Yellow Cardinal (*Gubernatrix cristata*) males respond more strongly to local than to foreign dialects

PABLO ANDRÉS FRACAS,*[1,2] (iD) JUAN MANUEL ROJAS RIPARI,[1] (iD) BETTINA MAHLER[1] & MARISOL DOMÍNGUEZ[3] (iD)

[1]*Departamento de Ecología, Genética y Evolución, Instituto de Ecología, Genética y Evolución de Buenos Aires (IEGEBA-UBA-CONICET), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, Ciudad Autónoma de Buenos Aires (C1428EGA), Argentina*

[2]*División Ornitología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-CONICET), 1405, Ciudad Autónoma de Buenos Aires, Avenida Ángel Gallardo 470, Argentina*

[3]*Unit of Evolutionary Biology/Systematic Zoology, Institute for Biochemistry and Biology, University of Potsdam, Potsdam, Germany*

Bird song is a culturally transmitted behavioural trait strongly tied to territory defence and mate attraction in oscine passerines. Divergent song variations can appear in different populations of the same species as a consequence of multiple factors generating geographically distinct songs also termed dialects. Most studies show that males react more strongly towards local dialects, potentially as a by-product of evolutionary divergence between populations, although other hypotheses have been suggested. In addition, females are hypothesized to show stronger responses to local songs as this may lead to greater reproductive success. In this context, song may become a prezygotic barrier for reproduction. The Yellow Cardinal *Gubernatrix cristata* is an endangered species of the South American thorny shrubland that has suffered from population fragmentation due to habitat destruction and its capture for the illegal wildlife trade. Genetically different groups that sing their own dialect have been studied in the context of a conservation programme that intends to restore and preserve natural populations by releasing individuals that are recovered from the illegal pet market back into their area of origin. Although dialects have been identified, it remains unknown whether there is vocal recognition between the populations. In this study, we performed playback experiments in two populations and found that male Yellow Cardinals reacted more strongly to the local dialect, although the foreign dialect was still recognized. This information is important as it is not always possible to genetically assign an individual to its geographical origin before release, which could contribute to a secondary contact scenario where dialects play a critical role for settlement and reproduction.

Keywords: behavioural isolation, birdsong, conservation, oscine passerines.

Songs of oscine passerines comprise a series of long and complex vocalizations usually produced by males during the breeding season (Clutton-Brock 2009, Odom *et al.* 2014, but see Austin *et al.* 2021). They are considered a cultural trait in this group as song is learned by imitation of other conspecifics and perfected over time (Catchpole & Slater 2008). Song functions as one of the main mediators in sexual interactions as males use it to attract conspecific females and stimulate their copulation display (Searcy *et al.* 1981, Searcy & Marler 1981, Catchpole 1987, Clayton 1990, Leboucher *et al.* 1994). Vocal learning allows for more complex acoustic signals, which may in turn be sexually selected by females (Slabbekoorn & Smith 2002). Songs are also important in the

*Corresponding author.
Email: pafracas@gmail.com

context of intraspecific competition between males that use them to signal an occupied territory, avoiding the need to spend energy in chasing and fighting another male to defend it (Catchpole & Slater 2008).

Within each species, song may vary along its distribution as a result of factors such as different dispersal capacities, cultural drift and/or cultural, natural or sexual selection (Mundinger 1980, Lynch 1996, Gordinho *et al.* 2015). Song variants may appear or disappear as a consequence of an inexact copy of the conspecific song (Slater *et al.* 1980, Lynch 1996, Lachlan & Slater 2003, Irwin 2012) or differences in the conditions in which the young are raised, which may allow some groups of individuals to perform differently in song learning (Nowicki & Searcy 2004). Some song variants can also be preserved over time through different mechanisms of sexual selection if females select males according to particular song traits (Slabbekoorn & Smith 2002). Acoustic differences between locations that are distinctive and consistent are considered here as dialects (Marler & Tamura 1962, Baker & Cunningham 1985, Podos *et al.* 2004, Podos & Warren 2007).

In species where dialects exist, song differences may become a prezygotic reproductive barrier (Servedio 2001) when, for example, females prefer local over foreign songs (Baker *et al.* 1981, Searcy *et al.* 2002, Danner *et al.* 2011) or, more rarely, when males respond more strongly to foreign songs, displacing the 'foreigners' and reducing their chances of mating (Slender *et al.* 2018). In this way, gene flow is reduced and populations with different dialects may become reproductively isolated (Keller & Waller 2002). In cases where habitat loss and fragmentation turn contiguous populations into small and isolated groups of individuals, not only do the individuals become physically separated, but also dialect formation can become accentuated (Laiolo & Tella 2007). Dialects as a prezygotic reproductive barrier become important for conservation when programmes managing endangered species include translocation of individuals to reinforce natural populations.

The Yellow Cardinal *Gubernatrix cristata* is a globally threatened oscine songbird of the family Thraupidae found in the thorny shrubland forest from the southern extreme of Brazil to central Argentina, including Uruguay (Ridgely & Tudor 1997). During the last century, large numbers of birds, mostly males, have been illegally captured for the cage

trade at the same time that habitat fragmentation was caused by the transformation of forests into agricultural landscapes and cattle pastures (Pessino & Tittarelli 2006, Ministerio de Ambiente y Desarrollo Sustentable & Aves Argentinas 2017, Reales *et al.* 2019). This means the species now occurs only in isolated populations with about 1500–3000 individuals left, prompting a categorization of Endangered by the IUCN (BirdLife International 2022). In Argentina and Uruguay, four main groups have been found to be genetically differentiated and were defined as isolated management units (MUs) (Domínguez *et al.* 2017). Moreover, differences between the songs of the MUs have also been described (Domínguez *et al.* 2016), leading to the conclusion that each forms a distinct dialect and should be considered a 'culturally significant unit' (Ryan 2006). However, inter-group recognition of dialects produced by birds from different MUs has not yet been tested.

Since Yellow Cardinal populations are currently small, isolated and exhibit different dialects, we analyse the role of behaviour (in this case recognition of conspecific songs) as a prezygotic reproductive barrier between different MUs. This is critical in light of the conservation programme that releases Yellow Cardinals recovered from wildlife trafficking back into the wild (Dominguez *et al.* 2019), where they might be reintroduced into a wrong MU, allowing a secondary contact scenario. Releasing individuals into the incorrect MU might compromise their fitness if the ability to integrate into the local population depends on their song. If dialects are differently recognized, foreign individuals might face a reduced reproductive success due to a lower capacity to attract females or compete with local males in territorial defence. Thus, long-term reintroduction success may depend on the ability of introduced individuals to acquire unfamiliar local dialects. However, song acquisition in passerines primarily occurs before the first reproductive attempt (Catchpole & Slater 2008), and it remains unclear whether reintroduced individuals can re-adapt their songs. To test the hypothesis that different song traits affect dialect recognition we used a playback experiment (call broadcast) to examine the response of males to simulated intruders singing vocal or foreign songs in two different MUs. This experimental approach has been encouraged when evaluating premating reproductive isolation between populations as it provides a stronger measure than

acoustic trait analysis (Freeman & Montgomery, 2017). Several studies have shown that songbirds respond more strongly to local dialects, and this has been associated with evolutionary divergence between populations (Parker *et al.* 2018). In this context, we discuss the biological implications both for the individuals released and the MU that is intended to be preserved, to contribute to future management decisions in the conservation programme.

METHODS

Study site

We conducted fieldwork at two sites, each in a different MU (see Domínguez *et al.* 2017 for MU delimitation): Estancia La Colorada (36°48′13.99″S, 64°37′12.94″W), in La Pampa Province (southern MU), and Estancia La Paz (29°12′40.87″S, 58°15′54.37″W), in Corrientes Province (northern MU). These areas are located within a thorny shrubland habitat where the dominant vegetation is xerophilous forest, with a predominance of tree species of the genus *Prosopis* (Cabrera 1971). As Yellow Cardinals are year-round residents in their entire distribution (Jaramillo 2020), we selected the most distant MUs in Argentina to inspect vocal recognition. Ensuring the greatest geographical distance between sampling localities we minimized the possibility of previous contact between the individuals of both populations.

Pilot study and experiment setup

In 2016, we performed pilot experiments *in situ* to test the distance at which the stimulus was perceived and to identify the variables that represented the response to the song played. At a site not included in the experiment, male Yellow Cardinals that were paired with females were caught and colour-banded, and their songs and the volume at which they sang were recorded. These birds were then exposed to 3 min of another conspecific and their response was recorded. We found that males sang with an intensity of 55–65 dB within a 10 m range, and males within at least 100 m were able to hear the stimulus played around those levels, as they all interrupted their activities, approached the speaker, sang and flew around the speaker around a 20 m range throughout the 3 min. The time in which the response

ceased was variable between individuals, from within a minute after the stimulus stopped to a continued response for several minutes. In 2017, individuals were marked and experiments were performed at both MUs. We located male adult Cardinals that were paired with a female and were defending their territory. These individuals were captured via mist netting and banded with an aluminium ring and a unique combination of two colour rings. We also recorded each banded male's song with a digital handy audio recorder (Zoom H4N, Zoom Corporation, Haup-Page, NY, USA) in wav format at a 44.1 kHz sampling rate and 16-bit resolution, and measured the intensity of the songs with a digital sound level meter (ColeMeter GM1351, Benetech, Shenzhen, China) at 10 m (values ranged from 50 to 70 dB).

These recordings and others obtained in a previous study (Domínguez *et al.* 2016) were used for the creation of the playback stimuli. To ensure that responses were exclusively directed to conspecific songs, we used the software Raven Pro 1.4 (Charif *et al.* 2010) to select full clear songs of a single male, where no other heterospecific songs were recorded in the background at the same time. Then we used Audacity v3.0.0 (Audacity Team 2017) to compile songs (which each lasted 3–8 s) from a single male, with a 10–15 s interval between songs (similar to the silent periods between songs typical of cardinals), into a final 3-min wav-format playback file, containing 10–13 different songs and up to 13 songs from each male, for each treatment. The same process was conducted for the creation of the control playback stimulus, with 14 different songs of different local Rufous-collared Sparrows *Zonotrichia capensis* (Passerellidae; Fig. 1), that lasted 3 s and with a 10 s interval between songs. We selected this species because of its high abundance in both MUs and its conspicuous song (Rising & Jaramillo 2020). We assumed that it was well known by the Cardinals and therefore would not provoke an aggressive response.

Playback experiment

We conducted the experiments during the early morning (06:00–10:00 AM) and in the afternoon (5:00–7:00 PM), when birds are most active (Ralph *et al.* 1996). Within each of the identified territories, we searched for the focal male using 8 × 42 m binoculars. After it was spotted, we selected a conspicuous tree in which the speaker was hidden between

the branches, and played one of the 3 min stimuli: Local (L, songs from the same MU), Foreign (F, songs from the other MU) or Control (C, songs of a local *Z. capensis*). The playback volume level was standardized at values near 60 dB ($\pm$2 dB) at 10 m from the speaker using the same digital sound level meter used during the recordings. We recorded the male's behaviour during the Playback period and during a silent Post-Playback period of at least 10 min, to avoid overlapping between responses. After both periods, we repeated the procedure sequentially with the other two stimuli. We controlled for pseudoreplication in mutiple ways: (1) the order in which the different stimuli were reproduced was randomly sorted before the experiments, and each male was assigned a different combination; (2) none of the local males were exposed to their own song as the local stimulus; (3) the foreign and control songs belonged to different individuals in each experiment; and (4) the control songs always belonged to different local *Z. capensis*.

Aggression measures

We combined the Playback and Post-Playback periods *a posteriori* into a response period in which we recorded four aggression measures (based on the pilot experiments): (1) time (s) spent singing within 100 m from the speaker, (2) time (s) spent within 20 m from the speaker, (3) distance (m) of the closest approach and (4) response time (s) calculated as the total time since the start of the stimulus until the bird lost interest in it. We considered that the individual lost interest in the stimulus played when it was eating or outside the 100-m radius from the speaker for a 3.5-min interval. We chose this time interval because there is an abrupt decay in the number of cardinals that resumed their response after this time elapsed (Fig. S1).

Statistical analysis

All statistical analyses were conducted using R software version 4.0.5 (R Core Team 2021). The four aggression measures were standardized, reduced and combined through a principal components analysis using the *prcomp* function from the base package *stats* (R Core Team 2021). According to the broken-stick criterion (Legendre & Legendre 2012, Silva *et al.* 2020), we retained the only principal component (PC) that explained more variance than would be expected by

randomly dividing the variance into the components (Fig. S2) as a single combinatory behavioural measure (hereafter 'overall behavioural response'). We extracted the males' scores in the PC and performed a Pearson's correlation with the original variables to check that all the aggression measures were significantly represented. To determine if there was an effect of the song (L, F or C) in the response of the males, we analysed these scores with a general linear mixed model built with the package *nlme* 3.1-157 (Pinheiro *et al.* 2022) and *identity* link, where the stimulus was included as a fixed factor. We controlled for the effect of the order in which the stimuli were played and the origin of the Cardinals tested including order and MU as fixed factors. The variance of each male was controlled by including individual identity as a random factor. Variance was modelled through the VarIdent function, allowing a different variance for each stimulus. Tukey's multiple comparisons tests were perfomed *a posteriori* to analyse if the response differed between the stimuli with the package *multcomp* 1.4-20 (Hothorn et al. 2008). Significance levels were established at 0.01. Normality was corroborated through Shapiro–Wilk's test (W = 0.98, P = 0.95), and homoscedasticity was checked through graphics of residuals versus predicted values from the model.

Ethical note

Due to the conservation status of our focal species, all procedures were performed between September and early October during the early breeding season, when males are establishing their territories with their breeding pairs (Domínguez 2015). In this way we minimized disruption of their breeding activities. Experimental procedures were carried out under legal authorization of the Governmental Offices of La Pampa and Corrientes Provinces, and our experimental protocol (No. 147) was approved by the Institutional Commission for the Care and Use of Laboratory Animals of the University of Buenos Aires.

RESULTS

Aggression measures

A total of nine experiments (n = 9 individuals, Data S1) were conducted Yellow Cardinal male responses varied for all aggression measures
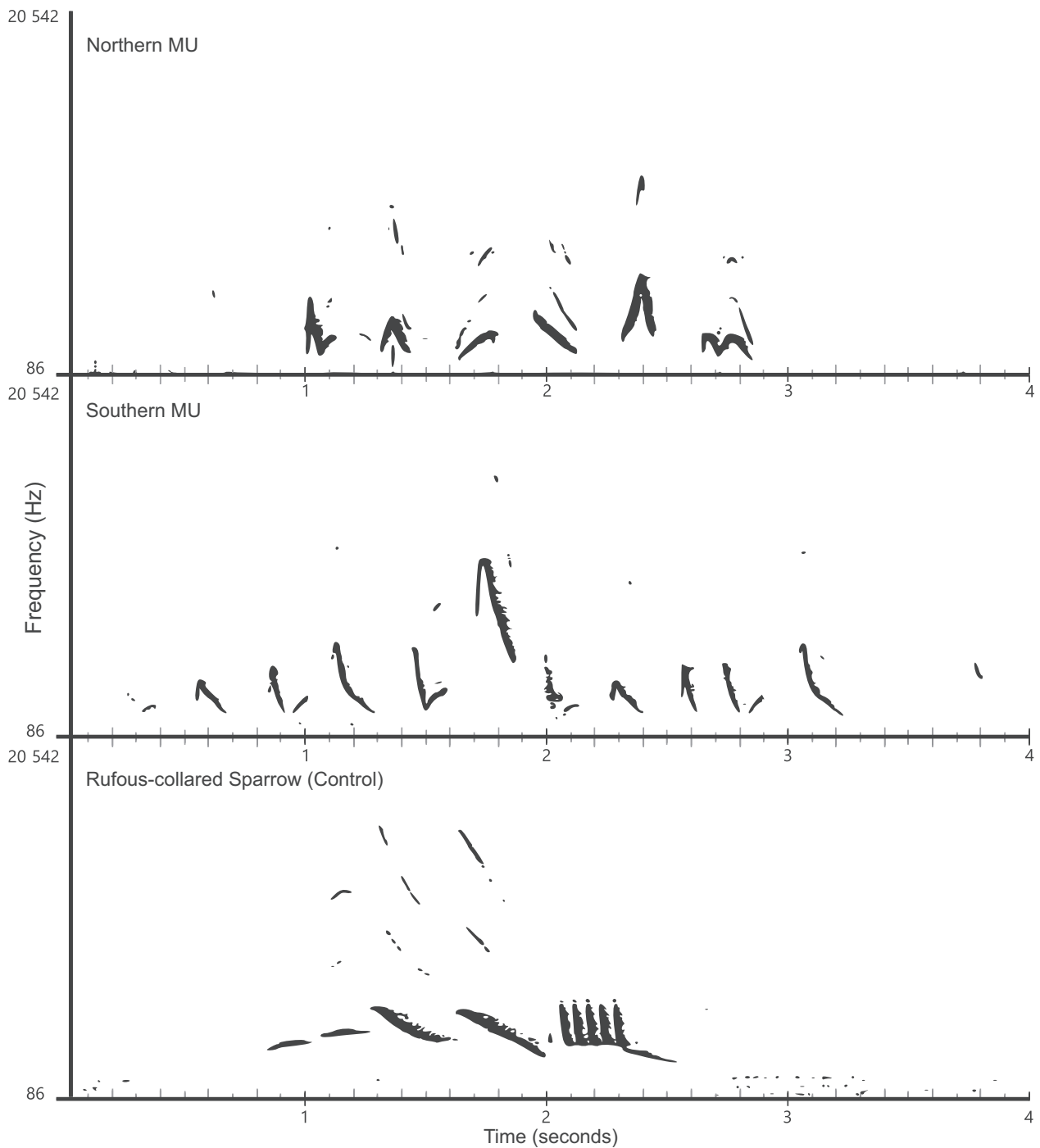
Figure 1. Examples of songs used in experiments. Spectrogram comparing two of the Yellow Cardinal's dialects (southern and northern management units (MUs)) and a heterospecific song from a species present in both MUs, the Rufous-collared sparrow *Zonotrichia capensis*. Parameters were set as follows in Sonic Visualizer (Cannam *et al.* 2010): Hann window of 1024 samples, bandwidth: 86–20 542 Hz, frequency scale: linear, gain: 13.5 dB, window size: 1024 samples, window overlap: 93.75%, oversampling: 1×, all Bins displayed.

recorded depending on the type of song played (Fig. 2a). When the heterospecific song was played, the males sang (average time singing 17.89 ± 8.84 s) but did not enter the 20-m area surrounding the speaker in any case (average closest approach was 72 ± 9 m) and the mean response time was 295 ± 85 s. In response to conspecific foreign songs the males also sang (average time singing 31.56 ± 8.46 s), but in this case they did enter and stayed in the 20-m area (average time spent within 20 m 107.22 ± 48.95 s) and the average closest approach to the speaker was at a shorter distance than when the heterospecific song was played (average closest approach 38 ± 9.05 m). Despite these differences, the average response time was similar (average response time 448.56 ± 95.40 s). In contrast, when the conspecific local song was played the males sang during more time than in the other cases (average time singing 51.78 ± 6.75 s) and, similar to when the foreign song was played, they entered and remained in the 20-m area (average time spent within 20 m 174.22 ± 54.89 s), but in this case, the average closest approach to the speaker was at an even shorter distance than for the other songs (21.11 ± 4.23 m). Lastly, the average response time was the longest (664.22 ± 75.70 s).

Overall behavioural response

The first PC explained 65.98% of the total variance and was able to represent the four variables (correlation between original variables and PC scores > |0.7|, Table 1), suggesting that the PC is indeed a good indicator of male Yellow Cardinal overall response to the playbacks. Birds with high PC scores represent individuals that had long response periods during which they spent a long time singing within 100 m, remained for a long time within 20 m of the speaker, and approached it more closely.

Yellow Cardinal males' overall behavioural response differed according to the song played (Wald's χ^2 = 51.64; df = 2; P < 0.001). There was no effect of the order in which the different stimuli were played (Wald's χ^2 = 5.24, df = 2, P = 0.07) nor of the management unit of origin of the tested individuals (Wald's χ^2 = 1.24, df = 1, P = 0.27, Table S1). The overall behavioural response of the males was stronger towards conspecific songs (Tukey's test F–C P < 0.001; Tukey's test L–C P < 0.001). All the individuals tested responded more strongly to a local than to a foreign playback (Tukey's test L–F, P = 0.007, Table 2, Fig. 2b).

DISCUSSION

General results

We provide evidence that Yellow Cardinals are able to distinguish between dialects, eliciting stronger responses towards local songs. In particular, Yellow Cardinals showed longer response periods during which they remained closer to the speaker, sang for a longer time and approached the audible stimulus at the closest distance when confronted with a local dialect. These results reinforce the importance of the recommendation that Yellow Cardinals should be genetically assigned before release as their fitness might be compromised when released in the incorrect MU. To our knowledge, this is the first time this kind of experiment has been performed on an endangered songbird species with the particular aim of directly contributing to its conservation management.

Vocal communication is a conspicuous behaviour, well described in many bird species (Lovette & Fitzpatrick 2016), and the response of either males or females to different dialects has been widely studied. The results vary depending on the species, including similar responses of territorial males towards different dialects (Ratcliffe & Grant 1985, McGregor et al. 2002, Danner et al. 2011), stronger responses towards foreign dialects (Baker et al. 1981, Petrinovich & Patterson 1981, Ratcliffe & Grant 1985, McGregor et al. 2002, Hansen 2007, Danner et al. 2011) and, in most cases, stronger reaction to familiar dialects, followed by foreign and finally heterospecific songs (Slabbekoorn & Smith 2002). According to our results, male Yellow Cardinals follow the latter pattern. In non-migratory species, this response is presumed to emerge as a by-product of evolutionary divergence between populations, although it has also been suggested to originate from a cognitive process that discriminates conspecific from heterospecific songs, and for which foreign songs are less readily recognized as conspecific (Parker et al. 2018). Either or both mechanisms might be occurring in Yellow Cardinal populations that remain isolated, where individuals do not interact due to habitat fragmentation and sing different dialects. This isolation might have narrowed
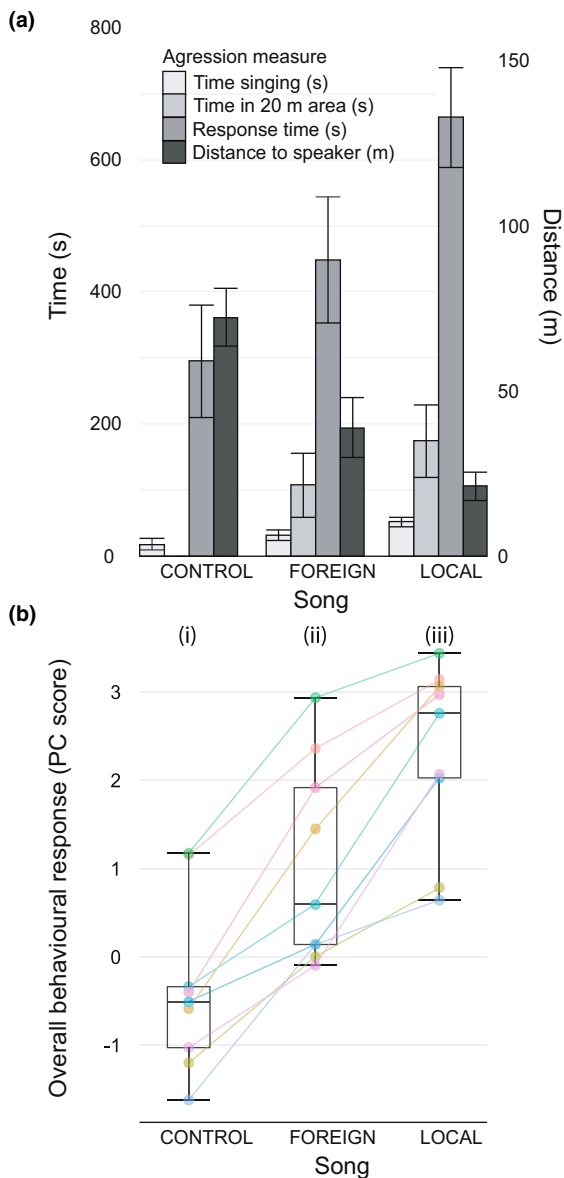
Figure 2. Male Yellow Cardinal behavioural responses towards different dialects. (a) Responses to control, foreign and local dialects, measured as mean (±standard error) time spent singing within 100 m of the speaker (s), time spent within 20 m of the speaker (s), response time (s) calculated as the total time since the start of the stimulus until the bird lost interest in it (left vertical axis) and distance of the closest approach (m, right vertical axis). (b) Overall behavioural responses to control, foreign and local dialects. Whiskers represent the minimum and maximum values, while the limits of the box represent lower and upper quartiles. The middle thick line inside the box represents the median. (i), (ii) and (iii) indicate significant differences ($P < 0.01$) between songs played. Different dots and lines represent each male's response.

Table 1. Aggression measures in the overall behavioural response. Pearson's correlation coefficients (loadings) of the aggression measures in the extracted principal component (PC) that explained 65.98% of the total variance.

Aggression measure	Load in first PC
Time in 20-m radius	0.74
Time singing	0.81
Minimum distance to speaker	0.83
Response time	0.87

Table 2. Different overall behavioural responses towards different dialects. Estimates, 95% confidence intervals (CI), standard errors and *P* values for the Tukey tests.

Contrast	Estimate	95% CI	Standard error	P value
Foreign–Control	1.48	0.78–2.18	0.30	< 0.001
Local–Control	2.82	1.82–3.82	0.43	< 0.001
Local–Foreign	1.33	0.32–2.35	0.44	< 0.006

the window of what is perceived as a conspecific song in each population, where individuals respond more strongly towards a local song and perceive the foreign dialect less strongly as one of their own species.

Although differences in song structure between dialects are evident, with Yellow Cardinals of the southern MU singing longer songs with shorter internote intervals (Fig. 1; Domínguez *et al.* 2016), our results show that the foreign dialects were still recognized by local males. Yellow Cardinals are vocal learners, which can promote song variation (Slabbekoorn & Smith 2002). However, song variation can also increase within populations, and thus slow the evolutionary rate of discrimination between premating signals, as greater absolute differences between songs are required to achieve discrimination (Freeman *et al.* 2017). This suggests that songs might not have diverged enough between Yellow Cardinal populations to render them unrecognizable as conspecific. Despite this fact, playback experiments provide a consistent assessment for premating reproductive isolation between populations at least when divergence in acoustic traits is low to moderate (Freeman &

Montgomery, 2017) and the stronger response towards local dialects suggests that behavioural isolation due to lack of dialect recognition might emerge in cases of secondary contact. Songbirds may respond weakly to foreign conspecific dialects because of lack of experience with them (Colbeck et al. 2010). However, alternative explanations have been proposed, such as the decptive mimic hypothesis which states that immigrants match local songs to appear local and reduce risks of aggression from established local individuals (Payne 1983, Rohwer 1982). Yellow Cardinals are residents and habitat fragmentation has isolated the MUs, probably limiting dispersal and the chances of deceptive mimicry occurring. In addition, the risk of responding to heterospecifics should drive increased discrimination, especially when closely related species are present (Hamao 2016, Parker et al. 2018). While the Yellow Cardinal distribution is shared with many confamilials (eight in the southern MU and 30 in the northern MU; Winkler et al. 2020), our study did not detect response differences between MUs.

Biological implications for males

Birdsong is a sexual signal, so it has direct consequences on reproduction, as it primarily mediates sexual interactions such as mate attraction and territorial defence (Kroodsma & Byers 1991). The song control system itself is part of the extended brain circuitry that mediates not only singing activity but appetitive and consummatory reproductive behaviours through steroid hormones (Ball & Balthazart 2020). Due to its role in mating and as a cultural trait, previous evidence in other bird species suggests that it may even drive the early stages of speciation (Whitehead et al. 2019). Therefore, it can indirectly affect population growth rates and it is considered a cultural trait relevant for population persistence and conservation (Laiolo 2010). For example, the Thick-billed Grasswren *Amytornis modestus* (Maluridae) occurs as two parapatric subspecies with different dialects. Genetic introgressions have occurred between the two subspecies (*A. m. indulkanna* towards *A. m. raglessi*), and this is associated with the fact that *A. m. indulkanna* males had a stronger aggressive response towards *A. m. raglessi* (subspecies in vulnerable condition due to cattle overgrazing) songs, while the latter had a similar response towards both songs, making them unable to defend their territories appropriately and

producing an asymmetric gene flow between the subspecies (Slender et al. 2018). In the endangered Regent Honeyeater *Anthochaera phrygia* (Meliphagidae), the production of atypical songs carried reproductive costs: males whose songs differed from the norm were less likely to be paired with a female (Crates et al. 2021). Our results suggest that, in cases of secondary contact, Yellow Cardinal males singing a foreign song may receive a weaker response from the local males which, at first, might seem an advantage by reducing the aggressive interactions between them. However, this may carry reproductive costs, as those individuals might be unable to defend their territory successfully or attract a female partner, thus being unable to mate and produce offspring with local females.

Biological implications for females

We focused on male responses because male–male competition is usually more tractable than female choice in experiments (e.g. Reichard 2014), particularly in this species, where males are the ones that sing and react aggressively in territorial defence (P. A. Fracas pers. obs.). This experimental approach has been widely used (De Rosa et al. 2022), assuming that males' responses reflect females' choice (Dingle et al. 2010, Hamao 2016). Moreover, studies that have assessed the response of both sexes have found no evidence that males were more discriminating than females (Uy et al. 2018). We expect females to be even more selective than males and therefore to respond in a similar way, as mistakes in song recognition might lead to hybridization (Qvarnström et al. 2006). However, in the southern MU, hybrids with Diuca Finch *Diuca diuca* have been documented (Bertonatti & López Guerra 1997, 2001, Pessino et al. 2002, Rodriguez & Bertonatti 2018). These events were associated with the lack of males in the region due to illegal trapping, in conjunction with song convergence between the species (Domínguez et al. 2016). Evidence suggests that, with conspecific male scarcity, Yellow Cardinal females may have reduced their vocal signalling thresholds for mate selection.

Male scarcity may also occur in other populations. According to our results, a released Yellow Cardinal male singing a foreign dialect can be recognized by local conspecifics and, considering that song recognition is not the only requirement for reproduction (Forslund & Pärt 1995), it

might have a chance to mate. However, in the presence of local males, the fitness of foreign males is likely to be reduced by the preference of local females for familiar songs. The behavioural response of female Cardinals in the field is difficult to measure as they are usually in the company of a territorial male, to which their behaviour is closely tied (P. A. Fracas pers. obs.). Future studies performed in captivity might help to distinguish the individual response of females to foreign and local dialects, and the relevance of dialects as a prezygotic barrier for reproduction in Yellow Cardinals.

Conservation management

Cultural traits such as song dialects can influence reproductive (Potvin *et al.* 2015) and social (Barker *et al.* 2021) behaviours, which ultimately affect fitness or even population viability (Laiolo *et al.* 2008). The study of vocal communication is becoming an important dimension within conservation management for endangered species (Ryan 2006, Laiolo 2010, Brakes *et al.* 2019, 2021, Lewis *et al.* 2021, Whiten 2021) and currently there is an emerging trend of research applying animal behaviour to this field (Rowe & Bell 2007, Kidjo *et al.* 2008, Bradley *et al.* 2014, Martínez & Logue 2020, Crates *et al.* 2021). To preserve each population's unique genetic and cultural traits, and hence the species' diversity, the use of individuals from the same source population or that present the same cultural traits has been recommended for translocations (Lewis *et al.* 2021). The source population of the Yellow Cardinals recovered from illegal trapping is usually unknown, because confiscation takes place close to selling points and not capturing points. Therefore, genetic assignment is crucial for a successful reintroduction programme (Dominguez *et al.* 2019). If male Yellow Cardinals are released back into another MU and sing a different dialect, they might create a disruptive environment for the local individuals by introducing new song variants and, according to our results, might receive weaker recognition from local birds and therefore will not be able to maximize their fitness.

CONCLUSIONS

We found evidence that male Yellow Cardinals recognize both foreign and local conspecific

dialects, but respond more strongly to the latter. These results reinforce the importance of the steps taken by the current Yellow Cardinal conservation programme (Dominguez *et al.* 2019) where individuals retrieved from the illegal trade are genetically assigned to their source population before release. These measures have proved to be effective, because genetically assigned Yellow Cardinals released back to nature in their corresponding MU have been observed with mating partners, defending territories and nesting (Atencio *et al.* 2020). While song type could potentially be used to assign males to their MU, only males vocalize and only during the reproductive period. Response to playbacks is particularly strong at the beginning of the reproductive season and then declines, and is very low during the non-reproductive period. Thus, song type is of limited use as a standardized method for geographical assignment. Releasing individuals without genetic assignment is a risk that grants only one benefit: maintaining population numbers in the short term. However, if these individuals receive a weaker response from local individuals and are not able to defend their territories and mate, or even disrupt genetic and cultural traits of the management unit, the costs of the management programme might be greater than the benefits. Therefore, we strongly recommend that efforts to assign each cardinal to its source population continue into the future.

CONFLICT OF INTEREST STATEMENT

The authors have declared no conflicts of interest.

ETHICS STATEMENT

The protocols and procedures were ethically reviewed and approved prior to the start of the study by the Comisión Insitucional de Cuidado y Uso de Animales de Laboratorio - FCEyN - UBA (protocol No. 147).

AUTHOR CONTRIBUTIONS

FUNDING

Data Availability Statement

The data that support the findings of this study are available in the Supporting Information of this article and in Open Science Framework.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. End of response period.

Figure S2. Broken stick criterion.

Table S1. Primary results.

Data S1. Contains all the behavioural variables raw data analysed with individual identity (Id), management unit (MU) association, stimulus played in each experiment and the order in which the stimulus was played.

Data S2. Data Analysis Script.