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Cover: A color banded White-crested Elaenia (*Elaenia albiceps chilensis*) prhotographed at its breeding grounds in Patagonia, Argentina. In this issue Presti *et al.* investigated the role of climate and food supply on its demographic parameters. Photo author: Victor Cueto.

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ARTICLE

Behavior and seasonal abundance of Neotropic Cormorant *Nannopterum brasilianus* (Gmelin, 1789) in southeastern, Brazil

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ABSTRACT: The Neotropic Cormorant *Nannopterum brasilianus* (Gmelin, 1789) is one of the most common and abundant species in Brazil's aquatic environments, but little is known about its natural history. This study elaborates and quantitatively evaluates the ethogram and seasonal abundance of this species at Lake Açu, in Rio de Janeiro, Brazil. Between August 2013 and July 2014, behaviors were registered by the *ad libitum* sampling method and quantified by the continuous recording during 30-min sessions. The mean number of sighted individuals per month was 30.41 ± 4.79. Abundance was higher during the dry season (41.5 ± 5.36) compared to the rainy season (19.33 ± 4.81) (t = 3.07, P = 0.01). A total of 42 behaviors were described and grouped into five behavioral categories: maintenance (83.59%), ingestion/excretion (10.67%), locomotion (3.48%), play (1.65%), and agonistic behavior (0.61%). The time spent in these categories did not vary significantly between the morning and afternoon periods. This study can be used as a starting point for further ethological studies on the species.

KEY-WORDS: feeding, Lake Açu, maintenance, Phalacrocoracidae, seasonality.

INTRODUCTION

The Phalacrocoracidae family includes about 40 species of long-beaked piscivorous waterbirds, with mostly monochromatic plumage and webbed feet, commonly called Cormorants (Kennedy & Spencer 2014). Despite morphological similarities, the typical behaviors among species in this family may differ according to the inhabited area, due to worldwide distribution (Bernstein & Maxson 1982). Among different behaviors, wing spreading may be absent or occur only rarely in some Cormorants, in order to avoid loss of heat in cold regions (Cook & Leblanc 2007).

The Neotropic Cormorant, *Nannopterum brasilianus* (Gmelin, 1789), the only representative of the family in Brazil, is distributed from the southern United States to southern South America (Sigrist 2009). It presents gregarious habits and inhabits inland waters and seafronts (Sick 1997). The species display brown plumage when young and black when adults, with the presence of white filoplumes on the sides of the head and neck during the reproductive period (Bó 1956). In Brazil, they reproduce in colonies in the Amazon, Pantanal and on islands near the coast of Rio de Janeiro (Sick 1997, Alves *et al.* 2011).

Although the species is widely distributed and of common occurrence, few studies concerning its natural history have been published. Most include general behavior (*e.g.*, Oliveira & Costa 2003, Sazima 2008, Branco *et al.* 2009), distribution patterns (*e.g.*, Alves *et al.* 2011, Silva *et al.* 2014) and feeding (*e.g.*, Barquete *et al.* 2008, Alarcón *et al.* 2012, Casaux *et al.* 2012) descriptions.

Ethograms are basic tools used in natural history studies (Sakamoto *et al.* 2009). They consist of a list of behavioral units and their respective descriptions and can be accompanied by qualitative and quantitative analyses (Yamamoto & Volpato 2011). Ethograms are reference sources, which may be used in phylogenetic analyses and in the elaboration of hypotheses regarding behavior functionality (Kennedy *et al.* 1996, Gokula 2011).

Behavior descriptions of *N. brasilianus* are scarce. Previous studies have been described some aspects related to maintenance (Branco *et al.* 2009), foraging (Gheler-Costa *et al.* 2018), agonistic (Oliveira & Costa 2003), play (Sazima 2008), feeding associations with piscivorous birds (D'Angelo & Sazima 2013) and dolphins (Santos *et al.* 2010, Espinoza-Rodríguez *et al.* 2015), and diving behaviors (Quintana *et al.* 2004). However, an ethogram has not been produced for the species.

Due to the lack and importance of studies related to natural history, this study elaborates and quantitatively analyses Neotropic Cormorant ethogram and seasonal abundance of the species in an artificial lake in southeastern Brazil. Ethogram was then compared to others previously described for Phalacrocoracidae.

METHODS

Study area

This study was performed at the campus of the Universidade Federal Rural do Rio de Janeiro (22°46'9.56''S; 43°41'13.12''W) in Seropédica, located in the Baixada Fluminense district. The campus comprises 3024 ha (Chiquieri *et al.* 1995), covering countryside, grazing areas, Atlantic Forest fragments, spontaneous wetlands, and four lakes, three artificial and a natural one (Ferreira *et al.* 2010). The climate is classified as "*Cw*" by Koppen's International System, as humid subtropical with a dry season in winter (Alvares *et al.* 2013).

Observations were carried out on an artificial lake, Lake Açu, located near the Agronomy Institute. The lake comprises an area of 98,538.08 m^2 with a depth of 1.75 m. The surrounding vegetation is composed of grasses and sparse trees, including *Ziziphus joazeiro*, *Syzygium cumini* and *S. malaccense*; and palms (Arecaceae), including *Caesalpinia echinata*, *Ficus* sp., *Mangifera indica*, and *Psidium guajava*.

Field procedures

Observations were carried out between August 2013 and July 2014. Sixty field trips were performed, totaling 168 h of sampling effort, where 100 h comprised the quantitative analyses. Behavioral units were registered by the *ad libitum* sampling method and quantified by the continuous recording (Altmann 1974). The observed behaviors were photographed, filmed and recorded using spreadsheets. A focal individual was chosen randomly by chance in each session. Therefore the same individual could or could not be chosen in the next session. During each 30-min session, the duration of each individual behavior was counted in minutes. At the end of each session, 10-min intervals were taken, followed by a new session. A total of 100 sessions were sampled in the morning (06:30 h to 11:59 h) and 100 in the afternoon (12:00 h to 18:00 h). The division and nomenclature of each behavior were based on the studies carried out by Schleidt *et al.* (1984), Prestes (2000) and Oliveira & Costa (2003). Individuals were classified as young if plumage was brown and as adults if plumage was black. Adults with white filoplumes on the sides of the head and neck displayed breeding plumage. The highest number of individuals observed per month was adopted as a measure of monthly abundance.

Statistical analyses

Data normality (Shapiro-Wilk's test) and homogeneity of variances (Levene's test) were first tested. The difference between the number of individuals sighted during the dry (April to September) and rainy (October to March) seasons was analyzed by Student's *t*-test. The behavioral categories were evaluated regarding differences in duration between morning and afternoon periods by the Student's *t*-test after log-transformation. All tests were performed using the PAST software v. 3.12 (Hammer *et al.* 2001), adopting a 5% significance level. Data are presented as means ± standard error.

RESULTS

The monthly average of Neotropic Cormorants at Lake Açu was 30.41 ± 4.79 individuals, reaching higher and lower values in June 2014 and December 2013, respectively (Fig. 1). Abundances differed between seasons ($t = 3.07$, $P = 0.01$), higher in the dry season (41.5 ± 5.36) compared to the rainy season (19.33 ± 4.81). The population was composed by young individuals, except for a record of three adults in reproductive plumage in November 2013.

Forty-two behaviors were identified and described, grouped into five behavioral categories: maintenance (83.59%), ingestion/excretion (10.67%), locomotion

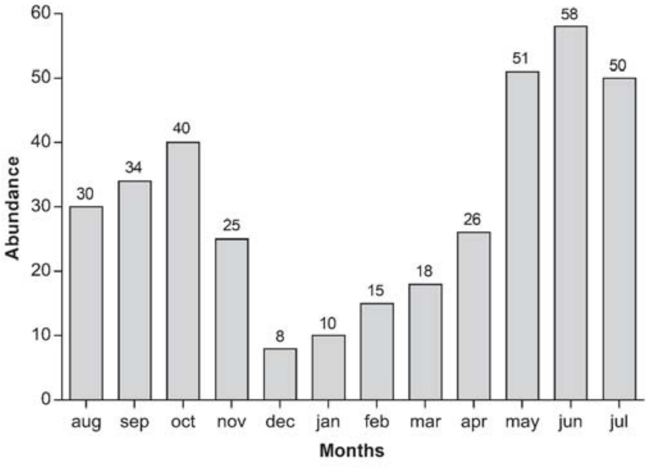

Figure 1. Abundance (highest monthly value) of *Nannopterum brasilianus* from August 2013 to July 2014 in the Lake Açu, southeastern Brazil.

(3.48%), play (1.65%) and agonistic behavior (0.61%) (Fig. 2). These categories did not vary significantly between the morning and afternoon periods (maintenance: t = -0.21, P = 0.83; ingestion/excretion: t = -0.02, P = 0.98; locomotion: t = -0.85, P = 0.41; play: t = -1.09, P = 0.34; and agonistic behavior: t = -1.17, P = 0.27).

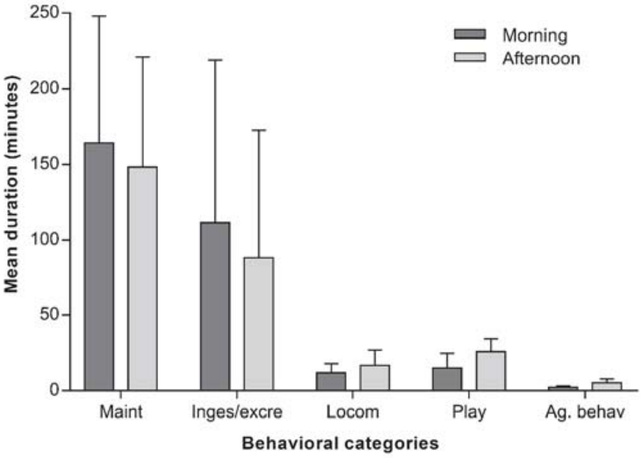

Figure 2. Mean duration and standard error of behavioral categories during the morning (06:30 h to 11:59 h) and afternoon (12:00 h to 18:00 h) periods (in minutes). Maint - Maintenance, Inges/excre - Ingestion/excretion, Locom - Locomotion, Play, and Ag. behav - Agonistic behavior.

Maintenance

These include behaviors related to resting, body care and plumage activities (Fig. 3).

Head scratching: the bird tilts its head to its chest and lifts one leg toward it. It then moves the tarsi quickly against the head, in top-to-bottom movements. These movements may also be directed to the chin and throat (Fig. 3A).

Back head scratching: the bird moves its neck towards its back, swinging the head against it in quick lateral movements (Fig. 3B).

Tarsus scratching: the bird lifts its leg up close to the abdomen and tilts its head towards the tarsi, with rapid half-open beak movements on the tarsi (Fig. 3C).

Preening: with its wings half-open and low, the bird moves its half-open beak toward the base of the feathers, aligning them, carrying out this movement for feathers throughout the whole body, tilting its head to the region where the feathers will be aligned (Fig. 3D).

Plumage shaking: the bird, with its body leaning forward after exiting the water, shakes its whole body in one quick movement, causing excess water to leave the feathers. This can be followed or preceded by wing, head and tail shaking (Fig. 3E).

Figure 3. Behavioral conducts of *Nannopterum brasilianus* in the maintenance category: (**A**) Head scratching, (**B**) Back head scratching, (**C**) Tarsus scratching, (**D**) Preening, (**E**) Plumage shaking, (**F**) Wing shaking, (**G**) Wing spreading, (**H**) Bathing, (**I**) Sitting resting, (**J**) Back head resting, (**K**) Bipedal resting, (**L**) Unipedal resting, (**M**) Gular-fluttering, (**N**) Neck lowering, (**O**) Head lowering, (**P**) Beak opening, (**Q**) Neck shrinking (adult with breeding plumage), (**R**) Wing leg stretching.

Wing shaking: after leaving the water, the bird tilts its body forward, opens its wings and shakes them in fast and beating movements. Variation: slow wing beating (Fig. 3F).

Head shaking: after leaving the water, the bird swings its head sideways, slow at first, increasing frequency until slowing down again. This also occurs during foraging, after the bird takes its head out of the water.

Tail shaking: after leaving the water, the bird leans its body forward and swings its tail horizontally in short and fast movements.

Wing spreading: after leaving the water, the bird opens its wings horizontally and keeps them still (Fig. 3G).

Bathing: during movement in the water after foraging, the bird leans its body forward and flaps its wings against the water, raising its body from the surface. This may be followed by diving. The bird alternates between displacement in water, dipping, and bathing (Fig. 3H).

Sitting resting: the bird remains with its body lowered over its legs, with the abdomen in contact with the substrate (Fig. 3I).

Back head resting: the bird tilts its neck towards its back, positioning the head between the wings with the beak tucked beneath scapulars. Eyes remain closed (Fig. 3J).

Bipedal resting: body erect and supported with both legs on the substrate, relaxed neck, closed wings and lowered tail. Lateral head and gular-fluttering movements may be present (Fig. 3K).

Unipedal resting: similar to bipedal resting, but the body rests with one leg on the substrate, while the other is retracted near the abdomen (Fig. 3L).

Gular-fluttering: the bird remains with its beak half open and vibrates its gular region. This behavior is prevalent during bipedal resting but can be performed during other behaviors. It is common on hot days (Fig. 3M).

Neck lowering: the bird lowers its neck vertically towards the substrate (Fig. 3N).

Head lowering: similar to neck lowering, but the bird lowers only its head vertically toward the substrate (Fig. 3O).

Beak opening: the bird opens its beak quickly then closes it, as in a yawn. Variation: with its head lowered, the bird opens its beak slowly, accompanied by lateral movements of the head (Fig. 3P).

Neck shrinking: the bird shrinks its neck close to the body, forming an "s" (Fig. 3Q).

Wing leg stretching: the bird may or may not tilt its body slightly forward, then stretch its wing, followed by the tarsus on the same side of the body (Fig. 3R).

Ingestion/excretion

These behaviors are related to feeding and hydration activities (Fig. 4).

Foraging: the bird plunges in the water in search for fish by impelling the anterior part of the body, first submerging the head, then the trunk and, finally, the tail. Upon returning to the surface, only the neck and part of the back are exposed. Foraging can be carried out individually or in groups, and usually takes place on the lakeshore. During group foraging, individuals move in rows, forming a barrier to facilitate fish catching (Fig. 4A).

Eating: The bird feeds when it emerges after diving during foraging, bringing a fish in its beak. It swings its head sideways to arrange the fish into a cranial position in the beak, then tilts the head and neck back and swallows the prey. It may drink water after feeding (Fig. 4B).

Drinking: the bird tilts its body under the water, lowers its neck and places its head inside the water (Fig. 4C). It picks up some water with its beak and vertically raises its head to swallow, with the beak half open (Fig. 4D).

Defecating: the body is slightly inclined forward, the feathers close to the cloaca become erect, the tail is lifted and stool is expelled (Fig. 4E).

Locomotion

These are behaviors related to changes in location, unrelated to feeding (Fig. 5).

Water moving: body in the water with exposed neck, tail and back. The bird slowly moves in the water by leg movements, without diving (Fig. 5A).

Open wings water moving: body in a position similar to water moving, but with wings open, high and close to the bird's head as it moves in the water. This behavior precedes flight (Fig. 5B).

Figure 4. Behavioral conducts of *Nannopterum brasilianus* in the ingestion/excretion category: (**A**) Foraging, (**B**) Eating, (**C**, **D**) Drinking, (**E**) Defecating.

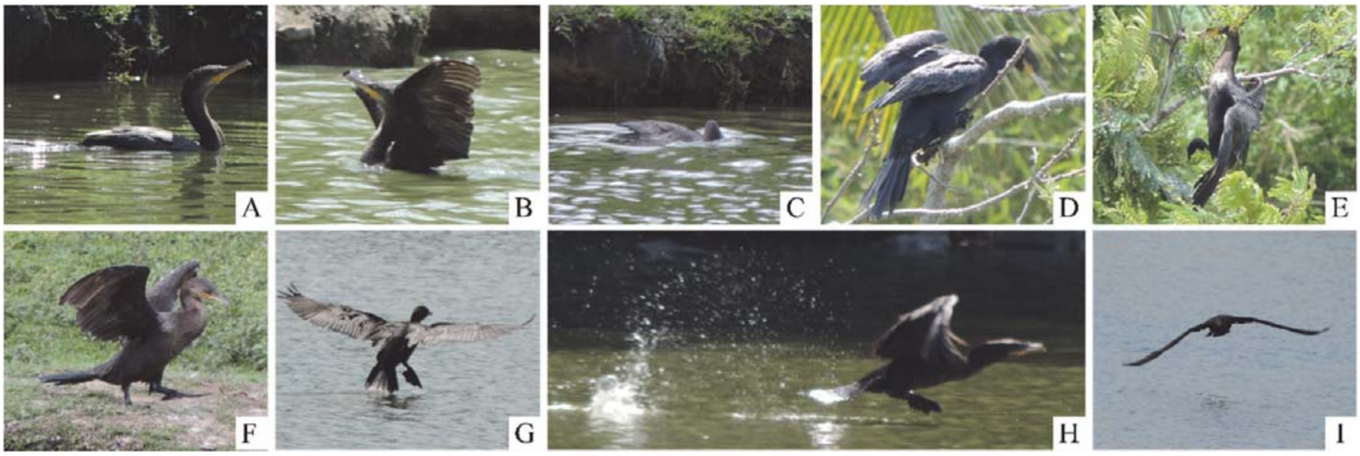

Figure 5. Behavioral conducts of *Nannopterum brasilianus* in the locomotion category: (**A**) Water moving, (**B**) Open wings water moving, (**C**) Head dive water moving, (**D**) Tree branch moving, (**E**) Falling, (**F**) Ground moving, (**G**) Water landing, (**H**) Water takeoff, (**I**) Flying.

Head dive water moving: body in a position similar to water moving, however, the bird repeatedly plunges its head and part of the neck underwater while moving in the water. This can be followed by head shaking when the head emerges (Fig. 5C).

Tree branch moving: the bird moves laterally on a branch with its body tilted forward and wings slightly open and slightly raised, moving one leg at a time in the target direction. It can rotate the body 180° to change position and perform short jumps to move between nearby branches (Fig. 5D).

Falling: when the bird lands or moves on a branch in trees, it can become unbalanced and fall onto the substrate (the lake, in the case of the present study). To try to remain on the branch, it supports its head or body parts on the branch, with wings and tail open, but this does not usually prevent the fall (Fig. 5E).

Ground moving: the bird moves with one leg at a time in the target direction with its body slightly inclined forward, with wings semi-open or closed and raised tail, leaning the body towards the leg that supports it on the ground. The bird can rotate its body 180° to change position (Fig. 5F).

Water landing: body tilted, wings open and raised, tarsi extended forward and tail open and lowered. The bird flies toward the water, flaps its wings and slides its legs into the water surface, with the tarsi being the first part of the body to come into contact with water. When sliding, the bird slows down, until the abdomen touches the water, after which the wings close immediately (Fig. 5G).

Water takeoff: with the body in the open wings water moving position, the bird flaps its wings and remains with the tail and tarsi in the water. Simultaneously, it moves its legs against the water surface, pushing its body out of the water until flight takes place (Fig. 5H).

Flying: head, neck, trunk, and tail stretched and aligned horizontally, tarsi extended close to the body and tail open. The bird performs a beaten flight and can glide for a few seconds (Fig. 5I).

Play

These behaviors are related to the search and movement of inanimate objects with the beak (Fig. 6).

Single playing: happens on the ground, branches or water. On the ground, the bird grabs an inanimate object (branch, leaf or root) with its beak and swings it with its head in lateral movements until the object falls. It then picks up the same object and repeats the movement. On branches, the bird moves its head towards branches with leaves and tries to pull them out with its beak in rapid movements. In water, the bird catches an inanimate object with its beak and moves in the water with it and can swing its head laterally (Fig. 6A).

Group playing: when an individual carries an inanimate object in its beak, another bird approaches, vocalizes and tries to take the object with its beak (Fig. 6B). This second individual can pick it up from one end and both then pull on it, like on a tug of war. Other individuals can vocalize and perform a wing-waving display while approaching the bird with the object. In this display, the bird slightly tilts its body forward, the tail is open and raised, and the wings beat slightly. This can be accompanied by vocalization (Fig. 6C).

Ground searching: the bird tilts its body, lowers its neck towards the ground and, with its beak, looks for dry branches or leaves among the vegetation to play with. The bird may walk on the ground or remain in the same place (Fig. 6D).

Agonistic behavior

These are behaviors related to aggressive intra- and interspecific activities (Fig. 6).

Figure 6. Behavioral conducts of *Nannopterum brasilianus* in the play and agonistic behavior categories: (**A**) Single playing, (**B**) Group playing, (**C**) Group playing - wing-waving display, (**D**) Ground searching, (**E**) Fighting, (**F**) Ground chasing, (**G**) Spot stealing, (**H**) Escaping, (**I**) Threat searching.

Fighting: body tilted, with wings open or closed. The bird stretches and moves its neck horizontally towards its opponent, and may peck it, preferably on the head or neck. The gular bag expands and the bird vocalizes (Fig. 6E).

Ground chasing: the bird pursues the escaping opponent in a rapid ground displacement during fighting on the ground. The opponent (2) can either face the first individual (1) or continue to run (Fig. 6F).

Spot stealing: when resting on the substrate, another individual approaches and begins a fight. If the first individual does not change location, it climbs on the back of the opponent, flaps its wings, vocalizes and pecks the opponent on the neck and head (Fig. 6G). The attacked bird vocalizes and expands its gular bag. In most cases, it loses its balance and leaves the area, while the attacker occupies the free spot. The attacking bird may also give up stealing the spot and look for another resting place.

Escaping: displacement of the bird on the ground, branch, air or water, away from an intra- or interspecific threat. When escaping by ground, branch, and water, the bird moves short distances (1 to 2 m), usually during intraspecific agonistic interactions, such as fighting or spot stealing. Regarding air movement, the bird flies at greater distances (> 2 m), preferably during interspecific interactions, such as the approach of people or dogs. When it escapes through the air in areas near water, it propels its body through tarsi movement on the water surface, similar to water takeoff (Fig. 6H).

Threat searching: the bird moves its head horizontally in the direction of possible threats (Fig. 6I). The body can move laterally.

Vocalization: occurs mainly during agonistic and play interactions. The bird opens its beak, expands its gular bag and vocalizes repeatedly with the proximity of another individual (oak, oak, oak ...). Variation: small hoarse (oak) during resting or foraging.

DISCUSSION

Lake Açu represents a valuable food, rest and overnight area for Neotropic Cormorants in urban surroundings. The resident population displayed seasonal variations during this monitoring, with greater abundance during the dry season. A similar pattern was reported for the nearby Guanabara Bay, southeastern Brazil (Alves *et al.* 2011). However, the opposite was recorded in wetlands in the south and north of Brazil (Branco 2002, Barquete *et al.* 2008, Silva *et al.* 2014). These variations may be related to migration between feeding and breeding sites during the year, which may differ locally (Sick 1997). Although adults displaying breeding plumage were found, no reproduction activities were observed. The population decreases during the rainy season correspond to migration to reproductive sites, usually islands, such as the Tijucas Islands (Alfavaca and Pontuda) in Rio Janeiro (Alves *et al.* 2011).

Neotropic Cormorant, as well as others cormorants, spend most of their daylight time in maintenance activities (King *et al.* 1995, Gwiazda 2000, Branco *et al.* 2009). The ethogram raised herein lists behaviors commonly found in Phalacrocoracidae family (*e.g.*, Bartholomew *et al.* 1968, Oliveira & Costa 2003, Nelson 2005). However, some behaviors seem to have different roles in Neotropic Cormorant. One of the most common behaviors of the family, wing spreading, is absent in several species belonging to the blue-eyed shag complex (Bernstein & Maxson 1982), but was frequent in Neotropic Cormorant. The purpose of such behavior is controversial and may include thermoregulation (Clark-Jr. 1969), plumage drying (White *et al.* 2008) or intraspecific display of foraging success (Jones 1978). At Lake Açu, this behavior was carried out with wet plumage, followed or not by feeding and associated with behaviors to remove excess water, indicating a primary plumage drying purpose.

Behaviors associated with reproduction in other cormorants were recorded in non-reproductive situations among young individuals, indicating possible alternative purposes. The wing-waving display performed during group playing is a male advertising carried out during courtship to attract females or claim possession of the nest (van Tets 1965, Childress & Bennun 2002). However, it can also be used in the defense of rest perches in *Phalacrocorax carbo* (Galván 2004). In the observed context, its function would relate to the claim of the inanimate object acquired by another individual. Spot stealing, the posture assumed by one individual when climbing on the back of another and pecking its neck, refers to mating behavior (Berry 1976). In addition, playing behaviors, such as looking for and manipulating leaves and branches, are similar to collecting material for the nest. Such behaviors among young individuals may favor the learning and practice of innate responses, facilitating communication between adults (Sazima 2008).

In conclusion, this study provides important information about the natural history of Neotropic Cormorant and can be used as a starting point for further ethological studies on the species.

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Kleptoparasitism and territoriality in the Snail Kite *Rostrhamus sociabilis* (Accipitriformes: Accipitridae) in the Complejo Güija, El Salvador

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ABSTRACT: We present the observations of some kleptoparasitic and territorial interactions in the Snail Kite (*Rostrhamus sociabilis*), following focal individuals from January to May 2017 in two wetlands of El Salvador. Those interactions were performed during their food searching and managing of prey on perch. We observed two attempts of kleptoparasitism from Great-tailed Grackle (*Quiscalus mexicanus*) to *R. sociabilis*. On the first case, a flock of *Q. mexicanus* chased an adult Snail Kite, which had captured a snail; on the second case, a male of *Q. mexicanus* tried to steal a young Snail Kite's prey, which was managing its prey on perch. On both cases in response to the attack, two individuals chose to change perch to complete the consumption of its prey. We also observed an intent of kleptoparasitism between two male Snail Kites, after the attack, on perch the chased bird released the snail and moved to another site, meanwhile, the attacker ended up eating the snail. We attribute this observation to a kleptoparasitic behavior, related to water stress and variations in prey availability. We recorded Snail Kite's territorial behavior between the species and against other raptors, as a way to protect their feeding territories. With these observations, we provide some information about the ecological behavior of the species in El Salvador. We stress the need to carry out research related to the interaction between *R. sociabilis* and *Q. mexicanus* on its feeding sites, focusing in the effect of water scarcity and snail availability on the behavior of the Snail Kite.

KEY-WORDS: ethology, Great-tailed Grakle, raptors, specialist, wetlands.

INTRODUCTION

In a community structure, the interaction of species can be either positive or negative (Jaksic & Marone 2001). The result of the interactions generates a dynamic equilibrium that determines the structure of the community and the richness. Among interactions that contribute to this dynamic flow are: competition, predation (including parasitism) and mutualism (Dhondt 2012). Competition is an interaction between individuals of the same (intraspecific) or distinct (interspecific) species, it is caused by the common need of a limited resource in the habitat that species share, which leads to the reduction of survival, growth and/or reproduction of the competing individuals (Begon *et al*. 1995).

Food theft or kleptoparasitism, can occur in many groups of animals, however, is more common among birds, where parents which provide food to their offspring may be more vulnerable to be attacked by organism of the same species (intraspecific attacks) or other species (interspecific attacks) (Brockmann & Barnard 1979, Gaglio *et al.* 2018). This could lead to a decrease in the feeding rates, due to the time spent in avoiding kleptoparasitic attacks (Gaglio *et al.* 2018).

The Snail Kite (*Rostrhamus sociabilis*) has a wide geographical distribution from Florida (USA) to Uruguay and Argentina (Sick 1997), it is probably one of the most morphologically specialized species among raptors, since its hook-shaped, thin and curved beak allows it to easily cut the connecting muscle and to extract the meat completely from the shell, which is the main prey that makes up its diet (Méndez *et al.* 2006, Rueda & Wiebe 2014, Chapman & Bolen 2015). In this study we present observations of kleptoparasitism and territoriality in *R. sociabilis* populations in two wetlands of the Complejo Güija, with the aim of describing those behaviors and contributing to the knowledge of the ethology of this species in the country.

METHODS

Complejo Güija is located in western El Salvador, in the Santa Ana department, municipality of Metapán (14°17'N; 89°29'W). It is a RAMSAR site (MARN 2016) and its extension includes 47.200 ha. The main lake has an area of 42 km^2 of which 76.7% corresponds to El Salvador and the rest to Guatemala. This complex includes the Metapán Lagoon, the Güija Lake and portions of the Natural Protected Area San Diego y La Barra (Herrera & Rivera 2001, Herrera 2005). We made the observations in the northern sector of the Güija Lake (14°17.584'N; 89°31.983'W) (Site 1), and in the sector of Rincón del Cuje, in the Metapán Lagoon (14°18.548'N; 89°29.288'W) (Site 2).

We performed 11 visits to each site in the period of January to May 2017, from 7:00 h to 12:30 h. The information of the bird's behavior was obtained using the focal individual method (Lehner 1998), which is, briefly, a selection of an individual that started to forage being the focus of the observation for 10 min, at a distance no less than 15 m, to prevent the species from modifying its behavior due to disturbance. In each observation, we recorded intra and interspecific interactions, with emphasis on territoriality. At the end of the observation of one focal individual, we waited for 10 min to select a new one, making sure that the specimen was not the same that we were observing previously.

RESULTS & DISCUSSION

Great-tailed Grakle *vs.* Snail Kite

We observed agonistic interactions from *Quiscalus mexicanus*, which in Site 1 performed flock chases on an adult *R. sociabilis* which had captured a snail. These persecutions were carried out as an attempt to steal the snail captured by the species. Due to these persecutions the Snail Kite moved to another place with its prey, without presenting aggressive behavior against its persecutors. Similar behavior of kleptoparasitism was observed on a juvenile, which was managing its prey on the perch and was frequently interrupted by a male *Q. mexicanus* (Fig. 1A), which made attempts to steal the snail and made a constant vocalization. In response to the attack, the juvenile chose to change the perch to end the consumption of its prey. On Site 2 we observed the displacement by an individual of *Q. mexicanus* against a female *R. sociabilis* (Fig. 1B). This behavior of kleptoparasitism against *R. sociabilis* has been observed by Sykes-Jr. (1987) in *Q. major*, a species that made constant attacks against Snail

Figure 1. Attacks and intent of kleptoparasitism of a male *Quiscalus mexicanus* towards a juvenile *Rosthramus sociabilis* (**A**). Displacement of a female *R. sociabilis* by a male *Q. mexicanus* (**B**).

Kites, while it was on a perch or in flight. With our observations we documented for the first time in the zone this behavior between *R. sociabilis* and *Q. mexicanus*. We even observed an individual of *Q. mexicanus* carrying a snail in its beak. Therefore, we suggest that future studies focused on the feeding interaction of these species.

Snail Kite *vs.* Snail Kite

In Site 1 we observed an intraspecific attack of *R. sociabilis* against another individual of the same species, which had a prey on a feeding perch. Due to the attack, the Snail Kite released the snail and moved to another site. The Snail Kite which finished the attack ended up eating the snail. We attribute this observation to a kleptoparasitic behavior. Miller & Tilson (1985) observed kleptoparasitism between *R. sociabilis* against Limpkin *Aramus guarauna,* when the availability of snails was low, due to the decrease in water level or the increase in vegetation height. We observed similar conditions (in relation to the availability of snails) to those observed by Miller & Tilson (1985) on the day of the kleptoparasitic interaction, because snail hunted per h was low: 0.52 snails/h. This kleptoparasitic behavior may be more frequent according to wetland conditions, such as low water levels and low prey availability. For this reason, it is important to evaluate the behavior of the Snail Kite during these periods of stress.

Territoriality

On Site 1, we recorded interactions of *R. sociabilis* with other raptors: on one occasion, two juvenile *Geranoaetus albicaudatus* were displaced by persecution and vocalization by a male *R. sociabilis* who was hunting. Similar observations were made by Haverschmidt (1970) in Suriname, who documented the persecution of *R. sociabilis* against *Buteogallus meridionalis*, which had captured a small mammal. In our observations, the attack was probably carried out because *R. sociabilis* was in foraging activities and both individuals of *G. albicaudatus* slightly interrupted their activity, since the diet of this species is composed mainly by rodents, amphibians, reptiles, carrion and even small birds (Dunne *et al.* 2012), making improbable territorial behavior.

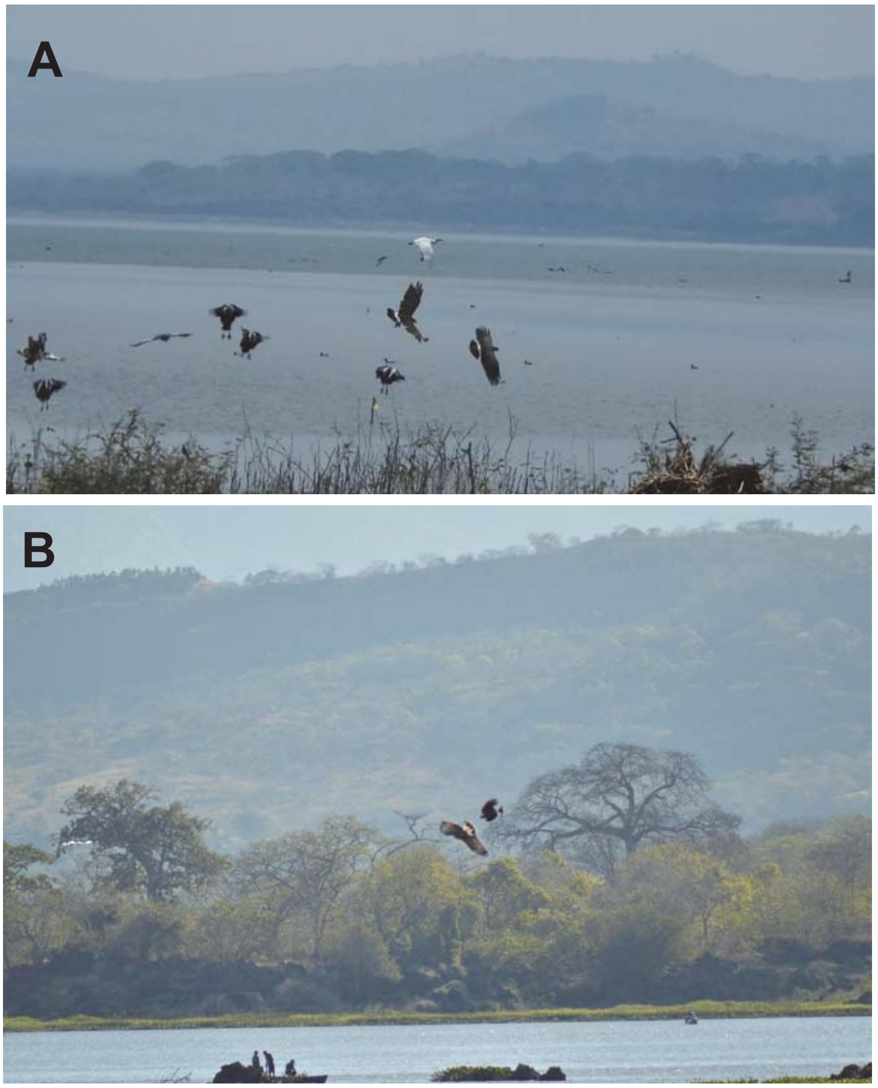

Figure 2. Territorial behavior for the food resource among *Rosthramus sociabilis* in both studied sites (**A** = site 1; **B** = site 2).

On Site 2, we observed a territorial fight between a female *R. sociabilis* and *Caracara cheriway*: the female vocalized while in flight to get *C. cheriway* away from the sector, in the same way it made attacks with its claws without making contact. We also recorded interactions against *Buteogallus anthracinus*; in this case, it was this species which removed *R. sociabilis* from the site with vocalizations and without presenting aggressiveness with its claws. This area has been described as a feeding and hunting site for *B. antrhacinus* (Molina 2013). In the same way we observed an active nest to the east of the foraging site of *R. sociabilis*, so the attacks could be related to territoriality.

We registered territorial behaviors among Snail Kite's in both sites. In Site 1, an adult male was attacked while moving with its prey (Fig. 2A), causing consumption of its prey approximately 20 m away from the site where the attack occurred. In the interaction site, the capture of snails by Snail Kites was frequent. Snyder & Snyder (1970) mention that *R. sociabilis* forages in common feeding areas and sometimes some individuals usually exhibit territorial behaviors in defense of small areas (2.25 km^2) where they constantly capture snails, preventing other individuals from hunting. The defense of its territory is carried out when the availability of snails is high, while in conditions of low abundance. The defense of territory is not carried out, because this implies energy expended (Snyder & Snyder 1970). Unlike these observations, the day of the interaction the snail intake was low, with 1.33 snails consumed per h. In Site 2 we recorded the displacement of individuals in search of food or feeding on the perch. This behavior is attributed in this case to the defense of food territories due to a high abundance of snails, similar to the observations of Snyder & Snyder (1970). On the day of observation, we recorded the maximum amount of snails consumed/h (7.33). Bourne (1985) and Posso *et al.* (2012) also describe this territorial behavior exhibited by males, with vocalizations and persecutions against intruders in their food territories. We conclude that the territorial behavior of the Snail Kite in both wetlands is frequent and this can increase in periods of low snail availability.

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Stilts do not protect against crawlers: Limpkins preyed on by Tegu Lizards at an urban park

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ABSTRACT: Limpkin (*Aramus guarauna*) is a long-legged wading bird that forages mostly in wetlands in the open and occasionally under tree cover. This large bird is cautious and frequently scans its immediate environs when active or resting. Records of adult Limpkin predators are scarce and restricted to two very large aquatic reptiles, the American Alligator (*Alligator mississippiensis*) in North America and the Yellow Anaconda (*Eunectes notaeus*) in South America. Herein we report on two Limpkins killed and eaten by Black and White Tegus (*Salvator merianae*) at an urban park in southeastern Brazil. One of the Limpkins was still alive when we came across the predation event, whereas the other Limpkin seemed freshly killed. The first Limpkin was already sprawled on the ground and occasionally opened the bill, vocalised hoarsely and flapped the wings, while the Tegu repeatedly bit the bird on several body parts, which gradually weakened the bird. The Limpkin died when the Tegu bit hard the bird on the head and crushed the skull. In the second event the bird was bitten on several body parts and, thus, we assume that it was also killed by the Tegu that was eating the fresh corpse. The two events comprised two Tegu individuals recognisable by natural marks. Limpkins killed and consumed by Tegus probably are a rare occurrence. Tegus are large by Neotropical lizard standards, but are small compared with the other two very large reptiles known to prey on Limpkins. Presently, only three reptilian species are documented as predators of adult Limpkins.

KEY-WORDS: Aramidae, predation, Teiidae, urban area, wading bird.

Limpkin (*Aramus guarauna*) is a long-legged wading bird that forages mostly in wetlands in the open and occasionally under tree cover (Bryan 1996, 2002). This large bird is cautious and frequently scans its immediate vicinity when active or resting, especially if sitting on the ground (I.S., pers. obs.). Records of adult Limpkin predators are scarce and restricted to two very large aquatic reptiles, the American Alligator (*Alligator mississippiensis*) in North America and the Yellow Anaconda (*Eunectes notaeus*) in South America (Strussmann 1997, Bryan 2002). Herein we report on two Limpkins attacked and eaten by Black and White Tegus (*Salvator merianae*) at an urban park in southeastern Brazil.

We recorded the two predation events of Limpkins by Tegus at the *Parque Ecológico Professor Hermógenes de Freitas Leitão Filho* (22°48'42''S; 47°04'26''W) in Campinas, São Paulo state, southeastern Brazil. The park has a total area of 0.13 km^2, of which about 75% is occupied by a large pond surrounded by native and exotic vegetation composed of trees, bushes and grass patches. We observed the Limpkins and the Tegus with bare eye and recorded their interactions in video and photos with a digital camera at a distance of 2–3 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 two predation events are on file at the *Museu de Zoologia da Universidade Estadual de Campinas* (ZUEC).

On 08 February 2018 at early afternoon we recorded a Tegu crawling under tree cover, while a Limpkin walked nearby well aware of the large lizard (Fig. 1A). Shortly after, we heard a thrashing noise and hoarse calls nearby. Then we came across the first predation event, the Limpkin still alive but sprawled on the ground. It occasionally opened the bill, vocalised hoarsely and flapped the wings (Fig. 1B), while the Tegu repeatedly bit the bird on several body parts. This biting gradually weakened the Limpkin, which died when the Tegu bit hard the bird on the head and crushed the skull drawing blood at the base of the bill (Fig. 1C). After the kill, the Tegu pulled off feathers from the bird's body (Fig. 1D) and began to tear flesh pieces to consume.

On 16 February 2018 we recorded the second predation event, also at early afternoon. When we became aware of this event, the Limpkin seemed freshly killed and was bitten on several body parts. Consequently, we assumed that it was killed by the Tegu that was tearing flesh from the corpse (Fig. 2A & B). The two events we recorded comprised two Tegu individuals recognisable by natural marks.

Figure 1. An adult Tegu *Salvator merianae* (foreground) moves close to an adult Limpkin *Aramus guarauna* (**A**). Note relative size of both animals and the Limpkin's long legs ("stilts"). A wounded Limpkin sprawled on the ground, its eyes and bill partly open (upper left) and a Tegu with feathers protruding from its mouth (lower right) (**B**). The Limpkin's head is bitten hard by the Tegu, crushing the skull and drawing blood on the base of bill (**C**). Feathers from the bird's body and wings are pulled off by the Tegu (**D**). Photo author: J.V. Hipolito.

Figure 2. The fresh body of a second killed Limpkin provides food for another adult Tegu (**A**), eight days after the first Limpkin kill. The vivid red parts on the Limpkin corpse (centre) indicate a recent death (**B**). Photo author: J.V. Hipolito.

To the best of our knowledge, the predation events we recorded are the first instance of adult Limpkins killed and consumed by a medium-sized reptile. Limpkins are large and long-legged wading birds, with about 70 cm total length and about 60 cm tall (Bryan 1996, 2002, Sick 1997). The Black and White Tegu is large by Neotropical lizard standards, with about 120 cm total length (Pianka & Vitt 2003). Thus, predation on Limpkins by these lizards may be a rare event, the more so as birds this size remain unrecorded as prey for the Black and White Tegu, which is mostly an omnivorous scavenger at the study site and hunts considerably smaller prey (Sazima & D'Angelo 2013). Moreover, both Tegus and Limpkins are a common sight at the study site (Corbo *et al.* 2013, Sazima & D'Angelo 2013), but these birds killed and devoured by the lizards were never recorded before.

We were unable to tell whether the first predation event was favoured by a weakening condition such as disease or injury or the Limpkin sat and did not perceive the approaching Tegu in time to evade the attack. Limpkins sit rarely (Bryan 2002) but at our study site this behaviour is not rare, especially at open places where the bird has a good view of the immediate surroundings (I.S., pers. obs.). Apart from the possibility of the Tegu attacking an inattentive Limpkin sitting under a tree cover, there still remains the chance that the Limpkin was partly disabled. Whatever the case, two Limpkins killed and eaten by two Tegus at the same site in the interval of about a week is noteworthy.

At present, only three reptile species are documented as predators of adult Limpkins: American Alligator, Yellow Anaconda, and Black and White Tegu (Strussmann 1997, Bryan 2002, present paper). Alligators prey on medium-sized and large aquatic birds, including rails, cormorants, anhingas, ibises, and herons (Wolfe *et al.* 1987, Rice 2004, Saalfeld *et al.* 2011), and the same does the Yellow Anaconda, which may prey on birds as large as storks, ibises, and screamers (Strussmann 1997). These are very large reptilian predators when compared with the Tegu, which indicates the probable rarity of predation events on Limpkins by Tegus. Additional, natural history-oriented studies and observations may test this assumption.

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ARTICLE

Status of the Ibera Seedeater *Sporophila iberaensis*

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ABSTRACT: Paraguayan records of the recently described Ibera Seedeater *Sporophila iberaensis* are compiled and reviewed. Observations of birds identifiable to this species in Paraguay date from at least 1998, with the first photographic documentation in December 2004. The species has now been recorded at a minimum of 11 localities in the departments of Cordillera, Itapúa, Misiones, San Pedro and Presidente Hayes. The first two records of the species from Brazil (both from Mato Grosso do Sul) are also listed. Most Paraguayan records are of singing males, and breeding has been documented (a pair feeding fledglings) at one locality in Cordillera department, significantly expanding the known breeding range of the species. At least three localities appear to hold small populations (observations of multiple territorial males and/or pairs). In Paraguay, as in Argentina, the species appears to prefer wet tall grasslands bordering wetland areas. Its preference for tall grasslands makes the species particularly susceptible to habitat loss and degradation through overgrazing, frequent burning, and conversion to agriculture. These threats are all present at the principal localities for the species in the country. A reassessment of the species global conservation status taking into consideration the Paraguayan range and population suggests that it may best be treated as "Vulnerable".

KEY-WORDS: Brazil, conservation, distribution, grassland, South America, Thraupidae.

INTRODUCTION

Sporophila is a genus of about 40 species of seedeaters, almost entirely restricted to the Neotropics (Ridgely & Tudor 2009). Classification of the genus *Sporophila* has been difficult at all levels, from family placement to the specific or morph status of several forms. Traditionally classified within the Emberizidae, recent morphological and molecular studies have revealed the genus to belong to the Thraupidae (Mason & Burns 2013). Systematics have been particularly confusing for the "capuchino" group, which is primarily found in the grasslands of central and southern South America (Campagna *et al.* 2013). Recently, a new species of capuchino seedeater, Ibera Seedeater *Sporophila iberaensis*, was described from northern Argentina based on an analysis of vocalizations and plumages (Di Giacomo & Kopuchian 2016). The male *S. iberaensis* plumage type has been observed in northern Argentina since at least late 1990s (López-Lanús *et al.* 2013), but its taxonomic status had been unclear due to its similarity to the pre-definitive plumages of other capuchino species.

Currently the species is listed as "Endangered" on the IUCN (International Union for Conservation of Nature) Red List. This categorization was recommended by López-Lanús *et al.* (2013) due to the very small population size of the species, that is thought to be declining as a result of habitat loss and degradation and potentially it being captured for trade (BirdLife International 2017). A reassessment of the currently species categorization is needed, taking into consideration all the information about its distribution in Paraguay and Brazil.

To date, 15 species of *Sporophila* have been recorded in Paraguay (SACC 2016). Here we present an overview of the known records of *S. iberaensis* in the country (five of which were mentioned by Di Giacomo & Kopuchian 2016) and discuss the status of the species. We also present the first two records of the species in Brazil (one of which was mentioned by Di Giacomo & Kopuchian 2016).

METHODS

Records of *S. iberaensis* were compiled from published literature and technical reports, our field observations and those of other observers, eBird (www.ebird.org) and the Guyra Paraguay biodiversity database. The previously unpublished record from Brazil was discovered by reviewing photos in WikiAves (http://www.wikiaves.com.br/). This species differs from other species of *Sporophila* since males present a leaden gray crown and forehead that contrast with the nape, coverts, ear coverts, and blackish brown chin and throat. The back and rump are olive brown; breast, belly and under tail coverts are pallid yellow to buffish; white base rectrices same color as the dorsal wing-bar, which is slightly larger from the other seedeaters. Females of this species are alike other species of seedeaters (López-Lanús 2015, Di Giacomo & Kopuchian 2016). Previously, *S. iberaensis* has been confused with individuals of *Sporophila ruficollis* (Dark-throated Seedeater) which has an odd pre-definitive plumage. After revision of both species, they were separated due to behavior (vocalizations and breeding area) and morphological attributes (López-Lanús 2015, Di Giacomo & Kopuchian 2016). The location of each record was digitized using ArcGIS software, and habitat information was gathered when available.

All confirmed records of the species were used to generate the Minimum Convex Polygon for the species' distribution. To select an optimal grid size for assessing Area of Occupancy (hereafter AOO) and Extent of Occurrence (hereafter EOO), the distances between all locations were calculated, and the average distance in km used to determine grid size (15 × 15 km). For the extent of occurrence all grids within a 10 km radius from each point were selected, in recognition of the likelihood of the species occurring in similar habitats in areas adjacent to known localities.

Nomenclature follows the South American Classification Committee - SACC (http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm), with the exception of *S. iberaensis* (as the taxon has yet to be recognized by SACC). For the latter, Di Giacomo & Kopuchian (2016) and IUCN (2017) are followed.

RESULTS

Records of *S. iberaensis* in Paraguay date from at least October 1998, when a male was observed by R.C. close to a locality where the species is now regularly recorded. The first known documentation of the species in the country are photos of a male at km 97, Ruta 3 by F. Fragano (*in litt.*) on 05 December 2004, the photo is available on this link, (http://www.faunaparaguay.com/sporophila_iberaensis.html). Increasing awareness of this distinctive plumage-type led to more reports from *c.* 2008 onwards, and the species has now been reported from 11 localities in the departments of Cordillera, Misiones, Itapúa, San Pedro and Presidente Hayes (Table 1, Fig. 1).

Many records of the species are from the Important Bird Area (IBA) PY025 Arroyos y Esteros, which is dominated by humid grasslands with species of the Poaceae family and the presence of annual and perennial herbs (Cartes & Clay 2009, TNC 2005). This area is very similar to others where the species has been recorded such as the IBA PY034 Campo Llano, which is characterized by the presence of flooded grasslands with marshes and gallery forest (Fig. 2; Josse *et al.* 2003, Cartes & Clay 2009).

To date, all but one record of the species have been in eastern Paraguay. The one record from western Paraguay (the Humid Chaco) is from an area of open flooded palm savanna with the predominant grass species being Poaceae family (TNC 2005, Cartes & Clay 2009).

Nearly all Paraguayan records of *S. iberaensis* are from the austral spring (September to December) and summer (December to January), with just one record from the austral winter (June 2004). Apart from this one exception, regular visits to appropriate habitat (including a confirmed breeding site) outside of September to January have not recorded the species.

Apparent pairs and singing males have been recorded at three localities during October to January, with breeding confirmed at one (a pair feeding young in two consecutive years at Ruta Juan de Mena, O. Bordón, *in litt.* 2017), representing a northward extension of the breeding range by about 300 km. Multiple males have

Table 1. Locations and first observations of *S. iberaensis* in Paraguay.

Date	Locality	Observer
31 October 1998	Ñu Guazú, General Artigas, Itapúa department.	R.C.
07 January 1999	Río Tacuary wetlands, Itapúa department.	R.C.
June 2004	Campo Llano, Misiones department.	A.J. Lesterhuis
05 December 2004	km 97, Arroyos y Esteros, Cordillera department.	F. Fragano
October 2008	Ruta Juan de Mena, Cordillera department.	P. Smith
October 2008	Bajo Chaco, Presidente Hayes department.	C. Morris
06 October 2011	San Cosme y San Damián, Itapúa department.	C.D. Timm
08 December 2014	Yabebyry, Misiones department.	A.J. Lesterhuis
January 2016	Santiago, Misiones department.	T.G., R. Ruiz, S. Rojas
November 2017	Colonia Volendam, San Pedro department.	M. Fast, M. Ens
13 December 2017	Estero San Mauricio, Itapúa department.	T.G., V. Rojas

been recorded at all three localities, with a high count of nine males at Ruta Juan de Mena in December 2016 and January 2017 (Fig. 2).

Di Giacomo & Kopuchian (2016) list one record of *S. iberaensis* from Brazil, a male photographed and videoed by J. del Hoyo at Pousana Aguapé, Mato Grosso do Sul state on 09 January 2005 (http://ibc.lynxeds.com/species/dark-throated-seedeater-sporophila-ruficollis). A second record, clearly identifiable as *S. iberaensis* was photographed at Miranda, Mato Grosso do Sul state by N. Cabral on 26 August 2015 (http://www.wikiaves.com.br/1933758&p=27&t=s&s=11672).

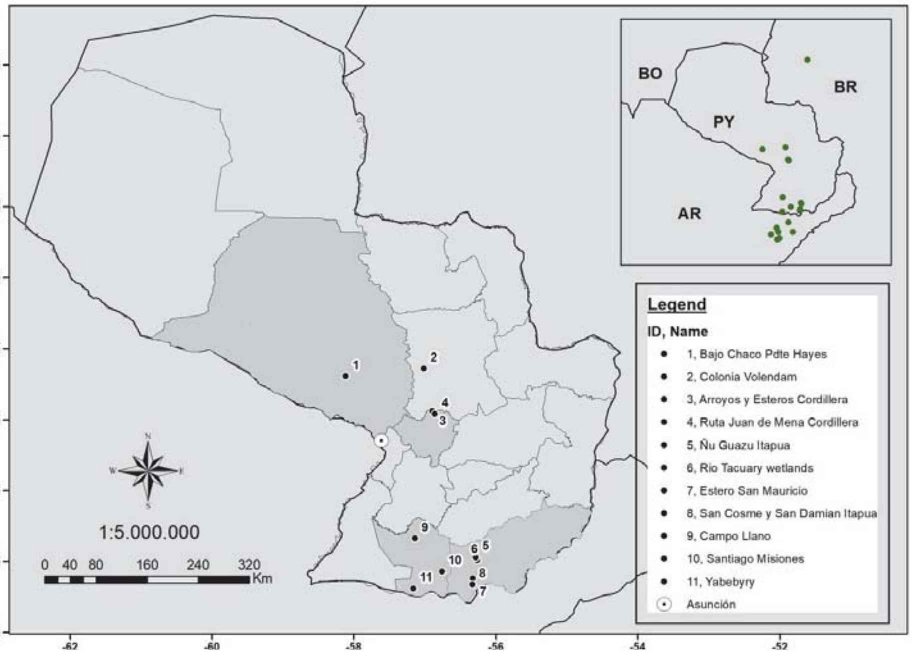

Figure 1. Records of *Sporophila iberaensis* in South America. Gray triangles: new localities with records of *S. iberaensis* including records from literature and other sources (Denton 2010, Smith & del Castillo 2012, López-Lanús 2015, Smith & Clay 2015).

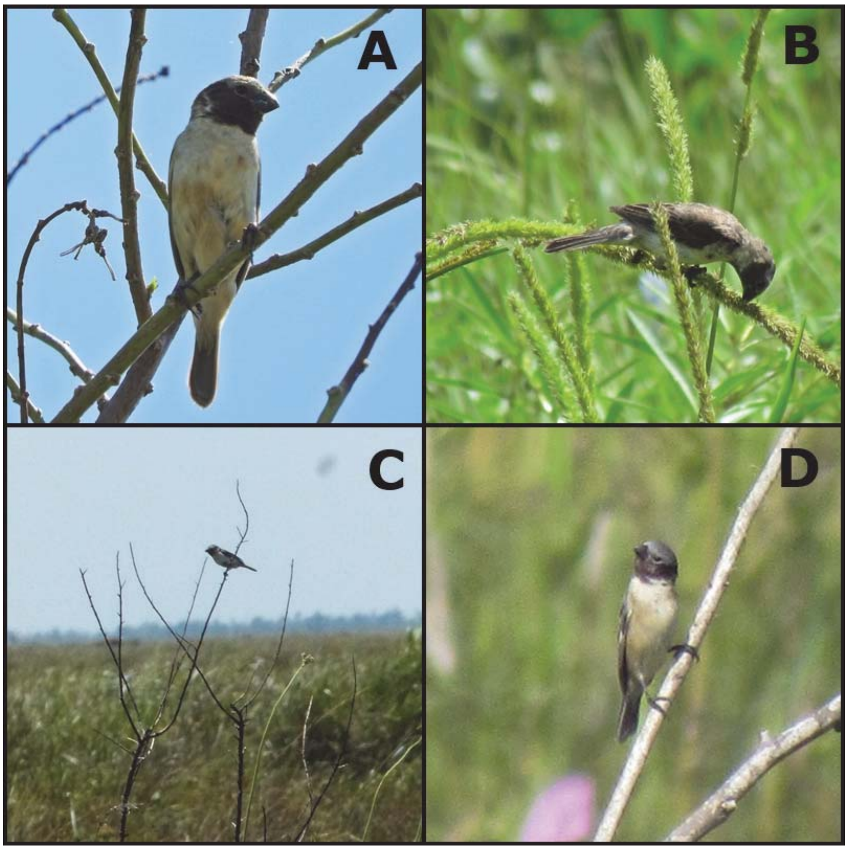

Figure 2. *Sporophila iberaensis* in Santiago, Misiones (**A** & **B**); in Campo Llano, Misiones (**C**); in Juan de Mena, Cordillera (**D**). Photo authors: R. Ruíz (**A**), T. Galluppi (**B** & **D**), H. Cabral (**C**).

Conservation status

Ibera Seedeater is currently listed as "Endangered" at a global level under the criterion C2a(*ii*) of the IUCN Red List (IUCN 2017). This assessment was based on the species known distribution in Argentina, where it appears to be restricted to the Ibera Marshes and adjacent grasslands in Corrientes province (IUCN 2017). Given this restricted distribution, it was assumed to be one subpopulation, and to number less than 1000 mature individuals (Di Giacomo & Kopuchian 2016, IUCN 2017).

With documentation of the species range to include southeastern and central Paraguay, its conservation status warrants reassessment. Taking into consideration the species apparent breeding range in Paraguay, *S. iberaensis* has an EOO of 62,046 km^2 in Argentina and Paraguay, and an AOO of 12,365 km^2 (Fig. 3). The two Brazilian records have been excluded from these calculations given that they may be part of the non-breeding range of the species.

While judging the limits of subpopulations of a migratory species can be particularly difficult, it seems plausible that there are at least two subpopulations within Paraguay, one located in the extreme southeast (Itapúa and Misiones departments, and likely connected to the subpopulation in Argentina) and one in the center (Cordillera and San Pedro, and potentially Presidente Hayes departments). However, the apparent gap in distribution could also be the result of undersampling or local extinctions.

Although the Paraguayan records significantly expand the range of the species, the numbers recorded at any one site are low, and it seems very likely that the total number of mature individuals in the overall population is less than 10,000 (and possibly not more than 1000). Combined with an estimated and projected continuing decline in mature individuals due to habitat loss of at least 10% in 10 years, this triggers Red List criterion C1 in the category "Vulnerable". If further research reveals that there are discrete subpopulations, then a higher level of threat may be warranted under C2a.

The species population is considered to be declining primarily due to habitat loss (IUCN 2017). Its preference for tall grasslands makes it particularly susceptible to habitat loss and degradation through overgrazing, frequent burning, and conversion to agriculture. These threats are all present at the main localities for the species in Paraguay. Worryingly, the species is not currently known from any formally protected areas in Paraguay.

DISCUSSION

Southern and central Paraguay is clearly an important part of the range of *S. iberaensis*, with records of multiple individuals and apparent pairs in appropriate habitat and

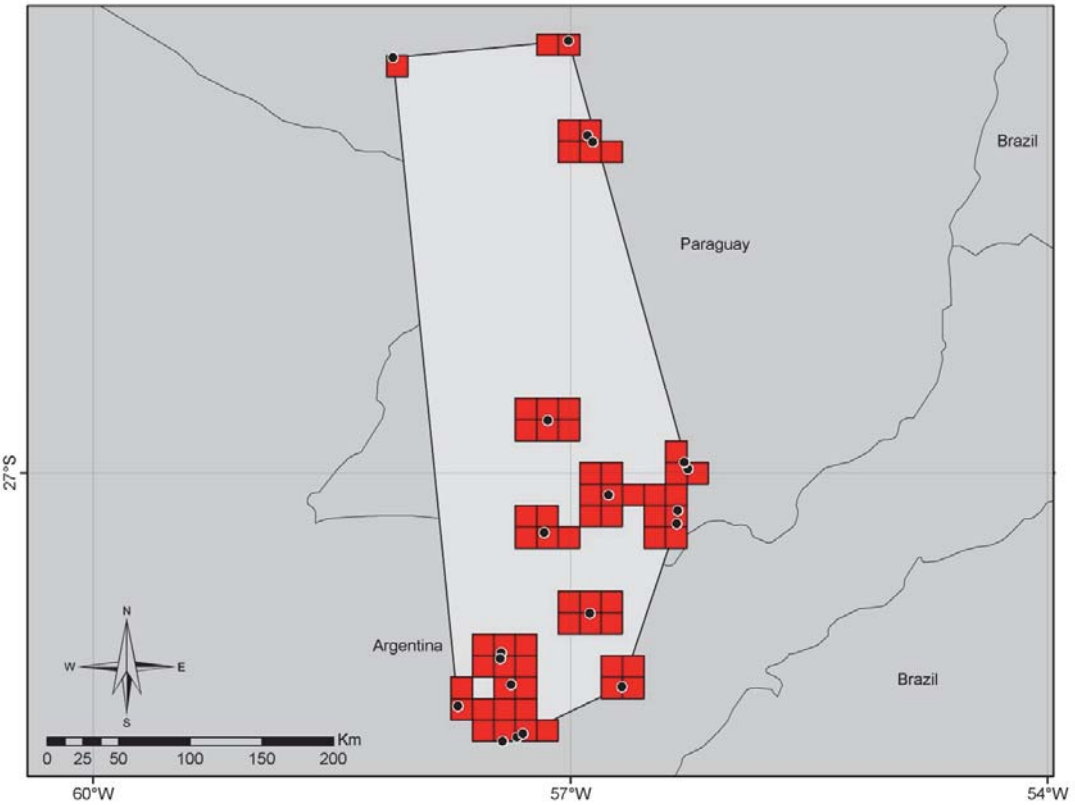

Figure 3. Area of occupancy (AOO) of *Sporophila iberaensis*. The species has been recorded from or is considered likely to occur in 54 grid squares of 15 × 15 km.

breeding confirmed in one area in Cordillera department. Records are primarily from the austral summer, and it seems likely that as with other capuchino seedeaters, *S. iberaensis* winters to the north, in Brazil. The two records from Mato Grosso do Sul state support this, though the first is an atypical date for a wintering bird (or migrant), and perhaps represents a bird over-summering on the wintering grounds, though it also raises the possibility that the breeding range may extend into southwestern Brazil.

Paraguayan localities for the species are primarily from the Mesopotamian Grasslands and Humid Chaco ecoregions (Dinerstein *et al.* 1995, del Castillo & Clay 2004), where the species has a preference for tall wet grasslands, and may be an indicator of the degree of ecological integrity of such grasslands (as proposed by López-Lanús *et al.* 2013). The one confirmed breeding location and the record from San Pedro department are in grasslands associated with the Humid Chaco ecoregion (Dinerstein *et al.* 1995, del Castillo & Clay 2004), but in a transitional zone toward more Cerrado-like grasslands.

Ibera Seedeater can often be found in proximity to other threatened grassland birds such as Strange-tailed Tyrant *Alectrurus risora* and Chestnut Seedeater *Sporophila cinnamomea*. All three species and the habitats they depend upon are all increasingly threatened in Paraguay from conversion to agriculture, overgrazing, frequent burning, and the drying of wetland habitats.

A reassessment of the global conservation status of the species taking into account its Paraguayan range and population suggests that the species should perhaps best be considered "Vulnerable" under criterion C1. The Paraguayan National Red List assessment is currently being updated, and the species has been proposed as "Vulnerable" under criteria C1. Given the significant overlap in range and threats as other capuchino seedeaters, similar conservation measures should be implemented for *S. iberaensis*, including listing on Appendix I of the Convention of Migratory Species, creation of a protected area within its Paraguayan range, and working with ranchers to set-aside areas of appropriate habitat during the breeding season. Furthermore, observers are encouraged to document new records and localities for the species. These records could include the department of Paraguari, in order to sustain the idea that there are two subpopulations of the species; and in particular to search for it in southwestern and central Brazil during the austral winter.

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ARTICLE

Demography of the Neotropical austral migrant *Elaenia albiceps chilensis* (Tyrannidae) on its breeding grounds: climate and food offer effects

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ABSTRACT: The White-crested Elaenia (*Elaenia albiceps chilensis*) is a Neotropical austral migrant that breeds in Patagonian forests and overwinter in South America tropics. We investigated White-crested Elaenia demography and the environmental conditions the specie is subjected at the northwest of Patagonia as a first attempt to elucidate its population dynamic. We studied the species abundance, individuals' body condition, survival, productivity of young and site fidelity according to changes in rainfall patterns and food supply, during three breeding seasons (2009 to 2012). We color banded 361 adult and juvenile White-crested Elaenias. During the first studied season, precipitations were remarkably above the mean and ripe fruit supply was lower than in the other seasons, whereas the abundance of arthropods remained similar along the study. The species abundance decreased 50% across the study, while adult apparent survival rate, the number of breeding females, young productivity and site fidelity were 50% lower in the first season in comparison to the following seasons. Females presented lower body condition at arrival in the first two studied periods. Site fidelity diminished after unfavorable breeding season (*i.e.* low young productivity and fruit supply), especially for males, although they were more faithful than females and had a slightly higher apparent survival rate. Our results suggest that White-crested Elaenia demography is affected by changes in its main food resource supply (fleshy fruits) during the breeding season, indicating that this part of the annual cycle could be fundamental for its population dynamic.

KEY-WORDS: body condition, breeding season, frugivory, Patagonian forest, population dynamic, site fidelity, survival, White-crested Elaenia.

INTRODUCTION

The study of demography and the factors that regulate populations are among the most important approaches to understand population trends. Birds demographic (abundance, survival and reproductive success) and behavioral features (site fidelity, space use and dispersal) are regulated by both intrinsic and extrinsic factors (*e.g.* physical and nutritional traits of individuals and food or weather variations, respectively; Martin 1996, Newton 1998). These factors interact with each other in positive and negative ways, and their implications in a population are expected to vary according to the species life history (Newton 1998).

Among demographic features, differences in life history between North and South Hemisphere birds suggest that Southern hemisphere species have lower reproductive success (as indicated by smaller clutch sizes, higher nest predation rates, more nesting attempts and greater parental care) that is compensated with higher adult survival (see review in Martin 1996 & Russell *et al.* 2004). Throughout South America information is contrasting, with some studies indicating a higher adult survival from tropical to temperate latitudes (Martin 1996) and others pointing to a lack of such trend (Karr *et al.* 1990, França & Marini 2010), or even to variations among phylogeny and regions for tropical birds (Blake & Loiselle 2013). Although this trend has been mainly suggested for resident species, it also applies to species that perform regional or long distance migrations (Martin 1996, Russell *et al.* 2004, Blake & Loiselle 2013).

Among behavioral features site fidelity is one that can be affected by species life history as well as by environmental quality, conditioning migratory birds' abundance (Holmes & Sherry 1992). Site fidelity will be favorable if the area allows individuals to pair a previous successful partner or be more competitive because of prior territory ownership, as well as if they are able to identify the distribution and availability of resources as food, refugees or nestling sites (Newton 2008). Contrary, site fidelity will be disadvantageous for migrants if the site diminishes in quality or represents an unpredictable habitat (Switzer 1993). In addition, site fidelity can differ according to sex, age and competitive condition, generating differences in dispersal and habitat use patterns (Latta & Faaborg 2002).

Environmental factors are relevant causes of demographic variation in resident and migratory bird populations. Food limitation can be a fundamental factor affecting body condition and, consequently, breeding success and survival (Martin 1987). Factors such as precipitation, habitat quality and resource spatial distribution, will affect food abundance and availability, affecting differently the population (Wilson *et al.* 2011). The effects of those environmental factors on the population can be quantified by measuring different external variables that indicates habitat quality (Benson & Bednarz 2010) as well as estimating the individuals' body condition by their body mass or fat deposits (Labocha & Hayes 2012). On the other hand, unusual weather conditions, sometimes related with periodic climatic events, affect the sizes of bird populations (Sillett *et al.* 2000). Some studies suggest that southern temperate birds' survival either is reduced after periods with unusual precipitation, rainy (Thomson & Estades 2012) or dry (Sagario 2010). Therefore, it is expected that climate variations also affect migratory birds' demography at southern South America.

All these theories about the factors controlling population dynamics remain slightly evaluated in passerine birds of South America, been mainly studied in tropical species (Karr *et al.* 1990, Martin *et al.* 2000, Parker *et al.* 2006, Blake & Loiselle 2013). Thus, there is still little information for temperate latitudes of South America and migratory birds of the Neotropical austral system, despite some advances for different passerine families in survival (Willson & Pendleton 2008, Sagario 2010, Thomson & Estades 2012), site fidelity (Jahn *et al.* 2009) and life history traits (*e.g.* parental care, Llambías *et al.* 2015).

The White-crested Elaenia (*Elaenia albiceps chilensis*) is the most abundant Neotropical austral migrant passerine at the Patagonian forest (Grigera *et al.* 1994, Ippi *et al.* 2009). This tyrant flycatcher arrives up to mid-October to breed and start its migration to the tropics between mid-February and March (Fitzpatrick 2004, Bravo *et al.* 2017). It is a frugivorous-insectivorous species with an important role as the main disperser of seed of endemic plants of the Patagonian forest (Armesto *et al.* 1987, Amico & Aizen 2005) and as a controller of herbivorous insects of *Nothofagus* trees (Mazia *et al.* 2009). There are studies of White-crested Elaenia abundance (Brown *et al.* 2007), diet (Grigera 1982, Brown *et al.* 2007), foraging behavior (Chust *et al.* 2012, Cueto *et al.* 2016a), functional role (Mazia *et al.* 2009, Cavallero *et al.* 2013, Bravo *et al.* 2015), and migration routes (Marini & Cavalcanti 1990, Capllonch *et al.* 2011, Cueto *et al.* 2016b, Bravo *et al.* 2017), but its survival has never been studied, as well as the relationship between its demographic parameters with environmental factors.

The aim of our study was to analyze the demography of the White-crested Elaenia through the analysis of changes in abundance, productivity of young, survival, site fidelity and body condition, related with food offer and precipitation variability during the breeding season. We aim to improve our knowledge about the factors affecting its population at temperate latitudes of South America.

METHODS

Study site

We conducted our study from October to March of three consecutive breeding seasons (2009/10, 2010/11 and 2011/12) in a Patagonian mixed forest of *Nothofagus dombeyi* (Coihue) and *Austrocedrus chilensis* (Ciprés de la Cordillera) at Steffen Lake (41°30'S; 71°35'W, 550 m a.s.l). This is a representative and well protected area of the temperate forest of southern South America inside Nahuel Huapi National Park, at the northwest of Argentinean Patagonia (Mermoz *et al.* 2009). At the study site, the forest is characterized by a canopy above 20 m of height and an understory (< 10 m) with fleshy fruit shrubs, mainly *Aristotelia chilensis* (Maqui) and *Schinus patagonicus* (Laura).

The climate is cold-temperate with precipitations concentrated in autumn and winter (April–September). Annual mean precipitation in the study area is 1264 mm (for 1993–2012 period) and annual mean temperature is 9.1°C (for 2000–2012 period), with a maximum mean temperature of 15°C (January) and a minimum of 3.5°C (July) (data from Station N° 2300 "Lago Steffen", *Red Hidrológica Nacional, Subsecretaría de Recursos Hídricos de la Nación*).

We established two permanent plots on the northern margin of the lake, separated 1000 m by a small bay. The plots area were 4 ha (Plot 1) and 7 ha (Plot 2) and we gridded them in 25 *x* 25 m squares, for bird and food resource surveys (68 squares for P1 and 109 squares for P2). Both plots had the same vegetation composition and structure, representing a well-preserved mixed forest with three types of patches: open areas, young forest and old forest (see Bravo *et al.* 2015), therefore we pooled the data for the analysis.

Bird surveys

Scientific nomenclature and common name follow the recommendation by the South American Checklist Committee (Remsen-Jr. *et al.* 2018). To get demographic data of the White-crested Elaenia we used capture-mark-recapture method. We captured birds using 24 mist nets of 12 m × 3 m, 38 mm mesh size (12 per plot). Nets were distributed along the area separated at least 50 m from each other, arranged in fixed places at every capture session to register the mist net of every captured and recaptured bird in order to study site fidelity. During every breeding season, nets were opened for two consecutive days per month in both plots (in similar month dates along every session), since sunrise and for at least five hours.

Every captured bird was banded with numbered aluminum and a unique combination of color bands. We weighted birds to the nearest 0.1 g with a 30 g spring scale in every capture occasion and measured their tarsus length to estimate their arrival and departure body condition (details below). We aged individuals by the presence (adult) or lack (juvenile) of the characteristic white crown (Schulenberg 2009). To determine the sex and reproductive status of birds, we registered the development of the incubation patch (females) and cloacal protuberance (males) following Ralph *et al.* (1993), and used the differences in wing and tail length between females and males for sexing non-breeding birds following Cueto *et al.* (2015). When an individual did not match with those criteria of sexing it was classified as "unsexed adult".

From November to February, after net sampling, we surveyed each plot to relocate those banded birds that remained at the study site to complete their capture history for survival and site fidelity estimates. Searches were carried out systematically by walking through the study area during five hours after sunrise and three hours before sunset, at least once per day for a mean of 10 days or until no new banded birds were seen after searching for 10 h. We registered the identity of each banded bird found and its location on the grid. The position of every relocated bird was recorded estimating the distance and angle respecting a reference point of the grid, using a compass. We also recorded eventual encounters while collecting environmental data.

Arthropods and fruit abundance

Arthropod abundance was estimated using blue sticky traps (Young 2005). We used blue because it is neutral in terms of attracting or repelling insects (Ausden & Drake 2006). Each trap was of 10 × 20 cm, attached inside a plastic transparent cylinder of 15 cm diameter to prevent that leaves, branches and rain affect its capture efficiency. We used 28 blue sticky traps (14 per plot) that were randomly placed, tided horizontally on an exposed branch of a shrub or tree, two meters above the ground, operated for an average of 15 days per month depending on weather conditions. After the survey, we counted the number of captured individuals at each trap.

We evaluated fruit production of *Aristotelia chilensis* (Elaeocarpaceae), the main fleshy-fruited shrub consumed by White-crested Elaenia at the study site (Bravo *et al.* 2015). We randomly selected 10 individuals in each plot and counted the number of ripe fruits every 15 days from November to March. We used a semi-quantitative index from 0 to 5 (Saracco *et al.* 2004), where 0: no fruits, 1: 1–10 fruits, 2: 11–50 fruits, 3: 51–100 fruits, 4: 101–500 fruits, and 5: 501–1000 fruits.

Precipitation patterns

To assess the potential effect of climate on the White-crested Elaenia's demography and their food abundance, we analyzed the variations on precipitation at the study site. Precipitation data were available from the weather station N° 2300 - "Lago Steffen" (*Red Hidrológica Nacional, Subsecretaría de Recursos Hídricos de la Nación*), for the period 1993–2012. We considered wet or dry months to be those with monthly rainfall above or below one standard deviation of the average monthly rainfall for a 20-years period of climatic data (Ropelewski & Folland 2000).

Data analysis

Bird abundance and productivity of young: In order to compare bird abundance among breeding seasons, we calculated the season capture rate for each bird category (female and male in breeding and non-breeding conditions; and juveniles) as the total number of captures per 100 h of net effort. We used the data from November to February, and excluded from the analysis birds captured in October and March that did not remain in the study site in the summer (*i.e.* those individuals that were just passing through). Juveniles capture rate in every season was used as a measure of productivity of young (du Feu & McMeeking 1991).

Relative body condition: We generated an index of body condition using the residuals of the linear regression between every bird tarsus length and their body mass (Labocha & Hayes 2012). Positive residuals indicated that birds were in relatively good condition, *i.e.* they were heavy for their size, and negative residuals indicated relatively poorer condition. We used a two-way ANOVA to examine the differences of body condition between breeding seasons, arrival from spring migration (October–November) and departure from the breeding study site (February–March) of females and males. Given the unequal sample sizes, we used Type III method to compute the sum of squares (Shaw & Mitchell-Olds 1993). Comparisons of treatments after ANOVA were performed using the Kramer modification of Tukey's test (Day & Quinn 1989) using the free software InfoStat (2014).

Survival: We estimated apparent annual survival rate between two breeding season intervals (2009/10 to 2010/11 and 2010/11 to 2011/12) as the probability of an individual survive and return to the same breeding area. This is an approximation of the real survival rate, because it does not account for permanent or temporal emigration (Lebreton *et al.* 1992). We used captures, recaptures and relocation data of 269 birds, considering only adult birds as we never recaptured or relocated any marked juvenile. We excluded from the analysis the individuals that were captured just once and were not relocated during the season (*i.e.*, likely transient individuals). We fitted Cormack-Jolly-Seber (CJS) mark-recapture models to assess apparent annual survival rate and capture probability (Lebreton *et al.* 1992). We confirmed models goodness-of-fit and lack of over-dispersion using the median $\hat{c}$ procedure (Burnham & Anderson 2002). We modeled apparent survival probability (φ) as constant, varying in time (years) and between sexes, and examined the influence of these two covariates together, as additive and interactive effects. We considered capture-recapture-relocation probability (p) constant in time and equal among sexes. We based our decision on sampling effort as we systematically sampled the plots with mist nets and active search since the arrival of the birds till their departure, compensating possible differences in detection caused by changes in females and males behavior during their breeding period (as incubation and territorial defense). The relative importance of each model was compared using: Akaike›s Information Criterion adjusted for small sample size (AICc), the difference of AICc between models (ΔAICc), their weights (wi) and deviance (Burnham & Anderson 2002). Models with a ΔAICc < 2 of the top model were considered to have equal support, so we model-averaged survival estimates (Burnham & Anderson 2002). Model averaging generated an annual mean apparent survival rate for each sex and breeding period, with their standard errors and confidence intervals. We performed this analysis in R (version 3.1.1 2014, The R Foundation for Statistical Computing) using the RMark package (version 2.1.8; Laake & Rexstad 2008) that provides an interface to the software MARK (version 7.2; White & Burnham 1999).

Site fidelity: We analyzed it as the percentage of adult birds banded in a previous field season that were recaptured or relocated in a subsequent field season. We compared the differences in annual return rates between breeding seasons (2009/10 to 2010/11 *vs.* 2010/11 to 2011/12) for all returning White-crested Elaenias individuals and by sexes, through a difference of proportions test (Agresti 2002). We used a Bonferroni correction to adjust α when more than one test was performed on related data. We considered the data from November to March for the analysis and used the free software InfoStat (2014).

We estimated the displacement distance between the first capture and the first recapture or relocation of individuals in every breeding season. For this, the position of the mist nets and relocation position of every bird were georeferenced in a metric coordinate system, using the free software Quantum Gis 1.8.0-Lisboa (QGIS Development Team, 2012). We performed a T test (Agresti 2002) to compare the displacement distance between sexes and between returning periods: 2009/10 to 2010/11 versus 2010/11 to 2011/12, and 2009/10 to 2010/11 versus 2009/10 to 2011/12 displacement.

Arthropods and fruit variations: Abundance of arthropods was assessed by calculating a relative abundance index per trap (*RAI* = number of caught individuals / number of trapping days) and then estimated the average of all traps for the season. We evaluated differences in arthropod abundance among seasons by using one factor Analysis of Variance with Repeated Measures (Winer 1971), because we counted arthropods in the same points at every season. We used the Tukey multiple comparison test for comparing means when season factor was significant (Winer 1971). We tested equality and symmetry of covariance matrices (Winer 1971). Data violated the symmetry assumption, so we used the Greenhouse-Geiser procedure (Lower Bound Epsilon correction = 0.5) to adjust the degrees of freedom of within-subject effects (Winer 1971). For ripe fruit offer, we calculated the proportion of individuals that offered no ripe fruits (index 0), less than 50 ripe fruits (indexes 1 and 2), and those that offered more than 50 ripe fruits (indexes 3 to 5). For each category, we evaluated the difference in abundance of ripe fruit between seasons using a test for difference of proportions (Zar 2010). ANOVAs, the Tukey comparisons and all assumption tests were performed on the free software InfoStat (2014).

RESULTS

Bird abundance and productivity of young: We banded 361 adult and juvenile White-crested Elaenias and recaptured 44 individuals during 5394 mist netting hours (Table 1). Complementary we relocated 25 adults that were not recaptured in nets but detected by active search. We did not recapture or relocate any marked juvenile after its hatching year. Male capture during October-November represented 69% of all captures. The latest captured individuals towards the end of the breeding season (March) were mainly juveniles. Captures of new individuals decreased almost 50% between the first and last studied seasons (Table 1). During 2009/10 we registered the lowest percentage of breeding females (28%) and the lowest productivity of young, while for the following seasons the percentage of breeding females exceeded that of non-breeders (68% for 2010/11 and 73% for 2011/12) and the productivity of young increased (Fig. 1).

Relative body condition: White-crested Elaenias arrived in relatively good condition only during the 2011/12 breeding season ($F_{2,\,169}$ = 3.42, $P < 0.001$; Fig. 2A), presenting the lowest condition during 2009/10, especially females. The condition for the departure period did not present a statistical different variation between breeding seasons ($F_{2,\,66}$ = 1.72, P = 0.187; Fig. 2B) or sexes ($F_{1,\,169}$ = 21.58, P = 0.060).

Survival: The best fitted model indicated a variation in apparent annual survival rate between breeding seasons, being 50% lower for 2009/10–2010/11 interval in relation to 2010/11–2011/12 (0.41 ± 0.07 *vs.* 0.80 ± 0.15). Models that considered survival vary among seasons and sexes had a great support following AICc and ΔAICc criterion (Table 2). Results from model averaging revealed that the mean apparent annual survival rate was equally low for females and males for the first interval but males tended to increase its survival more than females towards the following breeding season (Table 3).

Site fidelity: From 231 banded and sexed adult White-crested Elaenias, 69 individuals returned the following breeding seasons. Within those faithful birds, 14 individuals returned all the studied seasons and 12 skipped from the first season (2009/10) to the third (2011/12), not being recapture or relocated during the second season (2010/11). Annual return rate varied significantly between breeding seasons, being higher for 2010/11 to 2011/12 period (Zc = -0.13, P = 0.028) in

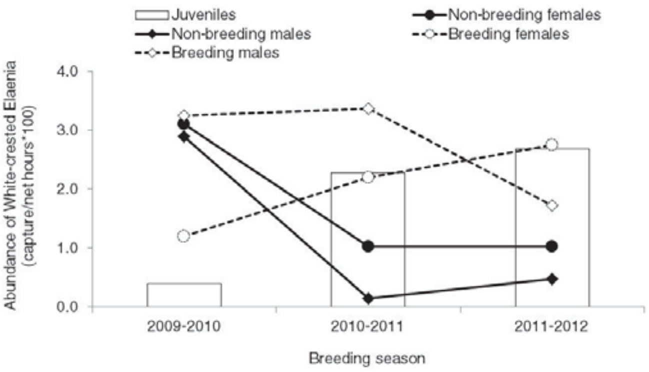

Figure 1. Abundance by sex reproductive status and juvenile productivity of the migratory White-crested Elaenia along three breeding seasons, at Nahuel Huapi National Park, Patagonia, Argentina. *Total adults*, includes all captured individuals with more than one year old (*i.e.* breeding and non-breeding individuals). *Breeding birds* were defined by the presence of developed incubation patch (female) and cloacal protuberance (male) and *Juveniles* by the lack of the white crown.

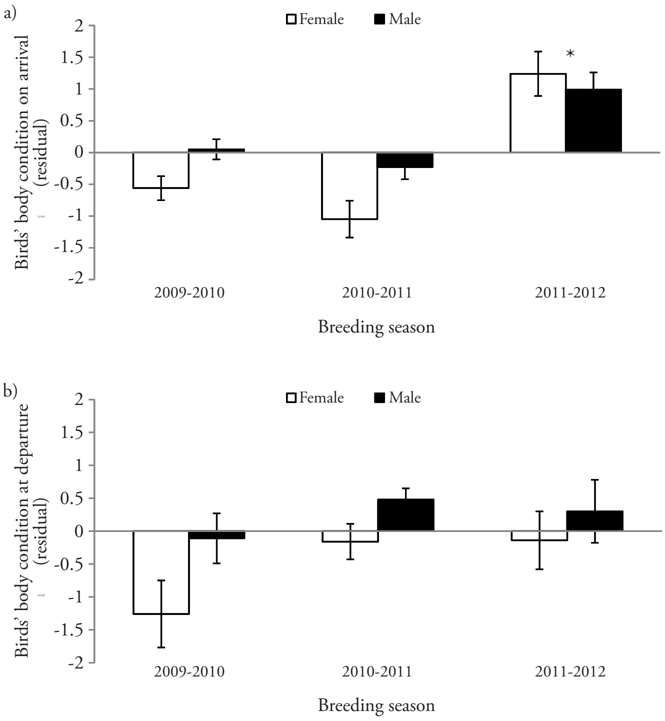

Figure 2. Body condition variation of the migratory White-crested Elaenia females and males, during: **a**) arrivals and **b**) departures in three breeding seasons, at Nahuel Huapi National Park, Patagonia, Argentina. Boxes represent the mean condition in every period (± SE - Standard Error). Condition was derived as the residuals of a linear regression between body mass and tarsus length. Positive residuals indicate better condition. Asterisk indicates the statistically different season.

Table 1. Captures and recaptures of the migratory White-crested Elaenia by sex and age, in three breeding seasons (October to March) at Nahuel Huapi National Park, Patagonia, Argentina. Individuals that did not match with the criteria of sexing were left as "unsexed adults".

Breeding seasons	Total banded birds	Females	Males	Juveniles	Unsexed adults	Total captures and recaptures
2009–2010	152	61	85	3	3	152
2010–2011	136	55	68	27	4	154
2011–2012	73	46	33	23	2	104
Total	361	162	186	53	9	410

Table 2. Models results for the apparent annual survival rate (φ) and recapture (p) probability of the migratory White-crested Elaenia in three breeding seasons at Nahuel Huapi National Park, Patagonia, Argentina (*n* = 269). Models are arranged by Akaike's Information Criterion adjusted for sample size (AICc). (.) Parameter is constant; k: number of parameters; wi: model weight.

Model	*k*	AICc	ΔAICc	w_i	Deviance
φ (time) p (.)	3	373.38	0.00	0.49	4.75
φ (time * sex) p (.)	5	374.54	1.16	0.27	1.77
φ (time + sex) p (.)	4	374.86	1.48	0.23	4.17
φ (.) p (.)	2	382.42	9.04	0.01	15.84
φ (sex) p (.)	3	383.60	10.22	0.00	14.97

Table 3. Apparent annual survival rate and capture probability estimates (measured as capture, recapture and relocation) for the migratory White-crested Elaenia in three breeding seasons at Nahuel Huapi National Park, Patagonia, Argentina. Estimates correspond to model averaging of the best-fitted models that indicated that survival varied by time and sex-class.

Parameter	Breeding seasons interval	Sex	Estimate	SE	95% Confidence Interval	
					lcl	ucl
Survival (φ)	2009–2010 to 2010–2011	Female	0.40	0.09	0.25	0.58
		Male	0.41	0.08	0.28	0.56
	2010–2011 to 2011–2012	Female	0.74	0.17	0.34	0.94
		Male	0.84	0.17	0.30	0.98
Capture probability (p)	Constant in time	-	0.49	0.09	0.32	0.66

relation to the first interval (Table 4). Considering the birds that returned across the entire study and those that skipped the second studied season, site fidelity of 2011/12 season increased from 33% to 49% (54 individuals), increasing the above-mentioned difference with the first interval. Fidelity did not vary significantly between sexes (*Zc* = -0.11, *P* = 0.084), but males tended to return in greater proportion than females towards 2011/12 (Table 4).

With respect to territory fidelity, only three males moved between plots along the study, less than 1500 m. The mean displacement between seasons was: 94 ± 100 m for 2009/10 to 2010/11 seasons, 85 ± 71 m between 2010/11 to 2011/12 , and 102 ± 84 m for birds that were banded in 2009/10 and only relocated in 2011/12. There were no significant differences between the mean displacement of the first and second period (*t* = 0.42, *P* = 0.676), neither between the first and the third (*t* = -0.29, *P* = 0.772). Females tended to displace more than males when they returned (*n* = 30, 118 m ± 86 m *vs.* *n* = 54, 76 ± 78 m on average, respectively. *t* = 2.25, *P* = 0.027).

Precipitation variability: The first study year was an unusual rainy year, with an important input during the October–March period (638 mm) that was almost two standard deviations above the historical record (371 mm). At the following breeding seasons, precipitation was close to average (347 and 390 mm, respectively; Fig. 3).

Arthropods and fruit offer. Arthropod abundance was similar among seasons ($F_{2, 27}$ = 3.027; *P* = 0.093; Fig. 4) but ripe fruit production varied notably between seasons. The proportion of plants without ripe fruits was higher in the first study season than the two following breeding seasons (Fig. 5, test for more than two proportions, *Zc* = 22.86, *P* = 0.003), while plants with more than 50 ripe fruits were higher in the second and third seasons (*Zc* = 6.94, *P* = 0.031; Fig. 5).

Table 4. Site fidelity (annual return rate) of the migratory White-crested Elaenia in three breeding seasons at Nahuel Huapi National Park, Patagonia, Argentina. Estimation is presented as the percentage and number of adult birds that returned from a previous banding season, by sex-class and for the complete studied population. Total estimation includes birds captured at 2009/10 that returned at 2011/12, not being recaptured or relocated during 2010/11. Returns include both recaptures in nets and relocations of color-banded individuals.

Banding and returning seasons	**Returning individuals**		
	All	**Females**	**Males**
2009/2010 to 2010/2011	20% (29)	20% (12)	20% (17)
2010/2011 to 2011/2012	33% (28)	19% (9)	50% (19)
Total	30% (69)	24% (26)	35% (43)

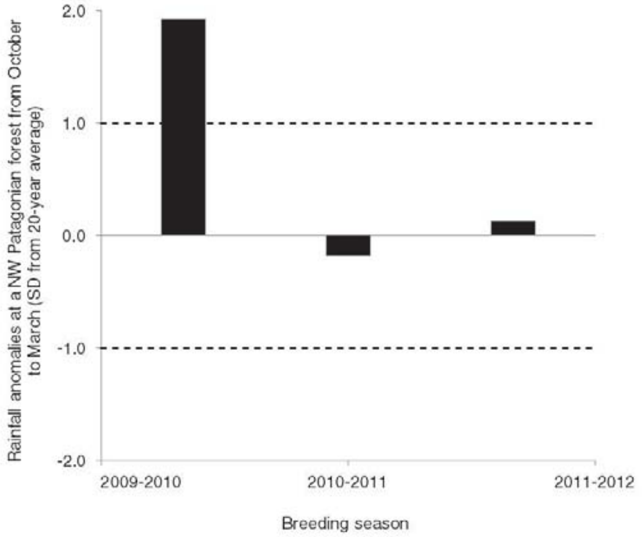

Figure 3. Rainfall anomalies during three breeding seasons of the migratory White-crested Elaenia at Steffen Lake, Nahuel Huapi National Park, Patagonia, Argentina. Values are expressed in standard deviations from an average climatic data of a 20-year period. Wet and dry years were those with annual rainfall respectively above and below one standard deviation (dashed lines) from the mean.

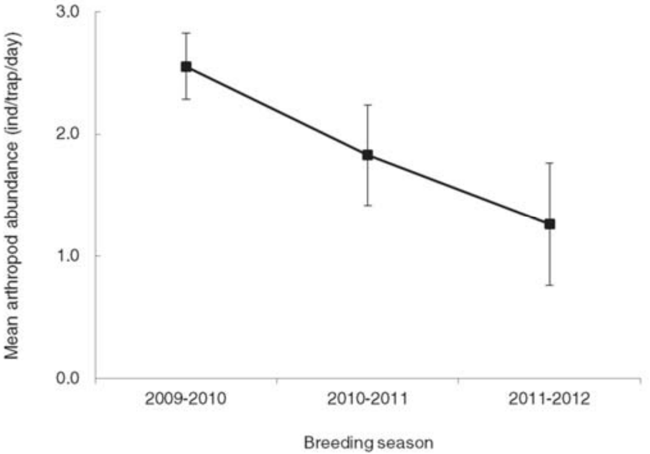

Figure 4. Variation in arthropods abundance between three breeding seasons of the migratory White-crested Elaenia, at Nahuel Huapi National Park, Patagonia, Argentina. Values represent the mean arthropods abundance index (number of individuals captured per sticky trap per survey days, ± SE - Standard Error) for every season.

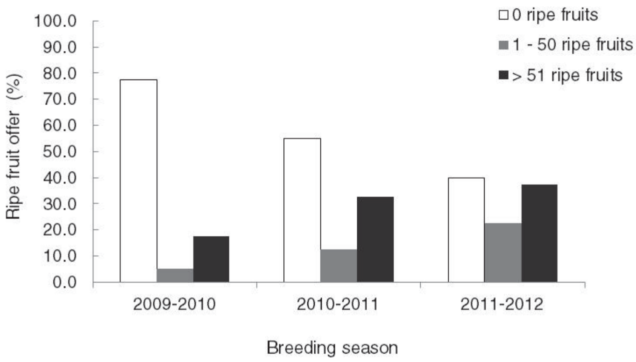

Figure 5. Differences in *Aristotelia chilensis* ripe fruit offer between three breeding seasons of the migratory White-crested Elaenia, at Nahuel Huapi National Park, Patagonia, Argentina. The percentage of *Aristotelia chilensis* plants within every fruit offer score is shown for each season.

DISCUSSION

Our results suggest that the demography of migratory White-crested Elaenia is affected by environmental changes on its breeding grounds. The three seasons of our study had contrasting climatic conditions, with the first season having a remarkable increase in rainfall respecting the historical average for the study area. This climatic variation was reflected in changes in the supply of ripe fruits of *Aristotelia chilensis*, but not in the abundance of understory arthropods. The increase in rainfall during the first season resulted in few days of full sun, likely leading to the inability of *Aristotelia chilensis* shrubs to produce ripe fruits, a relationship widely documented for others species (Aalders *et al.* 1969, Patten & Proebsting 1986, Spayd *et al.* 2002). During that first season a lower proportion of females became reproductive (28%), which was reflected in a low productivity of young. Besides, birds' relative body condition tended to be lower than the following seasons and both survival and site fidelity diminished by 50% after that period.

Previous studies have shown the impact of food limitation in reproductive status and success of resident and migratory birds, as birds adapt their reproductive cycle according to food availability (Martin 1987, Sherry & Holmes 1995, Marshall *et al.* 2002, Jahn *et al.* 2014). For example, females of *Parus major* are able to modify their laying date so it coincides with periods of higher caterpillar abundance (their main food item) and higher temperatures, promoting nesting success (van Noordwijk *et al.* 1995). With respect to the influence of arthropods supply on White-crested Elaenias demography, we found that slightly variations in foliage arthropods abundance did not affect bird's reproductive status and productivity of young, neither body condition or survival. Similar results were reported for Nearctic-Neotropical migrants (*Vireo olivaceus*, Marshall *et al.* 2002, and *Seiurus aurocapilla*, Vernouillet *et al.* 2014) and for White-crested Elaenias breeding at central Chile (González *et al.* 2004). Consistent with Cueto *et al.* (2016a) that found changes in the species foraging behaviour related with fruit offer variations at the same study site, we conclude that fruit is the main food resource affecting White-crested Elaenia reproductive success and demography during the breeding period. Our work represents a primary approximation of the effect of food limitation in White-crested Elaenia demography and reinforces the importance of more detailed study for a complete understanding of the role of food resources on the species population dynamic.

Decrease in new individuals capture rate along our study years could be considered as an indirect measure of low immigration rate, caused by a poor influx of new birds to the population (Newton 1998). This could be due to events of lower reproductive success (as in the first studied season), or higher mortality during the non-breeding period. As White-crested Elaenia present high migratory connectivity between their non-breeding and breeding areas (Bravo *et al.* 2017), the decrease in their captured rate could also be related with environmental variations at their wintering sites on the Brazilian Cerrado and Atlantic Forest (for example, see Wilson *et al.* 2011).

Our study represents the first survival estimation for a Neotropical austral migrant species and revealed that survival varied across seasons. For Nearctic-Neotropical migrants breeding at temperate latitudes of North America and wintering in the tropics, the temporal variation in survival has been attributed to weather anomalies across the areas used by birds along their life cycle (Mazerolle *et al.* 2005), as they promote decreases in food availability diminishing survival and productivity of young (Sillett *et al.* 2000, Mazerolle *et al.* 2005). Our results are consistent with those studies, as survival of White-crested Elaenia decreased after years with rainfall anomalies that affected ripe fruit supply. Unfortunately, there are not similar studies at the species wintering sites that allows linking the entire annual cycle survival process. Nevertheless, recent studies revealed White-crested Elaenias returns to their wintering areas in the Brazilian Cerrado and Atlantic Forest by routes with different habitat structure and refueling opportunities (Bravo *et al.* 2017), indicating that a good body condition at departure could be fundamental to survive the journey between breeding and wintering sites. According to that, the poor relative body condition of birds during arrival and departure of the first season could enhance birds' mortality during autumn migration, diminishing survival values between breeding seasons. This relationship between rainy breeding seasons with the reduction in the species departure body condition has also been reported by previous studies (González *et al.* 2004). Our results reinforce the need of demographic studies across the entire annual cycle to improve our knowledge of White-crested Elaenia population dynamic.

In addition, our mean apparent annual survival estimate (60%) is higher than the mean reported for other migratory Flycatchers of comparable size and behavior, breeding at temperate North America (50%; Karr *et al.* 1990, Koronkiewicz *et al.* 2006) but similar to tropical resident flycatchers (Johnston *et al.* 1997, França & Marini 2010, Blake & Loiselle 2013). Our results reinforce the hypothesis of higher survivorship of southern hemisphere tropical and temperate birds respecting to northern hemisphere ones (Martin 1996). Nevertheless, this trend requires more research including the hypothesis of reproduction cost, nest predation rate and adult mortality, that have been mainly verified for North American and tropical birds (Martin *et al.* 2000, Martin 2015).

Regarding migratory behavior, the higher capture rate of White-crested Elaenia males comparing to females at the beginning of the breeding season suggest that males could be arriving earlier, a behavior that is expected in territorial birds as a manner of territory acquisition (Kokko *et al.* 2006). The later departure of juveniles than of adults was also reported in studies at the austral extreme distribution of the species (Brown *et al.* 2007), and is usual in immature birds without prior migration experience (Whitaker & Warkentin 2010). Concerning site fidelity, comparisons between seasons showed a tendency for greater dispersal after breeding periods with low reproductive success, suggesting that White-crested Elaenias could be more predisposed to relocate after seasons with low productivity, as were reported for Nearctic-Neotropical migrants (Haas 1998).

On the other hand, our results of site fidelity are higher than previous studies that just considered recaptured birds on its estimations reporting returning rates only up to 11% (*e.g.* Espinosa & Egli 1997, Amico & Aizen 2005, Brown *et al.* 2007), even in long term studies (Rozzi & Jiménez 2013). Include data of relocations prevent underestimations of returning rates and improves apparent annual survival estimation (Martin *et al.* 2017).

However, if we considered only recaptured birds our result of site fidelity remains higher for Steffen's Lake (19% at 41°S) comparing to the estimation of a long term study at the species austral distribution in Navarino Island (10% at 56°S). The lower faithfulness at Navarino could respond to its habitability conditions, as summer precipitations and temperatures are lower than our study area, the vegetation structure varies widely in short distances and the main fruit item consumed by elaenias (*Drymis winteri* fruits) are available in autumn during their departure (Rozzi & Jiménez 2013). These factors could be promoting higher replacement rates of birds breeding at that higher latitude, indicating that Navarino Island could be a marginal habitat for the species.

Conclusions and future perspectives

Previous studies have emphasized the importance for species with low reproductive success to compensate this demographic feature with higher adult and juvenile survival (Martin 1996, Stahl & Oli 2006). However, migratory individuals face variable conditions along their life cycle that will impact on their survival indicating that there must be other mechanisms acting in their demographic dynamics. White-crested Elaenia has a diet and foraging behavior plasticity that allows them to adapt their food consumption to what is available according to the environment and rainfall variations, all along their geographical distribution (Johnson 1967, Grigera 1982, Celis-Diez 2002, Cueto *et al.* 2016a). Therefore, the compensation to a low productivity of young with a higher survival rate could be mediated by the White-crested Elaenia feeding plasticity, allowing the species to live in diverse and changing habitats.

Nevertheless and beyond the species plasticity, there is a connectivity between breeding and wintering areas as well as migratory routes (Bravo *et al.* 2017) that can force changes in the species demography, as those areas are being negatively affected by climatic change and human activities affecting the annual cycle of the birds. For example, the species' main wintering and stopover biomes (Atlantic Forest, Yungas and Cerrado, respectively) are highly threatened by deforestation for agricultural purposes (Malizia *et al.* 2012, Ferreira *et al.* 2014). Therefore to improve our knowledge of White-crested Elaenia population dynamic it is essential to promote long term studies that connect studies in demography, behavior, habitat use and food supply, with processes developed in wintering areas and throughout the routes the species uses during migration.

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Plumage polymorphism and variation in the *melanocortin-1 receptor* gene in the Fuscous Flycatcher, *Cnemotriccus fuscatus* (Wied, 1831)

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ABSTRACT: We investigated the possible mechanisms behind the variation plumage color of the Fuscous Flycatcher, *Cnemotriccus fuscatus*, by sequencing the *melanocortin-1 receptor* (*MC1R*) gene, which has been associated with the variation in plumage coloration in birds. *C. fuscatus* is widely distributed in South America and includes seven subspecies, which differ in their plumage coloration. Here we tested the hypothesis that the variation in the *MC1R* gene explains the plumage polymorphism found in *C. fuscatus*. We sequenced the *MC1R* gene in six subspecies, representing two groups: group 1 (yellow morph), with three subspecies, *C. f. duidae*, *C. f. fumosus*, and *C. f. fuscatus*, and group 2 (white morph), with the remaining subspecies, *C. f. bimaculatus*, *C. f. beniensis*, and *C. f. fuscatior*. The only variation we found among the *C. fuscatus* sequences were six non-synonymous substitutions from 22 variable sites, none of which were associated systematically with either plumage morph. The result of the neutrality test indicated that the polymorphism of the *MC1R* gene is not suggestive of significant selection pressure. We conclude that variation in plumage coloration in *C. fuscatus* does not appear to be determined by the *MC1R* gene, and that it may be related to other loci or under the influence of environmental factors.

KEY-WORDS: birds, *MC1R* gene, mutation, pigmentation, Tyrannidae.

INTRODUCTION

The variation in plumage coloration has been studied from ecological, evolutionary and genetic perspectives (Hoekstra & Price 2004, Mundy 2005, Uy *et al.* 2016). Such diversity has been related to visual communication, and may have evolved in response to the evolution of the avian visual system (Osorio & Vorobyev 2008), although there is also some evidence that changes in plumage coloration may be a response to varying pressures in different types of habitat (Gomez & Théry 2004, McNaught & Owens 2002). Many questions remain unresolved, however, on the evolution of plumage coloration and its relation to speciation in birds (Stoddard & Prum 2011, Seddon *et al.* 2013), such as the mechanisms that mediate the change in coloration between juveniles and adults (Galván & Jorge 2015), and the factors determining changes in coloration despite the considerable energetic costs of this process (Legagneux *et al.* 2012, Mercadante & Hill 2014).

Previous studies (*e.g.*, Robbins *et al.* 1993, Vidal *et al.* 2010, Johnson *et al.* 2012) have suggested that the *melanocortin-1 receptor* (*MC1R*) gene may be involved in the differentiation of the plumage in avian species, due to the association between mutations in this gene and the phenotypic variation found in a number of different groups of wild birds (Johnson *et al.* 2012, Ran *et al.* 2016). For example, single non-synonymous mutations in the *MC1R* gene were associated with plumage polymorphisms in the bananaquit (*Coereba flaveola*) and the chestnut-bellied monarch, *Monarcha castaneiventris* (Theron *et al.* 2001, Uy *et al.* 2009). Studies in birds have also shown that the *MC1R* gene controls the amount of both eumelanin (brown/black) and pheomelanin (red/yellow) produced (Takeuchi *et al.* 1996, Wen *et al.* 2015). In particular, García-Borrón *et al.* (2005) showed that the yellow (pheomelanin) phenotype is produced by recessive *MC1R extension* (e) alleles.

In this context, we investigated the variation in coloration found among the subspecies of the Fuscous Flycatcher, *Cnemotriccus fuscatus*, a monotypic genus widely distributed in South America (Fig. 1). There are seven *C. fuscatus* subspecies, which are differentiated not only on the basis of their morphological characters, but also their vocalizations and ecology (Fitzpatrick *et al.* 2004). These subspecies can be divided into two groups, based primarily on the coloration of the belly, which is either white or yellow. These flycatchers can be found in a variety of habitats, including fluvial islands, rainforest, dry forests, riparian habitats, and lowland and secondary forests (Rasmussen & Collar 2002). It is thus important to understand which factors may influence the variation in the coloration of plumage found among the different subspecies of the Fuscous Flycatcher (Farnsworth & Lebbin 2017). In particular, if a relationship can be found between genotype and phenotype, it might represent evidence of the role of natural selection in the fixation of subspecific coloration patterns (Hewitt 1988, Chunco *et al.* 2007).

Here we investigated the possible mechanisms that determine differentiation in plumage amongst the subspecies of *C. fuscatus*. Specifically, we tested whether non-synonymous mutations in the sequence of the *melanocortin-1 receptor* (*MC1R*) gene were associated systematically with variation in plumage coloration amongst the six subspecies, and whether these mutations are suffering selection pressures.

METHODS

We sequenced 27 samples of *Cnemotriccus fuscatus* muscle tissue (Table 1), representing six of the seven described subspecies. The samples were provided by the Goeldi Museum (MPEG: Museu Paraense Emilio Goeldi) in Belém, and the National Museum (MNRJ) in Rio de Janeiro. We followed the classification of Fitzpatrick *et al.* (2004) to allocate the subspecies to two groups (yellow and white morphs). Group 1 (yellow morph) was composed of *Cnemotriccus fuscatus duidae* (*n* = 5 specimens), *Cnemotriccus fuscatus fumosus* (*n* = 7), and *Cnemotriccus fuscatus fuscatus* (*n* = 5), which are ventrally yellow to light yellow. Group 2 (white morph) contained the other three subspecies, *Cnemotriccus fuscatus bimaculatus* (*n* = 5), *Cnemotriccus fuscatus beniensis* (*n* = 3), and *Cnemotriccus fuscatus fuscatior* (*n* = 2), which are ventrally white or light gray. Both male and female specimens were included, as *C. fuscatus* is not dichromatic (Fitzpatrick *et al.* 2004).

Total DNA was isolated from the muscle tissue using the Wizard© Genomic DNA purification kit (Promega), following the manufacturer's instructions. To obtain a partial sequence of the *MC1R* gene, we amplified the samples by PCR using the primers described by Cheviron *et al.* (2006): lcorMSHR9 (5' – CTG GCT CCG GAA GGC RTA GAT – 3') and lcorMSHR72 (5' – AYG CCA GYG AGG GCA ACC A – 3'). The PCR conditions were the same as those used by Cheviron *et al.* (2006), and the PCR products were sequenced by Sanger's didesoxiterminal method (Sanger *et al.* 1977), using an ABI 3500 automatic sequencer.

The DNA sequences were aligned and their nucleotides were compared to those from the bananaquit, *Coereba flaveola* (GenBank access numbers AF362598 and AF362601) and *Gallus gallus* (AB201631) using Bioedit

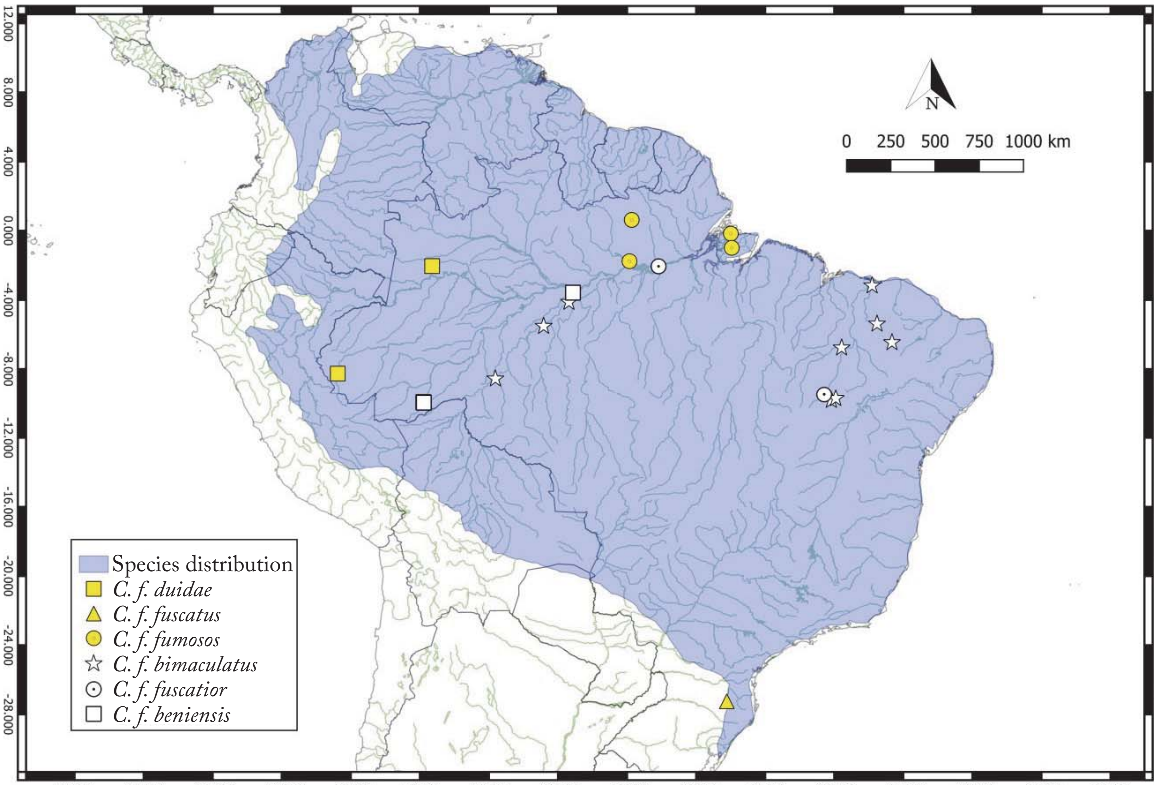

Figure 1. Map showing the distribution of samples of *Cnemotriccus fuscatus* sequenced in this study. Yellow points represent specimens with yellow bellies and white points denote specimens with white bellies.

Table 1. Location, coordinates, subspecies, voucher number, identification code, and source of tissue used in this study.

Locations (Coordinates)	Subspecies	Voucher number	Identification of the tissue	Institutions
Óbidos - PA (00°37'50''N; 55°43'40''W)	*C. f. fumosus*	CN1410, CN1378,	Cfu1410, Cfu1378	MPEG[*]
Chaves - PA 00°12'29.2''S; 49°58'39.2''W	*C. f. fumosus*	MARJ117, MARJ118	Cfu118, Cfu117	MPEG
Marajó - PA (00°59'21''S; 49°56'24''W)	*C. f. fumosus*	MAYA008	Cfu008	MPEG
Oriximiná - PA (1°45'36.89''S; 55°51'30.28''W)	*C. f. fumosus*	ORX336, ORX359	Cfu336, Cfu359	MPEG
Porto Walter - AC (08°20'35.7''S; 72°36'19.7''W)	*C. f. duidae*	UFAC1021	Cfu1021	MPEG
Japurá - AM (02°02'31.5''S; 67°17'16.6''W)	*C. f. duidae*	JAP225, JAP267, JAP270	Cfu225, Cfu267, Cfu270	MPEG
Porto Walter - AC (08°20'35.7''S; 72°36'19.7''W)	*C. f. duidae*	UFAC0976	Cfu0976	MPEG
Uruçuí - PI (07°14'2.00''S; 44°33'1.55''W)	*C.f. bimaculatus*	URC171	Cfu171	MPEG
Curimatá - PI (09°41'284''S; 44°14'200''W)	*C.f. bimaculatus*	SRV005	Cfu005	MPEG
Redenção do Gurgueia - PA (9°38'022''S; 44°08'807''W)	*C.f. bimaculatus*	SRV042	CfuS042	MPEG
Borba, Puruzinho, Ilha - AM 04°07'42''S; 59°21'55.4''W	*C. f. bimaculatus*	MAD500	Cfu500	MPEG
Autazes, Uricurituba, Ilha - AM 03°34'47''S; 59°07'50''W	*C.f. bimaculatus*	MAD608	Cfu608	MPEG
Santa Catarina - SC (27°14'32.42''S; 50°13'7.88''W)	*C. f. fuscatus*	TERNA210, TERNA398,TERNA1068, TERNA1349, Cachimbo470	Cfu210, Cfu398, Cfu1068, Cfu1349, Cfu470	MNRJ[†]
Rio Branco - AC (09°57'32.3''S; 67°43'57.2''W)	*C. f. beniensis*	UFAC1199, UFAC1297, UFAC273	Cfu1199, Cfu1297, Cfu273	MPEG
Monte Alegre - PA (2°3'14.72''S; 54°10'24.49''W)	*C. f. fuscatior*	PEMA042, PEMA037	Cfu042, Cfu037	MPEG

* Museu Paraense Emilio Goeldi.
† Museu Nacional do Rio de Janeiro.

v. 7.2.5, to confirm the position of amplified fragment. We then assessed if aminoacid sequence presented stop codons and indels, which could indicate pseudogenes. The potential association of variable sites with the plumage morphotype of each species was confirmed by visual inspection. We calculated Tajima's D (Tajima 1989) in DnaSP (version 3.51, Rozas *et al.* 2003) to verify whether the *MC1R* gene was under selection pressure in the two groups.

RESULTS

A total of 744 base pairs were sequenced for each of the 27 *C. fuscatus* samples, representing nucleotides 129–873 of the *MC1R* gene of *Gallus gallus*, which includes all the sites known to be associated with plumage polymorphisms in birds (Theron *et al.* 2001). Only 21 samples were considered (pp >0.6) after the resolution of the gametic phases (Harrigan *et al.* 2008, Table 2). In the BLAST (NCBI: National Center for Biotechnology Information) analysis, the sequences were 95% similar to that of *Gallus gallus* (Kerje *et al.* 2003) and 97% similar to that of *Coereba flaveola* (Theron *et al.* 2001).

We identified 22 variable sites in the 21 *C. fuscatus* samples (Table 2), including all six subspecies. These variable sites of the *MC1R* locus determined six non-synonymous mutations for the codification of amino acids, A8G, S9R, S10N, S89N, V226I, and L240I (Table 3). None of these sites were associated with the coloration patterns of either the two groups or any of the subspecies. Tajima's D was not significant (-1.603, $P > 0.05$), indicating that the variation found in the study locus in *C. fuscatus* is neutral, with a signal of recent demographic expansion, against the constant demographic model. All the sequences generated in the present study were deposited in GenBank (www.ncbi.nlm.nih.gov) under access numbers MK102986 through MK103006 (Table 3).

DISCUSSION

Our study of *Cnemotriccus fuscatus* indicates that there is no clear association between the plumage polymorphism found in this species and mutations of the *MC1R* gene. As in previous studies of bird species such as *Phylloscopus toutinegras* (MacDougall-Shackleton *et al.* 2003), *Lepidothrix coronata* (Cheviron *et al.* 2006), *Dendrocolaptes platyrostris* (Corso *et al.* 2013), *Philomachus pugnax*

Table 2. MC1R variable sites found in the sequences of *Cnemotriccus fuscatus*.

Voucher – Subspecies	**Nucleotidic sites**																							**Belly Plumage**
						1	**1**	**1**	**2**	**2**	**2**	**2**	**3**	**3**	**4**	**4**	**5**	**6**	**6**	**6**	**6**	**7**	**7**	
	1	**2**	**2**	**2**	**7**	**3**	**7**	**7**	**1**	**4**	**6**	**7**	**1**	**2**	**6**	**9**	**0**	**3**	**4**	**7**	**8**	**1**	**2**	
	5	**3**	**5**	**9**	**5**	**8**	**2**	**2**	**3**	**3**	**6**	**6**	**8**	**7**	**5**	**8**	**4**	**3**	**8**	**6**	**7**	**8**	**3**	
Cfu008 - *C. f. fumosus*	G	C	A	G	A	C	C	C	G	C	G	C	C	T	C	C	C/G	T	C	G	C	C/A	C	Yellow
Cfu117- *C. f. fumosus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Yellow
Cfu118 - *C. f. fumosus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Yellow
Cfu1410 - *C. f. fumosus*	.	.	.	.	.	.	.	.	.	.	A	T	.	.	.	.	.	.	T	.	.	.	.	Yellow
Cfu359 - *C. f. fumosus*	.	.	.	.	A/G	.	.	.	.	.	.	.	.	.	T	.	.	.	T	G/A	T	.	T	Yellow
Cfu225 - C. *f. duidae*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	T	.	.	.	T	Yellow
Cfu267- *C. f. duidae*	.	.	.	.	.	.	.	.	.	.	A	T	.	.	.	.	.	.	T	.	.	.	C/T	Yellow
Cfu0976 - *C. f. duidae*	.	.	.	.	G/A	.	.	.	.	.	G/A	C/T	.	.	.	.	.	.	T	.	.	.	.	Yellow
Cfu1021 - *C. f. duidae*	.	.	.	.	A/G	.	.	.	.	.	.	.	.	.	.	.	.	.	C/T	.	.	.	.	Yellow
Cfu270 - *C. f. duidae*	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	Yellow
Cfu210 - *C. f. fuscatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Yellow
Cfu398 - *C. f. fuscatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C/T	Yellow
Cfu1068 - *C. f. fuscatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Yellow
Cfu273 - *C. f. beniensis*	.	G	C	G/A	.	.	.	.	.	.	.	.	.	.	.	C/A	.	.	.	.	.	.	.	White
Cfu1297 - *C. f. beniensis*	.	.	.	.	.	.	.	C/T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	White
Cfu500 - *C. f. bimaculatus*	A/G	.	.	.	.	.	.	C/T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	White
Cfu608 - *C. f. bimaculatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	White
Cfu005 - *C. f. bimaculatus*	.	.	.	.	G	.	.	.	A/G	T/C	.	.	C/T	C	C/T	.	.	.	.	.	.	.	.	White
Cfu042 - *C. f. bimaculatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	White
Cfu171 - *C. f. bimaculatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	White
Cfu042 - *C. f. fuscatior*	.	.	.	.	.	T/C	T/C	.	.	.	.	.	.	.	.	.	.	C/T	.	.	.	.	C/T	White

Table 3. Position of non-synonymous variations within the amino acid *Cnemotriccus fuscatus*. GenBank access numbers for the samples analyzed.

Voucher – Subspecies	**Amino acid positions**						**Belly Plumage**	**Access number GenBank**
	8	9	10	89	226	240		
Cfu008 - *C. f. fumosus*	A	S	S	S	V	L/I	Yellow	MK102986
Cfu117 - *C. f. fumosus*	.	.	.	.	.	.	Yellow	MK102987
Cfu118 - *C. f. fumosus*	.	.	.	.	.	.	Yellow	MK102988
Cfu1410 - *C. f. fumosus*	.	.	.	N	.	.	Yellow	MK102989
Cfu359 - *C. f. fumosus*	.	.	.	.	V/I	.	Yellow	MK102990
Cfu225 - C. *f. duidae*	.	.	.	.	.	.	Yellow	MK102991
Cfu267 - *C. f. duidae*	.	.	.	N	.	.	Yellow	MK102992
Cfu0976 - *C. f. duidae*	.	.	.	S/N	.	.	Yellow	MK102993
Cfu1021 - *C. f. duidae*	.	.	.	.	.	.	Yellow	MK102994
Cfu270 - *C. f. duidae*	.	.	.	.	.	.	Yellow	MK102995
Cfu210 - *C. f. fuscatus*	.	.	.	.	.	.	Yellow	MK102996
Cfu398 - *C. f. fuscatus*	.	.	.	.	.	.	Yellow	MK102997
Cfu1068 - *C. f. fuscatus*	.	.	.	.	.	.	Yellow	MK102998
Cfu273 - *C. f. beniensis*	G	R	S/N	.	.	.	White	MK102999
Cfu1297 - *C. f. beniensis*	.	.	.	.	.	.	White	MK103000
Cfu500 - *C. f. bimaculatus*	.	.	.	.	.	.	White	MK103001
Cfu608 - *C. f. bimaculatus*	.	.	.	.	.	.	White	MK103002
Cfu005 - *C. f. bimaculatus*	.	.	.	.	.	.	White	MK103003
Cfus042 - *C. f. bimaculatus*	.	.	.	.	.	.	White	MK103004
Cfu171 - *C. f. bimaculatus*	.	.	.	.	.	.	White	MK103005
Cfu042 - *C. f. fuscatior*	.	.	.	.	.	.	White	MK103006

(Farrell *et al.* 2014) and the genus *Antilophia* (Luna *et al.* 2018), our findings reinforce the conclusion that this gene does not always play a role in the variation in plumage coloration found among populations or species. In this case, other genes or mechanisms may determine this variation, as observed in a number of birds (McLean & Stuart-Fox 2014).

A number of new genes associated with plumage coloration have been identified in recent years, although they have been analyzed in only a few species (Oribe *et al.* 2012, Bourgeois *et al.* 2016). Miwa *et al.* (2007), for example, found an association between mutations of the *endothelin receptor B2* (*EDNRB2*) gene and the coloration of *Cortunix japonica*, with a non-synonymous substitution that alters an amino acid (*R332H*) being associated with the "panda" pattern, in contrast with the standard "dotted white" pattern. Other genes that may be involved in pigmentation in birds include the *tyrosinase-related protein 1*, *TYRP1* (Xu *et al.* 2013, Bourgeois *et al.* 2016), *SRY-Box containing 10*, *SOX10* (Gunnarsson *et al.* 2011), Agouti protein, ASIP (Oribe *et al.* 2012, Zhang *et al.* 2013), and *Corin* (Bourgeois *et al.* 2016) genes, and the proopiomelanocortin (*POMC*) gene cluster, which includes *MC1R* (Kang & Kim 2015).

In addition to genetics, the variation found in the coloration of *C. fuscatus* may be related to environmental factors, given the diversity of habitats occupied by the species (Fig. 1). Uy *et al.* (2009), for example, found that natural selection may favor distinct coloration in different habitats based on the existence of several population patterns, with habitats dominated by short-wavelength light (*e.g.*, shaded woodland) favoring darker birds, and habitats rich in long-wavelength light (*e.g.*, forest clearings with direct sunlight) favor lighter-colored species.

Furthermore, the studied part of the gene *MC1R* includes all the main sites that were showed in previous research with plumage polymorphism of birds (Mundy 2005, Cheviron *et al.* 2006). Overall, our results reinforce the conclusion that understanding the evolution of plumage coloration in *C. fuscatus* with varying patterns of eumelanin/pheomelanin pigmentation requires a more profound investigation of the genes in the melanocortin pathway and their potential variation, as well as other loci and environmental factors. Unlike many other bird species (see *e.g.*, Cheviron *et al.* 2006, Corso *et al.* 2013, Farrell *et al.* 2014, Luna *et al.* 2018), the variation in the plumage coloration of *C. fuscatus* does not appear to be related to mutations of the *MC1R* gene.

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Scientific names must be shown in *italic*, and authors are encouraged to follow the latest systematic sequence, spelling and taxon authors of the Brazilian (Piacentini *et al.* 2015. *Rev. Bras. Ornitol.* 23: 91–298) or South American (www.museum.lsu.edu/~Remsen/SACCBaseline.html) bird lists, when pertinent and at their discretion. When using one of each of those sources, please be explicit about which one is being used, following it consistently throughout the manuscript. Common names should also follow those recommended by Brazilian or South American lists). Common names should be capitalized (*e.g.*, Kaempfer's Woodpecker, Common Tern).

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Each Table should be on a separate page, numbered in Arabic numerals, with its own heading.

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The following *abbreviations* should be used: h (hour), min (minute), s (second), km (kilometer), m (meter), cm (centimeter), mm (millimeter), ha (hectare), kg (kilogram), g (gram), mg (milligram), all of them in lowercase (not capitals) and with no "periods" ("."). Use the following *statistical notations: P, n, t, r, F, G, U, df* (degrees of freedom), χ^2, ns (non-significant), CV (coefficient of variation), SD (standard deviation), SE (standard error). With the exception of temperature and percentage symbols (*e.g.*, 15°C, 45%), leave a space between the number and the unit or symbol (*e.g.*, $n = 12$, $P < 0.05$, 25 min), also in figures and tables.

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Articles

Fargione J., Hill J., Tilman D., Polasky S. & Hawthornez P. 2008. Land clearing and the biofuel carbon debt. *Science* 319: 1235–1238.

Santos M.P.D. & Vasconcelos M.F. 2007. Range extension for Kaempfer's Woodpecker *Celeus obrieni* in Brazil, with the first male specimen. *Bulletin of the British Ornithologists' Club* 127: 249–252.

Worthington A.H. 1989. Adaptations for avian frugivory: assimilation efficiency and gut transit time of *Manacus vitellinus* and *Pipra mentalis. Oecologia* 80: 381–389.

Books and Monographs

Sick H. 1985. *Ornitologia brasileira, uma introdução, v. 1*. Brasilia: Editora Universidade de Brasilia.

Book Chapters

Thiollay J.M. 1994. Family Accipitridae (hawks and eagles), p. 52–205. In: del Hoyo J., Elliott A. & Sargatal J. (eds.). *Handbook of birds of the world, v. 2 (New World vultures to guineafowl)*. Barcelona: Lynx Editions.

Theses and Dissertations

Novaes F.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, Ciencias e Letras de Rio Claro.

Cavalcanti L.M.P. 2014. *Sazonalidade na estação reprodutiva de aves de uma área de Caatinga e sua relação com a precipitação.* Bachelor's Monograph. Mossoró: Universidade Federal Rural do Semiárido.

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IUCN. 1987. A posição da IUCN sobre a migração de organismos vivos: introduções, reintroduções e reforços. http://iucn.org/themes/ssc/pubs/policy/index.htm (access on 25 August 2005).

Dornas T. 2009a. [XC95575, *Celeus obrieni*]. http://www.xeno-canto.org/95575 (access on 25 February 2012).

Pinheiro R.T. 2009. [WA589090, *Celeus obrieni* Short, 1973]. http://www.wikiaves.com/589090 (access on 05 March 2012).

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