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ARTICLE

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

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

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

INTRODUCTION

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

Home range is an area where an individual restricts its activities during the year or period (Odum & Kuenzler 1955). When part of or all home range is defended against other conspecifics it is defined as a territory (Nice 1941, Odum & Kuenzler 1955). Home range is a cognitive map of resources that individuals keep up-to-date to fulfil their requirements (Powell & Mitchell 2012). Social and breeding behavior affect the territorial and home range dynamics, such as their sizes, boundaries, acquisition, dispersal, among others. Because natural habitats are usually fragmented to some degree, small patches may not have sufficient area for home ranges and also increase predation and parasitism near edges (Beier *et al.* 2002), as well as the patch isolation may have negative effects on dispersal (Pavlacky-Jr. *et al.* 2012).

Cooperative breeding is a social system characterized by a breeding pair and one or more individuals that did not breed, but collaborate to rear a brood (Woolfenden & Fitzpatrick 1984, Burt *et al.* 2007). These individuals are called nest helpers (hereafter, helpers). Why some individuals tend to postpone their own reproduction and help to rear a brood from others has intrigued scientists for decades. Studies have tried to explain how the cooperative breeding evolved (Poiani & Jermiin 1994, Du Plessis *et al.* 1995, Arnold & Owens 1998, Heinsohn & Legge 1999, Doerr & Doerr 2006, Russell *et al.* 2007, Hatchwell 2009, Cockburn & Russell 2011, Jetz & Rubenstein 2011, Feeney *et al.* 2013, Downing *et al.* 2015, Drobniak *et al.* 2015), but life-histories differ considerably between species and there is not a one-size-fits-all hypothesis (Cockburn 1998, Berg *et al.* 2012, Gamero *et al.* 2014). There are more than 10,000 extant bird species in the world, and 9% are estimated to present cooperative breeding (Cockburn 2006), and among the oscines 18.5% (Cockburn 2003). The Neotropics is the region with highest biodiversity on Earth, but it is the relatively less studied in terms of bird behavior (Stutchbury & Morton 2001). It is estimated that 6% (218 species) of all Neotropical birds have cooperative breeding (Jetz & Rubenstein 2011), but the effective number of species that breed cooperatively may be slightly higher as the breeding systems and natural histories of more birds are being described.

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

METHODS

Study area

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

Data collection

We began with a pilot study from November 2012 until January 2013. We then carried out observations from October to February, during two breeding seasons (2013–2015) of the only known population of Yellow Cardinal in Brazil. Population size, sex ratio, and longevity were estimated using banded birds, and unmarked individuals when it was possible to identify them by unique marks on plumage. We searched for Yellow Cardinals at the beginning of each breeding season (October) and captured adults using mist nets and marked with an aluminum ring (standard CEMAVE/ICMBio; the Brazilian Banding Agency) and a unique combination of colored plastic rings. Ten days old nestlings or chicks that just fledged were also marked. We measured birds following Eck *et al.* (2011): wing chord, tail length, tarsus length, bill and culmen length, nostril to bill tip, and total length, using a precision caliper (0.1 mm) and a ruler (1.0 mm). Body mass was measured using a precision dynamometer (0.5 g) of kind Pesola© Swiss Micro 20060. Plumage categorization follows Wolfe *et al.* (2010).

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

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

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

Statistical analysis

To assess differences on morphometric measurements between sexes and parental care between nestling phases we used the non-parametric Mann-Whitney *U*-test (Wilcoxon rank-sum test). Comparison of the frequency of visits to the nest of each group member (male, female and helper) were run with Kruskal-Wallis *H* tests, followed by post-hoc pairwise Mann-Whitney *U*-tests. Values are presented as mean ± SD and considered statistically significant when $P < 0.05$.

RESULTS

Capture, morphometric and demographic data

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

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

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

Social/mate system

The Yellow Cardinal is socially monogamous and the mated pairs may stay together for more than one breeding season, and only two divorces were observed. Additionally, two males lost their mates and mated again. In 2013, from nine mating pairs, one female disappeared and one divorced. After a successful nest, the divorced female and her two offspring disappeared in December 2013, but all three were seen again in October 2014. At that time, the female had found another male, and the two offspring became helpers. In 2014, one female at a nest was lost to predation and a second female divorced. All other pairs remained together. The divorced female of 2014 was later found paired in a neighboring territory in 2015. On a territory where both individuals of the pair were marked, we ringed a nestling at the nest in January 2013. In May 2013, the female disappeared, but the young was observed with the male. In October 2013, we found father and daughter on their territory and apparently paired, which was confirmed in December 2013 when we found a nest with nestlings. This male remained alone during the second breeding season. It is the first record of inbreeding in the Yellow Cardinal. A fledgling from this pair was ringed, but all young and the female were not seen since January 2014.

Nest helpers

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

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

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

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

Productivity and nesting success

Mean productivity per successful nest was 1.6 ± 0.74 fledglings ($n = 8$). Successful nests without helpers fledged a mean of one chick (4 fledglings/4 nests), and with helpers fledged two (8 fledglings/4 nests). The apparent success of nests with and without helpers was 57% (4/7) and 31% (4/13), respectively. The Mayfield Nesting Success was 40% and 13% for nests with and without helpers, respectively (18% for all nests pooled). There was no difference between nests with and without helpers in probability of survival for incubation (0.544 ± 0.239 *vs.* 0.403 ± 0.117; Z = 0.53; P = 0.60), nor nestling stage (0.732 ± 0.231 *vs.* 0.318 ± 0.125; Z = 1.58; P = 0.11).

Parental care

We observed about 12 h of parental care at three nests and recorded 6 h at one nest. The total frequency of visits to the nest was 12.28 ± 5.26 visits/h and we found a significant difference between initial and final nestling phases (9.91 ± 3.88 *vs.* 16.0 ± 5.16 visits/h; U = 14, P = 0.03, n = 18). Males made 4.39 ± 1.69 visits/h, females 5.06 ± 3.13 visits/h and helpers 2.83 ± 1.72 visits/h (Figure 1). There was a significant difference on visit rate between family members during the complete nestling period (H_2 = 7.92; P = 0.02), especially between helpers and females (2.83 ± 1.72 *vs.* 5.06 ± 3.13 visits/h; U = 89.5; P = 0.02), and helpers and males (2.83 ± 1.72 *vs.* 4.39 ± 1.69 visits/h; U = 84; P = 0.01). Only females increased significantly their visit rate from initial to final nestling phase (3.64 ± 2.58 *vs.* 7.29 ± 2.69 visits/h; U = 12.5; P = 0.02). There was no difference between frequency of visits per group member on initial phase (H_2 = 4.32; P = 0.12), but there was significant difference on final phase (H_2 = 7.75; P = 0.02) between helpers and females (3.71 ± 1.38 *vs.* 7.29 ± 2.69 visits/h; U = 5; P = 0.01).

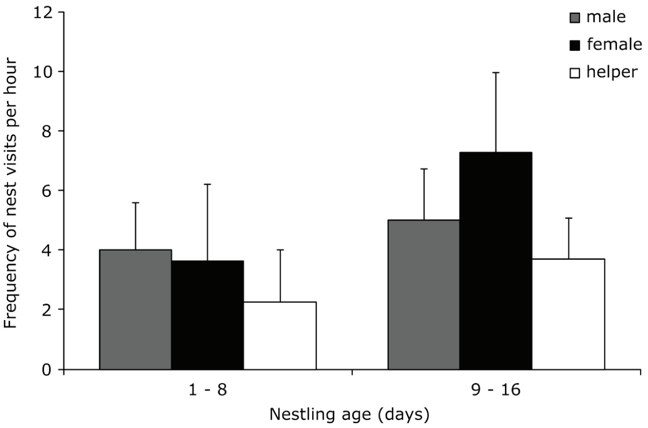

Figure 1. Frequency of visits to the nest of male (grey bars), female (black bars), and helper (white bars) on nestling age of the Yellow Cardinal (*Gubernatrix cristata*). Bars represent mean ± 1 SD.

Breeding territories

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

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

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

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

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

DISCUSSION

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

We are confident that the entire Brazilian population of Yellow Cardinal from Espinilho savanna was monitored by searching all potential areas of occurrence of the species. Small populations are likely to have genetic and demographic problems through time, such as inbreeding (Lande 1988, Stacey & Taper 1992, Pimm *et al.* 1993), which we observed in this population. Unmarked individuals that appear in definitive basic plumage may be immigrants from Argentina (about 4 km) or Uruguay.

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

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

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

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

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

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

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

Breeding territory and home range sizes may be considered large for a passerine of its size (~47 g). However, our estimations could be biased due to small sampling effort, and may be considered with caution, especially for home ranges estimates. Other grassland birds have smaller territories and home ranges. It was estimated that mean territory size for Lesser Grass-finch (*Emberizoides ypiranganus*, 20 g) is 1.1 ha (maximum 2.4 ha) (Chiarani & Fontana 2015), 3.7 ha for White-banded Tanager (Soares 2007). Chiarani & Fontana (2015) found that 83% of Lesser Grass-finch territories had the same males defending it in both breeding seasons. Pereira (2015) found a density of one territory/100 ha for Yellow Cardinal in the same study site, reflecting its large territories. Dardanelli *et al.* (2006) studied the minimum area requirements of a bird community in Argentina, and they found that, from 54 woodland species, 80% needed no more than 3 ha. However, they also found that nine species needed fragments of 80 ha or more, six of which also occur in our study site: Sharp-shinned Hawk (*Accipiter striatus*), White-fronted Woodpecker (*Melanerpes cactorum*), Tufted Tit-Spinetail (*Leptasthenura platensis*), Scimitar-billed Woodcreeper (*Drymornis bridgesii*), Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), and Suiriri Flycatcher (*Suiriri suiriri*).

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

Conservation actions

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

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REFERENCES

Altmann J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49: 227–267.

Alves M.A.S. 1990. Social system and helping behavior in the White-banded Tanager (*Neothraupis fasciata*). *Condor* 92: 470–474.

Arnold K.E. & Owens I.P.F. 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. *Proceedings of the Royal Society of London B: Biological Sciences* 265: 739–745.

Azpiroz A.B., Alfaro M. & Jiménez S. 2012. *Lista roja de las aves del Uruguay*. Montevideo: Dirección Nacional de Medio Ambiente.

Barker F.K., Burns K.J., Klicka J., Lanyon S.M. & Lovette I.J. 2013. Going to extremes: contrasting rates of diversification in a recent radiation of New World passerine birds. *Systematic Biology* 62: 298–320.

Beier P., van Drielen M. & Kankam B.O. 2002. Avifaunal collapse in west African forest fragments. *Conservation Biology* 16: 1097–1111.

Berg E.C., Aldredge R.A., Peterson A.T. & McCormack J.E. 2012. New phylogenetic information suggests both an increase and at least one loss of cooperative breeding during the evolutionary history of *Aphelocoma* jays. *Evolutionary Ecology* 26: 43–54.

BirdLife International. 2015. Species factsheet: *Gubernatrix cristata*. http://www.birdlife.org/datazone/speciesfactsheet.php?id=9078 (acessado em 21 December 2015).

Burns K.J., Shultz A.J., Title P.O., Mason N.A., Barker F.K., Klicka J., Lanyon S.M. & Lovette I.J. 2014. Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. *Molecular Phylogenetics and Evolution* 75: 41–77.

Burt D.B., Coulter P.F. & Ligon J.D. 2007. Evolution of parental care and cooperative breeding, p. 295–326. In: Jamieson B.G.M. (ed.). *Reproductive biology and phylogeny of birds, Part B: sexual selection, behavior, conservation, embryology and genetics*. Enfield: Science Publishers.

Calenge C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516–519.

Canestrari D., Marcos J.M. & Baglione V. 2009. Cooperative breeding in Carrion Crows reduces the rate of brood parasitism by Great Spotted Cuckoos. *Animal Behaviour* 77: 1337–1344.

Chiarani E. & Fontana C.S. 2015. Breeding biology of the Lesser Grass-Finch (*Emberizoides ypiranganus*) in southern Brazilian upland grasslands. *Wilson Journal of Ornithology* 127: 441–456.

Cockburn A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics* 29: 141–177.

Cockburn A. 2003. Cooperative breeding in Oscine passerines: does sociality inhibit speciation? *Proceedings of the Royal Society of London B: Biological Sciences* 270: 2207–2214.

Cockburn A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society of London B: Biological Sciences* 273: 1375–1383.

Cockburn A. & Russell A.F. 2011. Cooperative breeding: a question of climate? *Current Biology* 21: R195–R197.

Dardanelli S., Nores M.L.M. & Nores M. 2006. Minimum area requirements of breeding birds in fragmented woodland of central Argentina. *Diversity and Distributions* 12: 687–693.

Doerr E.D. & Doerr V.A.J. 2006. Comparative demography of treecreepers: evaluating hypotheses for the evolution and maintenance of cooperative breeding. *Animal Behaviour* 72: 147–159.

Domínguez M., Reboreda J.C. & Mahler B. 2015. Impact of Shiny Cowbird and botfly parasitism on the reproductive success of the globally endangered Yellow Cardinal *Gubernatrix cristata*. *Bird Conservation International* 25: 294–305.

Downing P.A., Cornwallis C.K. & Griffin A.S. 2015. Sex, long life and the evolutionary transition to cooperative breeding in birds. *Proceedings of the Royal Society of London B: Biological Sciences* 282: 20151663.

Drobniak S.M., Wagner G., Mourocq E. & Griesser M. 2015. Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding. *Behavioral Ecology* 26: 805–811.

Du Plessis M.A., Siegfried W.R. & Armstrong A.J. 1995. Ecological and life-history correlates of cooperative breeding in South African birds. *Oecologia* 102: 180–188.

Eck S., Fiebig J., Fiedler W., Heynen I., Nicolai B., Töpfer T., van den Elzen R., Winkler R. & Woog F. 2011. *Measuring birds/Vögel Vermessen*. Wilhelmshaven: Deutsche Ornithologen-Gesellschaft.

Edwards S.V & Naeem S. 1993. The phylogenetic component of cooperative breeding in perching birds. *American Naturalist* 141: 754–789.

Ekman J. & Griesser M. 2016. Siberian jays: delayed dispersal in the absence of cooperative breeding, p. 6–18. In: Koenig W.D. & Dickinson J.L. (eds.). *Cooperative breeding in vertebrates: studies of ecology, evolution, and behavior*. Cambridge: Cambridge University Press.

Faria L.P., Carrara L.A. & Rodrigues M. 2007. Dimorfismo sexual de tamanho no Fura-barreira *Hylocryptus rectirostris* (Wied) (Aves, Furnariidae). *Revista Brasileira de Zoologia* 24: 207–212.

Feeney W.E., Medina I., Somveille M., Heinsohn R., Hall M.L., Mulder R.A., Stein J.A., Kilner R.M. & Langmore N.E. 2013. Brood parasitism and the evolution of cooperative breeding in birds. *Science* 342: 1506–1508.

Gamero A., Székely T. & Kappeler P.M. 2014. Delayed juvenile dispersal and monogamy, but no cooperative breeding in White-breasted Mesites (*Mesitornis variegata*). *Behavioral Ecology and Sociobiology* 68: 73–83.

Gressler D.T. 2012. *Razão sexual e sobrevivência em* Neothraupis fasciata. Ph.D. Thesis. Brasília: Universidade de Brasília.

Gressler D.,T., Pereira Z.P. & Marini M.Â. 2014. Brood sex allocation in the Neotropical cooperative White-banded Tanager *Neothraupis fasciata*. *Journal of Ornithology* 155: 713–719.

Hatchwell B.J. 2009. The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 364: 3217–3227.

Heinsohn R. & Legge S. 1999. The cost of helping. *Trends in Ecology and Evolution* 14: 53–57.

Hensler G.L. & Nichols J.D. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. *Wilson Bulletin* 93: 42–53.

Hilty S. 2011. Tanagers (Thraupidae), p. 46–155. In: del Hoyo J., Elliott A. & Christie D. (eds.). *Handbook of the birds of the world, v. 16 (tanagers to New World blackbirds)*. Barcelona: Lynx Edicions.

Jacob A.A. & Rudran R. 2006. Radiotelemetria em estudos populacionais, p. 285–342. In: Cullen-Jr. L., Rudran R. & Valladares-Padua C. (eds.). *Métodos de estudos em biologia da conservação e manejo da vida silvestre*. Curitiba: Ed. Universidade Federal do Paraná.

Jaramillo A. 2011. Yellow Cardinal, p. 641. In: del Hoyo J., Elliott A., & Christie D. (eds.). *Handbook of the birds of the world: tanagers to New World blackbirds*. Barcelona: Lynx Edicions.

Jetz W. & Rubenstein D.R. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology* 21: 72–78.

Klimkiewicz M.K. & Futcher A.G. 1987. Longevity records of North American birds: Coerebinae through Estrildidae. *Journal of Field Ornithology* 58: 318–333.

Koenig W.D., Pitelka F.A., Carmen W.J., Mumme R.L. & Stanback M.T. 1992. The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* 67: 111–150.

Lande R. 1988. Genetics and demography in biological conservation. *Science* 241: 1455–1460.

Langen T.A. 2000. Prolonged offspring dependence and cooperative breeding in birds. *Behavioral Ecology* 11: 367–377.

Liker A., Freckleton R.P. & Székely T. 2014. Divorce and infidelity are associated with skewed adult sex ratios in birds. *Current Biology* 24: 880–884.

López-Lanús B., Grilli P., Di Giacomo A.S., Coconier E.E. & Banchs R. (eds.). 2008. *Categorización de las aves de la Argentina según su estado de conservación*. Buenos Aires: Informe de Aves Argentinas/AOP y Secretaría de Ambiente y Desarrollo Sustentable.

Manica L.T. & Marini M.Â. 2012. Helpers at the nest of White-banded Tanager *Neothraupis fasciata* benefit male breeders but do not increase reproductive success. *Journal of Ornithology* 153: 149–159.

Marchiori J.N.C. & Alves F.S. 2011. O Inhaduvá (*Prosopis affinis* Spreng.) no Rio Grande do Sul. 8 - Aspectos fitogeográficos. *Balduinia* 29: 13–20.

Marini M.Â., Duca C. & Manica L.T. 2010. Técnicas de pesquisa em biologia reprodutiva de aves, p. 295–312. In: von Matter S., Straube F.C., Accordi I.A., Piacentini V.Q. & Cândido-Jr., J.F. (eds.). *Ornitologia e conservação: ciência aplicada, técnicas de pesquisa e levantamento*. Rio de Janeiro: Technical Books.

Mayfield H.F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87: 456–466.

Nice M.M. 1941. The role of territory in bird life. *American Midland Naturalist* 26: 441–487.

Odum E.P. & Kuenzler E.J. 1955. Measurement of territory and home range size in birds. *Auk* 72: 128–137.

Paquet M., Covas R., Chastel O., Parenteau C. & Doutrelant C. 2013. Maternal effects in relation to helper presence in the cooperatively breeding Sociable Weaver. *PLoS ONE* 8: e59336.

Pavlacky-Jr. D.C., Possingham H.P., Lowe A.J., Prentis P.J., Green D.J. & Goldizen A.W. 2012. Anthropogenic landscape change promotes asymmetric dispersal and limits regional patch occupancy in a spatially structured bird population. *Journal of Animal Ecology* 81: 940–952.

Pereira M.S. 2015. *Assembleia de aves territorialistas na formação Espinilho: densidade e seleção de habitat reprodutivo*. MSc. Dissertation. Porto Alegre: Pontifícia Universidade Católica do Rio Grande do Sul.

Pimm S.L., Diamond J., Reed T.M., Russell G.J. & Verner J. 1993. Times to extinction for small populations of large birds. *Proceedings of the National Academy of Sciences of the United States of America* 90: 10871–10875.

Poiani A. & Jermiin L.S. 1994. A comparative analysis of some life-history traits between cooperatively and non-cooperatively breeding Australian passerines. *Evolutionary Ecology* 8: 471–488.

Powell R.A. & Mitchell M.S. 2012. What is a home range? *Journal of Mammalogy* 93: 948–958.

R Core Team. 2015. *R: a language and environment for statistical computing*. https://www.r-project.org (access on 15 December 2015).

Russell A.F., Langmore N.E., Cockburn A., Astheimer L.B. & Kilner R.M. 2007. Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science* 317: 941–944.

Schaub R., Mumme R.L. & Woolfenden G.E. 1992. Predation on the eggs and nestlings of Florida Scrub Jays. *Auk* 109: 585–593.

Seaman D.E., Millspaugh J.J., Kernohan B.J., Brundige G.C., Raedeke K.J. & Gitzen R.A. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63: 739–747.

Martins-Ferreira C., Bencke G.A., Fontana C.S., Dias R.A., Repenning M., Damiani R.V., Mauricio G.N., Gianuca A.T., Krügel M.M., Franz I., Rovedder C.E., Rupp A.E., Pereira M.S., Vizentin-Bugoni J., Joenck C.M., Straube F.C., Reinert B.L., Bornschein M.R., Dias D., Vieira B.P & Serafini, P.P. 2013. *Plano de Ação Nacional para a conservação dos Passeriformes ameaçados dos Campos Sulinos e Espinilho*. Brasília: Instituto Chico Mendes de Conservação da Biodiversidade. Série espécies ameaçadas 31.

Soares, C.G.D. 2007. *Biologia e conservação de* Neothraupis fasciata *(Aves: Thraupidae) no cerrado do Brasil central.* Ph.D. Thesis. Brasília: Universidade de Brasília.

Stacey P.B. & Taper M. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2: 18–29.

Stutchbury B.J.M. & Morton E.S. 2001. *Behavioral ecology of tropical birds*. London: Academic Press.

Székely T., Liker A., Freckleton R.P., Fichtel C. & Kappeler P.M. 2014. Sex-biased survival predicts adult sex ratio variation in wild birds. *Proceedings of the Royal Society of London B: Biological Sciences* 281: 20140342.

Székely T., Lislevand T. & Figuerola J. 2007. Sexual size dimorphism in birds, p. 27–37. In: Fairbairn D.J., Blanckenhorn W.U. & Székely T. (eds.). *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*. Oxford: Oxford University Press.

Welty J.C. & Baptista L.F. 1988. *The life of birds*. New York: W. B. Saunders.

Wolfe J.D. Ryder T.B., Pyle P. 2010. Using molt cycles to categorize the age of tropical birds: an integrative new system. *Journal of Field Ornithology* 81: 186–194.

Woolfenden G.E. & Fitzpatrick J.W. 1984. *The Florida Scrub Jay: demography of a cooperative-breeding bird*. Princeton: Princeton University Press.

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