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Effects of fragmentation and landscape matrix on the nesting success of grassland birds in the Pampas grasslands of Argentina

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The loss of grasslands in southeastern South America has negatively affected grassland birds, leading to marked declines in their populations. However, the extent to which habitat transformation impacts on their reproductive performance, and whether the magnitude of these effects may be modulated by landscape matrices, is unknown. We assessed the effect of fragmentation on grassland bird reproduction by comparing the combined influence of fragmentation and landscape matrix on nesting success, brood parasitism and productivity of the Spectacled Tyrant *Hymenops perspicillatus* and the Brown-and-yellow Marshbird *Pseudoleistes virescens*. Surveys were undertaken in small grassland patches embedded within different landscape matrices (urban and agro-ecosystem) and in a large patch within a reserve. Reproductive performance was adversely affected by fragmentation. However, these effects were conditioned by matrix type, and the response was not the same for the two species. For Brown-and-yellow Marshbird, fragmentation resulted in higher rates of brood parasitism and lower productivity regardless of the matrix type, whereas for Spectacled Tyrant, we found a negative effect only in an agricultural matrix. The lack of extensive grasslands makes small patches important; however, knowing the effects of different matrix types is critical to predicting the conservation value of grassland patches, and the response of different species is not uniform.

Keywords: brood parasitism, *Cortaderia selloana*, *Hymenops perspicillatus*, nest predation, nest survival, *Pseudoleistes virescens*, South America.

Grassland is one of the most modified biomes on Earth because a high proportion has been replaced by crops or is subject to livestock grazing (Hannah *et al.* 1995). Loss and degradation of grasslands have negatively affected biodiversity worldwide (Foley *et al.* 2005) and particular species have undergone reductions in their distribution and numbers because of grassland loss (Donald *et al.* 2006, Askins *et al.* 2007, Azpiroz *et al.* 2012).

Grassland loss and modification usually result in habitat fragmentation, with a reduced patch size and increased distances between patches (Wilcove *et al.* 1986, Andrén 1994). In general, population declines have been associated with the fragmentation process, because grassland birds have lower nesting success in relatively small patches as a result of increased predation (Johnson & Temple 1990, Winter & Faaborg 1999, Herkert *et al.* 2003), and higher rates of brood parasitism (Johnson & Temple 1986, 1990, Walk 2001, Jensen & Finck 2004, Patten *et al.* 2006). Despite broad support for these general trends, inconsistencies have been documented even in well-studied systems. For example, nesting success may not be clearly influenced by patch size (Winter *et al.* 2006, Walk *et al.* 2010), or the effects may be small and variable (Davis *et al.* 2006) or nesting success may even be greater in relatively small patches (Skagen *et al.* 2005). Brood parasitism is

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mainly associated with forest edges (Johnson & Temple 1990, Patten *et al.* 2006), but Pietz *et al.* (2009) found lower rates of brood parasitism where tree cover in the landscape was greater. Regardless of the presence or otherwise of trees in the landscape, parasitism rates can also be strongly related to regional cowbird *Molothrus* sp. abundance (Herkert *et al.* 2003). As effects are ambiguous, the greatest challenge to understanding the effects of habitat fragmentation on grassland birds is the variability of observed responses to fragmentation or differential sensitivity (Walters 1998) across regions, landscapes, habitats, species and populations.

In a fragmented landscape, remaining habitat patches are immersed within a matrix composed of habitats that are different from the original (Wilcove *et al.* 1986). Different matrices can contain diverse assemblages and numbers of predators and thus differentially affect nest predation in fragmented habitats (Andrén 1995). Effects of fragmentation therefore vary depending on the matrix type, and may be even more important than the patch size itself (Burger *et al.* 1994, Winter *et al.* 2000). The greater the difference between the landscape matrix and the original habitat, the larger the expected effect. It has been found that nesting success of grassland birds declines closer towards woody edges, but not towards roads or agricultural fields (Winter *et al.* 2000, Walk *et al.* 2010). In this regard, nest survival has been shown to be greater in grasslands near abandoned crop fields or pastures than near forest edges (Bollinger & Gavin 2004). However, nest predation rates have been found to be similar between grasslands with forest edges and those bordering crop fields (Jensen & Finck 2004, Renfrew *et al.* 2005), and higher nest survival has even been found along forest edges (Ribic *et al.* 2012). In addition, Perkins *et al.* (2013) found that although birds avoided nesting near edges, daily nest survival did not differ among different types of edge. Furthermore, it is known that density and abundance of grassland bird species correlate negatively with urbanization (Bock *et al.* 1999, Haire *et al.* 2000, McLaughlin *et al.* 2014). However, the effects of the urban matrix on reproductive performance of grassland birds have been little studied.

Recently, Buxton and Benson (2015) found that nests in urban landscapes had lower nest predation rates than nests in more rural landscapes, and that brood parasitism was also less frequent in more urbanized landscapes. Accordingly, evidence for matrix effects on grassland habitats has been equivocal (Johnson 2001, Lahti 2001). Explanations are many, but one important consideration is the identity of nest predators (Chalfoun *et al.* 2002), possibly because of landscape-mediated differences in the predator community (e.g. Chalfoun *et al.* 2002, Rodewald & Kearns 2011). Predation of grassland bird nests is not due solely to edge predators and brood parasites but also to predators that live in the grassland habitat itself (Pietz & Granfors 2000, Renfrew & Ribic 2003), as well as predators that are habitat generalists (Thompson *et al.* 1999, Renfrew & Ribic 2003). Therefore, the relative importance of matrix effects probably depends on the species composition, abundance and activity of nest predators (Ribic *et al.* 2009, 2012).

Grasslands in southeastern South America form one of the most extensive grassland ecosystems in the Neotropics and have been transformed by development of a vast livestock industry, arable agriculture and afforestation (Soriano *et al.* 1991, Overbeck *et al.* 2007). Habitat homogenization in the agro-ecosystems of the region has negatively affected bird diversity, leading to local extinctions and marked population declines over the past 100 years (Fraga *et al.* 1998, Di Giacomo & Di Giacomo 2004, Codesido *et al.* 2011). As a result, 22 species are considered globally threatened or near threatened, and many others are considered endangered at national or regional levels (Azpiroz *et al.* 2012). The Pampas region in particular has been greatly transformed (Baldi *et al.* 2006), and most native tall-grasslands are only preserved in the eastern parts of the region, mainly because these areas are unsuitable for intensive agriculture as they have brackish or sandy soils or are frequently flooded (León *et al.* 1984, Viglizzo *et al.* 2001). These remnants consist primarily of tall-grasslands dominated by *Cortaderia selloana* (Bilenca & Miñarro 2004). These grasslands are a critical habitat for the conservation of Pampas grassland birds, which are highly dependent on them to obtain food and nest-sites (Pretelli *et al.* 2013). Tall-grasslands are represented by patches of varying size, from large and uniform extensions growing in nature reserves (Bilenca & Miñarro 2004) to reduced patches within heterogeneous landscape matrices such as suburban areas and agro-ecosystems (Pretelli *et al.* 2013).

Although fragmentation is a key factor in bird population declines, no studies on the reproductive success of Pampas grassland birds have yet been undertaken. Most of our knowledge on the effects of grassland fragmentation and edge effects on nest success of grassland birds comes from northern hemisphere temperate grasslands (e.g. Winter *et al.* 2000, Herkert *et al.* 2003, Ribic *et al.* 2009). A recent review of the ecology of grassland birds of southeastern South America highlights the need to assess how habitat transformation and matrix effects impact reproductive performance (Azpiroz *et al.* 2012). Our aim was therefore to assess the effect of fragmentation on grassland bird reproduction by comparing the combined influence of fragmentation (small patches vs. a continuous patch) and landscape matrix (urban vs. agro-ecosystem) on nesting success, brood parasitism and productivity of two grassland-nesting species, Spectacled Tyrant *Hymenops perspicillatus* and Brown-and-yellow Marshbird *Pseudoleistes virescens*.

METHODS

Study site

The study was conducted along a 135-km-long coastal strip in the southeast Pampas region (Cabrera 1976) of Buenos Aires Province, Argentina. The northernmost of our five sampling sites along this strip was located near Villa Gesell city (37°13′S, 57°05′W), and the southernmost site near Miramar city (38°14′S, 57°48′W). The study area included the Mar Chiquita Coastal Lagoon Biosphere Reserve (37°40′S, 57°23′W) of 26 488 ha, hereafter 'the reserve' (part of the UNESCO Man and the Biosphere Programme; Isacch 2008). The reserve is one of the most important in the Pampas region, as it supports a high biodiversity and conserves a variety of habitats (Isacch 2008). The landscape surrounding the reserve is dominated by a mosaic of natural habitats and agro-ecosystems, which includes crops and cultivated pastures, natural grasslands, ponds and streams, exotic forest and urban areas (Vervoorst 1967, Isacch *et al.* 2006). The primary use of natural grasslands is cattle grazing (80%); croplands occupy < 10% of the area (León *et al.* 1984). The mean annual temperature is *c.* 15 °C, with warm summers and cool winters (January mean temperature range: 21.5–23.5 °C, July mean temperature range: 7.5–9.5 °C; Soriano *et al.* 1991). Mean annual precipitation ranges from 800 to 1000 mm, with more intense precipitation in summer (December–March) and less in winter (June–July; Martos *et al.* 2004).

Study species

Spectacled Tyrant is a member of the family Tyrannidae and inhabits open lands, grassy areas near water bodies, marshes, and fields and pastures (Fitzpatrick 2004). In our study area, Spectacled Tyrants are present in spring and summer (Pretelli *et al.* 2013), and consistently use tall grasslands of *C. selloana* to nest from mid-October to late January (Pretelli & Isacch 2013) where they build open-cup nests. The modal clutch size is two. Brown-and-yellow Marshbird is a member of the family Icteridae that inhabits marshy areas and humid grasslands in northeastern Argentina, Uruguay and southern Brazil (Ridgely & Tudor 1989). In our study area, this species is present year-round (Pretelli *et al.* 2013), and breeds from late September to mid-December (Mermoz & Reboreda 1998). They build open-cup nests 0.5–1.5 m above the ground in grasses and small shrubs. Clutches usually consist of four to five eggs. Marshbirds have a cooperative breeding system with helpers that assist in rearing young and defending nests against predators and brood parasites (Orians *et al.* 1977). Brown-and-yellow Marshbird is frequently parasitized by Shiny Cowbird *Molothrus bonariensis* (Mermoz & Reboreda 1998).

Spectacled Tyrant and Brown-and-yellow Marshbird were selected as model species as they are conspicuous, abundant and have a high affinity for tall grasslands of *C. selloana* for nesting (Pretelli *et al.* 2013). While both species are classified by IUCN as Least Concern (BirdLife 2014), they have declined in abundance and even disappeared from vast areas of the Pampas region following replacement of native tall grasslands with croplands and pasturelands (Codesido *et al.* 2011).

Sampling design

To assess the effect of grassland fragmentation, we compared the reproductive success of each species between a large unfragmented site (the reserve), which represents the original condition of the grassland, and fragmented grasslands in small patches immersed in a landscape matrix of different land-uses. We selected two grassland patches

in each of two dominant matrix types. In the reserve, where grassland covers a large continuous area, we sampled in two sites (equivalent in size to fragmented patches) to include variability. With this sampling design, we evaluated the effect of the fragmentation of grassland habitat (patches vs. reserve) and the effect of the matrix type on small grassland patches.

Two small grassland patches (0.7 and 4.5 ha) were situated within an agricultural matrix (hereafter 'agro-patches') and two (2.2 and 4.4 ha) within an urban matrix ('urban-patches'). During the sampling period, agro-patches were surrounded by a combination of short grasses and crops (wheat and maize). Urban-patches were small areas of grassland within urban areas dominated by houses and green areas with scattered trees. The urban study area comprised an urban agglomeration which includes Miramar city and El Marquesado coastal village, in the southeastern Buenos Aires Province, with a population of 25 129 inhabitants (INDEC 2010). Each patch was surrounded by its respective matrix to a distance of at least 1.5 km from the centre of the patch. As patch shape could modify effects of the landscape matrix itself, we selected patches with similar perimeter-to-area ratios (Helzer & Jelinski 1999). The area and perimeter of each patch were determined using an online tool (http://www.freemap-tools.com/area-calculator.htm). The study site was covered by an image from Google EARTH with high resolution (date 1 July 2011) in which previously geopositioned patches were easily recognized. The perimeter/area ratio on average was 4.55 for agro-patches and 4.05 for urban-patches. In the reserve, *C. selloana* grassland covers *c.* 900 ha, but we searched for nests in two 10-ha permanent plots located > 1.5 km from the reserve edge.

Cortaderia selloana grasslands in the reserve and agro-patches host a diversity of potential nest predators including raptors (e.g. *Milvago chimango*, *Circus buffoni*), passerines (e.g. *Pitangus sulphuratus*, *Embernagra platensis*, *Phacellodomus striaticollis*), mammals such as opossums (*Monodelphis dimidiata* and *Didelphis albiventris*), Hog-nosed Skunks *Conepatus chinga*, Pampas Foxes *Lycalopex gymnocercus*, Geoffroy's Cats *Oncifelis geoffroyi*, Lesser Grisons *Galictus cuja*, small mammals (e.g. *Oxymycterus rufus*), and reptiles (Canepuccia *et al.* 2008, Baladrón *et al.* 2012, Cardoni *et al.* 2012, Pretelli *et al.* 2013, M.G. Pretelli pers. obs.). In addition, other predators occur in urban-patches, such as Domestic Dogs *Canis lupus familiaris*, Domestic Cats *Felis catus*, and rats *Rattus* spp. (M.G. Pretelli pers. obs.).

Nest monitoring

We systematically searched for nests in patches and in the reserve during two breeding seasons (September 2011–January 2012; September 2012–January 2013). Once found, we recorded nest locations with GPS and marked the nest area with plastic tape to facilitate subsequent monitoring. Nests were visited at intervals of 3–5 days following standard procedures to avoid attracting predators to nests (Martin & Geupel 1993). Nests were checked until they were abandoned, predated or produced fledglings. At each visit, we recorded egg or chick loss and the presence of adults near the nest. The continued presence of eggs after the estimated date of hatching and/or the absence of parents was taken as evidence that a nest had been abandoned. We considered a nest to have been predated when the complete clutch disappeared between two subsequent visits or when the chicks disappeared from their nests before they were old enough to fledge. We considered a nest successful if one or more chicks fledged. For 29 Spectacled Tyrant nests found that failed during incubation, we estimated clutch-initiation dates by assuming that the observed period was halfway between the end of laying and hatching. The same criterion was applied for 12 Marshbird nests. We considered the presence of parasite eggs, eggs punctured by cowbirds or cowbird chicks evidence of parasitism. Eggs pecked by Shiny Cowbirds usually have one or more small punctures (Massoni & Reboreda 2002).

Data analysis

We estimated nest success rates using the daily-survival estimator in program MARK (White & Burnham 1999). Daily survival rate (DSR) was then used to estimate cumulative probabilities for nest survival. The duration of the nestling period (i.e. from egg-laying to fledging) was obtained from the literature as 31 days for Spectacled Tyrant (Pretelli & Isacch 2013) and 28 days for the Marshbird (Mermoz & Reboreda 1998). Variance for cumulative survival probabilities and 95% confidence intervals were approximated using the delta method (Rotella 2005, Powell 2007). Post-hoc comparisons of survival among locations (i.e.

agro-patches, urban-patches and reserve) for each species and between species for each location were done using CONTRAST (Hines & Sauer 1989). This program uses a chi-square approach that is analogous to ANOVA in order to control for experiment-wise error and adjust for Type I errors (Hines & Sauer 1989). Values of DSR and cumulative survival are presented as means ± 1 se in order to make them comparable with other studies.

We were able to determine clutch initiation dates for the sample of nests found during construction and egg-laying ($n = 21$ for Spectacled Tyrant and $n = 26$ for Marshbird). Clutch-initiation dates were assigned by backdating from hatching dates ($n = 54$ nests for Spectacled Tyrant and $n = 29$ nests for Marshbird) for nests found during incubation and by using nestling weights (Mermoz 1996 and M.G. Pretelli unpubl. data) for nests found after hatching ($n = 21$ nests for Spectacled Tyrant and $n = 19$ nests for Marshbird). For Spectacled Tyrant, we standardized the observation period for each nesting attempt by setting a maximum length of 31 days (17 days for the egg-laying and incubation stages and 14 days for the nestling stage; Pretelli & Isacch 2013). For the Marshbird, a successful nesting attempt lasts 28 days (17 days for the egg-laying and incubation stages, and 11 days for the nestling stage; Mermoz & Reboreda 1998). Observation periods started either the day the first egg was laid (for nests found during construction) or the day a nest was found.

We used a generalized linear mixed model (GLMM) with a Poisson error structure and a logit link function to assess differences among the three treatments (agro-patches, urban-patches and reserve) in the number of nestlings fledged per nest and productivity of successful nests (i.e. number of chicks fledged per successful attempt). Also, we compared brood parasitism rate (i.e. number of nests parasitized) among the three treatments, again using a GLMM, but in this case with a binomial error structure (two possible values for the response variable: 0 if no parasitism occurred, 1 if it did) and a logit link function (Crawley 2007). Nest-patch identity and year were included as random terms to account for non-independence of data. Moreover, as one agro-patch was relatively small in comparison with the other three patches, we tested for the statistical significance of this random term using the *lrtest* function of the *lmtest* package. Model fits were visually assessed by inspecting plots of standardized deviance residuals for each model. We assessed goodness-of-fit for all models and estimated the variance inflation factor ($\hat{c}$) as residual deviance divided by degrees of freedom (Crawley 2007). We fitted GLMMs using the *glmmadmb* function of the *glmmADMB* package (Skaug *et al.* 2013) with R version 3.0.1 (R Development Core Team 2013). The level of significance in all tests was set to $P < 0.05$. Values are reported as means ± 1 sd.

RESULTS

Thirty-eight Spectacled Tyrant nests were monitored in agro-patches (18 in 2011–2012 and 20 in 2012–2013), 20 in urban-patches (10 in 2011–2012 and 10 in 2012–2013) and 38 in the reserve (12 in 2011–2012 and 26 in 2012–2013). We monitored nests at agro-patches over 60 days (23 October–22 December), at urban-patches over 54 days (26 October–19 December) and at the reserve over 54 days (24 October–17 December) for a total of 260, 267 and 565 exposure days, respectively. Twenty-one nests were found during construction or egg-laying, 54 during incubation and 21 after chicks had hatched. The fate of nests is shown in Table 1. The proportion of successful nests did not differ between breeding seasons (reserve: $\chi^2_1 = 1.54$, $P = 0.21$; urban-patches: $\chi^2_1 = 0.95$, $P = 0.32$; agro-patches: $\chi^2_1 = 0.75$, $P = 0.38$).

Thirty-six Marshbird nests were monitored in agro-patches (nine in 2011–2012 and 27 in 2012–2013), 17 in urban-patches (six in 2011–2012 and 11 in 2012–2013) and 21 in the reserve (eight in 2011–2012 and 13 in 2012–2013). We monitored nests at agro-patches over 63 days (18 September–20 November), at urban patches over 56 days (5 October–30 November) and at the reserve over 63 days (18 September–20 November) for a total of 317, 169 and 204 exposure days, respectively. Twenty-six nests were found during construction or egg-laying, 29 during incubation and 19 after chicks had hatched. The fate of nests is shown in Table 1. The proportion of successful nests did not differ between breeding seasons (reserve: $\chi^2_1 = 1.17$, $P = 0.28$; urban-patches: $\chi^2_1 = 0.01$, $P = 0.94$; agro-patches: $\chi^2_1 = 0.21$, $P = 0.65$).

Nest survival

Daily survival rate for Spectacled Tyrant nests varied depending on year and site (Table 2). Cumula-

Table 1. Number and outcome of Spectacled Tyrant and Brown-and-yellow Marshbird nests in the reserve, urban-patches and agro-patches during two breeding seasons (September 2011–January 2012; September 2012–January 2013) in the southeast Pampas region, Argentina. Nesting outcome is defined as successful (S), predated (P) or abandoned (A).

	Reserve			Urban			Agro		
Species	S	P	A	S	P	A	S	P	A
Spectacled	23	15	0	14	6	3	11	27	0
Tyrant	60%	40%	0%	60%	26%	14%	29%	71%	0%
Brown-and-yellow	16	5	1	10	7	2	14	18	4
Marshbird	72.7%	22.7%	4.5%	53%	37%	10%	39%	50%	11%
Total nests	39	20	1	24	13	5	25	45	4

tive probability of nest survival for the 2 years combined was 0.073 in agro-patches, 0.535 in urban-patches and 0.467 in the reserve. Post-hoc comparisons of site-specific survival showed significant differences between reserve and agro-patches ($\chi^2_1 = 24.83$, $P < 0.001$), and urban-patches and agro-patches ($\chi^2_1 = 11.20$, $P < 0.001$) but no differences between urban-patches and reserve ($\chi^2_1 = 0.18$, $P = 0.664$; Fig. 1). DSR for Marshbird nests also varied depending on year and site (Table 2). Cumulative probability of nest survival for the 2 years combined was 0.200 in agro-patches, 0.362 in urban-patches, and 0.526 in the reserve. Post-hoc comparisons showed significant differences between reserve and agro-patches ($\chi^2_1 = 7.10$, $P = 0.007$) but no differences between urban-patches and agro-patches ($\chi^2_1 = 2.32$, $P = 0.127$), and urban-patches and reserve ($\chi^2_1 = 1.00$, $P = 0.315$; Fig. 1). There were differences between the two species in agro-patches ($\chi^2_1 = 8.45$, $P < 0.001$), but no differences in the urban-patches ($\chi^2_1 = 0.97$, $P = 0.322$), or in the reserve ($\chi^2_1 = 0.17$, $P = 0.670$; Fig. 1).

Total fledglings, fledglings per nest, productivity of successful nests and parasitism

A total of 16 nestlings of Spectacled Tyrant fledged from agro-patches (0.42 ± 0.72 fledglings per nest, $n = 38$ nests), 29 from urban-patches (1.26 ± 1.13 fledglings per nest, $n = 23$ nests) and 42 from the reserve (1.10 ± 1.00 fledglings per nest, $n = 38$ nests) (Supporting Information Table S1). The number of nestlings fledged per nest in agro-patches was lower than in the reserve (GLMM: $Z = 2.97$, $P < 0.01$) and in urban-patches ($Z = 3.51$, $P < 0.01$). The number of nestlings fledged per nest from the reserve and urban-patches was similar ($Z = 0.84$, $P = 0.40$) (Supporting Information Table S2). However, productivity of successful nests was similar between agro-patches (1.45 ± 0.52 fledglings per nest, mode = 1, $n = 11$ nests) and the reserve (1.91 ± 0.42 fledglings per nest, mode = 2, $n = 23$ nests; $Z = 0.93$, $P = 0.35$), and between agro- and urban-patches (2.07 ± 0.61 fledglings per nest, mode = 2, $n = 14$ nests; $Z = 1.14$, $P = 0.26$) (Table S2). Productivity was also similar between reserve and urban-patches ($Z = 0.34$, $P = 0.74$) (Table S2). There were no effects of patch identity on productivity ($\chi^2_1 = 0.30$, $P = 0.58$). No young Spectacled Tyrants were found starved in the nest at any nesting sites.

A total of 39 Marshbird nestlings fledged from agro-patches (1.21 ± 1.4 fledglings per nest, $n = 32$), 19 from urban-patches (1.11 ± 1.10 fledglings per nest, $n = 17$) and 42 from the reserve (2.0 ± 1.34 fledglings per nest, $n = 21$) (Supporting Information Table S3). The number of nestlings fledged per nest was significantly higher in the reserve than in agro-patches ($Z = 1.97$, $P < 0.048$) and urban-patches ($Z = 2.10$, $P < 0.035$). The number of nestlings fledged per nest from agro- and urban-patches was similar ($Z = 0.09$, $P = 0.92$) (Supporting Information Table S4). Productivity of successful nests was similar between the reserve (2.5 ± 1.0 fledglings per nest, mode = 2, $n = 16$) and agro-patches (2.6 ± 1.2 fledglings per nest, mode = 3, $n = 14$; $Z = 0.23$, $P = 0.818$) and between the reserve and urban-patches (1.9 ± 0.7 fledglings per nest, mode = 2, $n = 10$; $Z = 0.95$, $P = 0.342$) (Table S4). Productivity was similar between agro- and urban-patches ($Z = 1.12$, $P = 0.262$) (Table S4). Patch identity did not affect productivity ($\chi^2_1 = 0.002$, $P = 0.96$). No Marshbird

Table 2. Daily survival rates (DSR) for Spectacled Tyrant and Brown-and-yellow Marshbird nests in the reserve, urban-patches and agro-patches, estimated using MARK. Data are mean DSR (with se) for each year and site, and combined across years.

Species	Reserve			Urban-patches			Agro-patches		
	2011 2012	2012 2013	All years	2011 2012	2012 2013	All years	2011 2012	2012 2013	All years
Spectacled Tyrant	0.986 (0.007)	0.968 (0.008)	0.975 (0.006)	0.975 (0.012)	0.984 (0.011)	0.979 (0.008)	0.903 (0.025)	0.927 (0.019)	0.916 (0.015)
Brown-and-yellow Marshbird	0.989 (0.009)	0.964 (0.017)	0.977 (0.010)	0.973 (0.018)	0.958 (0.017)	0.964 (0.013)	0.949 (0.022)	0.938 (0.013)	0.944 (0.012)

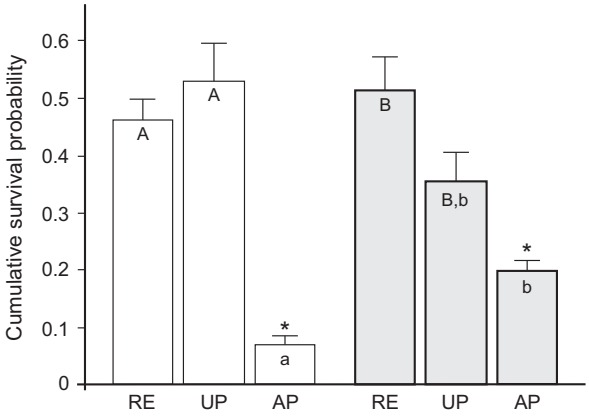

Figure 1. Cumulative nest success showing site-specific variation for Spectacled Tyrants (open bars) and Brown-and-yellow Marshbirds (grey bars) nesting at three locations (RE: reserve, UP: urban-patches, AP: agro-patches) in the south-eastern Pampas region, Argentina. Cumulative survival is the probability a nest will survive for both incubation and nestling periods. Standard errors were calculated using the delta method. Different letters (A, a for Spectacled Tyrant; B, b for Brown-and-yellow Marshbird) indicate significant differences between groups. Asterisks above columns indicate significant differences between species.

nestlings were found starved in the nest at any of the sites. Marshbirds had significantly lower rates of brood parasitism in the reserve (three of 21 nests; 14.2%) than in either agro-patches (26 of 36 nests; 72.2%) or urban-patches (10 of 17; 58.8%; $Z = 4.12$, $P < 0.01$ and $Z = 3.18$, $P < 0.01$, respectively), and there were similar parasitism rates between agro- and urban-patches ($Z = 0.91$, $P = 0.36$) (Supporting Information Tables S5 and S6). The proportion of successful parasitized nests was 67% in the reserve (2/3), 10% in urban-patches (1/10) and 27% in agro-patches (7/26), which successfully fledged two, one and nine Shiny Cowbirds, respectively.

DISCUSSION

The reproductive performance of Spectacled Tyrant and Brown-and-yellow Marshbird was affected by grassland fragmentation, being generally higher in the reserve than in the patches. However, these effects were notably conditioned by the landscape matrix surrounding grasslands, and responses were not the same for both species. For the Marshbird, fragmentation caused higher rates of brood parasitism and lower numbers of nestlings per nest regardless of matrix type. For Spectacled Tyrant,

we found a negative effect only when the patches were immersed in an agricultural matrix. In both species, productivity of successful nests was similar irrespective of nesting site.

Spectacled Tyrant nesting success was 84.4 and 86.4% lower in agro-patches than in the reserve and urban-patches, respectively, and nesting success for Marshbirds was 62% lower in agro-patches than in the reserve. The negative effect of the agricultural matrix contrasts with previous studies for other regions (Winter *et al.* 2000, Jensen & Finck 2004, Walk *et al.* 2010, Perkins *et al.* 2013) that reported no effect of this type of edge. In general, reproductive success is related to patch size, and nest predation is higher in smaller patches (Johnson & Temple 1990, Winter & Faaborg 1999, Herkert *et al.* 2003, but see Skagen *et al.* 2005, Walk *et al.* 2010). In this sense, these differences could be due to the larger patch size sampled in other studies (0.7–4.5 ha, this study; 31–1084 ha, Winter *et al.* 2000; 8–97 ha, Jensen & Finck 2004; 3–142 ha, Walk *et al.* 2010; 13.2–38.3 ha, Perkins *et al.* 2013), which could reduce access to predators and parasites. They could also be due to environmental differences between the grasslands and agro-ecosystems of Northern and Southern Hemispheres (e.g. number and types of predators; Ribic *et al.* 2009).

For Spectacled Tyrant, we also noted differences in response between agro- and urban-patches. Because of this, one might initially assume that differences in nest predation between sites may have been due to changes in predator abundance or type of predator, including fewer important predators in urban areas (Rodewald & Kearns 2011, Stracey 2011). It may also be that some predators in urban landscapes may specialize in alternative food sources, which in turn may reduce the predation pressure on bird nests and contribute to the lower nest predation rates often observed in urban landscapes (Rodewald *et al.* 2011, Fischer *et al.* 2012). Beyond the abundance or activity of any given predator species, higher nest predation rates in agricultural grasslands may also result from having a more diverse predator community in these areas (e.g. McKinney 2008). Increased predator diversity may result in a greater probability that a nest will be discovered and predated. Differences may have occurred due to a decrease in abundance of predators in urban-patches, with a dominance of aerial, visually orientated predators. Our presumption is based on the higher predation rate of Marshbird nests, which are larger and typically higher in the vegetation and hence more exposed to aerial predators than are Spectacled Tyrant nests.

Spectacled Tyrant nesting success in urban-patches was relatively high and similar to that in the reserve, and was 39% greater than that of Marshbirds. The effects of urbanization on nesting success of grassland birds have been little studied. However, our results agree with those recently described by Buxton and Benson (2015), who found that nests of grassland birds (mostly of Red-winged Blackbird *Agelaius phoeniceus*) in urban landscapes had lower nest predation rates than nests in more rural landscapes (but see Grandmaison & Niemi 2007). Rodewald *et al.* (2011) found that an urbanizing landscape matrix can decouple interactions between breeding birds and their nest predators, basically because many synanthropic predators are heavily subsidized by anthropogenic food sources (Marzluff & Neatherlin 2006, Withey & Marzluff 2009). However, reproductive success could be a partial indicator of the performance of individuals, as Shipley *et al.* (2013) observed that the nesting success of the Spotted Towhee *Pipilo maculatus* nesting in forests near urban edges was relatively high but the predation rate on juveniles was also high. Nevertheless, our results suggest that the effect of fragmentation shown in urban-patches may depend on a species' reproductive strategy.

Grassland fragmentation is correlated with greater rates of brood parasitism in our study system. In general, higher rates of parasitism occur near forest edges (Johnson & Temple 1990, Patten *et al.* 2006, but see Pietz *et al.* 2009). By contrast, patches with crop edges and low woody cover have lower rates of brood parasitism (Winter *et al.* 2000, Walk *et al.* 2010). In our study, even though agro-patches had no trees around them, we recorded the highest rate of brood parasitism (72%). Mermoz and Reboreda (1998) found that the rate of brood parasitism of Marshbirds nesting mostly in patches of thistles *Cynara cardunculus* growing in field margins along secondary unpaved roads was 65.4%, a value similar to that found in this study (agro-patches: 72.2% and urban-patches: 58.8%). Also for grassland birds, Buxton and Benson (2015) observed that brood parasitism by Brown-headed Cowbirds *Molothrus ater* was greater in rural areas than in urban areas, indicating that this pattern may be similar irrespective of grassland-host species, and that it relates mainly to the abundance of brood parasites, as in both study

areas the abundance of cowbirds decreased with urbanization in the landscape (Buxton & Benson 2015, Pretelli 2015). Higher brood parasitism and productivity of parasite nestlings in agro-patches would generate a system that promotes a negative feedback process whereby parasite populations benefit to the detriment of native hosts.

Decreased reproductive rates due to brood parasitism could promote a decline at the population level for Marshbirds. For some forest birds of North America, the presence of buildings near nesting areas negatively affected the breeding success of birds by increasing brood parasitism (Tewksbury *et al.* 2006, Rodewald 2009). Similarly, Burhans and Thompson (2006) found that rates of brood parasitism were twice as high in urban than rural landscapes for shrubland birds. Our results show that, regardless of the type of habitat, fragmentation is a process that promotes brood parasitism, which can be enhanced even more by the type of matrix surrounding remnant patches of habitat.

In recent decades, increased human habitat modification may be exacerbating the degree of food limitation for many birds (Evans 2004); nevertheless, the results suggest that the availability of food in the different situations considered here does not limit the number of fledglings in successful nests. Furthermore, as productivity is also limited by parental aptitude and life-history traits of a particular species, the high productivity of successful nests may not be sufficient to compensate for the high nest predation. As a consequence, the viability of populations in small agro-patches may be restricted, and their persistence may depend on the migration rate between different subpopulations (Levins 1969). Migration rate may depend on the extent to which a patch is isolated within to the landscape matrix, and the ability of species to move through that matrix (Fahrig 2007). In the study area, the agricultural matrix is dominant and is unlikely to be an impediment to dispersal. Marshbirds are present year-round in the study area (Pretelli *et al.* 2013). The evidence suggests that the reserve is functioning as a source and the patches as sinks (Pulliam 1988). Although we do not know whether the number of young produced can be enough to sustain subpopulations in the patches, the Marshbird has declined in abundance and even disappeared in vast areas of the Pampas region in conjunction with large grasslands (such as the reserve) following replacement of native tall grasslands by croplands and pasturelands (Codesido *et al.* 2011).

Whereas most of the land use in the Pampas region is agricultural, urbanization is increasing, mostly at the expense of natural environments (Faggi *et al.* 2010, Isla 2013). Our findings on the relatively better reproductive performance of species in urban-patches than in agro-patches is an important aspect to consider in land planning, highlighting the role that maintaining native vegetation can have in urbanization projects. Despite the low nesting success of birds breeding in agro-patches, they may still be important in improving connectivity between continuous grasslands and maintaining biodiversity in agro-ecosystems at the landscape scale (Altieri 1999, Donald & Evans 2006). These small patches are of great importance for grassland bird movements and for nesting (Pretelli *et al.* 2013) despite the low nesting success, but our results strongly suggest the need to retain larger areas of grassland to conserve grassland birds.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Number of fledgling Spectacled Tyrants *Hymenops perspicillatus* per nest in agro-patches, urban-patches and at the reserve (patch size in hectares) in the southeast of the Pampas region, Argentina.

Table S2. Results of comparison of productivity of Spectacled Tyrant.

Table S3. Number of fledgling Brown-and-yellow Marshbirds *Pseudoleistes virescens* per nest in agro-patches, urban-patches and at the reserve (patch size in hectares) in the southeast of the Pampas region, Argentina.

Table S4. Results of comparison of productivity of Brown-and-yellow Marshbird.

Table S5. Number of Brown-and-yellow Marshbirds *Pseudoleistes virescens* nests parasitized by Shiny Cowbirds *Molothrus bonariensis* in agro-patches, urban-patches and at the reserve (patch size in hectares) in the southeast of the Pampas region, Argentina.

Table S6. Results of comparison of brood parasitism on the Brown-and-yellow Marshbird.