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ANTHROPOGENIC NESTING SITES ALLOW URBAN BREEDING IN BURROWING PARROTS *CYANOLISEUS PATAGONUS*

SITIOS DE NIDIFICACIÓN DE ORIGEN ANTRÓPICO PERMITEN LA REPRODUCCIÓN DEL LORO BARRANQUERO *CYANOLISEUS PATAGONUS* EN MEDIOS URBANOS

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Summary.— How birds adapt to urban life is a key question in evolutionary and conservation biology since urbanisation is one of the major causes of habitat loss worldwide. Some species are able to deal with these anthropogenic changes but a shortage of nesting sites may preclude them from breeding in cities. We conducted a baseline survey of the cliff-nesting burrowing parrot *Cyanoliseus patagonus* around Bahía Blanca (Argentina), estimating a minimum total of 1,361 pairs breeding at 24 sites (colonies) in 2013. The species showed facultative colonial behaviour, colony size varying between 1 and 300 pairs. Most colonies (68%) and pairs (74%) occupied human-made substrates, mostly quarries but also water wells. Colony size was strongly correlated to the extent of both natural and anthropogenic nesting substrates, suggesting an ideal free distribution of pairs according to the availability of nesting resources. Anthropogenic substrates have certainly allowed population expansion in what is a rather flat landscape with a shortage of cliffs and ravines, as well as urban breeding by a large part (61%) of the surveyed population. This is currently one of the largest populations of burrowing parrots, a previously abundant species that is progressively threatened by persecution and nest poaching for the international pet trade.

Key words: coloniality, nest-site innovations, nest-site shortage, Psittacidae, quarries, urbanisation.

Resumen.—Dado que la urbanización es una de las causas principales de pérdida de hábitat a escala mundial, resulta clave desde el punto de vista evolutivo y de conservación comprender cómo las aves se adaptan a vivir en este tipo de medios. Algunas especies son capaces de adaptarse al medio urbano, pero la escasez de lugares para nidificar puede impedir su reproducción. En este trabajo realizamos un seguimiento del loro barranquero *Cyanoliseus patagonus* en los alrededores de Bahía Blanca (Argentina),

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estimando una población reproductora mínima de 1.361 parejas distribuidas en 24 colonias en 2013. El tamaño de las colonias varió entre 1 y 300 parejas, mostrando un comportamiento colonial facultativo. La mayor parte de las colonias (68%) y de las parejas reproductoras (74%) ocuparon sustratos de origen humano, fundamentalmente canteras, aunque también se instalaron en pozos de agua. El tamaño de las colonias estuvo fuertemente correlacionado con el tamaño de los sustratos de nidificación, tanto naturales como artificiales, sugiriendo una distribución libre ideal de las parejas acorde con la disponibilidad de lugares para nidificar. Los sustratos de origen antrópico seguramente permitieron una expansión poblacional en un paisaje llano, con escasez de quebradas y barrancas, pero también una colonización del medio urbano por buena parte de la población reproductora censada (61%). Esta puede constituir ahora una de las mayores poblaciones de loros barranqueros del mundo, una especie que antaño fue abundante pero que se vio progresivamente amenazada por la persecución humana y su explotación para el comercio internacional de mascotas.

Palabras clave: canteras, colonialidad, innovación de lugares de nidificación, limitación de lugares de nidificación, Psittacidae, urbanización.

INTRODUCTION

Since urbanisation is one of the leading causes of habitat loss and biodiversity impoverishment worldwide, unravelling the differences among bird species in their tolerance to urban habitats is of pivotal importance (Sol *et al*., 2013a). Behavioural adjustments and/or non-random sorting of individuals by behavioural traits may assist some species in becoming urban dwellers (Sol *et al*., 2013b). In this respect, urbanisation differs from other drivers of habitat loss and transformation in that the new habitats have an unusually high presence of humans, which may select for tame individuals to live in urbanised habitats (Carrete and Tella, 2010). A recent comparative study conducted in and around a young city (Bahía Blanca, Argentina) showed a contemporary process where species that cope well with urbanisation are those showing high inter-individual variability in their tolerance of humans (Carrete and Tella, 2011). Inter-individual variability in fear of humans, which is in turn positively correlated to the relative brain size of species, may thus satisfactorily explain why some species may become urban dwellers while others strongly avoid urban habitats (Carrete and Tella, 2011, 2013). However, tameness alone is not enough to allow species to colonize urban habitats if key resources, such as adequate nesting sites, are unavailable (Sol *et al*., 2013a). This may be the case for obligate hole-nesting species that require cliffs for breeding. Although some cliff-nesting species switch to breed in city buildings, others seem unable to use these novel nesting substrates (Newton, 1998) and are thus precluded from living in urban habitats.

We focus here on the nesting habits and breeding numbers of the burrowing parrot *Cyanoliseus patagonus*, a Neotropical cliff-nesting species showing high inter-individual variability in fear of humans and thus a large potential for dealing well with urbanisation (Carrete and Tella, 2011). We show how the use of new, anthropogenic nesting substrates (quarries and water wells) allows this species to maintain a significant breeding population in a rather flat landscape with a shortage of natural nesting sites, as well as allowing urbanised areas to hold even larger breeding numbers than rural areas.

METHODS

This study was conducted in Bahía Blanca and surrounding rural areas (southern Province of Buenos Aires, Argentina), covering a large area of flat landscapes with natural grasslands, pastures and cereal crops and the Eastern range of the Sierra de la Ventana (fig. 1). Bahía Blanca is a relatively young city, founded in 1828 (D'Orbigny, 1845), inhabited by c. 301,000 people in 2010.

Some nesting sites (n = 6) of burrowing parrots were opportunistically found during previous work aimed to study the behavioral responses of rural and urban birds to human disturbance in a variety of species, conducted during nine breeding seasons (December-January 2003-2011; Carrete and Tella, 2010, 2011, 2013). In December 2012, and more intensively in November-December 2013, we surveyed all previously known sites for burrowing parrots and searched for new ones. The burrowing parrot is considered a colonial species that digs its own nest burrows in cliffs (Masello *et al*., 2006). One of its colonies, El Cóndor, represents the largest known breeding aggregation of parrots in the world with *c*. 37,500 pairs (Masello *et al*., 2006). However, the spatial arrangement of nests often makes it difficult to define colonies (see e.g. Jovani and Tella, 2007). In this study, we defined "colonies" as those well-delimited nesting sites, such as natural cliffs, quarries and water wells, where the species was found to breed, even if some of them were occupied by just one pair. These sites greatly varied in suitable nesting surface, human disturbance and accessibility to predators. In a few instances, quarries offered several artificial cliffs occupied by burrowing parrots within a range of 400 m but, after Brown and Brown (1996), these reproductive cores were considered as single colonies given that all individuals reacted together against human or predator intruders. Therefore, although breeding birds from different colonies may share foraging grounds and communal roosts (see Discussion), the particularities of each nesting site may strongly affect breeding success and colony dynamics (Serrano *et al*., 2005) and thus justify this functional definition of a colony from a reproductive point of view.

Previous work conducted at El Cóndor colony estimated the number of breeding pairs by extrapolating the proportion of active nests to the total number of burrows recorded in the cliffs (Masello *et al*., 2006). This procedure was difficult to apply in our study area since we did not climb to the nests to confirm reproduction and indeed many active burrows were occupied by other species. These were mostly feral pigeons *Columba livia* var. *domestica*, which outnumbered burrowing parrots in several colonies, but there were also several other species including barn owls *Tyto alba* and American kestrels *Falco sparverius*. We therefore opted to count from a distance, using binoculars and a telescope, the number of pairs attending nests when feeding offspring in the early morning and evening (Masello *et al*., 2006), combining this methodology with estimates of the number of breeding pairs as the maximum number of adults observed simultaneously in flight when disturbed by people, divided by two. These methods, together with the fact that some pairs might have failed during the earlier stages of reproduction, produced relative estimates of colony sizes rather than an accurate census. The minimum size of the whole breeding population was estimated in December 2013 when most nests contained nestlings (only four fledglings were observed by the end of this month in 2013). However, two colonies (colony 11 holding eight pairs in 2008 and colony 10 holding one pair in 2012) could not be revisited in 2013 given the difficult access to the private properties where they were located, while colonies 3 and 24 (holding 4 and 13 pairs respectively in 2012) were unoccupied in 2013 (see fig. 1 and table 1 for their locations and characteristics). These colonies did not contribute to the breeding population census conducted in 2013 but were used to describe colony characteristics and to assess the relationship between number of pairs and surface area of colony nesting sites. Therefore, sample sizes slightly varied among analyses.

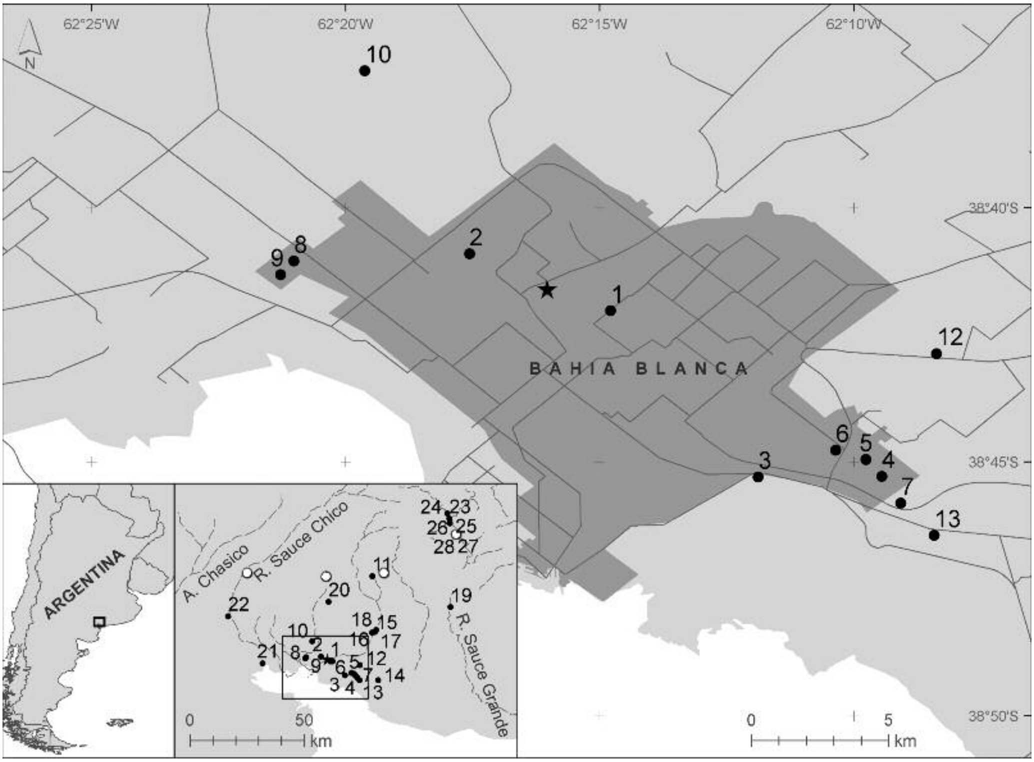

FIG. 1.—Study area showing the distribution of burrowing parrot colonies (filled circles), unoccupied potential nesting sites (open circles) and the urban communal roost (star). Number codes correspond to colonies cited in the table 1. The grayish polygon shows urbanized areas of Bahía Blanca city.
[Área de estudio, mostrando la distribución de las colonias de loro barranquero (círculos rellenos), de potenciales sitios de reproducción no ocupados (círculos vacíos) y del dormidero comunal urbano (estrella). Los números corresponden a las colonias detalladas en la tabla 1. El polígono gris muestra el área urbanizada de la ciudad de Bahía Blanca.]

The surface area of nesting sites was estimated as the product of the length by the average height of the vertical substrate, as calculated using a laser range finder. Google Earth maps (images from 2013) and GPS were used to measure the extent of the largest quarries.

Non parametric tests were used to explore relationships between variables since these were not normally distributed. However, for the description of colony size variability we show both mean and median values since the former are often used for comparative analyses of avian coloniality.

RESULTS

Nesting substrates

Burrowing parrots were found breeding in 28 colonies across the whole study period (see fig. 1 and table 1). Most colonies (67.8 %) were found in human-made substrates. Quarries

TABLE 1

Details of the burrowing parrot colonies surveyed, indicating code numbers (corresponding to those referred in the text and fig. 1), type of substrate, habitat, number of breeding pairs estimated in 2013, and the approximate surface (in m^2) of the nesting substrate.
[Detalles de las colonias de loro barranquero monitorizadas, indicando sus códigos numéricos (correspondientes a los señalados en el texto y fig. 1), el tipo de sustrato, el hábitat, el número de parejas reproductoras estimadas en 2013 y la superficie aproximada (en m^2) del sustrato de nidificación.]

Code	Substrate	Habitat	Area	# pairs	Surface
1	Quarry	Urban	Bahía Blanca	124	2000
2	Quarry	Urban	Bahía Blanca	3	140
3	Quarry	Urban	Bahía Blanca	0	320
4	Quarry	Urban	Bahía Blanca	64	1350
5	Quarry	Urban	Bahía Blanca	300	9440
6	Quarry	Urban	Bahía Blanca	47	1350
7	Quarry	Rural	Bahía Blanca	36	900
8	Quarry	Urban	Bahía Blanca	5	180
9	Quarry	Urban	Bahía Blanca	5	200
10	Quarry	Rural	Bahía Blanca	?	21
11	Water well	Rural	Bahía Blanca	?	96
12	Quarry	Rural	Bahía Blanca	299	3083
13	Quarry	Rural	Bahía Blanca	23	890
14	Quarry	Rural	Bahía Blanca	14	294
15	Roadside cutting	Rural	Bahía Blanca	1	60
16	River bank	Rural	Bahía Blanca	1	40
17	River bank	Rural	Bahía Blanca	2	60
18	River bank	Rural	Bahía Blanca	2	90
19	Quarry	Rural	Bahía Blanca	71	862
20	Water well	Rural	Bahía Blanca	1	64
21	Roadside cutting	Rural	Bahía Blanca	4	400
22	Quarry	Rural	Bahía Blanca	7	105
23	River bank	Urban	Sierra Ventana	13	126
24	River bank	Urban	Sierra Ventana	0	140
25	River bank	Rural	Sierra Ventana	73	660
26	River bank	Urban	Sierra Ventana	263	7396
27	River bank	Rural	Sierra Ventana	1	125
28	River bank	Urban	Sierra Ventana	2	40

provided nesting sites for 17 of the 28 colonies. Ten of these quarries were abandoned and five in use for the extraction of construction materials. In another two cases, the quarries were actually escarpments resulting from excavations during road construction (termed as “roadside cuttings” in table 1). Burrowing parrots were also found breeding underground, in the internal walls of two abandoned, dry, water wells. Elsewhere, nine colonies were located in natural substrates, namely in the banks of two of the four small streams that cross the study area (fig. 1). Five unoccupied potential although small nesting sites were identified (fig. 1).

The number of breeding pairs in the colonies correlated positively with the surface area of their nesting substrates (Spearman correlation, $r_S = 0.89$, $P < 0.001$, N = 28, fig. 2). This relationship held for both anthropogenic ($r_S = 0.88$, $P < 0.001$, N = 19) and natural substrates ($r_S = 0.83$, $P = 0.006$, N = 9) considered separately. The larger numbers of pairs breeding in anthropogenic (mean = 53.5, median = 8, range 1-300) compared to natural substrates (mean = 41.1, median = 2, range = 1-263) parallels the larger substrate surfaces of the former (anthropogenic median = 320 m^2, range = 21-9,440 m^2, natural median = 125 m^2, range = 40-7,396 m^2; Mann-Whitney U test, Z = –1.69, P = 0.089).

Breeding population size

The estimated total minimum breeding population in the study area was 1,361 pairs during the 2013 nestling period. Most pairs (74.1%) were located in 19 colonies in the area of Bahía Blanca city and surrounding plains, the rest nesting in five colonies in the Sierra de la Ventana (see table 1). Colonies ranged from 1 to 300 breeding pairs (mean = 57 ± 94 SD, median = 10, N = 24). Overall, 73.8% of the breeding population used anthropogenic nesting sites.

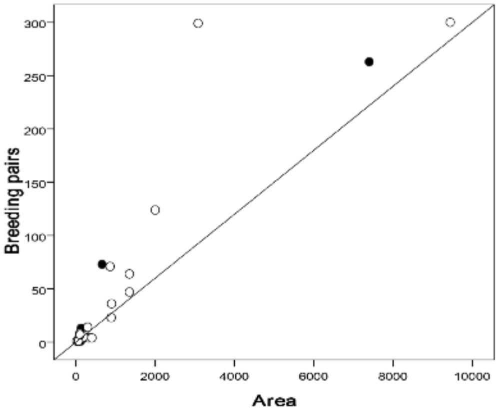

FIG. 2.—Relationships between the estimated number of breeding pairs and the surface (in m^2) of natural (filled circles) and anthropogenic (open circles) nesting substrates. The diagonal line represents an ideal free distribution (correlation = 1). *[Relaciones entre el número estimado de parejas reproductoras y la superficie (en m^2) de los sustratos naturales (círculos rellenos) y artificiales (círculos vacíos) usados para nidificar. La línea diagonal muestra una distribución libre ideal (correlación = 1).]*

Regarding the surrounding habitat, most of the population (60.7 %) was breeding in ten urban and suburban colonies, of which seven were quarries in Bahía Blanca and three were river banks in two small villages of Sierra de la Ventana (fig. 1 and table 1).

DISCUSSION

Shortage of nesting sites and urban breeding

The populations of cliff-nesting bird species are often limited by the shortage of nesting substrates (Newton, 1998). This seems to be the case for burrowing parrots around Bahía Blanca, where in a rather flat landscape just a few streams offer mostly small banks that can only accommodate small numbers. In this context, the adoption for nesting of new, anthropogenic nesting substrates may be considered as an innovation for the species, especially in the case of nesting in water wells. An anecdotal use of quarries and water wells as nesting sites was previously reported for burrowing parrots (Masello *et al*., 2011), and the use of quarries has been also shown for other cliff-nesting species limited by a shortage of natural nesting sites (Jefferson, 1984; Moore *et al*., 1997; Castillo *et al*., 2008). The use of these new substrates, together with the capacity of burrowing parrots to colonise urban habitats (Carrete and Tella, 2011), has allowed the city to hold a large part of the breeding population. Although historical data are not available, the overall breeding population is likely to have been smaller due to nest site limitation before human expansion in the area allowed the species to occupy quarries. It is worth noting that the naturalist Alcide D'Orbigny did not mention the presence of burrowing parrots during his pioneer exploration of our study area in 1828, despite devoting a great effort to exploring river banks both in the Bahía Blanca plains and Sierra de la Ventana (D'Orbigny, 1845).

Variability in colony size

The strong correlation between colony size and nesting substrate extent supports a nearly free distribution of breeding pairs, i.e. they seem to distribute among sites according to nest site availability (fig. 2), something rarely found in colonial species (see review in Brown and Brown, 1996). Colony size variation has been related to predation pressure in other bird species (e.g., Serrano *et al*., 2005), and the accessibility of nests to terrestrial predators could constrain the number of breeding burrowing parrots in the colonies. Terrestrial carnivores such as the Pampa fox *Pseudalopex gymmnocercus*, pampas cat *Leopardus colocolo*, Geoffroy's cat *Leopardus geoffroyi*, Molina's hog-nosed skunk *Conepatus chinga* and lesser grison *Galictis cuja*, and large reptiles such as black-and-white tegu *Salvator merianae* and Patagonia green racer *Philodryas patagoniensis*, were observed close to some colonies or their surroundings. These species could reach nest burrows sited close to the ground or on cliff tops, thus making large cliffs safer from terrestrial predators and reducing the suitability for successful reproduction of part of the available nesting substrate. In this regard, a recent study on selection of wall cavities by a hole-nesting bird species, the common swift *Apus apus*, has shown that cavities both close to the ground and close to the top are avoided, probably as a response to predation risk (Corrales *et al*., 2013).

Colony size variability in the studied population falls within the lower end of the range of colony size variation (5-37,000 pairs, N = 31 colonies) found by Masello *et al*. (2011), who sampled nearly the whole distribution of the species for phylogeographic analyses. Although these authors considered neighbuoring nesting sites as single colonies for genetic comparisons (J. Masello, pers. com.), thus making their results not directly comparable, it is worth noting that we found five instances of pairs breeding solitarily. These pairs were in substrates of limited extent where we observed only a single nesting burrow. One of them was in a recently excavated quarry, another in an old roadside cutting, another in a water well and two in natural banks, and they were 0.18-18.2 km from the nearest occupied nesting sites. Although colony size varied with substrate extent, there is little doubt that these five solitary pairs could have integrated into the surrounding larger colonies (see Serrano and Tella, 2012, for other colonial species).Very small colonies, and especially solitary nesting pairs can be easily overlooked, compared to large colonies, so it is highly probable that we underestimated the proportion of birds breeding solitarily or in very small groups. In general, the social breeding strategy of burrowing parrots resembles that of facultative colonial species, in which solitary pairs may pioneer the colonisation of new nesting sites (Jovani *et al.*, 2008), and could reflect a heritable polymorphism in breeding sociality (Serrano and Tella, 2007). Given that the most intensive work on the breeding and population ecology of burrowing parrots has been conducted in the largest colony known for the species (e.g., Masello and Quillfeldt, 2004a, 2004b; Masello *et al.*, 2006), more research is needed across the range of colony sizes to explore the above hypotheses.

Conservation threats and opportunities

The burrowing parrot has been legally persecuted as a pest for decades, due to unsubstantiated claims of damage to crops, and it is also intensively captured for the national and international pet trade (Masello *et al.*, 2011; Grilli *et al.*, 2012). As reported by CITES (www.cites.org), Argentina has captured and exported *c.* 140.000 individuals since 1979. These pressures, together with the loss of natural habitats, have caused the range reduction of the species, the reduction and endangerment of genetically differentiated populations, and even the extirpation of several colonies, including the largest known colony (of 50,000 pairs, Masello *et al.*, 2011). It seems to be another case of an otherwise abundant species that may quickly become threatened due to overharvesting and excessive persecution (Donald *et al.*, 2010). Currently our study area may hold the third-largest population of burrowing parrots after El Cóndor and La Lobería, in Río Negro Province, with 3,000 individuals (Masello *et al.*, 2011) gathering in a communal roost in the central park of the city (fig. 1). This roost reached *c.* 4,000 individuals during the 2013 breeding season (pers. obs.). Contrary to the behaviour recorded at El Cóndor colony (Masello *et al.*, 2006), almost all breeders in our study were observed to leave their nests before sunset to fly directly towards this large roost. The colonies at Sierra de la Ventana, where we found three smaller communal roosts (fig. 1), were an exception. The fact that the number of burrowing parrots joining this communal roost largely outnumbered the breeding population surrounding Bahía Blanca during the nesting period (*c.* 2,000 breeders, see table 1) suggests that it may draw a significant fraction of the non-breeding population. Immatures and nonbreeding adults may constitute a large population fraction in burrowing parrots (Masello *et al.*, 2006) and other long-lived parrot species (Tella *et al.*, 2013; Pacífico *et al.*, 2014), and further research is needed to elucidate the age structure and non-breeding population fraction in this population.

According to Masello *et al.* (2011), the studied burrowing parrot population belongs to Patagonus 1, a genetically distinct population from Patagonus 2 within the *patagonus* subspecies. Although Patagonus 1 and Patagonus 2 genotypes are phenotypically indistinguishable, and are often found together in breeding colonies, all individuals sampled in Bahía Blanca and Sierra de la Ventana showed only the Patagonus 1 haplotype (Massello *et al.*, 2011). This genetic trait adds conservation value to the important size of the studied population.

In the study area, direct persecution of burrowing parrots through poisoning seemed to have ceased in recent years (our last record was in summer 2008), and while professional nest poaching for the international pet trade removed hundreds of nestlings annually (mostly from colonies 4 and 5), this activity ceased with the European ban in wild-bird trade in 2005 (Carrete and Tella, 2008), which caused a collapse in international demand for wild-caught parrots (J. L. Tella and M. Carrete, unpubl. data). Although some nestlings are still obtained for the local or national trade, this threat is now much reduced compared with the past.

Urban-breeding birds may benefit from a reduction of predators in urban environments (Tella *et al*., 1996; Díaz *et al*., 2013). Indeed, although we frequently observed predators and/or predated eggs and chicks in rural colonies, such observations were rare in suburban colonies and nearly absent in the most urban one (colony 1). Studies of the breeding biology of this population would show whether breeding success is higher in urban habitats and large quarries compared to rural habitats and small, accessible ravines. On the other hand, the abandonment of currently exploited suburban quarries could further favour a population increase of the species. Moreover, the maintenance of quarry sites, or even the creation of new quarries, could be an effective management action for the conservation of burrowing parrots in areas where their populations may be limited by a shortage of nesting sites.

Urban breeding is not however free of some costs and threats. Feral pigeons breed in their hundreds in burrows dug by parrots and this species is a potential competitor for food and nesting sites and a vector of diseases (Rupiper, 1998; Marlier and Vindevogel, 2006). Host-parasite relationships among urban birds are however largely unknown (Delgado and French, 2012), and future studies should examine the potential transmission of pigeon diseases to parrots. Moreover, pigeons are hunted at night at one of the biggest parrot colonies (5) and killed with poisoned seeds nearby, which could account for some of the adult parrots we found dead in this suburban colony. Unlike the Chilean and southern Argentinean Patagonian populations (Masello *et al*., 2011), the burrowing parrot in our study area is not protected but is still considered an agricultural pest, even though its main diet does not include crops there (J. L. Tella and M. Carrete, pers. obs.). A concerted extermination campaign directed at it, or even at a companion species such as the feral pigeon, could easily eliminate this burrowing parrot population. Moreover, current urbanisation plans may result in the destruction of the whole of urban colony 1 in the near future, in the course of urban development or on the grounds that parrots may cause the erosion and collapse of the quarry. Under this plan, most of the quarry would be covered with concrete, thus eliminating almost all the nests, and it would be closely surrounded by a parking site and new buildings. This would be likely to lead to the loss of the largest known urban colony of parrots in the world (J. Masello, pers. com.), since it is the only one sited in the core of a city. This loss would not only affect this population of burrowing parrots but would also eliminate the opportunity to develop environmental education programmes and tourism in Bahía Blanca region centred on this unique parrot colony.

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