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Occurrence patterns of the endangered Yellow Cardinal *Gubernatrix cristata* in north-east Argentina: only in savannahs and at sites away from roads

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Summary

The endangered Yellow Cardinal Gubernatrix cristata is under pressure from habitat loss and from capturing for the cage bird trade. In north-east Argentina it is known to be associated with the Espinal ecoregion, but no information was available on habitat selection within this ecoregion. In Entre Ríos province, Argentina, we first sampled Yellow Cardinal presence in four environments: Espinal savannahs, Espinal open woodlands, riparian woodlands, and agricultural fields. Yellow Cardinals were only detected in savannahs. In a second set of surveys, transects were surveyed at sites with known presence of Yellow Cardinals and were placed within savannahs as well as nearby in open forests of only slightly different physiognomy. Yellow Cardinals were again only detected in savannahs. Tree density, shrub cover and height of herbaceous layer were lower in savannahs than in open woodlands. Ground-foraging Yellow Cardinals in savannahs foraged exclusively in grass patches with short grass of 3-12 cm height. Such short grass occurred in 75% of spots of savannahs sites, but only in 48% of open woodlands. Savannah sites with Yellow Cardinals were significantly further away from permanent roads than sites without Cardinals, likely a reflection of capture pressure near roads. We recommend establishing additional protected areas with a high proportion of savannah patches and with limited or no road access. The short grass used by foraging Yellow Cardinals requires maintenance through grazing. Rewilding with native herbivores in protected areas is preferable to attain natural herbivory, but during the initial stages of rewilding, cattle and sheep grazing are essential to avoid tree and shrub proliferation in savannahs. The Yellow Cardinal can also persist on private lands with Espinal vegetation under sustainable livestock grazing. Frequent and effective patrolling and road controls are essential to reduce illegal capturing.

Resumen

El Cardenal Amarillo Gubernatrix cristata, en peligro de extinción, está bajo presión por la pérdida de hábitat y por la captura para el comercio de aves de jaula. En el noreste de Argentina se sabe que está asociado con la ecorregión Espinal, pero no se dispone de información sobre la selección de hábitat dentro de esta ecorregión. En la provincia de Entre Ríos, Argentina, primero muestreamos la presencia del Cardenal amarillo en cuatro ambientes: sabanas del Espinal, bosques abiertos de Espinal, bosques ribereños, y campos agrícolas. Los Cardenales amarillos solo se detectaron en las sabanas. En un segundo conjunto de muestreos, las transectas se midieron en sitios con presencia conocida de Cardenales amarillos y se colocaron dentro de sabanas, así como cerca en los bosques abiertos de fisonomía ligeramente diferente. Los Cardenales Amarillos nuevamente solo se detectaron en las sabanas. La densidad de árboles, la cobertura de arbustos y la altura del estrato herbáceo fueron menores en las sabanas que en los bosques abiertos. Los Cardenales amarillos que se alimentan en el suelo en las sabanas, se alimentan exclusivamente en parches de pasto corto de 3 a 12 cm de altura. Este pasto corto se presentó en el 75% de los sitios en sabanas, pero solo en el 48% en los bosques abiertos. Los sitios de sabana con Cardenales Amarillos se encontraban significativamente más lejos de las carreteras permanentes que los sitios sin Cardenales, probablemente un reflejo de la presión de captura cerca de los caminos. Recomendamos establecer áreas protegidas adicionales con una alta proporción de parches de sabana y con acceso por carretera limitado o nulo. El pasto corto utilizado por los Cardenales amarillos en busca de alimento requiere mantenimiento a través del pastoreo.

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Es preferible repoblar con herbívoros nativos en áreas protegidas para lograr la herbivoría natural, pero durante las etapas iniciales de reintroducción de ganado vacuno y ovino, el pastoreo es esencial para evitar la proliferación de árboles y arbustos en las sabanas. El Cardenal Amarillo también puede persistir en tierras privadas con vegetación de Espinal bajo pastoreo de ganado sostenible. La vigilancia y los controles viales frecuentes y efectivos son esenciales para reducir las capturas ilegales.

Introduction

The presence of birds is closely related to the condition of their environments. The physical structure and composition of vegetation directly influence the use and selection of bird habitats (Milesi *et al.* 2008, Zhang *et al.* 2013, Fourcade *et al.* 2018). Among the factors that affect the habitat use of a species are its physiological and morphological limitations, the interaction with other species and the abundance and distribution of resources (Wiens 1989, Lombardini *et al.* 2001, Pigot *et al.* 2016, Girma *et al.* 2017). Forest birds are often seriously threatened, particularly in regions where habitat transformation and fragmentation are well advanced (Kajtoch *et al.* 2012, BirdLife International 2017).

The Yellow Cardinal Gubernatrix cristata is a member of the passerine Thraupidae family and the only representative of the genus (Campagna et al. 2011). It is distributed in southern Brazil, Uruguay and, principally, Argentina (Reales et al. 2019). In Argentina, its range extends from the north-east to the centre of the country, mainly in areas with a mixture of xerophilous woodlands and savannahs (Reales et al. 2019). This region is severely affected by habitat loss and fragmentation (Dardanelli et al. 2006, Calamari et al. 2018, Dardanelli and Bellis 2021). Populations of the Yellow Cardinal are currently small and are in decline due to habitat degradation and loss, and high capture pressure for the cage bird trade (Collar et al. 1992, BirdLife International 2021). This context led to Red List recognition in 1994 as a globally 'Endangered' species, as well as recognition as a nationally endangered species in Argentina and Uruguay (BirdLife International 2021), and as critically endangered in Brazil (Serafini et al. 2013). Most of the distribution of this species falls in Argentina, in the Espinal ecoregion, with several records in the neighbouring Monte and Chaco ecoregions (Reales et al. 2019, Domínguez et al. 2020).

Previous studies of the Yellow Cardinal addressed distribution (López-Lanús et al. 2016, Reales et al. 2019, Domínguez et al. 2020), reproduction (Domínguez et al. 2015, Beier et al. 2017, Beier and Fontana 2019, Segura et al. 2019), genetics (Domínguez et al. 2017, 2019) and brood parasitism (Azpiroz 2015, Domínguez et al. 2015, Beier and Fontana 2019). However, information is lacking on the structure and composition of vegetation used by the Yellow Cardinal. In Entre Ríos and Corrientes provinces, the species is associated with the Espinal ecoregion (Domínguez et al. 2015, Reales et al. 2019), a semi-arid region with thorny trees smaller than 5 m. Within the Espinal, there are different environments with subtle differences in vegetation structure and composition, but with different uses by birds (Calamari et al. 2018), though the exact habitat use by the Yellow Cardinal in the Espinal has not yet been described. We aimed to assess which environments are used by Yellow Cardinals in the Espinal. We first sampled occurrence of Yellow Cardinals in all environments in the Espinal landscape, including savannahs, open woodlands, farmland, and riparian vegetation, in proportion to availability in the landscape. As Yellow Cardinals were only found in savannahs, we tested whether the Yellow Cardinal is indeed associated with savannah environments and avoids the similar but slightly denser open woodlands in the same region, by sampling with standardized effort in the two environments at sites with known presence of the species, to exclude the possibility that absence in open woodlands was caused by a factor not related to habitat, such as capturing. We measured the structure and floristic composition of savannahs and open woodlands in the Nandubay District of the Espinal ecoregion and analysed the associated occurrence of the Yellow Cardinal. We assessed whether Yellow Cardinals preferentially forage in patches of short grass. As the Yellow Cardinal is heavily captured for the illegal cage bird market, we also investigated whether its local distribution was associated with savannah sites away from towns and permanently passable roads. The hypothesis behind this is that more remote sites may retain more Yellow Cardinals, because such sites will experience less capture pressure from poachers.

Methods

Study site

This study was conducted in north-east Argentina, in the departments of La Paz, Federal, Feliciano and Federación in the province of Entre Ríos (Figure 1).

Biogeographically, this area corresponds to the Chaqueño domain of the Neotropical realm. The Ñandubay District of the Espinal ecoregion mainly covers the south of the province of Corrientes and the north of the province of Entre Ríos. The dominant landscapes are undulating plains, low hills, floodplains, and alluvial valleys (Menéndez and La Rocca 2007, Oyarzabal *et al.* 2018). The climate of the region is subtropical with average annual rainfall between 1,000 and 1,300 mm, and average annual temperature between 18 and 20°C (Morello *et al.* 2012).

The vegetation of the Nandubay District of the Espinal is characterized by open xerophilous low woodlands (6–12 m high) dominated by ñandubay *Prosopis affinis* and espinillo *Vachellia caven* trees. The shrub layer, when present, is 2–4 m high with up to 50% cover (Menéndez and La Rocca 2007). The herbaceous stratum is dense and continuous, with grasses up to 1 m high, dominated by the genera *Paspalum, Axonopus* and *Andropogon*. The two most extensively occurring environments in this region are savannahs and open woodlands (Figure 2). Savannahs look like grasslands with sparsely distributed trees, and without shrub stratum. On the other hand, open woodlands had more of a shrub stratum and a higher tree density. The distinction between these vegetation types follows Oyarzabal *et al.* (2018).

The main economic activity in the region is cattle and sheep grazing (Menéndez and La Rocca 2007, Beier and Fontana 2019), with grazing occurring in both woodlands and savannahs. Increasingly, woodlands and savannahs in the study region are being



Figure 1. North-east Argentina (black line box), Nandubay District of the Espinal ecoregion (grey-dotted area), and study area in Entre Ríos province (grey striped circle).

cleared, primarily for agriculture (Maldonado *et al.* 2012, Guida-Johnson and Zuleta 2013).

Data collection

To select search areas for Yellow Cardinal populations we used Google Earth images, using as search criteria the presence of native vegetation (in satellite images readily distinguished by presence of irregularly scattered trees from featureless agricultural fields) and the presence of access roads. We ventured on foot up to 3 km from roads to avoid road-associated influences on habitats and bird populations. At the outset, no information was available on the preferential environments used by Yellow Cardinals within the Espinal ecoregion, so we sampled in all four environments within the Espinal: savannahs, open woodlands, riparian forests, and agricultural fields. We surveyed 36 search areas between May 2015 and July 2017, covering breeding and non-breeding seasons, in order to determine presence-absence of the species in the four environments. All study areas were on privately owned land with grazing by cattle and sheep, and occasionally horses, in Espinal woodland and savannahs, intermixed with agricultural fields of mostly soybean and corn crops. To locate Yellow Cardinals in each search area, we made up to three straight transects of 1 km in length covering all the different environments that were available in each site. Along each transect we performed three unlimited radius 10-minute point counts, at 500 m intervals (i.e. at 0, 500 and 1,000 m along each transect). At each point a recording of Yellow Cardinal song from southern Corrientes (provided by M. Dominguez, Aves Argentinas) was played to increase detections of the species. In addition, we surveyed 648 observation points with the use of playback from rural roads that connected the search areas. These rural roads were low-traffic dirt or

gravel access roads connecting villages and small towns with livestock farms and farmland. The points were located where roads crossed Espinal vegetation and emerged from travel across four departments in search of Yellow Cardinals, with 70% of point locations having savannahs on at least one side of the road, and the remainder of points in open woodland. At each roadside or transect point, we surveyed 10 minutes with four repetitions of 30 seconds of playback followed by two minutes of listening and observation (Bibby *et al.* 2000).

Because in the first exploratory set of surveys only portions of transects passed through patches of savannahs and open woodlands, and Yellow Cardinals may have been absent due to a factor not related to habitat (for instance, capturing), or may have been influenced by playback, we aimed to confirm the avoidance of Espinal open woodlands in spite of their close similarity in physiognomy to Espinal savannahs (Figure 2). In a second set of surveys, we determined at sites with known occurrence of Yellow Cardinals, without use of plavback, whether within Espinal vegetation Yellow Cardinals use savannahs or the similar open woodlands. We selected three sites (out of the original 36 search areas) with stable breeding populations of Yellow Cardinals, as evidenced by repeat sightings and presence of juveniles between 2015 and 2017. At each of these occupied sites, transects of 1 km were laid out, with each transect entirely in either an open woodland or savannah vegetation patch, and with pairs of savannah and open woodland transects laid out in parallel and separated by a standardized 300 m. The three sites were separated by 22 to 54 km, and in total contained 12 transects in savannah environments and nine in open woodland environments. We performed repeat transects of the same environment at a site separated by at least 250 m, determined as surpassing the maximum distance at which birds could be detected, thus avoiding



Figure 2. Two habitats surveyed for presence of Yellow Cardinals in the Espinal of northern Entre Ríos, Argentina: savannah (top) and open woodland (bottom).

pseudo-replication of detections. We surveyed the transects systematically for presence and abundance (number/km) of Yellow Cardinals, without playback, walked at a constant speed of 3 km/h, from dawn to 12h00 and from 15h00 to sunset, on days without rain and with wind speeds under 20 km/h. We performed surveys in spring and summer, four in 2017 and four in 2018 at each transect. The order in which each transect was visited was alternated. The total survey effort for these transect surveys was 84 h.

In order to relate presence of Yellow Cardinals to vegetation structure and composition in the two environments at the three sites, we measured the vegetation in three plots of 100 x 20 m perpendicular to each transect of 1 km. These plots were spaced at

the positions of 0, 500, and 1,000 m along each transect. In the plots, the following variables we measured: 1) height (cm) of the herbaceous stratum, 2) percentage of shrub cover and 3) tree density by species, for trees >20 cm DBH. The percentage of shrub layer cover were estimated visually, and the height of the herbaceous stratum was measured using a ruler (Braun-Blanquet 1979, Matteucci and Colma 1982). We also recorded the height of grass vegetation at spots where Yellow Cardinals foraged and contrasted this with the available, measured grass heights in savannah environments.

Out of the first set of 36 search areas, 22 included savannah environments. We used these 22 search areas with savannahs to examine the relationship between Yellow Cardinal presence at sites and the distance of these sites to towns and roads. For each search area the straight distance to the nearest gravel or asphalt road, and the road distance to the nearest town, were measured in Google Earth. Distances to asphalt or gravel roads were considered because these are permanently accessible whereas dirt roads are frequently not passable after rains. Towns were regional population centres of between 5,000 and 10,000 inhabitants (San José de Feliciano, Federal, Las Paz, San Jaime de la Frontera and Chajarí) where most poachers are located, as judged from interviews with local landowners as well as from press coverage of seizures by police of illegally captured birds.

Statistical analysis

Because our vegetation plots were separated by distances of 500 m, each plot was considered an independent measurement. Shapiro-Wilk tests indicated that our measurements of tree density, shrub cover and height of herbaceous layer in savannahs and open woodlands, as well as distances of savannahs with and without Yellow Cardinals to roads and towns, were not normally distributed. Contrasts in these measurements were tested with Mann-Whitney U tests. The use and availability of short grass patches by ground-foraging Yellow Cardinals, and frequency of short grass spots in savannahs versus open woodlands, were tested with Chisquare tests.

To compare the specific composition and density of tree species at transects with the two types of environments, we performed a non-metric multidimensional scaling (NMDS) analysis. To perform this analysis, iterations with random starts were made until the best solution for the ordering (the lowest stress value) was repeated in two runs. Additionally, to complement the NMDS, we performed similarity analysis (ANOSIM) to compare the degree of similarity in the composition of the tree stratum among the group transects (open woodland vs. savannah). ANOSIM is a permutation procedure that produces an R statistic, which is an absolute measure of distance between groups. Large positive values (up to 1) of R indicate low similarity between the groups while low values (close to 0) indicate high similarity between groups (Assis et al. 2015). For multivariate analyses (NMDS and ANOSIM) we used the Bray Curtis dissimilarity index on a matrix of density of tree species (Dixon 2003). We performed the analyses using the R 3.3.3 program (R Core Team 2017) using the vegan packages (Oksanen 2011). Significance was accepted when *P* < 0.05.

Results

Occurrence patterns: savannahs vs open woodlands

At 108 transects of 1 km randomly sampling the available environments of savannahs, open woodlands, riparian forest, and agricultural fields, and surveyed with playback, Yellow Cardinals were only detected in savannahs. We then placed 21 transects of 1 km entirely within savannah environments or nearby these (at 300 m distance) entirely within open woodland environments, at sites where we had established presence of Yellow Cardinal populations, and surveyed at standardized effort without playback. Yellow Cardinals were again only detected in savannah environments. During these standardized effort surveys Yellow Cardinals were detected at nine out of 12 transects in savannah environments, with a total of 24 detections and with one to four individuals recorded per detection.

Structure and composition of vegetation in savannahs and open woodlands

The similarity analysis (ANOSIM) between groups of transects showed differences between the vegetation structure of open woodlands and savannahs (ANOSIM: R = 0.275, P = 0.006). Non-metric multidimensional scaling (NMDS) based on the specific composition of the tree community and the tree density of the species showed a clear separation of transects corresponding to open woodlands or savannahs. Among the 12 transects in savannahs, no differences were found in the vegetation of transects with or without detections of Yellow Cardinal. No significant relationships were found between the number of Yellow Cardinal detections at savannah transects and the vegetation measurements height of the herbaceous stratum, percentage shrub coverage, and tree density. The tree species that were more strongly associated with savannah transects were ñandubay Prosopis affinis followed by espinillo Vachellia caven, while in open woodlands transects it was algarrobo negro Prosopis nigra, followed by espinillo and guayabo Myrcianthes cisplatensis, and to a lesser extent chañar Geoffroea decorticans, coronillo Scutia buxifolia and others (Figure 3).

The density of trees was higher in open woodlands $(139 \pm 88.5 \text{ trees/ha}, n = 36 \text{ plots})$ than in savannahs $(58 \pm 56.6 \text{ trees/ha}, n = 27 \text{ plots}, \text{Mann-Whitney } U = 792, Z = -4.24, P < 0.001).$ Similarly, shrub cover per plot was higher in open woodlands $(32.9\% \pm 26.5\%)$ than in savannahs $(13.5\% \pm 13.5\%, \text{Mann-Whitney } U = 715, Z = -3.17, P = 0.002)$. The herbaceous stratum was lower in savannahs $(10.2 \pm 8.7 \text{ cm}, n = 36)$ than in open woodlands $(15.6 \pm 10.5 \text{ cm}, n = 27, \text{ Mann-Whitney } U = 667, Z = -2.51, P = 0.01).$

Use and availability of short grass vegetation for groundforaging Yellow Cardinals

We observed 46 foraging events of 23 individuals of Yellow Cardinals in savannahs, with 11 foraging events from low perches and



Figure 3. Analysis of non-metric multidimensional ordering (NMS) of the relative abundance of tree strata species between different transects. Solid grey circles indicate savannah with Yellow Cardinal detections; open black squares indicate savannah without detections of Yellow Cardinal, solid black squares indicate open woodland. The open black triangles represent the relative position of the tree species in relation to the samples. *Myr cis: Myrcianthes cisplatensis, Vac cav: Vachellia caven, Pro nig: Prosopis affinis, Geo dec: Geoffroea decorticans, Scu bux: Scutia buxifolia.*

35 foraging events on the ground. On all occasions that Yellow Cardinals foraged on the ground in savannahs they were in patches with short grass of 3–12 cm height, using such short grass patches in a higher proportion than available ($\chi^2 = 11.7$, df = 1, *P* <0.001). The percentage of spots with short grass of 3–12 cm as used by ground-foraging Yellow Cardinals was higher in savannahs at 75% (out of *n* = 36) than in open woodlands at 48% (out of *n* = 27, $\chi^2 = 10.4$, df = 1, *P* = 0.001).

Presence-absence in savannahs vs distances to the nearest roads and towns

At 648 playback stations in Espinal vegetation along rural roads, not a single Yellow Cardinal was detected. Among 22 savannah sites that we searched for Yellow Cardinals, distances to permanent roads were significantly larger for sites with presence of Yellow Cardinals than for sites without Yellow Cardinals, with means of 6.1 km and 1.2 km respectively (Table 1). We examined whether absence of Yellow Cardinals from savannahs near roads could be explained by a difference in the size of savannah areas relative to distances to roads, but this was not the case: the 22 savannahs varied in area from 29 to 337 ha, and there was no relation in the area of the savannahs with distance to roads ($r^2 = 0.0009$, P =0.90). The mean distance to the nearest town was 30.8 km for savannah sites with presence of Yellow Cardinal and 18.1 km for sites with absence of Yellow Cardinal, but this difference was not significant (Table 1).

Discussion

Savannah habitat preference

Yellow Cardinals were only detected in savannahs, indicating that they have a clear preference for inhabiting this environment in the Espinal ecoregion in north-east Argentina. Savannahs are dominated in the tree stratum by ñandubay trees. Our finding of an association of Yellow Cardinal with ñandubay-dominated savannahs agrees with observations by Domínguez et al. (2015), Beier et al. (2017) and Beier and Fontana (2019). These studies described the nesting habitat of the Yellow Cardinal as savannahs in the province of Corrientes, in north-east Argentina and in the state of Rio Grande do Sul, in southern Brazil with a physiognomy and species composition with characteristics as we found in northern Entre Ríos. These studies reported that the majority of Yellow Cardinal nests were built in ñandubay trees, and this agrees with our nesting observations in northern Entre Ríos (Reales 2020). At our transects with presence of Yellow Cardinals we found that more than 50% of the trees were ñandubay, so it seems the cardinals mostly use these trees in proportion to availability. However, it is possible that Yellow Cardinals are tied to savannahs dominated by ñandubay trees for other factors such as foraging or predator visibility, and so used ñandubay trees for nesting simply because of availability in this environment, rather than for a preference for ñandubay trees because of nesting requirements. Segura et al. (2019) found Yellow Cardinal nests in the south of the geographical distribution solely in chañar trees.

We found in savannahs that the most representative tree species was ñandubay, and that the most representative species of open woodland was algarrobo negro, while espinillo follows it in order of importance in both environments. Oyarzabal *et al.* (2018) also mention that savannah environments are composed of ñandubay and espinillo trees. Thus, presence of ñandubay trees, in combination
 Table 1. Distances from sites with savannah environments to roads and towns and presence or absence of Yellow Cardinal Gubernatrix cristata.

Site number	Yellow Cardinal	Distance to the nearest permanent	Distance to the nearest
Site number	518185		Village (Kill)
1	Absent	0.5	19.0
2	Absent	2.0	23.5
3	Absent	2.5	16.0
4	Absent	0.5	5.0
5	Absent	0.5	8.5
6	Absent	0.5	6.0
7	Absent	0.5	26.0
8	Absent	0.5	33.0
9	Absent	0.5	17.0
10	Absent	0.5	19.0
11	Absent	0.5	25.0
12	Absent	6.0	15.5
13	Absent	0.5	3.0
14	Present	8.0	18.0
15	Present	1.5	11.0
16	Present	10.0	24.0
17	Present	0.5	26.0
18	Present	13.0	11.5
19	Present	0.5	24.0
20	Present	1.0	25.0
21	Present	14.0	62.0
22	Present	6.0	56.0
N Absent	13		
N Present	9		
Mean absent		1.2	18.1
Mean present		6.1	30.8
Median absent		0.5	19.0
Median present		6.0	24.5
Mann-Whitney U, W		22.5	34.0
Р		0.01	0.11

with a wide spacing of trees and low shrub cover, can be used as criteria for search areas for Yellow Cardinal populations in this part of their global range, and can be used to select areas to release birds that were confiscated from cage bird traders or keepers (Domínguez *et al.* 2017).

The mean height of the herbaceous stratum was shorter in savannahs than in open woodland environments. On all occasions that we observed Yellow Cardinals foraging on the ground in savannahs they were in patches with short grass of 3–12 cm height. The foraging cardinals used short grass patches in higher proportion than that they used tall grass patches. Short grass allows Yellow Cardinals to walk on the ground for foraging (Beier and Fontana 2019). In the absence of native herbivores, grazing by cattle and sheep can be beneficial to generate and maintain the

short grass patches that Yellow Cardinals uses for foraging. Menéndez and La Rocca (2007) indicated that livestock grazing is more intense in savannahs than in open woodlands. This difference in livestock grazing intensity between the two environments likely explains the difference in frequency of short grass spots we found and could contribute to the exclusive use of savannahs by Yellow Cardinals.

Native herbivores and livestock in savannahs

The effects of livestock grazing on bird assemblages are highly variable (Davies et al. 2010, Neilly and Schwarzkopf 2019), partly because the effects of grazing livestock on ecosystems vary with the type of herbivore (Sankaran et al. 2008). Moreover, livestock grazing effects are difficult to assess due to scarcity of areas without livestock grazing (Bellis and Muriel 2015). Clarke (2002) and Jones (2000) showed that grazing decreases the survival of woody plants (shrubs and young trees), and Lenzi-Grillini et al. (1996) found an increase in woody species because of the exclusion of grazing in a protected ecosystem. If extensive cattle ranching in the Espinal is contrasted with the complete exclusion of livestock, as is usually the case in protected areas, the Yellow Cardinal may be particularly affected when livestock are removed (Duval et al. 2019). An example of these dynamics relevant to the Yellow Cardinal is El Palmar National Park in Argentina. At the time of its creation, the park had a physiognomy of savannahs with palm, ñandubay and espinillo trees and a herbaceous stratum maintained by livestock grazing. Then, with the exclusion of livestock, and absence of abundant native herbivores, a marked invasion of trees and exotic shrubs occurred (Batista et al. 2014). There are records of the Yellow Cardinal from El Palmar before and shortly after the national park was established (Chebez and Morandeira 2005, R. Fraga pers. comm.). However, there are no recent records of presence of Yellow Cardinal in this national park (Marateo et al. 2009). The exclusion of grazing in systems that have evolved in the presence of large herbivores can reduce or locally extinguish bird populations adapted to grazing-controlled vegetation (Bock 1999, García et al. 2008). In these environments, moderate loads of livestock can have positive effects on some bird species (Bock 1999, Macchi and Grau 2012), since grazing prevents the dominance of a few plant species with highly competitive capacity, as proposed by the hypothesis of intermediate disturbance (Connell 1978, Olff and Ritchie 1998). Native herbivores reduce the growth rate and foliar biomass of small trees and shrubs, having a positive effect on herbaceous cover (Augustine and McNaughton 2004). Similarly, cattle grazing depresses the woody cover when the animal load is moderate and may have some positive effects on ecological processes. It can sometimes be used to promote ecosystem or landscape restoration, especially in ecosystems with a long history of human use where the reintroduction of native herbivores is not possible anymore, or during transition to rewilding (Verdú et al. 2007, Sankaran et al. 2008, Ba Diao 2020). Livestock may replace the role of herbivores that existed in grassland and savannah environments in historical times (de Lima et al. 2018). The majority of introduced species are functional surrogates for extinct species and many restore metabolic functional groups (Lundgren et al. 2020). In the case of the espinal in north-east Argentina, the main natural herbivory came from pampas deer Ozotoceros bezoarticus, plain viscacha Lagostomus maximus), grey brocket deer Mazama gouazoubira, and capybara Hydrochoerus hydrochaeris. In recent history, populations of these species were reduced due to the transformation of their habitat by agriculture expansion and livestock grazing and the impact of hunting (Ripple *et al.* 2015, Perez-Carusi *et al.* 2017, Puechagut *et al.* 2018, Di Bitetti *et al.* 2020).

A factor affecting Yellow Cardinal reproduction that should be weighed in a choice between native herbivores and livestock is brood parasitism by Shiny Cowbird *Molothrus bonariensis*. Shiny Cowbird is an extremely generalist brood parasite (Lowther 2018) and is a threat to Yellow Cardinal populations through a clear negative impact on its reproduction (Azpiroz 2015, Domínguez *et al.* 2015, Beier and Fontana 2019, Atencio *et al.* 2020). Habitat fragmentation, opening of habitats and livestock supplemental food provisioning (including corn, sorghum, and oats in food lots that are readily exploited by cowbirds) associated with livestock farming generate favourable conditions for Shiny Cowbird range expansion and increase their populations (Arendt and Vargas-Mora 1984, Post *et al.* 1993, Robinson *et al.* 1995). Grazing management of savannahs with native herbivores will result in fewer Shiny Cowbirds and less nest parasitism.

Yellow Cardinal occurrence away from permanent roads

In our wide-ranging search and transect counts in northern Entre Rios, Yellow Cardinals were only detected at savannah sites away from permanent roads, and this was independent from the sizes of savannahs relative to distance to roads. Capture pressure near roads likely explains this pattern of Yellow Cardinal absence, because most poachers work from roads with a car to carry poles, nets, a cage with a live lure Yellow Cardinal, and playback equipment, and are based in regional towns (Acosta 2013, Destro et al. 2019, Reales 2020), as also judged from personal observations, press coverage of illegal bird capturing, and conversations with local landowners and with police and gendarmes patrolling the study region. In a geographical analysis of the global distribution of the Yellow Cardinal, it was found that at 33% of points where the species was historically present but currently absent, suitable habitat remains as shown on satellite images. These absences were similarly interpreted as the result of capture pressure (Reales et al. 2019). López-Lanús et al. (2016) also pointed out the detrimental effect of captures on Yellow Cardinal populations. Alternative explanations for absence of birds near roads include habitat fragmentation, traffic noise, roadkill, and other disturbance, factors considered by Silva et al. (2017) to explain reduced species richness and abundance of birds near roads in an Espinal area in southern Brazil. However, Silva et al. (2017) found the main negative effects of these factors at only 10 m distance from roads, and that at 250 m negative impacts attenuated. As roads negatively affected Yellow Cardinal presence at a distance of up to 14 km, we consider capture pressure the more plausible explanation at such distances.

Conclusion

In north-east Argentina, a major global stronghold of the Yellow Cardinal, this 'Endangered' species is closely associated with savannah environments with ñandubay trees, and mostly persists at sites 0.5–14 km away from permanent roads. We recommend the establishment of additional protected areas in the region with a high proportion of savannah patches and with limited or no road access. Rewilding with pampas deer, plain viscacha, grey brocket deer, and capybara in these areas is preferable to attain

natural herbivory, to avoid Shiny Cowbird parasitism of Yellow Cardinals and to restore natural ecosystem interactions, but during the preparation and initial stages of reintroduction and recovery of native herbivores, it is essential to keep savannahs open with cattle and sheep grazing and avoid tree and shrub proliferation. The Yellow Cardinal can also persist in multipleuse areas on private lands with Espinal vegetation and livestock grazing, and there should be incentives for farmers to maintain this land use and avoid conversion to agriculture. In all areas with current or potential occurrence of Yellow Cardinal there should be frequent and effective patrolling and road controls to reduce illegal capturing.

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