant on the foliage during the dry season and on the ground in the rainy season. In this way, although the number of arthropods varied between seasons, it seems to be a sufficient resource to insectivorous birds feeding along the year. Besides, these birds can present some plasticity, changing the frequency of their foraging tactics repertoire in search of this feeding resource.

**KEY-WORDS:** arthropod abundance, foraging birds, seasonality, semideciduous forest, trophic ecology.

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## INTRODUCTION

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Insectivorous birds comprise most of the understory bird species in tropical forests (Cueto & Casenave 2000, Dário *et al.* 2002), and together with the food resources that they explore (insects and other arthropods), involve important issues on ecological interactions (Karr *et al.* 1982, Devey & Peres 2000, Codesido & Bilenca 2004). Some studies have evaluated the relationship between food resources and dynamics of populations and bird communities in many temperate and tropical regions (*e.g.* Loiselle & Blake 1990, Poulin & Lefebvre 1996, Burger *et al.* 1999, Malizia 2001). However, few studies have investigated the responses of insectivorous birds to the availability of their feeding resources in forest environments (Raley & Anderson 1990, Poulin *et al.* 1994, Manhães & Dias 2011).

The prey consumed by understory insectivorous birds, found both on the ground and foliage of trees and shrubs, can vary in different microhabitats due to the influence of abiotic conditions and vegetation structure (Smith *et al.* 1978). Furthermore, although arthropods

can be a highly abundant and regular resource when compared to flowers and fruits (Buskirk & Buskirk 1976, Poulin *et al.* 1994), they may also present seasonal variations, reducing their abundance in dry periods (Devey & Peres 2000). Consequently, the uneven spatial and temporal distribution of this prey resource can influence the number of individuals or the composition of insectivorous bird species in a community (Martin & Karr 1986, Horne & Bader 1990, Chesser 1995, Naranjo & Ulloa 1997).

Most studies relating the composition of the bird communities to the available food resources have been carried out with frugivorous birds (Moermond & Denslow 1985, Loiselle & Blake 1990), whereas studies with insectivores still remain restricted, mainly to the descriptive analysis of their diet (Ralph *et al.* 1985, Blake & Rougès 1997, Gomes *et al.* 2001, Rougès & Blake 2001). Thus, this study aimed to investigate the seasonal relationship between the richness and abundance of understory insectivorous birds and arthropods from different microhabitats (soil and foliage) in an area of the secondary Atlantic Forest in southeastern Brazil.

## METHODS

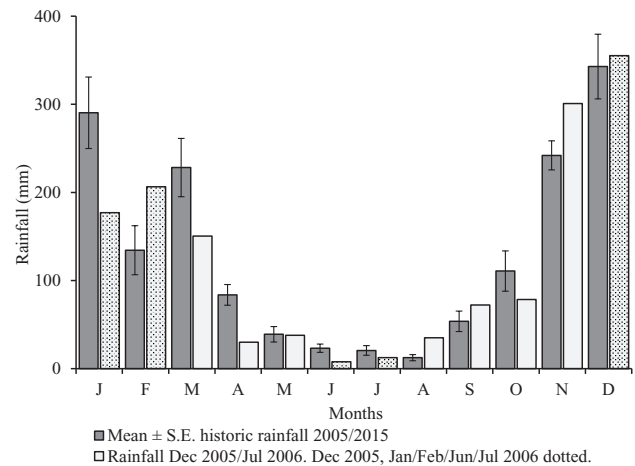
### Study area

The study area is a secondary Atlantic Forest fragment with 56 ha (Manhães *et al.* 2010), classified as a lower montane semideciduous forest (Oliveira-Filho *et al.* 2005) belonging to a private property named “Fazenda Continente”. The farm is located at 21°37'S; 43°21'W, between the municipalities of Juiz de Fora and Coronel Pacheco, Minas Gerais state, southeastern Brazil (Fig. 1). The altitude of the region varies between 670–800 m, and the climate is classified as Köppen Cwa (humid subtropical), with annual temperatures of around 20.2°C. The region has well-defined dry and rainy seasons (Granzinoli & Motta-Jr. 2006) and the annual rainfall varies around 1536 mm (Fig. 2).

### Bird samplings

Birds were captured during December 2005, January and February 2006 (rainy season), and June and July 2006 (dry season). Birds were captured by using 12 × 3 m mist-nets, with 38 mm mesh, installed at ground level in four pre-established transects (Fig. 1), standardizing 10 nets in line on each transect. Each transect was sampled twice for two consecutive days, with at least 20 days between the two samplings of the same transect, totaling 16 sampling days with mist-nets at each season. Captures began around

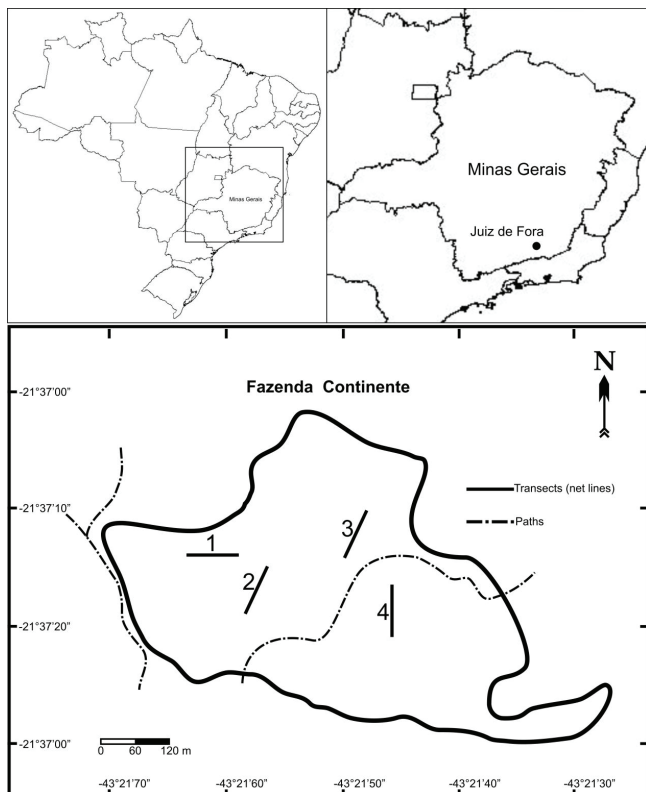
06:00 h and 06:30 h and continued for 10 h on the first day and 9 h on the second, settling intervals of 30–45 min to monitoring nets. The sampling effort totaled 3040 mist-net h, 1520 at each season. Birds captured were marked with numbered aluminum rings, provided by *Centro Nacional de Pesquisa e Conservação de Aves Silvestres (CEMAVE)* of *Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio)*, and they were subsequently released near the capture sites. The classification of birds followed Remsen-Jr. *et al.* (2015).



**Figure 2.** Rainfall Dec 2005/Nov 2006. Dec 2005, Jan/Feb/Jun/Jul 2006 dotted. Data from weather station of Juiz de Fora Federal University.

### Arthropod sampling

Foliage arthropods were sampled using a branch-clipping technique, a method that involves pruning branches of trees or shrubs in the collection bags (Cooper & Whitmore 1990). Samplings between the left and right sides of the mist-nets were alternated every visit to the transect. For each sample, we used eight plastic bags (40 × 60 cm), and the samples were taken at about 1.5 m height and at a distance of 2–5 m perpendicular to the nets, excluding the first and the tenth. Disturbance level in vegetation was maintained as low as possible. Branches were wrapped in bags and pruned. Bags with vegetation samples were weighed using 500 g Pesola® scales. Vegetation was then shaken vigorously inside the bags to dislodge trapped arthropods, before being discarded. The remaining vegetation in the bags was carefully inspected on a cloth when the arthropods, collected with forceps, were transferred to envelopes and allowed to dry in a freezer. The inner walls of the bags were also inspected to check for possible arthropods adhered to them. Subsequently, the collected arthropods were counted and identified according to Borror *et al.* (1976) and McGavin (2000). Due to the variation in the volume of vegetation in each sample, always higher than 100 g, the number of arthropods was adjusted to 100 g of vegetation (excluding the weight of the bag) in the seasonality analysis.



**Figure 1.** Map showing the localization of the study area and of the sampling transects (net lines). The “Continente Farm”, state of Minas Gerais, southeastern Brazil.

Soil arthropods on the ground were captured using pitfall traps, consisting of plastic pots with a diameter of 10 cm and depth of 15 cm, buried in the ground with borders at the surface level. Each pot was filled with 20 ml of a solution with water and inodorous soap (10%), modified from Haugaasen *et al.* (2003). Plastic screens were fitted for each trap at about 25 cm above the ground to prevent falling leaves and twigs from entering the pots. In each of the transects sampled with mist-nets, eight pitfalls were installed, from the second to the ninth net, located at a distance of 3–5 m perpendicular to the center of each one. The traps remained open simultaneously with the bird samplings, and capped after the end of these activities to avoid catching nocturnal arthropods. The right and left sides of the net lines were sampled alternately every sampling day. At the end of sampling, the contents present in the pots were transferred to filter paper and, after drying, analyzed under a 10× – 40× stereo microscope.

### Data analysis

The seasonal variability of the captures (including recaptures), the number of individuals and the number of species classified as foliage and ground foraging insectivores according to literature (*e.g.* Willis 1979, Rodrigues *et al.* 1994, D'Angelo-Neto *et al.* 1998) were measured with chi-square ( $\chi^2$ ) test. Seasonal variability in the abundance of arthropods was evaluated using a paired *t*-test after checking the data normality with the

Kolmogorov-Smirnov test, considering soil (“pitfalls”) and foliage (“branch-clipping”) arthropods separately. For statistical analysis, we used the BioEstat 5.3 (Ayres *et al.* 2007).

## RESULTS

There were 348 captures of insectivorous birds, totaling 243 individuals from 15 species of ground and foliage foraging insectivores. Foliage insectivores accounted for the vast majority of these species (12 species), with only three species of ground foragers: *Conopophaga lineata*, *Corythopsis delalandi* and *Pyriglena leucoptera* (Table 1). The highest number of captures (including recaptures) and individuals was also among the foliage insectivores, corresponding to more than 60% of the total. The number of captures ranged from one (three species) to 105 (*Platyrhinchus mystaceus*), and the most common species were *P. mystaceus* (26.3% of individuals captured), *Basileuterus culicivorus* (14.4%), *C. lineata* (14.4%), *P. leucoptera* (14.4%), *Anabazenops fuscus* (7.4%) and *Corythopsis delalandi* (6.2%). The species with highest proportion of recaptures was *P. mystaceus* ( $n = 41$ ; 39%) and the least was *B. culicivorus* ( $n = 9$ , 20.5%) (Table 1).

A total of 3416 arthropods were collected by both method. In the pitfall traps occurred 1782 and the most abundant groups were Hymenoptera Formicidae (28.3%) and Diptera (25.6%). Other prey categories, such as Coleoptera (18.7%) and Orthoptera (14.4%), were also

**Table 1.** Understory insectivorous bird species captured in the dry and rainy seasons in an area of secondary Atlantic Forest, southeastern Brazil. FI – Foliage insectivores; GI – Ground insectivores.

Species	Habit	Total of captures (%)	No. captures rainy season	No. captures dry season	Total of individuals (%)	No. individuals rainy season	No. individuals dry season	Total of recaptures (%)
Thamnophilidae								
<i>Thamnophilus caerulescens</i> Vieillot, 1816	FI	3 (0.9)	2	1	3 (1.2)	2	1	-
<i>Dysithamnus mentalis</i> (Temminck, 1823)	FI	5 (1.4)	2	3	4 (1.6)	2	3	1 (20.0)
<i>Pyriglena leucoptera</i> (Vieillot, 1818)	GI	52 (15.0)	31	21	35 (14.4)	23	20	16 (30.8)
Conopophagidae								
<i>Conopophaga lineata</i> (Wied, 1831)	GI	52 (15.0)	20	32	35 (14.4)	16	27	17 (32.7)
Furnariidae								
<i>Anabazenops fuscus</i> (Vieillot, 1816)	FI	25 (7.2)	16	9	18 (7.4)	13	8	7(28.0)
<i>Synallaxis ruficapilla</i> Vieillot, 1819	FI	16 (4.6)	6	10	11 (4.5)	6	9	5(31.3)
Tyrannidae								
<i>Corythopsis delalandi</i> (Lesson, 1830)	GI	22 (6.3)	10	12	15 (6.2)	9	10	7 (31.8)
<i>Leptopogon amaurocephalus</i> Tschudi, 1846	FI	7 (2.0)	5	2	7 (2.9)	5	2	-
<i>Hemitriccus diops</i> (Temminck, 1822)	FI	1 (0.3)	1	-	1 (0.4)	1	-	-
<i>Poecilatriccus plumbeiceps</i> (Lafresnaye, 1846)	FI	1 (0.3)	1	-	1 (0.4)	1	-	-
<i>Tolmomyias sulphureus</i> (Spix, 1825)	FI	11 (3.2)	6	5	10 (4.1)	6	5	-
<i>Platyrhinchus mystaceus</i> Vieillot, 1818	FI	105 (30.2)	55	50	64 (26.3)	46	36	41 (39.0)
<i>Myiophobus fasciatus</i> (Stadius Muller, 1776)	FI	1 (0.3)	-	1	1 (0.4)	-	1	-
<i>Lathrotriccus euleri</i> (Cabanis, 1868)	FI	3 (0.9)	2	1	3 (1.2)	2	1	-
Parulidae								
<i>Basileuterus culicivorus</i> (Deppe, 1830)	FI	44 (12.6)	24	20	35 (14.4)	21	20	9 (20.5)
<b>TOTAL</b>		<b>348 (100)</b>	<b>181</b>	<b>167</b>	<b>243 (100)</b>	<b>153</b>	<b>143</b>	<b>103 (29.6)</b>

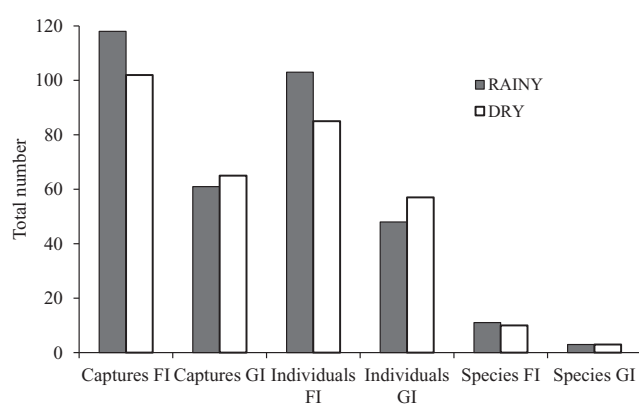
well represented, while the remaining 14 arthropod groups together accounted for less than 15% of the total (Table 2). Variations in the proportion of arthropod groups captured in different seasons were observed (Table 2). On the other hand, 1634 foliage arthropods, corresponding to 22 categories of at least 16 orders were collected using a branch-clipping method. Spiders were the most abundant arthropods (35.2%), followed by Isopoda (15.9%), Coleoptera (15.1%), Hemiptera Heteroptera (5.8%) and Hymenoptera Formicidae (5.4%). The proportions of

each group underwent minor variations between seasons (Table 2).

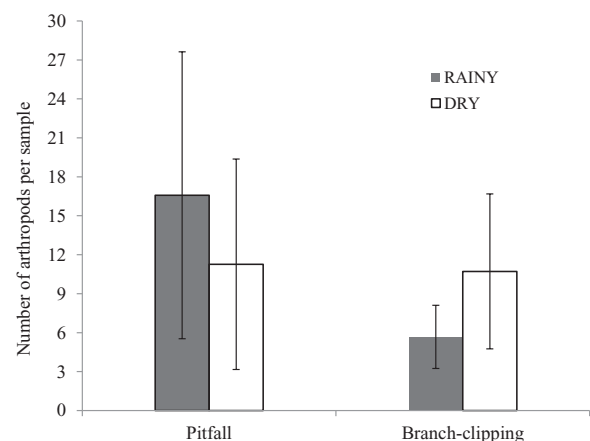
There was no seasonal variation in bird richness, the total number of captures and the number of individuals captured in any of the categories of insectivores (all  $\chi^2$  tests with  $P > 0.1$ ) (Fig. 3). The abundance of soil arthropods was higher during the rainy season ( $t = -2.89$ ;  $df = 63$ ;  $P < 0.01$ ) (Fig. 4), while a greater abundance of foliage arthropods was found in the dry season ( $t = -6.84$ ;  $df = 63$ ;  $P < 0.01$ ) (Fig. 4).

**Table 2.** Arthropods collected by “branch-clipping” (foliage) and “pitfall” (ground) methods in rainy and dry seasons. \* Number of individuals per 100 g of vegetation.

Category	Rainy		Foliage Dry		Total		Ground		TOTAL
	Frequency	$n^*(\%)$	Frequency	$n^*(\%)$	Frequency	$n^*(\%)$	Rainy $n(\%)$	Dry $n(\%)$	
Mollusca (non-arthropod)	1	0.5(0.2)	-	-	1(0.1)	0.5(0.1)	1(0.1)	-	1(0.1)
Orthoptera	25	14.5(4.0)	22	14.3(2.1)	47(2.9)	28.8(2.7)	131(12.4)	126(17.5)	257(14.4)
Phasmatodea	1	0.6(0.2)	-	-	1(0.1)	0.6(0.1)	-	-	-
Dermaptera	6	3.3(0.9)	1	0.7(0.1)	7(0.4)	4.0(0.4)	-	-	-
Mantodea	1	0.6(0.2)	-	-	1(0.1)	0.6(0.1)	-	-	-
Blattodea	4	2.2(0.6)	11	7.3(1.1)	15(0.9)	9.5(0.9)	1(0.1)	3(0.4)	4(0.2)
Isoptera	-	-	-	-	-	-	-	2(0.3)	2(0.1)
Hemiptera Heteroptera	19	11.9(3.3)	83	49.9(61.8)	102(6.2)	61.8(5.9)	15(1.4)	3(0.4)	18(1.0)
Hemiptera non-Heteroptera	40	24.5(6.7)	27	16.3(2.4)	67(4.1)	40.8(3.9)	18(1.7)	6(0.8)	24(1.4)
Coleoptera	84	50.1(13.8)	164	108.8(15.9)	248(15.2)	158.9(15.1)	293(27.6)	40(5.6)	333(18.7)
Diptera	9	5.4(1.5)	25	17.1(2.5)	34(2.1)	22.6(2.2)	154(14.5)	303(42.0)	457(25.7)
Lepidoptera	1	0.6(0.2)	9	6.1(0.9)	10(0.6)	6.7(0.6)	2(0.2)	-	2(0.1)
Hymenoptera non-Formicidae	15	9.1(2.5)	41	29.9(4.4)	56(3.4)	39(3.7)	25(2.4)	8(1.1)	33(1.9)
Hymenoptera Formicidae	45	27.3(7.5)	43	30.2(4.4)	88(5.4)	57.5(5.5)	352(33.2)	153(21.2)	505(28.3)
Isopoda	74	42.7(11.8)	183	124.6(18.2)	257(15.7)	167.3(15.9)	30(2.8)	15(2.1)	45(2.5)
Pseudoscorpiones	15	9.3(2.6)	3	2.5(0.4)	18(1.1)	11.8(1.1)	1(0.1)	13(1.8)	14(0.8)
Opilliones	17	9.9(2.7)	-	-	17(1.0)	9.9(0.9)	1(0.1)	-	1(0.1)
Acari	4	2.5(0.7)	-	-	4(0.2)	2.5(0.2)	1(0.1)	-	1(0.1)
Araneae	219	129.6(35.7)	360	240.0(35.0)	579(35.4)	369.6(35.2)	24(2.3)	19(2.6)	43(2.4)
Diplopoda	-	-	-	-	-	-	1(0.1)	-	1(0.1)
Larvae	12	7.1(2.0)	31	20.3(3.0)	33(2.0)	27.4(2.6)	9(0.9)	9(1.3)	18(1.0)
Nymph	2	0.9(0.3)	10	6.8(1.0)	12(0.7)	7.7(0.7)	1(0.1)	19(2.6)	20(1.1)
Pupae	3	1.7(0.5)	8	4.8(0.7)	11(0.7)	6.5(0.6)	-	-	-
Not identified	16	9.0(2.5)	10	6.7(1.0)	26(1.6)	15.7(1.5)	1(0.1)	2(0.3)	3(0.2)
<b>TOTAL</b>	<b>613</b>	<b>363.1(100)</b>	<b>1031</b>	<b>686.4(100)</b>	<b>1634(100)</b>	<b>1049.7(100)</b>	<b>1061(100)</b>	<b>721(100)</b>	<b>1782(100)</b>



**Figure 3.** Seasonal variation in the number of captures, individuals and species of insectivorous birds in a secondary Atlantic Forest area, southeastern Brazil.



**Figure 4.** Mean  $\pm$  standard deviation of arthropods individuals by sample captured by “pitfall” (ground) and “branch-clipping” (foliage) methods, in dry and rainy season in the Atlantic Forest area, state of Minas Gerais, Brazil.



## DISCUSSION

Some studies have shown seasonal variations in the abundance of food resources, and although these variations are more pronounced in temperate regions where winters are marked by severe food scarcity, they also occur in tropical areas (Karr 1976, Newton 1980, Loiselle & Blake 1990). The abundance of arthropods in the tropics is related to the regime of dry and rainy seasons, with its higher density generally associated with rainy periods (Develey & Peres 2000).

In the studied area, the higher abundance of soil arthropods was found in the rainy season, with a substantial decline during the dry season. The study area has its own characteristics of a semideciduous forest, marked by a relatively severe dry season, usually from April to September (Morellato & Haddad 2000, Oliveira-Filho & Fontes 2000), when the reduced availability of water can lead to a reduced number of arthropods, which could have difficulties in obtaining their water requirements (Janzen & Schoener 1968). In addition, the reproductive activities of arthropods associated with rainy periods increase their populations during this season (Orians 1980).

However, these patterns were not observed for the foliage arthropods, whose abundance was high in the dry season. Although the density of arthropods can be associated with a peak in vegetation productivity (Orians 1980) that is characteristic of the rainy season in the tropics, seasonal variations in the abundance of arthropods seem to be less pronounced in those regions than in temperate regions (Newton 1980). Another relevant factor is the frequent and intense rains, typical of tropical summers, which may hinder the permanence of arthropods on the foliage, making them less accessible to insectivorous birds foraging on the substrate, as previously suggested (Manhães 2007). While it still seems difficult to explain an increase in the number of arthropods during the dry season, Murakami (2002) suggests that the understory of semideciduous forests may harbor, during the dry season, arthropods that live in the canopy, as some plant species lose leaves in this period and arthropods need to search for food resources elsewhere.

Although the highest consumption of arthropods by insectivorous birds is associated with the breeding season of these birds (Develey & Peres 2000), which in the tropics occurs during the rainy season, along with the increased availability of arthropods (Orians 1980), the results indicated no relationship between the seasonal variations of the arthropods and the abundance of insectivorous birds. Although the rainy season has showed the greatest abundance of soil arthropods, ground foraging bird species remained the same in both seasons. Likewise, the foliage insectivores showed no seasonal variation,

although the number of foliage arthropods was higher in the dry season. Only a small difference in the bird species composition by season was observed, probably due to the capture of species with low representability, such as *Poecilatriccus plumbeiceps*, *Hemithriccus diops* and *Myiophobus fasciatus*, captured only once throughout the sampling periods. Codesido & Bilenca (2004) found similar results in a study on the seasonality of birds in the Chaco subtropical semiarid forest of Argentina, and did not find seasonal variations in the abundance of ground and foliage insectivores. In addition, this study revealed that seasonal variations experienced by some groups of insectivores occurred in migratory species, arriving in the tropical forests during summer, possibly attracted by a greater availability of arthropods. Lefebvre & Poulin (1996) observed relationship for some migrant species in mangrove forests of Panama. In the case of the current study area, we detected no migratory birds, with the insectivorous assemblage composed essentially by resident species, which may also have contributed to the absence of seasonal variations in the abundance of such birds, in addition to the composition of species. Cueto & Casenave (2002), in Argentina, attributed the lack of seasonality of coastal woodland insectivorous bird densities to a discrete temporal climate change, probably insufficient to generate an overall food scarcity. Thus, changes in the availability of food resources possibly cannot be the only factor responsible for variations that are occasionally found in the abundance of insectivorous species. Newton (1980) stated that food alone should not be considered a limiting factor for birds, because it is usually associated with several other factors, such as reproduction, territoriality and competition.

Another important factor to consider is the great plasticity of birds, which can be observed even in short periods of time (Tebich *et al.* 2004), allowing them to exploit other microhabitats to obtain food within a fragment. According to Newton (1980), the insectivorous birds consume only a small part of resources available in the environment and can therefore find food in the periods in which there is some reduction of these resources. According to Murakami (2002), birds may differ in response to seasonal variations in prey distribution, using different tactics and/or foraging substrates, and often change to new prey types to compensate for the reduced availability of feeding resources.

Despite having been carried out in a single forest patch, our results support those found in previous studies (Codesido & Bilenca 2004, Manhães 2007), whose variations in arthropod abundance in response to seasonality are not accompanied by a variation in the abundance of insectivorous birds in tropical forests. The presence of the most common bird species throughout the year suggests the absence of extensive migration of

insectivorous birds to the studied area, common in other locations (Lefebvre & Poulin 1996, Poulin & Lefebvre 1996), possibly explaining, to a large extent, the different patterns of responses from insectivorous birds in relation to the availability of their prey, according to the location studied.

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

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

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

## INTRODUCTION

Interspecific competition and aggression mediate species' spatial segregation and occupation in a number of avian communities (e.g. Robinson & Terborgh 1995, Jankowski *et al.* 2010). Evidence of assembly patterns suggest that these deterministic processes also shape the composition and structure of avian mixed-species flocks (e.g. Graves & Gotelli 1993, Colorado & Rodewald 2015). Mixed-species flocks are mutualistic associations between two or more species, and hypothesized advantages for birds that join such flocks are decreased predation risks and/or increased foraging efficiency (e.g. Morse 1977, Powell 1985). However, direct aggressive interactions in these associations can lead to local exclusion of subordinate bird species by the dominant species (Pierpont 1986, Graves & Gotelli 1993). Thus, avian mixed-species flocks offer an exceptional opportunity to investigate species interactions as many species, including closely related ones, can be found in the same flock. Evidence of competition among avian mixed-species flocking species come from research

programs performed in relatively well-preserved regions (e.g. Graves & Gotelli 1993, Colorado & Rodewald 2015) and no study has yet documented the interactions between invasive and native flocking species in human-modified landscapes. This is relevant because Neotropical avian social systems such as mixed-species flocks and army ant followers are known to be negatively affected by habitat disturbance, including forest fragmentation (Stouffer & Bierregaard-Jr. 1995, Maldonado-Coelho & Marini 2004, Mokross *et al.* 2014). In this study, we show that the Cerrado Woodcreeper, *Lepidocolaptes angustirostris* (hereafter “invasive woodcreeper”) is: 1) expanding its range into that of the native Atlantic Forest woodcreeper, *Lepidocolaptes squamatus* (hereafter “native woodcreeper”); 2) using the same forest fragments in which the native woodcreeper occurs; 3) regularly joining Atlantic Forest mixed-species flocks containing the native woodcreeper; 4) overlapping in foraging height with the native woodcreeper during flocking; and 5) engaging in aggressive encounters and excluding the native woodcreeper from flocks. The invasive species

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

## METHODS

### Species studied, study area and mixed-species flock observations

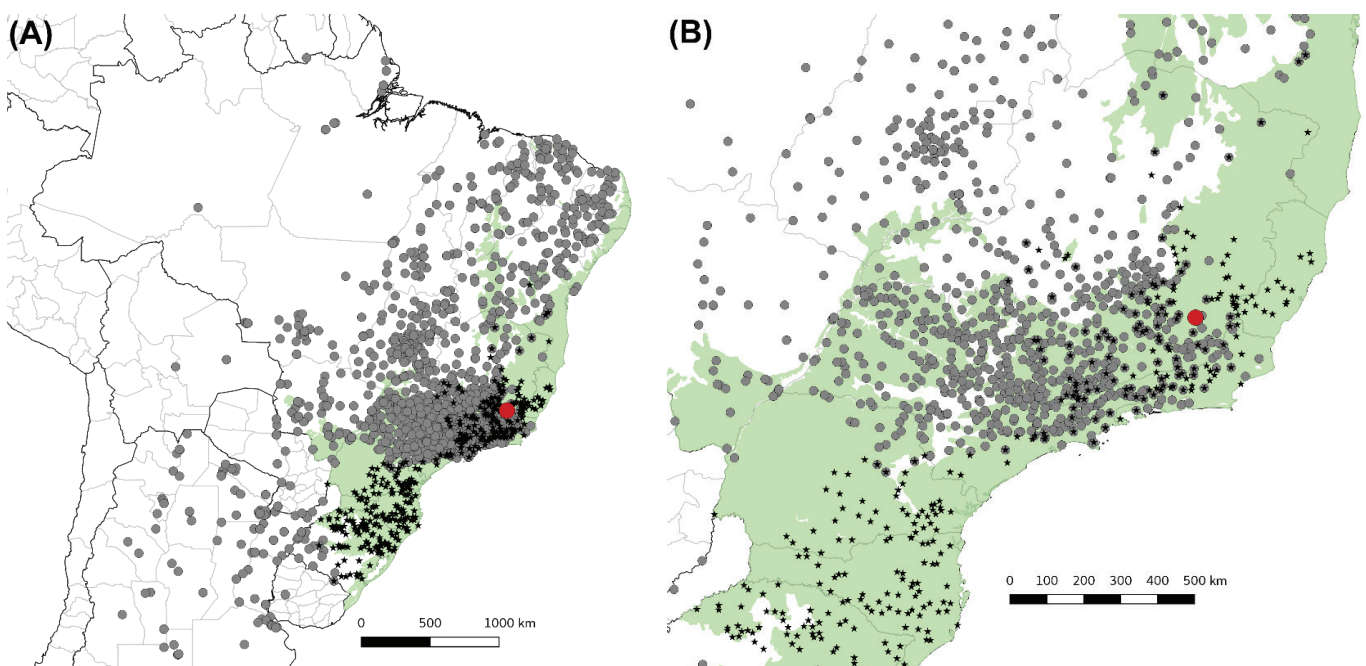
The native woodcreeper is commonly observed foraging in the canopy and sub-canopy of primary and secondary growth of moist, semideciduous and dry forests in eastern Brazil, where it regularly participates in mixed-species flocks (Develey & Peres 2000, Maldonado-Coelho & Marini 2004). The invasive woodcreeper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

The study region is located in the municipality of Viçosa and Paula Cândido (20°42'30" – 20°50'00"S;

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

### Geographic expansion of the invasive woodcreeper

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



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

### Forest fragment use and abundance of the invasive and native woodcreepers

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

### Mixed-species flocks participation by the invasive woodcreeper

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

### Foraging height use pattern of the invasive and native woodcreepers

The foraging observations on the native woodcreeper were carried out in all nine forest fragments in which flocks were studied, whereas foraging behavior of the invasive woodcreeper and all interactions between the two species were observed only in the 9.4 ha forest fragment (see above). Foraging observations were performed during the rainy and dry seasons and foraging heights were only obtained when the species were associated in mixed-species flocks. In a comparison of foraging height use,

the aim was to assess if the two woodcreeper species presented any differences in behavior when associated in mixed-species flocks. Seven 2 m classes of foraging heights were defined and estimated by eye. Information on each foraging bout was collected in intervals of 5 minutes to avoid pseudoreplication. In all recorded foraging bouts, the individuals were always searching for prey on tree trunks; hence, the foraging heights recorded were assumed to represent the actual foraging heights, even though individuals were only occasionally seen capturing prey.

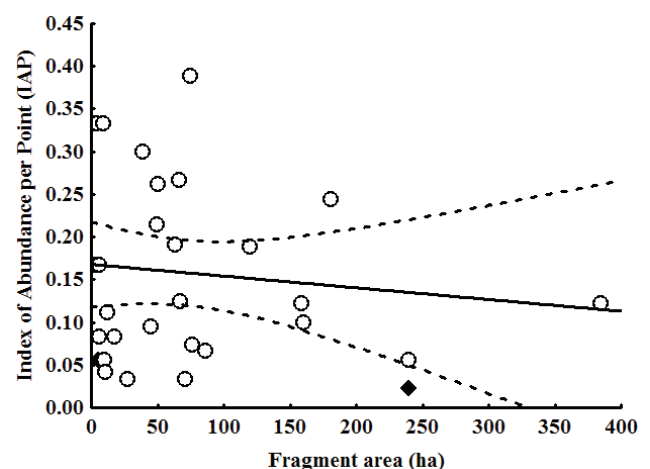
## RESULTS

### Geographic expansion of the invasive woodcreeper

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

### Forest fragment use and abundance of the invasive and native woodcreepers

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

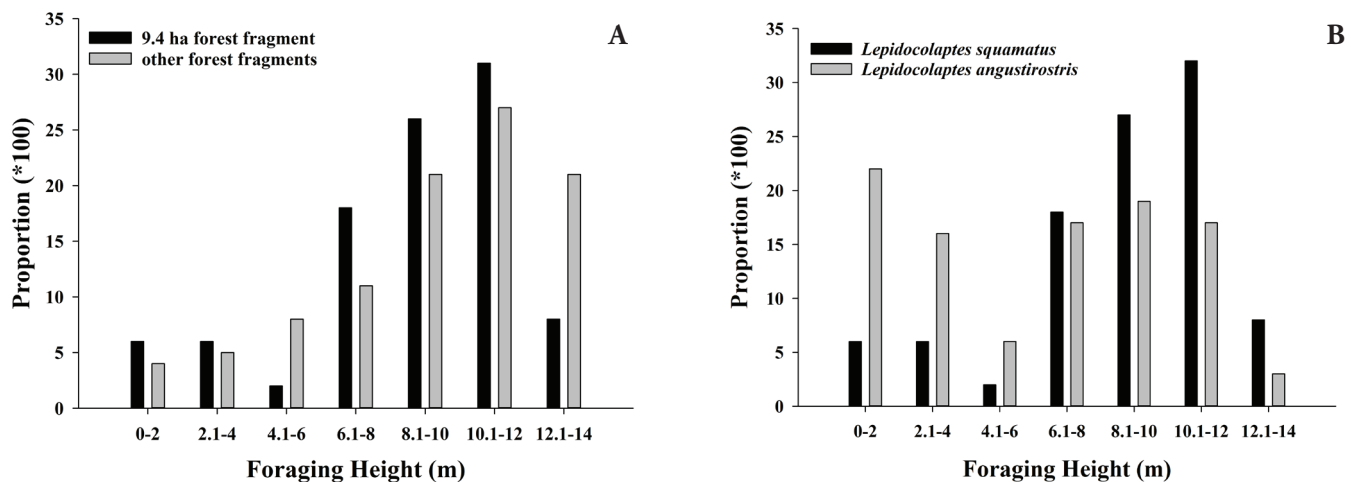


**Figure 2.** Abundance of the invasive (*Lepidocolaptes angustirostris*, black diamonds) and native (*Lepidocolaptes squamatus*, open circles) woodcreepers as a function of forest fragment size in the area of study. Unbroken and broken lines represent respectively the fit of a linear model and associated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

### Foraging height use pattern of the invasive and native woodcreepers

The analysis indicates that the two species differed in foraging height distribution (Kolmogorov-Smirnov two-sample test;  $D = 0.289$ ,  $P < 0.05$ ;  $n_{\text{invasive-woodcreeper}} = 64$ ,  $n_{\text{native-woodcreeper}} = 94$ ; Fig. 3). This difference in foraging height distribution is because individuals of the invasive woodcreeper did not show preferences in foraging height classes whereas individuals of the native woodcreeper exhibited a preference for the upper levels of trees. In the second comparison of foraging height use, the goal was to assess if there were any detectable behavioral

shifts in foraging height of the native woodcreeper in response to the presence of the invasive woodcreeper in mixed-species flocks. That is, we wanted to assess if individuals of the native woodcreeper exhibited a pattern of ecological character displacement (Pfennig & Pfennig 2009). Native woodcreepers in mixed-species flocks in which the invasive woodcreeper participated did not show differences in foraging height distribution from native woodcreepers in mixed-species flocks in which the invasive woodcreeper was absent (*i.e.* in the other eight forest fragments; Kolmogorov-Smirnov two-sample test;  $D = 0.131$ ,  $P > 0.05$ ;  $n_{9.4 \text{ forest fragment}} = 94$ ,  $n_{\text{other forest fragments}} = 323$ ; Fig. 3).



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

### Agonistic interactions between the invasive and native woodcreepers

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

## DISCUSSION

Competitive exclusion by more aggressive bird species is a common pattern in mixed-species flocks and over army ants. In such social organizations, the larger species

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

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

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

In the present study, we have shown that the process of Atlantic Forest fragmentation has led to the invasion of an aggressively dominant species from the adjacent Cerrado Biome. We have also shown that the native woodcreeper, which regularly join mixed-species flocks all year round (Maldonado-Coelho & Marini 2003), experiences foraging interference and flock exclusion as a result of agonistic interactions with the invasive species. It is reasonable to expect that such foraging interference and competitive exclusion will result in reduced fitness in the native woodcreeper, as the benefits of participating in mixed-species flocks would be lost or largely diminished. Those individuals disturbed when foraging, and certainly those excluded from flocks, are likely to experience a decrease in foraging efficiency and an elevated risk of predation. This can be critical because: i) the frequency of the invasive woodcreeper in flocks were higher during the period of food shortage (*i.e.* the dry season), ii) competitive exclusion from flocks can be detrimental to the fitness of the native species mainly in small and potentially food depleted forest fragments (*e.g.* Zanette *et al.* 2000), and iii) sympatry between the two woodcreepers is extensive in southeastern Atlantic Forest, and ongoing competition can be pervasive across their area of overlap. However, one positive finding of this study is the reduced abundance and occurrence of the invasive woodcreeper in the sampled forest fragments. This implies that the negative interactions reported here could have an impact on the native woodcreeper at the level of interacting individuals,

but they may not be extensive at the population level. Future studies should assess this possibility by comparing fitness of native woodcreeper individuals in the presence and absence of the invasive woodcreeper.

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

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# Genetic variation of the endangered Araripe Manakin (*Antilophia bokermanni*) indicates a history of demographic decline

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**ABSTRACT:** The Araripe Manakin (*Antilophia bokermanni*) is a “Critically Endangered” bird species endemic to northeastern Brazil. The habitat of the species has suffered intense fragmentation and degradation in recent years, resulting in a decline in population numbers. The present study evaluated the genetic diversity and structure of this population through the analysis of the Hypervariable Domain I of the mitochondrial Control Region and two nuclear introns (I7BF and G3PDH). Results revealed an absence of population substructuring and population decline beginning during the late Pleistocene, approximately 50,000 years ago. The evidence indicates that the effective population size of the Araripe Manakin has declined gradually over time ever since, a process that may have been intensified as a result of the recent anthropogenic impacts on the habitat of the species.

**KEY-WORDS:** coalescent theory, conservation, control region, Pipridae, population genetics.

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## INTRODUCTION

The Araripe Manakin (*Antilophia bokermanni*) is the world's most threatened species of manakin, according to the International Union for the Conservation of Nature (BirdLife International 2016). This species is endemic to a small tract of humid forest on the slopes of the Araripe Plateau in Ceará state in northeastern Brazil. The principal threats to the survival of the species are the ongoing anthropogenic degradation and loss of habitat, which is thought to contain less than one thousand individuals (Silva *et al.* 2011, BirdLife International 2016).

The risks faced by *A. bokermanni* highlight the need for the collection of reliable data for the effective management and conservation of the remaining populations, including insights into the evolutionary history of the species. Silva *et al.* (2011) estimated that the numbers of individuals have declined by more than a third over the past twenty years. This may have intensified the process of genetic drift, further reducing the genetic variability of its populations, while also increasing the probability of inbreeding, which favors the appearance of genetic anomalies and diseases,

and may lead to a loss of fitness (Frankham 2005). A recent study of the Araripe Manakin revealed slightly lower genetic diversity in comparison with its sister species, *A. galeata* (Rêgo *et al.* 2010).

Historical evolutionary processes are generally underestimated during the development of conservation policies for threatened species (Chaves *et al.* 2011), despite the importance of understanding the demographic history of threatened populations, such as those of *A. bokermanni*, for the development of reliable conservation programs (Cornetti *et al.* 2014). In this context, genetic data can support a better understanding of demographic processes that contributed to the current genetic diversity of the species (Chaves *et al.* 2011).

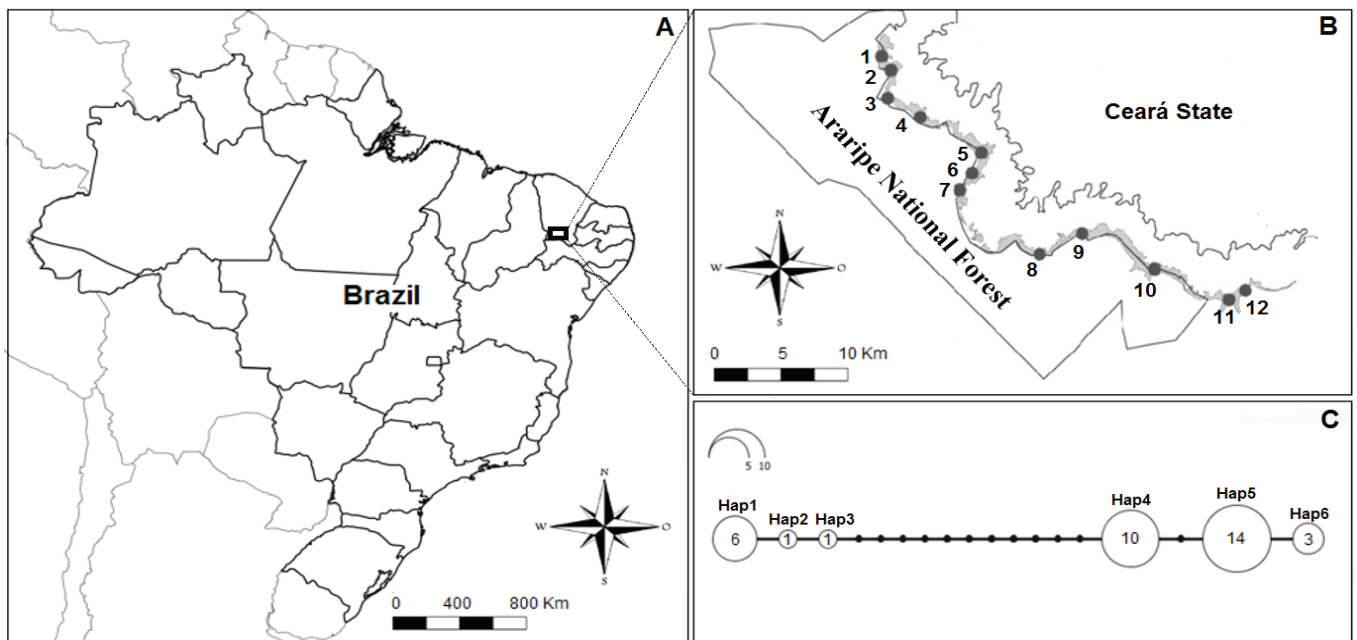
In the present study, the genetic diversity of *A. bokermanni* populations was analyzed based on sequences of the mitochondrial control region and two nuclear introns. Based on analyses of coalescent theory, the data were used to detect possible signs of historical demographic variation, and describe the spatial distribution of the genetic variation of the present-day population of the Araripe Manakin.

## METHODS

### Population sampling and laboratory procedures

Samples of blood or feathers were obtained from 37 Araripe Manakins obtained from 12 sites distributed throughout the geographic range of the species (Fig. 1A, B). Samples were stored in 95% ethanol at -20°C. Total genomic DNA was isolated using a Wizard® Genomic DNA Purification kit (Promega) according to the manufacturer's instructions. Polymerase Chain Reaction (PCR) was used to amplify Hypervariable Domain I (HDI) of the mitochondrial Control Region, which is widely used for the evaluation of diversity in studies of population genetics (*e.g.* Sammler *et al.* 2012, Jackson *et al.* 2013). We also selected two unlinked nuclear introns for multilocus analyses, intron 7 of the

Beta-Fibrinogen (I7BF) and intron of the glycerol-3-phosphate dehydrogenase 11 gene (G3PDH). Primers used were Dloop H-739 (Sorenson *et al.* 1999) and CytB-End (Bensch & Harlid 2000) for HDI, FIB-BI7H and FIB-BI7L (Prychitko & Moore 1997) for I7BF, and G3PDH13b and G3PDH14b (Fjeldså *et al.* 2003) for G3PDH. Amplification condition consisted of an initial denaturation at 94°C for 3 min, followed by 35 cycles of denaturarion at 94°C for 30 s, hybridization at locus specific temperatures and times (HDI, 52°C for 30 s; I7BF, 50°C for 35 s and G3PDH, 55°C for 30 s), extension at 72°C for 1 min and a final extension at 72°C for 10 min. PCR products were purified using Polyethylene Glycol 8000 (PEG, 1 g/mL), sequenced using BigDye® Terminator v. 3.1 Cycle Sequencing kit (Applied Biosystems™) and run in an ABI3500 XL automatic sequencer (Applied Biosystems™).



**Figure 1.** (A) Location of the Araripe Plateau in Ceará state, northeastern Brazil. (B) Distribution of *Antilophia bokermanni* and sites at which samples were collected in upland rainforest. (C) Haplotype network, only for HDI control region, and the number of individuals per haplotype.

### Genetic computational analysis

Sequences were aligned in Clustal-W (Thompson *et al.* 1994) and edited in Bioedit 7.2 (Hall 1999). Best-fit models of nucleotide evolution were determined in Mega 6 (Tamura *et al.* 2013), based on the Bayesian Information Criterion (BIC) with the HKY model being chosen for mtDNA, and the T93 model for the two nuclear introns, which were used in the Bayesian Skyline Plot analyses (see below). The possible recombination of the markers was verified using the *phi* test (Bruen *et al.* 2006), run in Splits Tree 4 4.14.4 (Huson & Bryant 2006). Genetic diversity was estimated based on the indices of haplotype (*h*) and nucleotide ( $\pi$ ) diversity, which were calculated in Dnasp 5.1 (Librado & Rozas 2009). Gametic phases of

the introns were established using the Phase algorithm (Stephens & Donnelly 2003), with posterior probabilities of at least 0.6 were considered to be resolved (Harrigan *et al.* 2008). A hierarchical analysis of molecular variance (AMOVA) was run in Arlequin 3.5.2.2 (Excoffier & Lischer 2010), for which we inferred the presence of two groups, one located in the northwestern portion of the distribution of the species (sites 1–7), and the other in the southeastern portion (sites 8–12), based on the discontinuity in the distribution of the humid forest (Table 1; Fig. 1) (see Rêgo *et al.* 2010, Silva *et al.* 2011). The number of independent *A. bokermanni* populations, based on the assumption of non-spatially hierarchical genetic mixing at an individual level, was inferred from the mitochondrial database using the Bayesian Analysis

of Population Structure software (Baps 6; Corander *et al.* 2008). A haplotype network was also inferred using the maximum likelihood approach in Haploviewer (Salzburger *et al.* 2011) to provide a visual representation of the relationships among haplotypes.

Two approaches were used to evaluate the occurrence of historic changes in the size of the *A. bokermanni* population. Firstly, deviations from neutral evolution was based on three tests, Fu's  $F_s$  (Fu 1997), Tajima  $D$  (Tajima 1989), and  $R_2$  (Ramos-Onsins & Rozas 2002), followed by a mismatch distribution analysis, in order to evaluate whether the *A. bokermanni* population is in equilibrium, expansion or has suffered a bottleneck (Rogers & Harpending 1992). These tests were computed in Dnasp 5.1. Secondly, Beast 1.8 software (Drummond & Rambaut 2007) was used to estimate a Bayesian Skyline Plot (BSP) for the mitochondrial data, while

an Extended Bayesian Skyline Plot (EBSP) was used for a simultaneous analysis of the three markers (Heled & Drummond 2008) to test historical fluctuations in population size. These analyses were run for  $200 \times 10^8$  generations with sample genealogies being sampled every 10,000 generations, in a strict molecular clock model, in which the first 10% of generations were discarded as burn-in. The calibration of the molecular clock was based on the intraspecific mutation rate estimated by Norman *et al.* (2014) for the HDI (0.0348 substitutions per site per lineage per million years), and 0.0135 substitutions per site per lineage per million years for nuclear introns (Ellegren 2007). One year was assumed as generation time in the calculation of the effective number of females ( $N_{ef}$ ). The BSP/EBSP and the Effective Sample Sizes (ESS) were determined in Tracer 1.6 (Rambaut & Drummond 2007).

**Table 1.** Sample sites and their geographic coordinates, number of samples analyzed, and the haplotypes observed for HDI control region only, on Araripe Manakin (*Antilophia bokermanni*).

	Sample sites	Geographic coordinates	No. of samples	Hap1	Hap2	Hap3	Hap4	Hap5	Hap6
Northwest	1	39°28'28"W; 7°13'48"S	6	-	-	-	2	4	-
	2	39°28'20"W; 7°14'18"S	2	1	-	-	-	1	-
	3	39°28'14"W; 7°15'41"S	2	1	-	-	1	-	-
	4	39°26'21"W; 7°17'01"S	2	-	1	-	-	1	-
	5	39°23'51"W; 7°18'43"S	3	1	-	-	1	1	-
	6	39°24'29"W; 7°19'42"S	1	-	-	-	-	-	1
	7	39°24'45"W; 7°19'58"S	2	-	-	-	2	-	-
Southeast	8	39°21'36"W; 7°22'49"S	1	-	-	-	-	1	-
	9	39°18'48"W; 7°21'57"S	6	2	-	1	2	1	-
	10	39°13'37"W; 7°24'46"S	2	-	-	-	-	-	2
	11	39°10'01"W; 7°24'24"S	3	1	-	-	-	2	-
	12	39°12'23"W; 7°24'34"S	5	-	-	-	2	3	-
	<b>Total</b>		35	6	1	1	10	14	3

## RESULTS

### Population genetic diversity and structure

Total dataset length and individual count was 348 bp for mitochondrial HDI from 35 specimens, 961 bp for I7BF from 37 specimens and 393 bp for G3PDH intron from 31 specimens, with no evidence of indels. GenBank accession numbers for the sequences of the different molecular markers analyzed: HDI (KY788006 – KY788011), G3PDH (KY788012, Hap1  $n = 24$ ; KY788013, Hap2  $n = 3$ ; KY788014 Hap3,  $n = 4$ ) and I7BF (KY788015, Hap1  $n = 34$ ; KY788016, Hap2  $n = 1$ ; KY788017 Hap3,  $n = 2$ ). The *phi* test found no evidence of any significant recombination in this marker ( $P > 0.9$ ). A total of 15 polymorphic sites was identified for the control region, with six haplotypes (Table 1), and haplotype diversity of 0.741 and nucleotide diversity

of 0.0161. By contrast, introns presented lower levels of genetic diversity, with only three haplotypes for each marker (Table 2), and lower levels of haplotype and nucleotide diversity for both I7BF (0.080 and 0.00008, respectively) and G3PDH (0.210 and 0.00055, respectively). Non-significant  $F_{st}$  values (Table 2) were obtained between the northwestern and southeastern segments of the population, indicating a lack of genetic sub-structuring in both mitochondrial (-0.007) and nuclear (-0.008) markers. The AMOVA indicated that all (100%) the molecular variability was contained within the population as a whole, rather than in the different subpopulations. The structural analysis in Baps indicated the existence of two groups ( $k = 2$ , marginal probability = -108.6688), but without independent lineages when the northwestern and southeastern groupings were included in the analysis (Appendix I). The haplotype network, represented only for HDI (Fig. 1C) shows that the most

common haplotypes (Hap1, Hap4, Hap5) are found throughout the population (Table 1).

### Historical demography

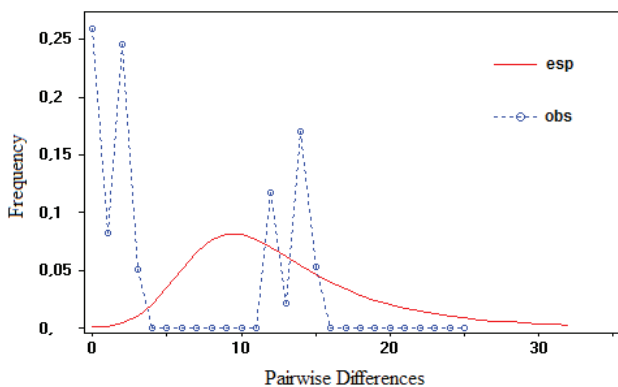
Significant positive results were obtained from the data for the HDI for  $D$  (1.7591;  $P < 0.05$ ),  $F_s$  (5.368;  $P < 0.01$ ) and  $R2$  (0.1868;  $P < 0.01$ ), rejecting the equilibrium population hypothesis. For the nuclear markers, the neutrality and population change tests did not return significant values (Table 2), and did not allow any reliable interpretation based on coalescence inferences. The mismatch distribution, performed only for the

mitochondrial marker, presented a bimodal pattern (Fig. 2), which was consistent with the haplotype network, but distinct from that of a population in equilibrium.

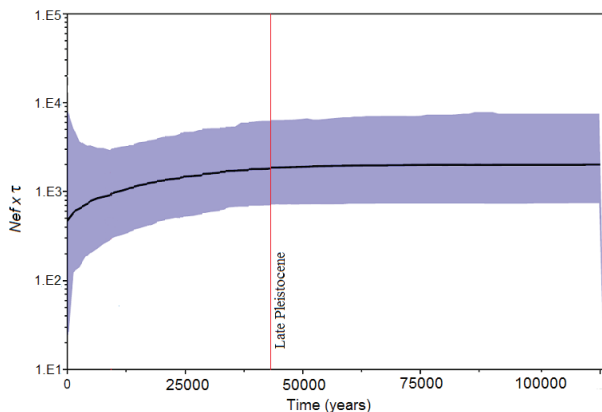
The evaluation of historic changes in population size based on the inferences derived from the EBSP found low ESS values ( $< 200$ ) in the different simulations. On the other hand, the demographic pattern outlined by the BSP (Fig. 3), focusing exclusively on the mitochondrial locus, indicates that mean values of effective size of the *A. bokermanni* population (females only) has been declining steadily over the past 50,000 years. However, the 95% confidence intervals indicated a scenario of relative stability or possibly, a recent expansion.

**Table 2.** Numbers of individuals and haplotypes sampled and summary statistics of indices of genetic diversity and population neutrality estimated for *Antilophia bokermanni*.  $n$  – number of samples; NH – number of haplotypes; S – variables sites;  $h$  – haplotype diversity;  $\pi$  – nucleotidic diversity, SD – standard deviation;  $D$  and  $F_s$  – Tajima and Fu tests, respectively;  $R2$  – Ramos & Rozas test. \*  $P < 0.05$  (significant); \*\*  $P < 0.02$  (significant).

Marker	Size of sequences	$n$	NH	S	$h \pm SD$	$\pi \pm SD$	$D$	$F_s$	$R2$	$F_{st}$
Control Region-DHI	348	35	6	15	0.741 $\pm$ 0.044	0.0161 $\pm$ 0.0027	1.7591*	5.368**	0.1868*	-0.007
I7BF	961	37	3	2	0.080 $\pm$ 0.043	0.0008 $\pm$ 0.00005	-1.3130	-2.853	0.0592	-0.008
G3PDH	393	31	3	2	0.210 $\pm$ 0.067	0.00055 $\pm$ 0.00018	-0.8350	-1.129	0.0541	



**Figure 2.** Mismatch distribution of the sequences of the HDI Control region of *Antilophia bokermanni*, based on the equilibrium population model. Expected (Exp) and observed (Obs) values are marked, respectively.



**Figure 3.** Bayesian Skyline Plot (for mitochondrial only) representing the effective size of the *A. bokermanni* population over time. The curve represents a gradual and constant decline beginning 50,000 years before present. The solid dark blue line represents the mean and the blue shaded area represents the 95% confidence interval of the historic effective size of the female population ( $N_{ef}$ ).

## DISCUSSION

### Genetic diversity and structure

Despite being among the world's most threatened bird species (BirdLife International 2016), the genetic diversity reported here for the mitochondrial marker of the Araripe Manakin (HDI  $h = 0.741$ ) is much higher than that found typically in the other threatened species of this group, such as *Aquila adalberti* ( $h = 0.321$ , Martínez-Cruz et al. 2004), *Pomarea dimidiata* ( $h = 0.000$ , Chan et al. 2011), and *Ardeotis nigriceps* ( $h = 0.261$ , Ishtiaq et al. 2011). The significantly lower levels of diversity in these species appear to have been produced by severe population bottlenecks, which do not appear to have occurred in *A. bokermanni*, suggesting that population size has been maintained above 500 individuals (Jackson et al. 2013). The unexpectedly high levels of genetic diversity found in the Araripe Manakin may be related to the retention of an ancestral polymorphism, associated with its relatively recent, and as yet incomplete separation from its sister species, *A. galeata* (Rêgo et al. 2010). Overall, then, the genetic diversity found in *A. bokermanni* is not consistent with any drastic reduction in population size (Jackson et al. 2013), but that there has been a slow and recent decline over the course of the evolutionary history of the species.

Despite the substantial fragmentation of the habitat found in the central portion of the range of this species, the results of  $F_{st}$  and the homogeneous distribution of haplotypes within the population (Table 1) indicate a lack of substructuring. A similar pattern was also

observed by Rêgo *et al.* (2010), in their analysis of the pseudo-control region. This may reflect either the relatively recent process of fragmentation, which has yet to affect the genetic structure of this type of marker, or the migration of individuals among fragments of forest. The latter hypothesis would be related to the behavior of the adult males of this species, which normally expel the juvenile offspring from their territories, obliging them to occupy new areas (Silva *et al.* 2011). This would result in high levels of gene flow, which would contribute to a reduction in the potential for inbreeding, and tends to increase in smaller, fragmented populations. This type of behavior also enhances the probability of adaptation to fragmented habitats (Canales-Delgado *et al.* 2012), although the exact genetic consequences of this dispersal pattern in *A. bokermanni* are still unclear.

### Historical demography

Despite the reduced resolution of the EBSP analysis, the demographic history of this species derived from the HDI sequence of the Control Region (derived from the BSP analysis) indicates a possible reduction in the *A. bokermanni* population approximately 50,000 years ago. The BSP derived from this analysis revealed a general trend of population decline, although the confidence intervals are also consistent with a stable population, or even a recent expansion. However, the lack of information derived from the low diversity of these loci limits phylogenetic estimates of the genealogy (Heled & Drummond 2008), and precludes reliable interpretation of the demographic events that have occurred in the Araripe Manakin population using only this approach.

Complementing these results, and supporting the assumption of a constant decline in the population size of the species, the demographic model presented in the mismatch distribution shows a pattern which may reflect the mixing of lineages that have separated recently or that have suffered a recent decline in numbers, with only the most common haplotypes surviving. The significant neutrality found in the HDI of the Control Region is also compatible with a historical reduction in population size. Assuming that the Araripe Manakin has had a relatively stable demographic history or has undergone a recent expansion, we would conclude that the considerable variation observed in the *N<sub>ef</sub>* values of the BSP resulted from the retention of ancestral polymorphisms. This feature is typical of the species of the genus *Antilophia*, as indicated by the recent separation of its lineages (Rêgo *et al.* 2010). This effect may generate false evidence of changes in population size, which emphasizes the need for caution in the interpretation of results (Grant *et al.* 2012, Heller *et al.* 2013). This restricts the potential for the inference of reliable estimates of effective population

size using this current method. It is also important to note that the mutation rate of the genetic marker analyzed in the present study, while adequate for the evaluation of recent demographic events on an evolutionary time scale (Zink & Barrowclough 2008), would not be sensitive enough to assess the effects of more recent anthropogenic impacts.

The possible recent reduction in the size of population of the Araripe Manakin, within the last 50,000 years, corresponds to the late Pleistocene. This epoch is characterized by successive periods of climate change (wet and dry cycles), which had a profound effect on the dynamics of the Neotropical biotas (Vuilleumier 1971), especially in the more rainforest and open biomes, such as the Cerrado and Caatinga (Werneck 2011), in which the species of the genus *Antilophia* are found.

The subsequent periods of glaciations and interglacials characterized by significant cooling, interspersed with shorter periods of intensely humid climate, resulted in the expansion and retraction of the majority of the gallery and scarp forests in northeastern Brazil (Behling *et al.* 2000), the type of habitat which the Araripe Manakin is associated. These climatic fluctuations may have provoked adverse conditions for the *A. bokermanni* population, which may have suffered a reduction in its genetic diversity during the adaptation process (Frankham 2005). In this context, the reduction and fragmentation of forest habitats may have led to a decrease in effective population size (Croteau *et al.* 2007), as observed in *A. bokermanni*. This indicates that the present-day genetic diversity of this population may have been determined primarily by past environmental and climatic events, during the evolutionary history of the species, rather than ongoing anthropogenic pressures, and the resulting reduction in population numbers (Silva *et al.* 2011).

As in *A. bokermanni*, studies of other passeriform populations in the forests of northeastern Brazil have also found evidence of a historical decline in population size during the same period. The ranges of species such as *Sclerurus scansor cearensis* (d'Horta *et al.* 2011), *Conopophaga lineata cearae* (Batalha-Filho *et al.* 2014), and *Pipra fasciicauda scarlatina* (Ferraz 2016), which are currently restricted to enclaves of humid cloud forest within the Caatinga, may have contracted progressively through the successive fluctuations in climate occurring during this period.

### Conservation implications

Based on the most recent census data, the population of this species may have suffered a loss of up to 36% over the past two decades, resulting from the deforestation of riparian zones, and the illegal catchment of springs, which typically results in the desiccation of the prime riparian

breeding habitat of the species (Silva *et al.* 2011). This type of impact, together with the historic decline in the *A. bokermanni* population, may have severe consequences in genetic terms, such as mating between closely-related individuals and increasing effects of inbreeding depression (Keller & Waller 2002).

The results of the present study emphasize the need for the preservation of the remaining genetic variability and the prevention of further losses, given the importance of this diversity for the adaptation of these organisms to random changes in the environment (Frankham 2005). These findings also reinforce need for the understanding of the genetic diversity of the *A. bokermanni* population. The main factor determining the loss of this diversity has yet to be identified. Further genetic analyses, based on more detailed methods and analyses (*e.g.* microsatellites and SNPs) may provide more conclusive answers for this problem and other important questions. One key objective is to integrate these data in the National Conservation Plan for the Araripe Manakin. These measures and other actions will determine the viability of this population over the medium- to long term, through the implementation of conservation measures and appropriate management actions.

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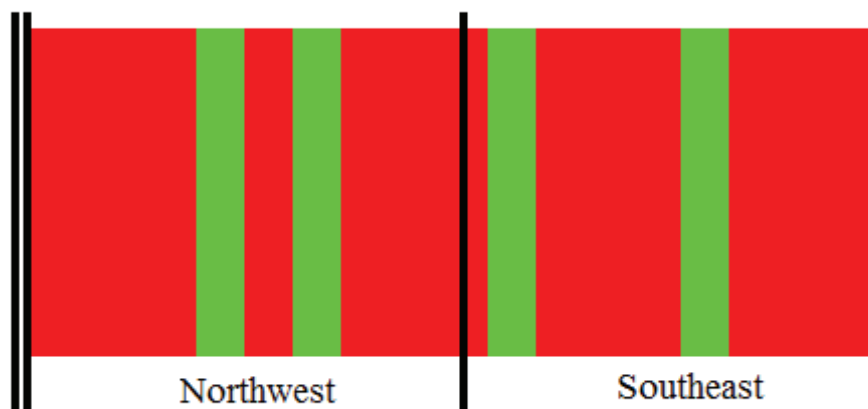
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## APPENDIX I

Hierarchical clustering from Bayesian Analysis of Population Structure. The individual level mixture analysis resulted in two groups in the optimal partition, but not suitable when placed geographically (northwest and southeast of the *Antilophia bokermanni* distribution).





# Peaceless doves: predators of two columbid species at an urban park in southeastern Brazil

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**ABSTRACT:** Doves are preyed on by a variety of vertebrate predators including mammals, birds, and snakes. In urban areas the predator diversity is restricted to a few species, and hawks are the commonest dove predators there. Herein we report events of predation on the Eared Dove (*Zenaida auriculata*) and the Picazuro Pigeon (*Patagioenas picazuro*) by two accipitrid raptors, the Roadside Hawk (*Rupornis magnirostris*) and the Plumbeous Kite (*Ictinia plumbea*), a falconid, the Aplomado Falcon (*Falco femoralis*), besides a dipsadid snake, the Eastern Green Whiptail (*Philodryas olfersii*), at an urban park. The doves were hunted mostly during their fledgling stages. The Plumbeous Kite hunted Eared Doves only during its breeding season to feed the offspring, whereas the Roadside Hawk preyed both on Eared Doves and the Picazuro Pigeon also during its non-breeding period. The Aplomado Falcon preyed on an adult Picazuro Pigeon, whereas the Eastern Whip Snake preyed on a nestling Eared Dove. The Roadside Hawk was the main predator of the Eared Dove in the studied park, and probably would prove to be an important predator of this and additional dove species at other urban areas.

**KEY-WORDS:** Accipitridae, anthropogenic area, Dipsadidae, raptors, snake.

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Neotropical pigeons and doves (Columbidae) dwell in diverse habitat types, but most species are found in open areas where they feed mainly on seeds (Baptista *et al.* 1997, Sick 1997, Dardanelli *et al.* 2011). Some dove species breed year-round and colonise anthropogenic habitats (Baptista *et al.* 1997, Sick 1997, Develey & Endrigo 2004, Corbo *et al.* 2013). Columbids fall prey to a diverse array of vertebrate predators including mammals, birds, and snakes (Silva & Faggioni 2015, Sarasola *et al.* 2016). Among raptors, a few hawk and kite species prey on doves, although birds are not their staple food (Thiollay 1994, Seavy *et al.* 1997, Sick 1997). Several Neotropical dove species dwell in urban areas, particularly in so called green areas, which harbour a few accipitrid and falconid raptor species as well (Thiollay 1994, Baptista *et al.* 1997, Sick 1997, Dardanelli *et al.* 2011, Corbo *et al.* 2013). In urban areas the predator diversity is restricted to a few species, and hawks are the commonest dove predators there (Thiollay 1994, Sick 1997). Besides raptors, in anthropogenic areas doves may fall prey to a few snake species that dwell there as well (Sazima & Marques 2007, Barbo *et al.* 2011).

Among the dove species that fare well in urbanised areas in Brazil, the Eared Dove (*Zenaida auriculata*) and the Picazuro Pigeon (*Patagioenas picazuro*) are the most

conspicuous and common ones (Develey & Endrigo 2004, Corbo *et al.* 2013). Herein we report events of predation on the Eared Dove and the Picazuro Pigeon by two accipitrid raptors, the Roadside Hawk (*Rupornis magnirostris*) and the Plumbeous Kite (*Ictinia plumbea*), besides a falconid, the Aplomado Falcon (*Falco femoralis*) and a dipsadid snake, the Eastern Green Whiptail (*Philodryas olfersii*) at an urban park in southeastern Brazil.

We observed predation on doves at the Parque Ecológico Prof. Hermógenes de Freitas Leitão Filho (22°48'42"S; 47°04'26"W, 587 m a.s.l) in Campinas, São Paulo state, southeastern Brazil. This recreational park is bordered by residential quarters and buildings of a local university (see map in D'Angelo *et al.* 2016). The park has a total area of 0.13 km<sup>2</sup>, of which about 75% is occupied by a large pond surrounded by native and exotic vegetation composed of trees, bushes and grass patches. The pond is bordered by a sandy path about 1.5 km long, used by people for walking, running, and promenading. Playgrounds, kiosks, benches and tables, as well as wastebaskets along the path accentuate the recreational nature of the study site.

Since observations of predation events on a particular prey type usually are fortuitous and circumstantial (Sazima 2008, 2015a), our records were opportunistic and spanned

six years, from 2010 to 2016, at different periods of the day and the year. We observed the predation events with bare eye, 10 × 15 binoculars, and through a 70–300 mm telephoto lens mounted on a SLR camera from a distance of 2 to 30 m. Throughout the observational sessions, we used the “*ad libitum*” and “sequence” samplings (Altmann 1974), which are adequate to record fortuitous or rare events. Voucher digital photographs of the predators and/or their prey are on file at the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC).

We recorded a total of 12 predation events involving two dove species, the Eared Dove and the Picazuro Pigeon, preyed on by three raptor species, the Roadside Hawk, the Plumbeous Kite, and the Aplomado Falcon, besides a snake, the Eastern Green Whiptail. The doves were preyed on mostly during their fledgling stages (Table 1). The Plumbeous Kite was observed to hunt Eared Doves only during its reproductive season and fed this prey type to the offspring, whereas the Roadside Hawk was observed to prey both on Eared Doves and the Picazuro Pigeon during its reproductive and non-reproductive periods. The Aplomado Falcon preyed on an adult Picazuro Pigeon, and the Eastern Whip Snake preyed on a nestling Eared Dove.

Most of the recorded predatory events consisted of raptors carrying their prey in talons and flying among the vegetation or in the open. On a few occasions we spotted the raptors perched on a branch and plucking feathers from, or tearing pieces of, the prey, only to fly upon the approximation of a passerby. However, some of the observed events allowed a description of an almost complete predation sequence. For instance, at midday of 04 May 2014, we observed an adult Roadside Hawk that grasped an Eared Dove nestling by the back from within an unattended nest, and carried the prey to a branch nearby. The still alive dove was held in right talons by its wing (Fig. 1A) and soon after alighting the hawk began to pluck the body feathers from the prey. The raptor pecked at the back of the prey first, and began to tear

and swallow small pieces from there. Our observation ended when a passerby caused the hawk to fly out of our visual reach.

At late afternoon of 14 July 2014, we observed a juvenile Roadside Hawk descending upon a juvenile Picazuro Pigeon that was foraging on the ground in the open. The hawk pulled the dove against the ground with both feet, then grabbed it by the neck and carried the prey in the right talons with visible effort and perched on a branch nearby. There, the hawk began to rip and swallow pieces of the prey's upper back. A passerby disturbed the hawk, which fled with the already dead prey to the understory. On the way it released the prey, which landed on the ground, the wounded back clearly visible (Fig. 1B). The hawk perched on a tree near the fallen dove, and after about 15 min it landed and carried the prey out of sight.

At midday of 10 October 2012, we observed a Plumbeous Kite flying low and striking in midair at the back of a clumsily flying Eared Dove fledgling that left a branch and was set to alight on another branch nearby. The kite carried the prey to a pole, where it plucked several feathers but did not rip or ate portions of the prey. Instead, the prey was carried to a nest nearby, where the kite (now clearly a male) delivered the dove to a female that was tending her single nestling. The female held the dove with right talons (Fig. 1C), tore small pieces of the prey and delivered them to the nestling.

At late morning of 27 December 2015 we observed an Eastern Green Whiptail foraging among branches (Fig. 1D) of a treelet that harboured an Eared Dove nest. The brooding adult flew off at the approximation of the snake. The now unattended nest contained a single, recently-hatched nestling, which the snake grabbed by the neck and began to swallow headfirst. Soon after, the snake was mobbed by a pair of Pale-breasted Thrushes (*Turdus leucomelas*) and a Streaked Flycatcher (*Myiodynastes maculatus*), which caused the predator to quickly retreat to a dense shrubbery, the nestling still in its mouth.

**Table 1.** Predators of two columbid species at an urban park in Campinas, São Paulo state, southeastern Brazil, over six years.

Predator	Prey	Life stage	Date
Roadside Hawk (adults)	Eared Dove	Fledgling	04 December 2010
	Eared Dove	Fledgling	09 January 2011
	Eared Dove	Fledgling	19 January 2013
	Eared Dove	Nestling	04 May 2014
	Eared Dove	Adult	20 August 2015
Juvenile	Picazuro Pigeon	Juvenile	14 July 2014
Adult	Picazuro Pigeon	Fledgling	12 June 2015
Plumbeous Kite (adults)	Eared Dove	Fledgling	10 October 2010
	Eared Dove	Fledgling	11 October 2015
	Eared Dove	Fledgling	25 October 2015
Aplomado Falcon (juvenile)	Picazuro Pigeon	Adult	21 December 2016
Eastern Green Whiptail	Eared Dove	Nestling	27 December 2015



**Figure 1.** Columbid predators at an urban park in southeastern Brazil. With an Eared Dove (*Zenaida auriculata*) nestling still alive in talons, a watchful Roadside Hawk (*Rupornis magnirostris*) adult perches on a branch (A); a Picazuro Pigeon (*Patagioenas picazuro*) juvenile killed and temporarily left on the ground by a Roadside Hawk juvenile (B); a Plumbeous Kite (*Ictinia plumbea*) female feeds her young pieces she rips from an Eared Dove fledgling (C); its head visible among leaves, an Eastern Green Whiptail (*Philodryas olfersii*) searches for nests among branches (D).

At mid-afternoon of 21 December 2016, we recorded a juvenile Aplomado Falcon feeding on an adult Picazuro Pigeon at the park. The falcon was on the ground with its wings spread over the prey, and tore pieces of the pigeon's chest. The prey's head and part of the chest and belly were already consumed, revealing seeds eaten by the dove. A passerby disturbed the falcon, which flew to a nearby tree and watched. However, it was spotted by a group of Chalk-browed Mockingbirds (*Mimus saturninus*), whose members mobbed the falcon until the raptor left the site.

At midmorning of 09 January 2011 we observed a Roadside Hawk perched on a branch, cleaning the toes and bill from vestiges (blood, small tissue pieces) of a recent meal. A few spotted plumes characteristic of a fledgling Eared Dove were found under the perch. During the cleaning session, the hawk was vigorously mobbed by a Streaked Flycatcher and a Greater Kiskadee (*Pitangus sulphuratus*) until it flew off the park.

The Roadside Hawk was the main predator of the two dove species at the studied park, where it is common and probably hunts there often (Corbo *et al.* 2013). This raptor feeds mostly on insects and rodents (Beltzer 1990, Thiollay 1994, Baladrón *et al.* 2011), but at the study park it was observed to feed on fledgling and nestling birds

only. Preying on Eared Dove fledglings and nestlings was observed at other sites near the park, and perhaps this feeding habit is more widespread than our results may indicate. A juvenile hawk was observed taking a nestling dove from within a nest in a backyard (G.B. D'Angelo, pers. comm.), and an adult was observed with a juvenile dove in talons at a parking lot adjacent to the study site (I.S., pers. obs.) to mention two additional records. Insect prey was observed only once near the park, a caterpillar caught on a tree by a juvenile hawk (Corbo *et al.* 2013).

In southern and southeastern Brazil, the Roadside Hawk breeds during the austral spring (Santos *et al.* 2009, I.S., pers. obs.). Thus, predation on doves by this hawk is not restricted to its breeding period. On the other hand, predation on birds, including the Eared Dove, seems restricted to the breeding season of the Plumbeous Kite, also in the austral spring (Loures-Ribeiro *et al.* 2003, Sazima 2008). However, in southern Brazil, only insects were fed to nestlings of this kite (Jacomassa 2011), which agrees with the general diet recorded for the Plumbeous Kite in Brazil and elsewhere in the Neotropics (Sick 1994, Seavy *et al.* 1997, Sazima 2008). Food delivered to nestlings both of the Roadside Hawk and the Plumbeous Kite, which demand an energetically rich diet, plausibly has an important proportion of vertebrates including

birds (Panasci & Whitacre 2000, Sazima 2008, present paper).

The Aplomado Falcon preys on insects and small vertebrates, including birds (White *et al.* 1994, Sick 1997). Studies on the feeding habits of this falcon in Mexico and Argentina indicate that birds are the most important component in the diet of this raptor, including the Picazuro Pigeon and the Eared Dove (Hector 1985, Bó 1999, Salvador 2012), which agrees with our observations at the study park.

The Eastern Green Whiptail feeds mostly on rodents and reptiles, but birds are present in its diet as well (Hartmann & Marques 2005). Indeed, this snake is a skilled bird hunter able to catch adult passerine birds and is mobbed whenever spotted by mockingbirds and other passerines (Sazima & Marques 2007, Sazima 2015b). Thus, its preying on an Eared Dove nestling would not come as a surprise, and possibly this snake is an important predator on the dove and other bird nestlings in anthropogenic areas.

In conclusion, at a small urban park in southeastern Brazil, a falconid and two accipitrid raptors seem to regularly prey on two dove species. Our observations indicate that the Roadside Hawk preys on doves throughout the year, whereas the Plumbeous Kite restricts predation on doves to its breeding season, when it migrates to the region (Corbo *et al.* 2013). Additionally, a dipsadid snake occasionally preys on one of the dove species.

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# A new population of the White Bellbird *Procnias albus* (Hermann, 1783) from lowland southern Brazilian Amazonia, with comments on genetic variation in bellbirds

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**ABSTRACT:** We report on a recently discovered population of the White Bellbird (*Procnias albus*) in southern Amazonia. Contrary to expectations based on geography and morphological analyses, a recently collected specimen from this new population is genetically closer to the northern subspecies, at the same time that it confirms the overall lack of genetic structure previously reported for the species. Our data reinforces the notion that the subspecies of *P. albus* may not be diagnosable by morphological and molecular characters. The discovery of a new *Procnias albus* population not far from the largest human settlement in Brazilian Amazonia underscores the need for more research to better understand avian distribution in this under-studied region.

**KEY-WORDS:** Cotingidae, distribution, phylogeography, subspecies, taxonomy.

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The White Bellbird, *Procnias albus* (Cotingidae) has a disjunct distribution in Amazonia; the nominate subspecies occurs north of the Amazon River in Venezuela, the Guianas, and northernmost Brazil, whilst *P. a. wallacei* occurs south of the Amazon River on the Serra dos Carajás in southeastern Pará state, Brazil (Snow & Sharpe 2016). *Procnias a. wallacei* is listed as “Vulnerable” according to the Brazilian list of threatened species (MMA 2014). The species was first reported south of the Amazon River by Wallace (1889) near the city of Belém, more than 450 km north of Carajás, but no voucher specimen for this record has been found and until now there have been no other records from the region. Thus, Wallace's (1889) record has either been disregarded for lack of documentation (Moura *et al.* 2014) or, alternatively, considered an instance of vagrancy or even a currently extinct population (Snow 1982). According to Berv & Prum (2014), the two subspecies currently recognized in *P. albus* are not distinct genetically, but more study is needed to clarify the taxonomy of this patchily distributed species. Here, we report on a newly discovered southern Amazonian population of *P. albus*, and comment on the genetic structure of the species.

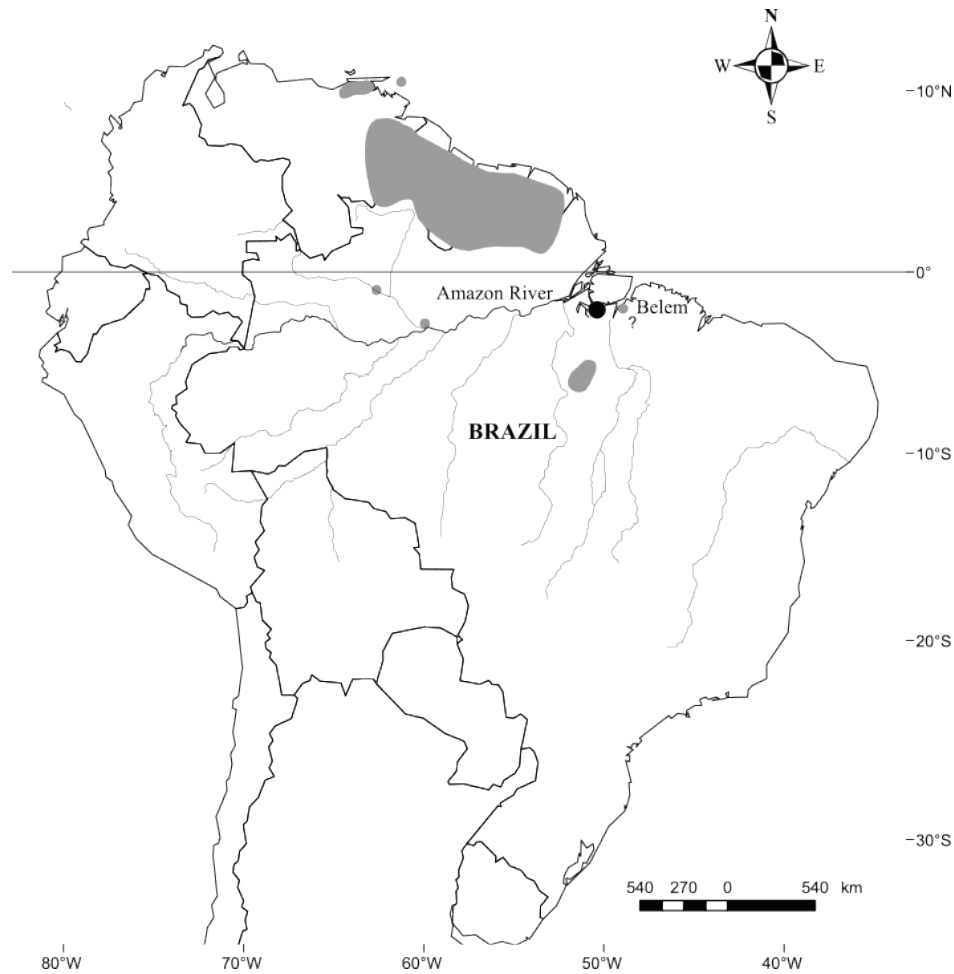
The new record was obtained during a biodiversity inventory of the northernmost part of the Xingu-Tocantins interfluvium at the municipality of Bagre, near

the Muratuba River (02°06'44.5"S; 50°22'15.8"W), c. 260 km (161 miles) to the west of Belém, in the state of Pará, Brazil. The region is covered by upland *terra firme* forest with canopy heights averaging 30 m, as well as *igapó* (black water forest), and *campinas* (white-sand forest). Four leks were found between 19 and 22 June 2015 in the municipality of Bagre (Fig. 1). Three leks were found in a *terra firme* forest area of approximately 25 km<sup>2</sup>. These three leks combined contained at least nine adult males, a young male and some females. A fourth lek was located in *várzea* forest. One adult male from the first lek was collected on 22 June 2015 (MPEG 80706; Table 1). Digital sound files were deposited in Xeno-canto ([www.xeno-canto.org](http://www.xeno-canto.org): XC261271, XC263193) and photographs were deposited in WikiAves ([www.wikiaves.com.br](http://www.wikiaves.com.br): WA1773951, WA1773933, WA1771028).

To compare morphometrics of this collected individual with those of known populations, S.M.D. measured six additional adult male specimens of *P. albus* deposited in the ornithological collection of Museu Paraense Emílio Goeldi (MPEG), as follows: *P. a. albus* (MPEG 32489 from Paru de Leste River, Aramapucú, state of Pará) and *P. a. wallacei* (MPEG 37213, 37214, 35042, 30543, all from Serra dos Carajás, Parauapebas, state of Pará). Measurements taken were bill length (exposed culmen), bill width at nostrils, bill height at

nostrils, left tarsus length, left wing length, and tail length. Measurements were taken with a Vonder electronic caliper to the next 0.01 mm and a ruler. The morphometric data was analyzed by plotting each measured specimen

with Principal Component Analysis (PCA) performed in XLSTAT (Addinsoft 2007). A Pearson's correlation matrix was used in the analysis, and the two factors that best explained the results were plotted against each other.



**Figure 1.** Currently known distribution of *Procnias albus* (gray), with the new location where the species has been documented shown in black. Question mark signs a location (Belém) where there is an historical report. Source: [www.birdlife.org](http://www.birdlife.org).

Plumage and soft color parts of MPEG 80706 were the same as in the nominate and *P. a. wallacei* subspecies (Oren & Novaes 1985), which shared a pure white plumage and tiny white plumes on the black wattle. The maxilla was black with a greyish edge and the mandible was grayish with a black tip, and the feet were gray. Females and one young male observed at the second lek were streaked yellow and olive below as in other *P. albus* populations (Kirwan & Green 2011).

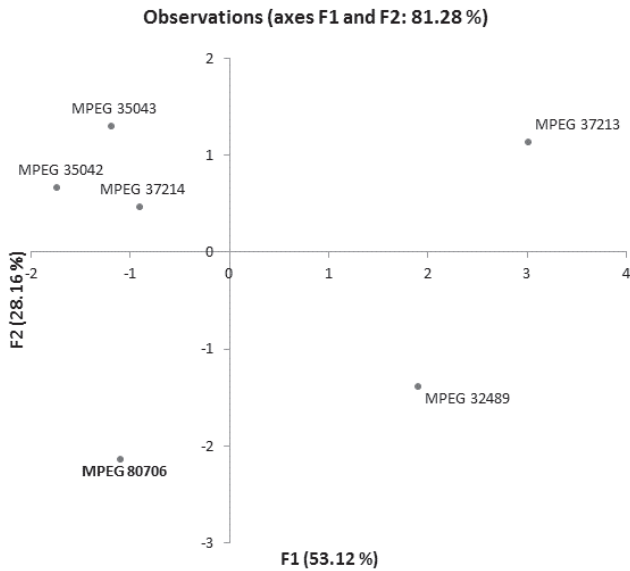
To explore possible genetic differences the DNA of MPEG 80706, the specimen collected during our avifaunal survey at Bagre, was extracted using a phenol-chloroform protocol (Sambrook & Russel 2001) and PCR-amplified for the mitochondrial gene NADH Dehydrogenase Subunit 2 (ND2); the PCR product was purified using a solution of 20% polyethylene glycol 8000 (PEG) and Sanger sequencing was performed on an ABI PRISM 3130 (Applied Biosystems). Sequences of ND2 for all *Procnias* species and outgroups were downloaded

from Genbank (Berv & Prum 2014) and used in the analysis. The downloaded sequences of *P. albus* were from samples AMNH 12002, KUNHM 1244 (both from subspecies *P. a. albus*) and MPEG 37214 (*P. a. wallacei*).

We conducted a phylogenetic analysis using Bayesian Inference (BI) with BEAST (Drummond & Rambaut 2007) and Maximum Likelihood (ML) using RAxML-7.0.3 (Stamatakis 2006). The best fitting model selected by jModelTest 2.1.3 (Darriba *et al.* 2012) was HKY (ti/tv = 5.1282). We also constructed a median-joining network (Bandelt *et al.* 1999) using NETWORK 4.5.1.0 ([www.fluxus-engineering.com](http://www.fluxus-engineering.com)).

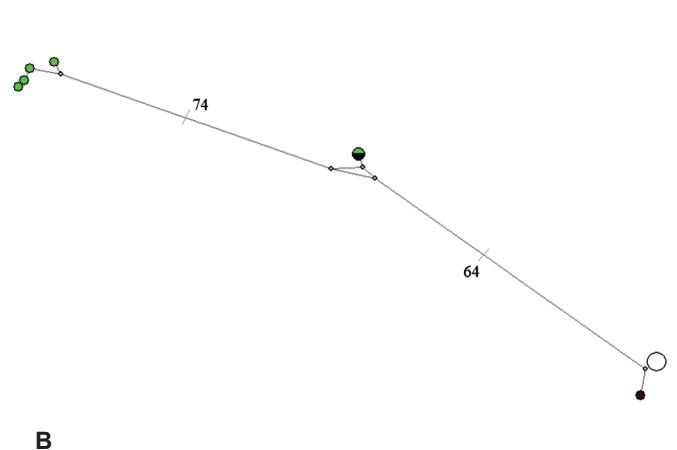
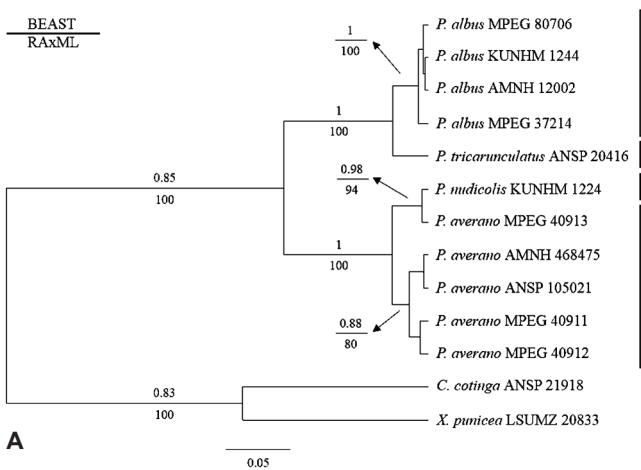
The first two axes of the PCA explained 81.23% of the morphometric variability among the examined specimens (eigenvalues F1 = 3.187 and F2 = 1.69) and were plotted against each other (Fig. 2). Axis 1 failed to discriminate between specimens of *P. a. albus* and *P. a. wallacei*, whereas axis 2 completely separated specimens of *P. a. albus* (with negative values) and *P. a. wallacei* (with positive values).

The Bagre specimen (MPEG 80706) grouped on axis 2 with the only *P. a. albus* specimen included in the analysis (Fig. 2), which is explained by the fact that these specimens shared similar tarsus and bill length values, the characters with the highest autocorrelation with axis 2 (*i.e.* 0.905 and 0.900, respectively).



**Figure 2.** Result of Principal Component Analysis (PCA). The first two axes of PCA are plotted against each other.

The ND2 sequence for MPEG 80706 is deposited in GenBank (Accession No. KY563658.1). Both ML and BI phylogenies, and the haplotype network recovered the same pattern of overall lack of genetic differentiation between subspecies of *P. albus* (Fig. 3). All specimens examined share the same haplotype (Fig. 3B) and although the clade uniting all *P. albus* specimens is strongly supported (Fig. 3A) the lack of haplotype variation within the species does not allow an assessment of relationships among these different populations/subspecies of *P. albus* and likely suggests that these subspecies are not real evolutionary entities.



**Figure 3.** (A) Gene tree generated by BEAST based on 1,001 bp of ND2 sequences of all *Procnias* species, including both *P. albus* subspecies (AMNH 12002 and KUNHM 1244 - *P. a. albus*/MPEG 37214 - *P. a. wallacei*) and outgroups. Numbers above and below branches are Bayesian posterior probabilities and RaxML bootstrap support values, respectively. (B) Median joining network of all haplotypes. The size of the circles is proportional to haplotype frequency and the colors correspond to the species colors on the tree in (A). Numbers under or above bars mean number of mutations between haplotypes.

This paper reports the second confirmed population of *P. albus* south of the Amazon River, the other being the Carajás population known since the 1980's (Roth *et al.* 1984). The presence of a young male and several singing males in at least four leks points to a breeding population rather than wandering individuals. However, according to some local people interviewed, the bellbirds sing only during the onset of the dry season (*i.e.* between May–July) and then either disappear or remain silent and inconspicuous. Thus, whether birds remain in the region outside the dry season remains to be established. Also, the Bagre record lies about 260 km west of Belém, therefore suggesting that the old Wallace (1848) record from near Belém is likely valid.

The PCA analysis indicated that bill and tarsus length are able to distinguish male specimens of *P. albus* subspecies (Fig. 3), corroborating Oren & Novaes (1985). The PCR analysis grouped the Bagre specimen (MPEG 80706) closer to the northern subspecies, *c.* 500 km far and separated by the Amazonas River, than to *P. a. wallacei* from Carajás, which are found *c.* 440 km to the south and not separated by any apparent geographic barrier. Therefore, our morphometric analyses suggest that the newly discovered population south of the Amazon belongs to the nominate form. However, these results should be interpreted with caution because we analyzed only one specimen of the nominate subspecies and therefore purported morphometric diagnoses between both *P. albus* subspecies may not hold when a larger series of specimens are analyzed. The genetic data presented herein suggest that the latter hypothesis is more likely to be correct. Despite the Carajás individual (MPEG 37214) have separated from the others in the ND2 tree, only one haplotype was recovered for *P. albus*. A possible explanation for this result is that the sequence for MPEG 37214, extracted from skin (Berv & Prum 2014), was much shorter than the others.

The lack of genetic differentiation between the Bagre specimen and other *P. albus* populations both south and north of the Amazon agree with Berv & Prum's (2014) suggestion that these subspecies "... are unlikely to be distinct evolutionary lineages that should be recognized as species". The nominate subspecies is a short distance migrant, and vagrants have been recorded in Brazil and Trinidad (Novaes 1980, Snow & Sharpe 2016). Therefore, it seems likely there are occasional dispersal events between both populations known south of the Amazon, which would be consistent with the lack of genetic divergence between the samples currently available.

The subspecies *P. a. wallacei* has recently been included in the Brazilian list of threatened species in the "Vulnerable" category (MMA 2014), in part because it has been documented only for Carajás in the Xingu area of endemism (*sensu* Silva *et al.* 2005), which is the second-most severely deforested Amazonian forest area of endemism (the Belém region is first, Silva *et al.* 2005, Bird *et al.* 2012). Therefore, despite the lack of consistent morphological and genetic differentiation between currently recognized subspecies of *P. albus*, it is premature to synonymize these taxa without analyzing a larger sample of specimens with a broader screen of molecular markers. This cautious approach is justified from a conservation standpoint. The Bagre region's forests and *campinas* have been exploited heavily for timber and sand extraction among other impacts, and there is much need for the creation of conservation units there, which would protect the second well documented populations of *P. albus* south of the Amazon as well as other remarkable codistributed species in a region that is continuing to yield significant ornithological discoveries (Lees *et al.* 2014).

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- Fargione J., Hill J., Tilman D., Polasky S. & Hawthorne P. 2008. Land clearing and the biofuel carbon debt. *Science* 319: 1235–1238.  
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- Sick H. 1985. *Ornitologia brasileira, uma introdução, v. 1*. Brasília: Editora Universidade de Brasília.

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- Novaes E.C. 1970. *Estudo ecológico das aves em uma área de vegetação secundária no Baixo Amazonas, Estado do Pará*. Ph.D. Thesis. Rio Claro: Faculdade de Filosofia, Ciências e Letras de Rio Claro.  
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 Pinheiro R.T. 2009. [WA589090, *Ceuleus obrieni* Short, 1973]. <http://www.wikiaves.com/589090> (access on 05 March 2012).

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