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Barn Swallows keep expanding their breeding range in South America

Juan Manuel Grande[A,B,C], *Miguel A. Santillán*[A], *Paula M. Orozco*[A,B], *María Soledad Liébana*[A,B], *Marcos Matías Reyes*[A], *Maximiliano Adrián Galmes*[A] *and Joaquín Ceregheti*[A]

[A]Centro para el Estudio y Conservación de las Aves Rapaces en Argentina, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Avenida Uruguay 151, Santa Rosa (6300), La Pampa, Argentina.
[B]Instituto de las Ciencias de la Tierra y Ambientales de La Pampa (INCITAP), Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET), Avenida Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina.
[C]Corresponding author. Email: manuhola@yahoo.es

Abstract. Barn Swallows (*Hirundo rustica*) breeding in North America traditionally wintered in South America. In the 1980s a small breeding population was found in coastal Argentina and since then the breeding range of Barn Swallows in the country has expanded. Our aims here were to examine the north-western limits of the breeding range of Barn Swallows in Argentina, and to analyse the factors that may determine selection of nesting site by the species. We surveyed and characterised culverts and bridges below roads, which are the most frequently used breeding sites of Barn Swallows in Argentina, in an area of 15 000 km^2 in northern La Pampa Province, central Argentina. We found 51 nests in 39 culverts and bridges sparsely distributed through most of the surveyed area. We also found 16 nests outside that area, in central Buenos Aires and La Pampa Provinces. Occupied culverts were higher and were more often associated with wetlands than unoccupied culverts. Most nests were in agricultural landscapes, with just a few in Caldén (*Prosopis caldenia*) forests. Our results confirm that the breeding range of the species in South America has expanded by about a third in relation to previous studies, but there is still a large area of suitable habitat for the species in Argentina, mostly to the north of La Pampa Province, suggesting that further expansion of the range of the species can be expected. Our study describes the expansion of this common species within South America and speculates on the underlying reasons.

Additional keywords: Argentina, distributional range, *Hirundo rustica*, artificial breeding substrate, nesting site, population expansion.

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Introduction

The range of breeding habitats occupied by a species is the result of a myriad of factors, including ecological and historical factors (Vuilleumier and Simberloff 1980). In the actual context of global change, there are many examples of changes in the distribution of bird species, both expansions and contractions (McKinney and Lockwood 1999). Identifying and tracking the occurrence of such changes in range allow exploration of the potential effects that environmental changes have on different populations of birds.

The Barn Swallow (*Hirundo rustica*) is one of the most widely distributed and abundant swallows in the world, occurring on all continents except Antarctica (although there are anecdotal records of the species even there; Korczak-Abshire *et al.* 2011), at least for parts of a year (Turner 2004). It breeds in open, cup nests made of mud and attached to walls in roofed and partly closed places. Originally, it probably bred in naturally occurring caves and crevices but now, and throughout its range, the species mainly nests in artificial structures, such as buildings, bridges, culverts and ditches (Møller 1994; Brown and Brown 1999). The use of artificial structures has allowed Barn Swallows to spread widely into habitats where natural breeding sites for the species did not occur (Møller 1994; Brown and Brown 1999). The species also shows broad ecological plasticity, which allows it to exploit successfully environments as diverse as high mountains (up to 3000 m asl), wetlands and deserts (Brown and Brown 1999). These are probably the main factors influencing its worldwide distribution.

Barn Swallows are predominantly long-distance migrants, with just a few sedentary subspecies and populations. It breeds throughout most of the northern hemisphere, and winters in the southern hemisphere, including South America, sub-Saharan Africa and Australia (Møller 1994; Brown and Brown 1999; Turner 2004). The species also stands out among birds because it is one of the few long-distance migratory species that has established breeding populations in former wintering areas, which can be thousands of kilometres from their original breeding grounds. Remarkably, two species of swallows – Barn Swallow and Common House Martin (*Delichon urbicum*) – are among the only five long-distance migratory birds known to have established breeding populations in their former wintering areas (the others are White Stork (*Ciconia ciconia*), European

Bee-eater (*Merops apiaster*) and Leach's Storm Petrel (*Oceanodroma leucorhoa*), all now breeding in southern Africa) (Sutherland 1998; Hockey *et al*. 2005). Another northern hemisphere breeding swallow that winters in the southern hemisphere, the Cliff Swallow (*Petrochelidon pyrrhonota*), has occasionally nested in Argentina although apparently not successfully (Petracci and Delhey 2004).

In South America, the Barn Swallow was a regular wintering non-breeding species until 1980, when six pairs were discovered breeding in Mar Chiquita, in south-eastern coastal Buenos Aires Province, Argentina (Martínez 1983). As breeding congregations of this species are conspicuous, and since the area where the species was first discovered breeding is regularly visited by an active ornithological community, it is likely that the breeding population settled in the area in or not long before 1980. Since then, population monitoring has shown that the breeding population has increased and may currently number thousands of individuals (Billerman *et al*. 2011). From its first-recorded breeding site, the population has also expanded south-west and north along the coast (Fiameni 2001; Larracoechea *et al*. 2013) and inland into the southern portions of Buenos Aires and La Pampa Provinces (Morici 2009, 2012). The species has also spread to the north and north-east of its original breeding site (Idoeta *et al*. 2011; Sánchez and Solis Fieg 2012).

Our aims in this study were to evaluate whether the species has expanded its breeding range further in central Argentina (La Pampa and Buenos Aires Provinces), and to assess the characteristics of the nesting sites used by Barn Swallows in Argentina. We also discuss the range expansion of the species and its foreseeable future limits.

Materials and methods

The discovery of a few nests of Barn Swallows in the 2011–12 and 2012–13 breeding seasons (mid October–late February) in western Buenos Aires Province and northern La Pampa Province led us to design and perform an intensive search for nests in the area. Most nests that have been reported in Argentina have been in culverts under roads or under bridges (Martínez 1983; Fiameni 2001; Petracci and Delhey 2004; Morici 2009; Idoeta *et al*. 2011; Morici 2012; Sánchez and Solis Fieg 2012; Larracoechea *et al*. 2013), and searching for nests in these structures is an efficient way to detect the presence of the species. In 2013, we performed intensive surveys along roads over four days (7 March, 17 April, 5 May and 15 November), looking for Barn Swallow nests in all culverts and bridges below roads in Northern La Pampa Province, covering an area of ~15 000 km^2 (hatched area in Fig. 1). Outside this intensively surveyed area, we also inspected a few culverts (although not systematically) along the Ruta Nacional 5 between Buenos Aires and Santa Rosa (La Pampa Province) on 5 September 2013 (9 culverts in 300 km) and in Ruta Provincial 188 between San Nicolás and General Villegas (Buenos Aires Province) on 24 February 2014 (10 culverts in 210 km), as well as a few in other roads in La Pampa and Buenos Aires Provinces (Fig. 1*b*). The search for nests was restricted to culverts and bridges below primary and secondary roads. Surveyed culverts and bridges were georeferenced with a GPS.

The intensively surveyed area is mostly within the western Pampas Grassland ecoregion, with only a small area in the Espinal ecoregion (see Fig. 1; Brown and Pacheco 2006). The area is generally flat with low hills in the west (100–350 m asl). The weather is subhumid to dry, with mean annual precipitation ranging from ~500 to ~850 mm and which falls mostly from October–November to March–April. Mean annual daily temperature is ~15°C (Cano 1980). In most of the survey area, the original vegetation (natural grasslands in the Pampas Grassland ecoregion, and open Caldén (*Prosopis caldenia*) forest in the Espinal) has been replaced by agriculture crops or pasture for livestock (SAyDS 2004; Lorda *et al*. 2008). The areas searched beyond the intensively surveyed area lay within the same two ecoregions and habitats were similar (Fig. 1*b*).

We also evaluated characteristics of culverts to determine factors that may influence use as nesting sites by Swallows. For example, low culverts could allow the access of predators to nests as well as the complete inundation of the culvert causing nesting failure. We measured the height of culverts and bridges, with a measuring tape, from the horizontal centre of the culvert or bridge from the ground to the ceiling of culvert or base of the bridge. Barn Swallows are also often associated with waterbodies (Brown and Brown 1999; Turner 2004). Because our study area is in a semiarid region and the presence of wetlands could influence the presence of the species, we also noted if culverts were associated with wetlands or not. To determine if there were differences in characteristics of occupied and unoccupied culverts within the intensively surveyed area, we ran generalised linear models (GLM) in JMP 8 software (SAS Institute Inc., Cary, NC). We used models with a binomial distribution and logit link to test for differences in height of the structure and proximity to wetlands. We found no nests in culverts and bridges inspected in the north-western part of the intensively surveyed area (Fig. 1*a*). Therefore, we considered them to be outside the breeding range of the species. Within the intensively surveyed area, we then compared the characteristics of culverts within and outside the breeding range of the species to see if there were differences that could explain the absence of the species in the latter. We analysed culvert height (modelled with normal distribution and identity link) and proximity to wetlands (modelled with binomial distribution and logit link) as dependent variables and location (within or outside occupied range) as the independent variable.

All means are reported ± standard error.

Results

In the intensively surveyed area, we checked 242 culverts and bridges along a total of 980 km of road, which comprises ~75% of the sealed roads in the survey area. We also checked 28 culverts and bridges along Ruta Nacional 5 and Ruta Nacional 188 in the centre of Buenos Aires and La Pampa Provinces (Fig. 1*b*). Most sampled culverts and bridges were square or rectangular in cross-section (89%, $n = 272$) and only a few culverts were cylindrical. We found no nests in any of the 15 cylindrical culverts examined. Of the 41 occupied culverts and bridges in the survey area, we recorded 56 nests (Fig. 1*a*). Outside the intensive survey area, we found another 23 nests in 14 occupied culverts and one nest found incidentally in a building in the east of La Pampa Province (Fig. 1*b*; for further details of the culverts and bridges surveyed, see Table S1 of the Supplementary Material, available online only). Within the intensive survey

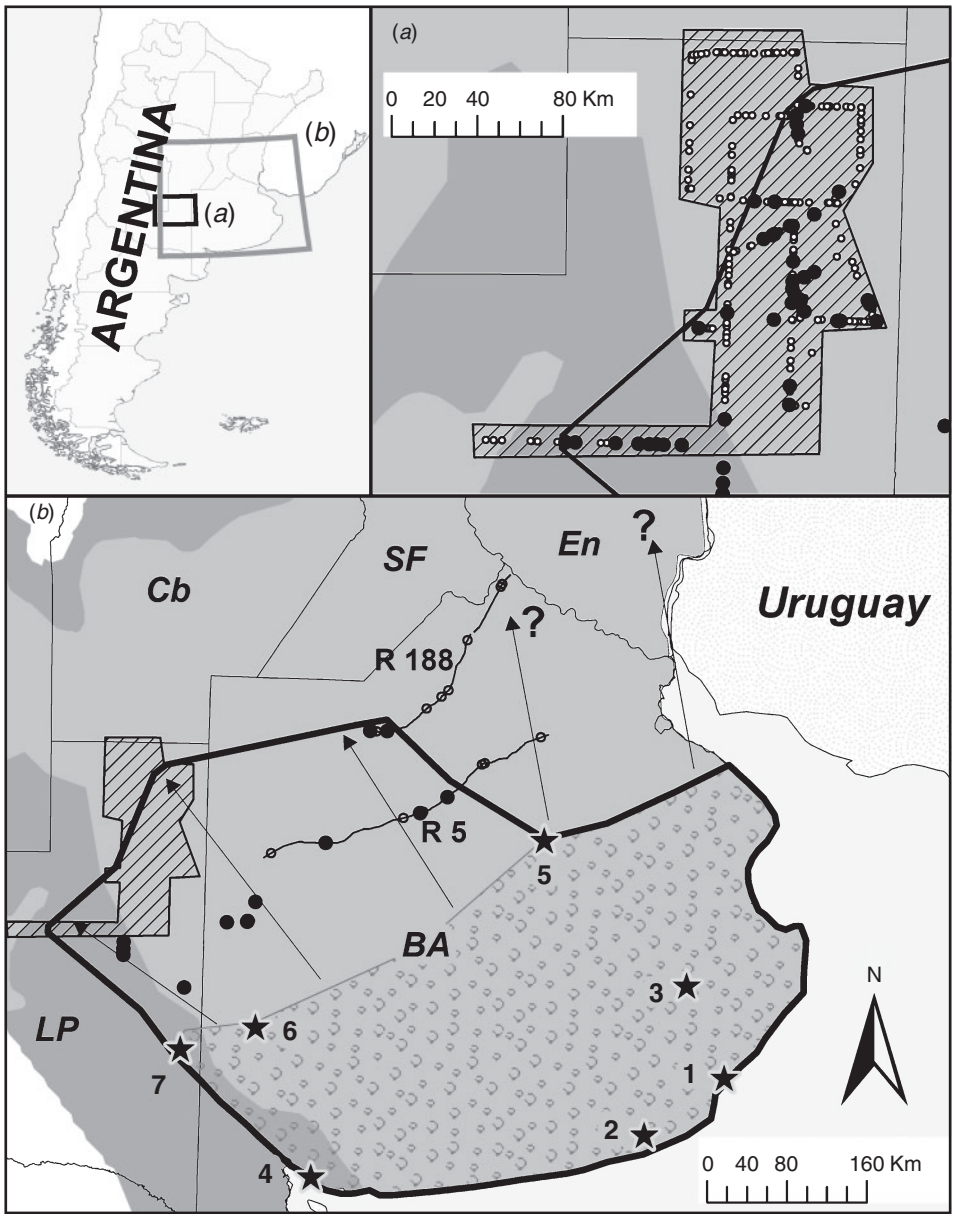

Fig. 1. The study area showing the distribution of the Barn Swallow breeding population in Argentina. (*a*) The hatched area shows the area searched intensively for Barn Swallow nests; solid black dots are sampled sites with nests, and white dots sampled sites without nests. The thick black line corresponds to the actual known limit of the distribution of the species, including records from this study. (*b*) Actual breeding distribution of Barn Swallows in Argentina (area limited by the thick black line) spread mostly through the Pampas Grassland ecoregion (light shading) with a small portion in the Espinal ecoregion (dark shading). Arrows show the spread of the species to the north-west while arrows with question marks indicate areas were we expect the species to be if it has spread to the north with the same intensity as to the north-west. The former distribution of the species according to previously published references is also shown (area covered by scattered trees symbol). Labelled stars correspond to published breeding records of the species in Argentina: 1) Martínez (1983); 2) Fiameni (2001); 3) Sánchez and Solis Fieg (2012); 4) Larracoechea *et al*. (2013); 5) Idoeta *et al*. (2011); 6) Morici (2009); 7) Morici (2012). Our study area and segments of roads surveyed in this study are also shown: R188, Ruta Nacional 188; R5, Ruta Nacional 5. Agentinean Provinces are shown as follow: En, Entre Ríos Province; BA, Buenos Aires Province; SF, Santa Fe Province; Cb, Córdoba Province; LP, La Pampa Province.

area, the mean distance to the next occupied culvert was 6.30 ± 0.76 km (range 0.9–23.4). The number of nests (active and inactive) per occupied structure was 1.41 ± 0.09 (range 1–4; number of occupied structures = 56 (41 culverts and bridges in intensive survey area, and 14 culverts and 1 incidental record in building outside this area)), although the maximum number of

active nests in a single culvert or bridge was three. Almost all nests (89.3% of 56 nests in the intensive survey area) were fixed to the walls of culverts, close to the roof (nest borders were generally 5–7 cm from the roof).

Occupied culverts within the survey area were higher than unoccupied structures (occupied culverts 101.16 ± 3.88 cm, $n = 37$; unoccupied culverts 70.58 ± 2.17 cm, $n = 178$; $\chi^2 = 34.794$, d.f. = 1, $P < 0.001$) and were more often associated with a wetland than unoccupied culverts (32% of occupied culverts were associated with wetlands cf. 7% of unoccupied culverts; $\chi^2 = 11.00$, d.f. = 1, $P < 0.001$, $n = 178$). The minimum height of occupied culverts was 50 cm. When comparing culverts outside the breeding range (culverts to the north-west of the solid black line in Fig. 1*a*) with those within it, we found that culverts from outside tended to be lower (within breeding range 80.32 ± 2.29 cm; outside breeding range 72.03 ± 3.44 cm; $\chi^2 = 3.35$, d.f. = 1, $P = 0.06$, $n = 209$) and were less likely to be associated with wetlands (13.1% associated with wetlands within the breeding range; 1.96% associated with wetlands outside; $\chi^2 = 6.15$, d.f. = 1, $P = 0.013$, $n = 188$).

Almost all nests were in structures in agricultural landscapes, including natural or exotic pastures, although we also found Barn Swallows nesting in culverts within two of the main urban areas in the surveyed area, Santa Rosa and General Pico, as well as a few nests associated with wetlands in patches of Caldén forest.

Discussion

Our results expand the known breeding distribution of Barn Swallows in Argentina ~ 270 km to the north-east and >430 km to the west of the closest previous records (Fig. 1*b*). This increases its known breeding range in South America by more than a third, and covering an area close to 244 000 km^2. We found a small number of nests, sparsely distributed in clusters, across much of the surveyed area, as is typical in the traditional breeding grounds of Barn Swallows in North America (Brown and Brown 1999). Nesting density and the number of nests per structure in the surveyed area is small compared with other areas of Argentina, where >40 nests may be found under single bridges (Petracci and Delhey 2004). This suggests that there could be some habitat limitation within our study site (e.g. resources are limited and do not support large colonies) or it is a consequence of the recent colonisation of the area. The latter suggestion is more plausible, because the species has progressively expanded in this way throughout the country and newly established breeding groups are small (i.e. bridges on the coast of Buenos Aires Province that now support tens of pairs held just a few nests when the species was first discovered breeding (Martínez 1983; Petracci and Delhey 2004)). In addition, habitats and land-uses in eastern La Pampa Province and much of central and southern Buenos Aires Province, where the species thrived, are very similar.

We found no nests in culverts or under bridges in the westernmost and northernmost areas surveyed in this study, suggesting that this was the limit of the distribution of the species at this time. Culverts and bridges in that area seem to be less suitable for Barn Swallows as they tend to be lower and are less often associated with wetlands. However, some culverts meet the characteristics apparently selected by the species and some pairs could probably establish there in the future. We do not know how far Barn Swallows have expanded to the north-east of our study area. In that region there is a complex of wetlands and channels (most of them manmade) that form the final section of the endorheic river, Río Quinto. The habitat certainly appears suitable for the species and, therefore, if Barn Swallows are still not there, they will probably be in the near future.

Taking into account the expansion of the species to the north-west, we estimated that Barn Swallows may have already occupied all the north of Buenos Aires Province (see Fig. 1*b*). However, the lack of records in the eastern culverts sampled along both Ruta Nacional 188 (six culverts) and Ruta Nacional 5 (three culverts), suggests that the species has not yet reached that area or did so only in low numbers.

The northern portion of the extensive treeless grassland plains that once formed the Pampas Grassland ecoregion of Argentina was used as a wintering area by Barn Swallows at least since the early 20th century (Pereyra 1938). However, this area was largely devoid of breeding substrates for the species until the arrival of Europeans. Roads and railways with associated culverts and bridges, as well as other structures, provide the only described breeding substrates for the species in Argentina (Martínez 1983; Petracci and Delhey 2004; Morici 2009; Idoeta *et al*. 2011; Morici 2012; Larracoechea *et al*. 2013) and seems to have allowed the establishment and subsequent expansion of the breeding range of Barn Swallows in Argentina. Breeding of Barn Swallows was formerly virtually restricted to the Pampas Grassland ecoregion (Martínez 1983; Fiameni 2001; Idoeta *et al*. 2011; Fig. 1*b*). More recently, there have been a few breeding records in the Espinal ecoregion, although most were in cropland or pasture landscapes or environments altered by people (Petracci and Delhey 2004; Morici 2012; Larracoechea *et al*. 2013). The few nests found in patches of native Caldén forest were associated with wetlands (this study). Although not common, there are wetlands in the Espinal ecoregion (Cano 1980; Brown and Pacheco 2006), suggesting that if the species finds suitable nesting sites there, expansion of the breeding range of Barn Swallows could be expected in this ecoregion.

Based on our findings within Argentina, which examined just two ecoregions where the species now occurs, Barn Swallows have >300 000 km^2 of potential habitat to the north of the current breeding range in Argentina into which to expand. This northern region is largely a continuous mix of crops and pasture. Furthermore, these northern areas have higher densities of people and roads, and far more rivers and wetlands, than the areas where the species currently breeds (Bianchi and Cravero 2010). Overall, there appears no clear, immediate environmental limit to the expansion of the breeding range to the north of its current range in Argentina.

Barn Swallows breeding in Argentina appear to have completely switched their moult phenology and developed their own migratory system; there is no evidence of breeding birds moulting actively in Argentina and no records of the species during winter (Garcia-Perez *et al*. 2013). It is not clear where the birds go, although stable isotope analyses suggest that they may go to the north-east of South America (specifically north Brazil, French Guiana, Suriname, Guyana, and Venezuela; Garcia-Perez

et al. 2013). The quality and extension of wintering grounds can have profound effects on the winter survival of a bird and, through carry-over effects, on their breeding and survival prospects in their next breeding attempt (Newton 2004; Norris *et al*. 2004). Barn Swallows breeding in South America could thus find the limit to their actual expansion is the carrying capacity of their new wintering grounds. Further research is needed to clarify where exactly they winter and the potential limitations the species may face there.

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