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Agricultural land-use, avian nesting and rarity in the Pampas of central Argentina

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Abstract. Human-mediated changes in land-use have affected many bird species in South America, and other regions where agroecosystems are now the most common environments. We evaluate how the rarity of landbird species in agroecosystems is influenced by their specialisation in nesting habitat. We estimated rarity of species by their local abundance and area of occupancy in the Pampas of Argentina. Relative local abundance was positively associated with area of occupancy. Most rare species (9 of 14) were specialists, whereas 15 of the 21 common species were generalists. Both woodland and grassland specialists had smaller areas of occupancy than generalist species. This pattern was expected for woodland specialists, owing to a lack of woodland in the agroecosystems of the Pampas. In the case of grassland specialists, the pattern might reflect the destruction of natural grasslands owing to an increase of agriculture. Wetland specialists were an exception within specialists, probably because they share characteristics with common species, such as flocking behaviour and use different feeding habitats. Our results show that some grassland species of increased conservation concern in the Pampas are facing the threat of extinction associated with low local abundance and limited distribution, emphasising the need for further conservation effort

Additional keywords: agroecosystems, area of occupancy, commonness, grassland birds, local abundance.

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Introduction

Rarity of species has received much attention since the beginning of ecology as a discipline (Darwin 1859; Preston 1948; Rabinowitz *et al*. 1986). One of the main reasons for studying patterns of abundance and distribution of rare species is because it is known that species with small populations and small distributions are more threatened with decline and extinction than abundant species with larger distributions (Shaffer 1981; Lande 1993; Purvis *et al*. 2000; Manne and Pimm 2001).

Many ecological and life-history attributes have been linked with rarity (for reviews, see Gaston 1994; Murray *et al*. 2002). In birds, for instance, empirical studies have identified several variables associated with rarity at the community level, including habitat specialisation (Kattan 1992; Goerck 1997; Brändle and Brandl 2001; Gillespie 2002) and the type of habitat used (Bock 1984; Böhning-Gaese and Oberrath 2001; Marsden and Whiffin 2003). Population decline and the degree of vulnerability to extinction have also been associated, among other factors, with habitat specialisation (Owens and Bennett 2000; Davies *et al*. 2004; Fairbanks 2004).

The consequences of landscape-level changes are a major theme in conservation biology (e.g. Lindenmayer and Fischer 2006) and there is growing interest in the contribution that modified landscapes can make to nature conservation (e.g. Vandermeer and Perfecto 2007). An important aspect of understanding these issues is to describe relationships between abundance, distribution and ecology of species. In agroecosystems, human activities that alter habitat often affect the abundance and distribution of species assemblages (Mack *et al*. 2000). However, these effects are not uniform for all species, so that human activities may generally benefit generalist species while negatively influencing specialist species (Diamond 1989; McKinney and Lockwood 1999; La Sorte 2006). We chose to investigate these relationships in the Pampas of Argentina, formerly an extensive grassland region that has become one of the largest agricultural regions of the world (Soriano 1991). Furthermore, there is an increasing concern for the conservation of grassland birds in the Pampas, with 24 species of grassland bird considered of conservation concern (Di Giacomo and Krapovickas 2005).

In the Pampas of central Argentina, land-use practices have deeply modified the original grassland over a fairly short period (Bilenca and Miñarro 2004; Aizen *et al*. 2009; Bilenca *et al*. 2009; Viglizzo *et al*. 2011). At present, <25% of these original grassland ecosystems remain uncultivated

(Viglizzo *et al*. 2011). The landscape of the Pampas has been altered structurally by the expansion of croplands and by the introduction of exotic trees around rural buildings and as shading woodlots for cattle (Zalba and Villamil 2002; Ghersa *et al*. 2002). These changes have affected several grassland birds that have already experienced range declines, such as the Saffron-cowled Blackbird (*Xanthopsar flavus*), Strange-tailed Tyrant (*Alectrurus risora*), Pampas Meadowlark (*Sturnella defilippii*) and Black-and-white Monjita (*Heteroxolmis dominicanus*) (Fraga *et al*. 1998; Fraga 2003; Di Giacomo and Di Giacomo 2004; Fernández *et al*. 2004; Codesido and Fraga 2009). In addition, the introduction of trees in the Pampas has been followed by the expansion of several species, including the Eared Dove (*Zenaida auriculata*), Picazuro Pigeon (*Patagioenas picazuro*) and Monk Parakeet (*Myiopsitta monachus*) (Gibson 1919; Daguerre 1936; Bruggers *et al*. 1998).

Recent studies on the avifauna of central Argentina has shown that the number of species across the phytogeographical provinces of the Pampas and the Espinal savanna is positively correlated with cover of native vegetation and negatively correlated with agricultural use (Schrag *et al*. 2009). In the Pampas, the abundance of 20 species is significantly correlated with the percentage of cropland. Responses of avian populations to increasing intensities of crop production along an agricultural gradient have been negative for most species but some responses have been positive (Filloy and Bellocq 2007). Codesido *et al*. (2011) found a significantly decreased area of occupancy of common grassland specialists, which may reflect the reduction of native grasslands owing to increased agricultural cultivation. However, there are no studies assessing the extent of commonness or rarity for landbirds and relating them to their habitat specialisation, particularly with regard to their nesting habitat. The aim of this study is to analyse how the nesting habitat of landbirds is related to rarity in the agroecosystems of central Argentina, and to test the hypothesis that specialist species are rarer than generalist species, by comparing local abundance and area of occupancy among generalist species with the different groups of specialist species (e.g. grassland-, woodland- and wetland-nesting species).

Materials and methods

Study area

The study was conducted within a region 500 × 450 km (33–39°S and 57–63°W; Fig. 1). The region includes five of the ecological units within the Pampas region of central Argentina, which show some differences in geomorphology, soils, drainage, physiography and vegetation: the Rolling, Flat Inland, West Inland, Flooding and Southern Pampas (Soriano 1991). The natural vegetation is a gramineous steppe dominated by grasses such as *Stipa*, *Piptochaetium*, *Aristida*, *Melica*, *Briza*, *Bromus*, *Eragrostis* and *Poa* (Soriano 1991). The region is almost flat, with a very slight slope towards the Atlantic Ocean, and a few hills and rocky outcrops in isolated sites. Mean annual temperature is ~15°C, with warm summers and cool winters (January mean temperature ranges 21.5–23.5°C, July mean temperature ranges 7.5–9.5°C); mean annual precipitation ranges from 800 to 1000 mm per year (Soriano 1991).

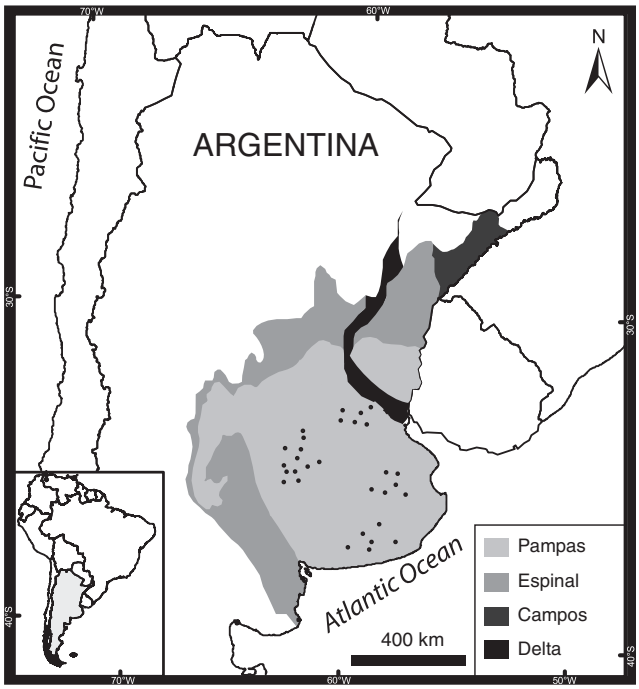

Fig. 1. Location of the 30 survey transects in the Pampas of Argentina.

Although the original vegetation was tall-grass steppe, intermingled with prairies, marshes and other edaphic communities, it has been heavily modified by human use (Soriano 1991), so that lands from the Pampas region are currently used intensively for cattle grazing or crop production (Aizen *et al*. 2009). Originally, trees were absent and occurring only marginally as native forests near the ecotonal areas with the neighbouring Delta and Espinal ecoregions (Burkart *et al*. 1999; Fig. 1). Stands of tall trees are novel in the Pampas and their introduction has added structural complexity to the previously more two-dimensional grasslands of this region. Nowadays, woodlands of both native and exotic species have been established in some places as riparian vegetation or along roadsides (Ghersa *et al*. 2002). In addition, scattered in the region are many seasonal ponds that are used as feeding and breeding habitat by a large suite of wetland birds (Gómez and Toresani 1998; Di Giacomo *et al*. 2007).

Sampling of birds

We restricted our sampling only to species of landbird, defined as species that use terrestrial habitats for most of their life cycle. Landbirds were surveyed on 30 transects along secondary and tertiary roads in agroecosystems of the Pampas region (Fig. 1). Six transects were placed randomly within each of the five Pampas ecological units described above (Soriano 1991). Each transect was 20 km long, with permanently marked survey points located every kilometre (20 points in total). Each transect was sampled by the same observer (MC) two times between 2006 and 2008. Surveys were conducted in summer (January–February). Climatic variables were fairly constant during the sampling times. Bird surveys were performed at each point using a point-count method (Bibby *et al*. 2000). Counts were

conducted in the morning, within 3 h of dawn, and in the evening, during the last 3 h before sunset. All landbirds seen or heard within a 200-m radius around each point in a 5-min period were identified and counted, resulting in a total sampling effort of 100 h. We did not census birds under extreme weather conditions (e.g. windy or rainy days; Bibby *et al*. 2000). We classified each species based on its nesting habitat as either habitat specialists (species that nest exclusively in either grassland, cropland, woodland, peridomestic habitat or wetlands; see 'Characterisation of land-use', below) or habitat generalists (species that use more than one habitat type for nesting) by means of a comprehensive review of the literature (see Codesido *et al*. 2011). We excluded from our analyses those species that inhabit but do not breed in the Pampas, either because they are Nearctic migrants (four species: Swainson's Hawk (*Buteo swainsoni*), Upland Sandpiper (*Bartramia longicauda*), American Golden Plover (*Pluvialis dominicus*) and Cliff Swallow (*Petrochelidon pyrrhonota*)) or because they are winter migrants arriving to the Pampas from Patagonia (three species: Black-faced Ibis (*Theristicus melanopis*), Austral Negrito (*Lessonia rufa*) and White-banded Mockingbird (*Mimus triurus*)) (Narosky and Di Giacomo 1993). In addition, we excluded from our analyses those species that were recorded only once in our surveys in order to avoid confounding effects of species rarity. These species are common in core areas of their distribution in the phytogeographical regions outside of our study region (e.g. the Espinal, the Chaco, and the Paraná Delta; Babarskas *et al*. 2003; De la Peña 2005; Pagano and Mérida 2009; Table S1 in the Supplementary material).

Characterisation of land-use

Surveys of bird populations and land-use were conducted simultaneously along each transect. The percentage cover of each of five land-use classes was visually estimated within 200 m of each survey point along the transect. We considered the following broad categories of land-use that are common in the study region and are characteristic of many agricultural landscapes around the world (Fuller *et al*. 1997; Haslem and Bennett 2008; Walk *et al*. 2010): (1) grasslands (including perennial pastures, short grasses and tall grasses); (2) croplands (including annual crops, stubble and ploughed or harrowed fields); (3) woodlands (including habitats with presence of natural woodlots or forest plantations >0.2 ha); (4) peridomestic areas (including all kind of infrastructure associated with barns and any type of rural housing); and (5) wetlands (including areas with floating or rooted vegetation on the banks of streams, ponds or along roadsides). The percentage cover for all survey points on a transect was averaged to give one value for each transect, and then the values for each transect and each year were averaged to give one overall value for each transect for the 2006–08 period.

Statistical analyses

Transects served as the sample unit for this study and, therefore, an average of all point values was taken to yield one value per transect and then averaged over the two annual surveys to produce the following variables: (1) local abundance of each species estimated only using transects on which the species was detected (Rey Benayas *et al*. 1999) and expressed as individuals per transect; and (2) the area of occupancy of each species estimated as the number of transects on which a species was recorded, reflecting a component of its present distribution in the study area (Gaston 1994). We evaluated the null hypothesis of no differences in local abundance and area of occupancy among groups of nesting bird species (i.e. generalists, and species nesting in grasslands, wetlands and woodlands) by a one-way analysis of variance (ANOVA). When variables did not meet assumptions for parametric tests they were transformed by applying a $\log_{10}$ transformation (Zar 1999). Then, considering our biological hypothesis (i.e. that specialists are rarer than generalists), we used a one-tailed Dunnett's test in order to test the null hypothesis of whether the means of local abundance and area of occupancy of the generalist group were significantly higher than the means of any of the specialist groups (Zar 1999).

Definitions of rarity and commonness are necessarily arbitrary but there is consensus that a species can be rare or common by its numbers or by the size of its distribution (Gaston 1994). In this study, common and rare species were assessed by considering both their relative local abundance and area of occupancy (Gaston 1994). We determined cut-off points for relative local abundance and area of occupancy (following Goodsell and Connell 2002) as: (1) rare, species with a small area of occupancy (present in <20% of transects) and low relative local abundance (comprising <1% of the total number of individuals); (2) common, bird with a large area of occupancy (present in >50% of the transects) and high relative local abundance (comprising >1% of the total number of individuals); and (3) intermediate rarity or commonness, which were species that did not meet the above criteria. We then analysed the association among relative local abundance and area of occupancy through simple correlation analysis (Zar 1999), and examined whether the proportion of common and rare species was independent of their nesting habitat specialisation (i.e. generalist and specialist) by means of a Chi-square test for mutual independence (Zar 1999).

Results

Landscape characterisation revealed that all types of habitats other than wetlands (i.e. grasslands, croplands, woodlands and peridomestic areas) were present in all surveyed transects of the Pampas agroecosystems; wetlands were present in only

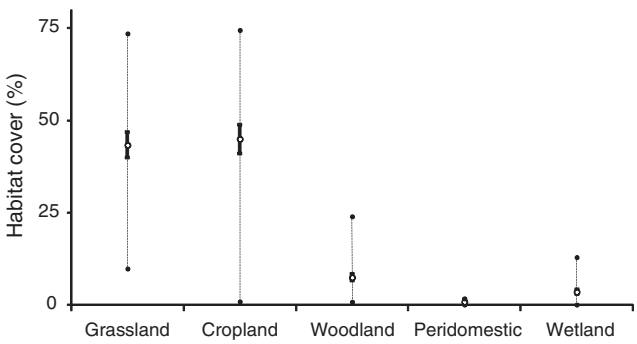

Fig. 2. Mean percentage habitat cover (percentage of transect) of the five habitat types surveyed in the Pampas study area of central Argentina. Error bars are ±1 s.e., and black points represent extreme values.

Table 1. Landbirds recorded in our surveys of the Pampas of central Argentina

Species with >1 record (species recorded only once are given in Supplementary material, Table S1) are classified according to their use of nesting habitat (generalist, grassland, woodland and wetland) and degree of rarity (common, rare or intermediate). Species are listed in order of decreasing relative abundance (%); area of occupancy is the number of transects in which a species recorded (maximum 30)

Species	Nesting habitat	Degree of rarity	Relative local abundance	Area of occupancy
Cattle Egret (*Bubulcus ibis*[A])	Wetland	Common	10.92	23
White-faced Ibis (*Plegadis chihi*)	Wetland	Common	9.02	23
White-rumped Swallow (*Tachycineta leucorrhoa*)	Generalist	Common	7.45	16
Southern Lapwing (*Vanellus chilensis*)	Generalist	Common	6.99	30
Grassland Yellow-Finch (*Sicalis luteola*)	Grassland	Common	6.37	30
Rufous-collared Sparrow (*Zonotrichia capensis*)	Generalist	Common	4.35	30
Brown-hooded Gull (*Chroicocephalus maculipennis*)	Wetland	Common	3.76	16
White-browed Blackbird (*Sturnella superciliaris*)	Generalist	Common	3.26	29
Chimango Caracara (*Milvago chimango*)	Generalist	Common	3.14	30
Greater Rhea (*Rhea americana*)	Grassland	Intermediate	2.92	4
Eared Dove (*Zenaida auriculata*)	Generalist	Common	2.74	30
Shiny Cowbird (*Molothrus bonariensis*)	Generalist	Common	2.28	29
Monk Parakeet (*Myiopsitta monachus*)	Generalist	Common	2.20	23
Double-collared Seedeater (*Sporophila caerulescens*)	Generalist	Common	2.18	30
Fork-tailed Flycatcher (*Tyrannus savana*)	Generalist	Common	1.84	30
Brown-and-yellow Marshbird (*Pseudoleistes virescens*)	Grassland	Intermediate	1.77	8
Rufous Hornero (*Furnarius rufus*)	Generalist	Common	1.48	30
Picazuro Pigeon (*Patagioenas picazuro*)	Generalist	Common	1.45	30
Barn Swallow (*Hirundo rustica*)	Generalist	Intermediate	1.45	6
Brown-chested Martin (*Progne tapera*)	Generalist	Intermediate	1.28	13
Southern Screamer (*Chauna torquata*)	Wetland	Common	1.13	16
Guira Cuckoo (*Guira guira*)	Generalist	Common	1.05	29
Grassland Sparrow (*Ammodramus humeralis*	Generalist	Common	1.05	25
Great Pampa-Finch (*Embernagra platensis*)	Grassland	Common	1.04	23
Bay-winged Cowbird (*Agelaioides badius*)	Generalist	Common	1.01	24
Maguari Stork (*Ciconia maguari*)	Wetland	Intermediate	0.86	17
Crested Caracara (*Caracara plancus*)	Generalist	Intermediate	0.85	26
Rock Dove (*Columba livia*)	Generalist	Intermediate	0.84	13
Chalk-browed Mockingbird (*Mimus saturninus*)	Generalist	Intermediate	0.80	29
Field Flicker (*Colaptes campestris*)	Generalist	Intermediate	0.78	29
Burrowing Owl (*Athene cunicularia*)	Generalist	Intermediate	0.76	28
Spotted Nothura (*Nothura maculosa*)	Generalist	Intermediate	0.75	29
Spectacled Tyrant (*Hymenops perspicillatus*)	Grassland	Intermediate	0.70	17
House Wren (*Troglodytes aedon*)	Generalist	Intermediate	0.63	29
House Sparrow (*Passer domesticus*)	Generalist	Intermediate	0.63	19
Saffron Finch (*Sicalis flaveola*)	Generalist	Intermediate	0.61	20
Tropical Kingbird (*Tyrannus melancholicus*)	Generalist	Intermediate	0.57	30
Great Kiskadee (*Pitangus sulfuratus*)	Generalist	Intermediate	0.57	24
Gray-breasted Martin (*Progne modesta*)	Generalist	Intermediate	0.53	6
Correndera Pipit (*Anthus correndera*)	Grassland	Intermediate	0.47	21
Firewood-gatherer (*Anumbius annumbi*)	Generalist	Intermediate	0.46	25
Gray-breasted Martin (*Progne chalybea*)	Generalist	Intermediate	0.42	6
Red-winged Tinamou (*Rhynchotus rufescens*)	Grassland	Intermediate	0.42	25
Hudson's Canastero (*Asthenes hudsoni*)	Grassland	Rare	0.38	5
Spot-winged Pigeon (*Patagioenas maculosa*)	Generalist	Intermediate	0.35	22
Whistling Heron (*Syrigma sibilatrix*)	Generalist	Intermediate	0.31	23
Picui Ground-Dove (*Columbina picui*)	Generalist	Intermediate	0.31	15
Screaming Cowbird (*Molothrus rufoaxiliaris*)	Generalist	Intermediate	0.27	16
Hooded Siskin (*Carduelis magellanica*)	Generalist	Intermediate	0.27	13
Rufous-bellied Thrush (*Turdus rufiventris*)	Generalist	Rare	0.26	3
Long-tailed Meadowlark (*Sturnella loyca*)	Generalist	Intermediate	0.25	6
Pampas Pipit (*Anthus chacoensis*)	Generalist	Intermediate	0.24	11
Sedge Wren (*Cistothorus platensis*)	Grassland	Intermediate	0.23	13
American Kestrel (*Falco sparverius*)	Generalist	Intermediate	0.22	26
Vermillion Flycatcher (*Pyrocephalus rubinus*)	Generalist	Intermediate	0.20	10
Aplomado Falcon (*Falco femoralis*)	Generalist	Intermediate	0.19	18

Table 1. (*continued*)

Species	Nesting habitat	Degree of rarity	Relative local abundance	Area of occupancy
Yellowish Pipit (*Anthus lutescens*)	Grassland	Intermediate	0.19	12
Bearded Tachuri (*Polystictus pectoralis*)	Grassland	Rare	0.19	2
Pale-breasted Spinetail (*Synallaxis albescens*)	Generalist	Intermediate	0.18	14
Green-barred Woodpecker (*Colaptes melanochloros*)	Generalist	Intermediate	0.17	19
Short-billed Pipit (*Anthus furcatus*)	Grassland	Rare	0.17	3
Warbling Doradito (*Pseudocolopteryx flaviventris*)	Grassland	Intermediate	0.16	9
White-tailed Kite (*Elanus leucurus*)	Generalist	Intermediate	0.15	20
Cattle Tyrant (*Machetornis rixosus*)	Generalist	Intermediate	0.15	12
Freckle-breasted Thornbird (*Phacellodomus striaticollis*)	Woodland	Rare	0.15	4
Roadside Hawk (*Buteo magnirostris*)	Generalist	Intermediate	0.14	19
Long-winged Harrier (*Circus buffoni*)	Grassland	Intermediate	0.12	12
Glittering-bellied Emerald (*Chlorostilbon aureoventris*)	Generalist	Intermediate	0.12	11
Masked Gnatcatcher (*Polioptila dumicola*)	Generalist	Rare	0.11	4
Bay-capped Wren-Spinetail (*Spartonoica maluroides*)	Grassland	Rare	0.11	5
Dark-billed Cuckoo (*Coccyzus melacoryphus*)	Woodland	Rare	0.10	5
White-crested Tyrannulet (*Serpophaga subcristata*)	Generalist	Rare	0.10	5
Creamy-bellied Thrush (*Turdus amaurochalinus*)	Generalist	Rare	0.10	2
Cinereous Harrier (*Circus cinereus*)	Grassland	Rare	0.10	2
Small-billed Elaenia (*Elaenia parvirostris*)	Generalist	Rare	0.09	3
Sooty-fronted Spinetail (*Synallaxis frontalis*)	Woodland	Rare	0.09	3
Short-eared Owl (*Asio flammeus*)	Grassland	Rare	0.06	2

[A]Following the South American Classification Committee (SACC) classification version of 2 February 2012.

23 of the 30 transects. Grasslands and croplands were the prevalent land-cover types in the region, even though there was considerable variation of cover of these land-use types among transects (Fig. 2). Among grasslands, tall-grass cover was 20%, followed by short-grass cover (12%) and pasture (11%), whereas among croplands, annual-crop cover was 42% and stubble cover was 3%. There was less and more variable cover of woodlands (8%), wetlands (4%) and peridomestic areas (<1%) habitat types in the in rural landscape (Fig. 2).

We recorded a total of 77 species of breeding landbird (Table 1). According to our classification system, most landbirds use woodlands, peridomestic areas and grasslands in which to nest in the rural landscape (Table 2), but none of these species use either croplands or peridomestic areas as its exclusive nesting habitat. Most landbird species ($n = 52$) were classified as generalists in their nesting habitat, whereas our classification of habitat specificity showed that grasslands hold the highest number of habitat-specialists ($n = 17$), followed by wetlands ($n = 5$) and woodlands ($n = 3$).

ANOVA revealed a significant difference in the local abundance of landbird species based on their nesting habitat ($F = 8.08$, d.f. = 3, 73, $P < 0.001$), even though the abundance of generalists was not higher than the local abundance of grassland and woodland specialists (one-tailed Dunnett's test: d.f. = 73, $P > 0.05$, in all cases; Fig. 3*a*). We found a clear difference in the area of occupancy of landbird species according to their nesting habitat (ANOVA: $F = 6.6$, d.f. = 3 and 73, $P < 0.001$; Fig. 3*b*), so that the area of occupancy of generalists was significantly higher than that of grassland and woodland specialists (one-tailed Dunnett's test: d.f. = 73, $P < 0.01$ for both groups), but did not differ significantly from that of wetland specialists (Fig. 3*b*).

Fig. 4 summarises the results of both criteria of common and rare species and their relationships with use of nesting habitat. As expected, relative local abundance was significantly associated with area of occupancy ($R = 0.36$, $n = 77$, $P < 0.01$; Fig. 4). According to both criteria, we identified 14 species as rare, 21 as common and 42 as species with an intermediate degree of rarity or commonness. There was a significant correlation between rarity of a species and its degree of specialisation in use of nesting habitat (Fig. 4). Most rare species (9 of 14) were specialist species in their use of nesting habitat, whereas 15 of the 21 common species were generalists ($\chi^2 = 8.05$, d.f. = 2, $P < 0.05$; Fig. 4). Wetland specialists were an exception to the above pattern as they were quite common species even though they are specialists in their use of nesting habitat.

Table 2. Summary of nesting habitat of the 52 generalist species (which nest in more than one habitat type) and the 25 specialist species (which nest in only one habitat type)

	n	Nesting habitat				
		Grassland	Cropland	Woodland	Peridomestic habitat	Wetland
Generalists	52	28	9	46	43	10
Specialists	25	17	0	3	0	5
Total	77	45	9	49	43	15

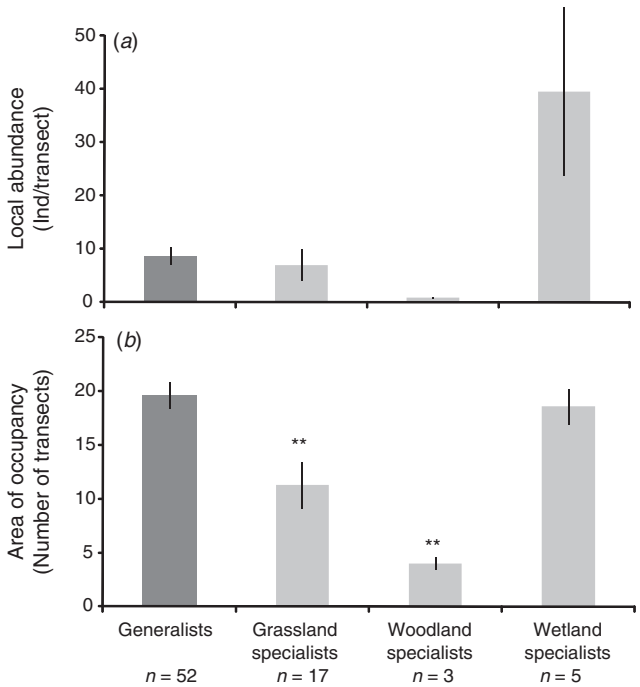

Fig. 3. (*a*) Mean (±s.e.) local abundance (individuals/transect); and (*b*) mean (±s.e.) area of occupancy (number of transects) for generalist species (dark grey), and grassland, woodland and wetland specialists (pale grey) in the avian assemblage of the Pampas of central Argentina. The area of occupancy of generalist species was significantly higher than that of grassland and woodland specialists (one-tailed Dunnett's test: d.f. = 73, $P < 0.01$ for both groups). **, $P < 0.01$.

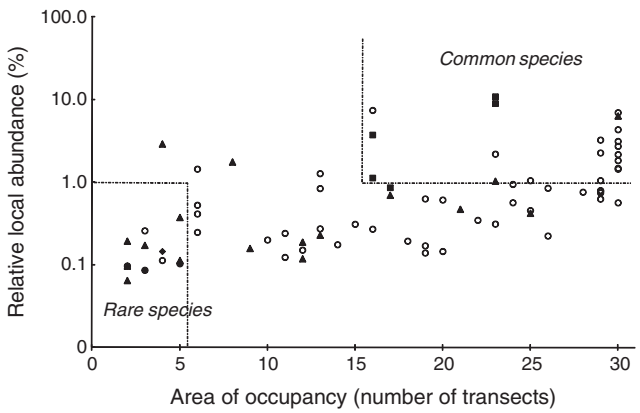

Fig. 4. Relative abundance and area of occupancy of 77 species of landbird in the Pampas of central Argentina classified according to their use of nesting habitat. ○, Generalist species (5 species rare, 32 intermediate and 15 common); ▲, Grassland specialists (6 rare, 9 intermediate and 2 common); ■, Wetland specialists (3 rare, 0 intermediate and 0 common); ◆, Woodland specialists (0 rare, 1 intermediate and 4 common).

Discussion

In general, our results showed that the degree of specialisation in use of nesting habitat is related to the commonness or rarity of landbirds in agroecosystems of central Argentina. Nesting specialists tend to be rarer than generalist species, and these associations are consistent with findings of previous studies showing that habitat specialisation is associated with rarity at the community level (Kattan 1992; Goerck 1997; McKinney and Lockwood 1999; Owens and Bennett 2000; Brändle and Brandl 2001; Gillespie 2002; Davies *et al*. 2004; Fairbanks 2004). In addition, the greater richness of generalist species in the avian assemblage of Pampean agroecosystems is consistent with studies that have shown that agricultural activities that alter habitat often benefit those species that take advantage of these changes and tend to then be common (Diamond 1989; McKinney and Lockwood 1999; La Sorte 2006).

Of all the terrestrial habitats in the Pampas rural landscape, grasslands support the highest number of nesting specialists, probably because of their fairly pristine condition and because they more closely resemble the natural grasslands of pre-European settlement times. Indeed, grassland specialists provide a particular identity to the Pampas (Stotz *et al*. 1996; Di Giacomo *et al*. 2007). In contrast, no species nested exclusively in croplands in the agroecosystems of the Pampas. This contrasts with the situation in western Europe, with its older history of human land-use in which some species depend on early successional habitats provided by agricultural activities (Sutherland 2004). Our results are, however, consistent with studies carried out in areas in which agriculture has been introduced more recently, such as Australia (Haslem and Bennett 2008) and west Africa (Söderström *et al*. 2003), which also have no species nesting exclusively in croplands.

Our findings show that the rarity of landbirds is associated with use of specialised nesting habitat. Most rare species were specialists, and all woodland specialists and many grassland specialists were classed as rare. Woodland specialists were expected to be rare because the lack of this habitat, in particular native woodland, provides little chance of settlement in the agroecosystems of the Pampas. In contrast, the rarity of grassland specialists might reflect the fragmentation of natural grasslands owing to an increase in agriculture (Baldi and Paruelo 2008).

Between 1986–90 and 2001–05 more than 4 260 000 ha has been converted to annual cropland in the Pampas, an increase of 10% of cropland with a corresponding decline in natural grasslands (adapted from Viglizzo *et al*. 2011). This has affected the continuity and biotic exchange among remnant patches of natural grassland (Baldi and Paruelo 2008). Moreover, grazing pressure may create grasslands with greater horizontal and vertical structural diversity. In particular, the reduction of areas of tall grassland could restrict the distribution of grassland specialists, such as observed in the Hudson's Canastero (*Asthenes hudsoni*) and Bay-capped Wren-Spinetail (*Spartonoica maluroides*), species that shelter, feed and nest in tall grass or on the ground surrounded by tall grass (Isacch and Martínez 2001; Isacch *et al*. 2003). Our results show that species with specific habitat requirements are more sensitive to human activities, something that had also been reported in other farmland ecosystems (Siriwardena *et al*. 1998; Murphy 2003; Caplat and Fonderflick 2009; Azpiroz and Blake 2009).

Wetland species were an exception to the pattern observed among the other groups of nesting specialists, since this group of species did not differ from generalists in either local abundance or area of occupancy even though wetland habitats are poorly represented in the rural landscape. The lack of

association between nesting specialisation of wetland species and their rarity or commonness could be related to other characteristics that wetland specialists may share with common species. For instance, wetland species have great dispersal capacity (Weller 1999), which is positively associated with range-size (reviewed in Gaston 1994). Furthermore, wetland specialists are able to use different habitats as feeding areas and have other characteristics of common species, such as flocking behaviour, which allows them to achieve greater anti-predator defence, greater mobility to use seasonal resources and colonial nesting to achieve greater reproductive success (Weller 1999).

In addition, it should also be noted that five species categorised as being generalist in their use of nesting habitats were rare in the Pampean agroecosystems even though these species are common in the neighbouring eco-regions of the Delta and the Espinal (Babarskas *et al*. 2003; Pagano and Mérida 2009). These species are associated with disturbed habitats (Parker *et al*. 1996) and in our study they were present in woodlots and peridomestic habitats. It is likely, therefore, that these species (e.g. Rufous-bellied Thrush (*Turdus rufiventris*) and Creamy-bellied Thrush (*Turdus amaurochalinus*)) are expanding into the interior of the Pampas using a novel habitat in the region (Narosky and Di Giacomo 1993).

Conservation implications

Changes in habitat – as has happened and continues to happen in the grasslands of the Pampas (Baldi and Paruelo 2008) – can cause specialists to become rarer and in some cases become locally extinct (Diamond 1989; McKinney and Lockwood 1999). According to Manne and Pimm (2001), rare and restricted species in the Neotropical avifauna are also the most threatened, a result consistent with the notion that they face the double jeopardy of extinction associated with low local abundance and restricted range (Johnson 1998). In this study, we identified six grassland species that face this double jeopardy in the temperate agroecosystems of Argentina (Fig. 4; Table 1). Of these six species, three are already listed as vulnerable species nationally (AOP–SADS 2008): Hudson's Canastero, Bay-capped Wren-Spinetail and the Bearded Tachuri (*Polystictus pectoralis*). According to our criteria of rarity, we should add to those species three other landbirds that share this double jeopardy in the study area: the Cinereous Harrier (*Circus cinereus*), Short-eared Owl (*Asio flammeus*) and Short-billed Pipit (*Anthus furcatus*), even though these species may not be considered as rare in grasslands outside the Pampas (AOP–SADS 2008; Azpiroz and Blake 2009). Moreover the Greater Rhea (*Rhea americana*) has also been mentioned as a threatened species (AOP–SADS 2008) since it is sensitive to agricultural development and their area of occupancy is decreasing (Bilenca *et al*. 2009; Alonso Roldán *et al*. 2009). Thus, the persistence of many grassland birds in the Pampas is a matter of concern given that they inhabit a region heavily affected, through loss of habitat associated with by human activities including agricultural expansion (Isacch and Martínez 2001; Isacch *et al*. 2003; Bilenca and Miñarro 2004; Codesido *et al*. 2008). The identification of species potentially at risk requires urgent action, especially considering that <1% of grassland areas in Argentina are protected and these lands remain vulnerable to further change (Bilenca and Miñarro 2004).

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