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Short Communication

Differing nest-defence behaviour in urban and rural populations of breeding Burrowing Owls

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Abstract. The behaviour of birds in urban habitats often differs from that of birds in surrounding natural and rural habitats, with the attenuation of fear responses to humans a primary behavioural adaptation to urban life. In breeding birds, fear responses and nest-defence have been linked to reproductive success. We studied the nest-defence behaviour of male Burrowing Owls in rural and urban habitats by measuring flight-initiation distance (FID), time to return to the nest following disturbance and aggressiveness of nest-defence in response to a person walking towards them during three stages of their breeding period: during incubation and during two nestling stages. Male Burrowing Owls breeding in rural habitat had longer FID than Owls breeding in urban habitat, but FID did not decrease over the breeding season whereas it did decrease over the breeding season in urban habitat. Male Owls in rural habitat were less likely to return to their nests within 10 min of disturbance than Owls in urban habitat. Lastly, aggressiveness of nest-defence of Owls breeding in rural and urban habitats was similar and increased throughout the breeding season in both habitats. Our results highlight the role of behaviour in explaining the ability of Burrowing Owls to live in a range of habitats, including successfully breeding in urban areas, and emphasise the importance of breeding stage on behavioural traits.

Additional keywords: aggression, *Athene cunicularia*, breeding stage, FID, flight-initiation distance, nest-return behaviour, urbanisation.

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Introduction

Urbanisation is a key threat to biodiversity (Chace and Walsh 2006; McKinney 2006) because it involves significant environmental change, such as the loss and replacement of natural vegetation with artificial structures, the availability of non-natural food resources, which are often spatially concentrated, increases in pollution, and changes in the predator community and in rates of disturbance (Marzluff 2001; Sol *et al*. 2013). Because such environmental changes are often drastic and rapid, it is to be expected that the limits of tolerance of many species are exceeded and that species diversity in urban habitats declines (Mc Kinney 2006; Sol *et al*. 2013). Nevertheless, urban habitats are ecological opportunities for some species, which are able to persist and thrive in these highly modified habitats (Bonier *et al*. 2007).

The behaviour of birds living in urban habitats often differs from that of the same species in surrounding non-urban habitats (Møller 2008*a*, 2009; Sih *et al*. 2011), with the attenuation of fear responses to humans a primary behavioural adaptation to urban life (Minias 2015). Some studies suggest that the ability to tolerate human disturbance reflects habituation by individuals over time (Cooke 1980; Rodríguez-Prieto *et al*. 2009; Li *et al*. 2011), whereas others suggest that it also reflects natural selection of individuals from species that have variable responses to human presence (Møller 2009; Carrete and Tella 2011, 2013).

Because urbanisation may act as a filter on the traits of species, birds that survive and reproduce in urban areas, and utilise urban resources, may share a suite of characteristics that explain their success in tolerating human impact, such as responses to novel stimuli, high explorative tendency, short escape distances and behavioural flexibility, among others (Møller 2009; Biondi *et al*. 2010, 2015; Sol *et al*. 2013).

The Burrowing Owl (*Athene cunicularia*) has successfully colonised urban areas. The species is a ground-nesting bird that inhabits open landscapes such as treeless plains and savanna; agricultural areas such as croplands, grazing lands and farmlands; golf courses; road verges; airfields; and urban and peri-urban areas (Poulin *et al*. 2011). This Owl, at its southernmost distribution in the Pampas of Argentina, is a year-round resident and excavates its own burrows (Marks *et al*. 1994). Mating pairs are territorial and highly conspicuous in daylight and are easily located near their nests (Marks *et al*. 1994). It has been suggested that Burrowing Owls can occupy modified environments, such as urban habitats, owing to its behavioural adaptability (Berardelli *et al.* 2010). However, recent studies have suggested that the species might be segregating spatially based on individual tolerances to urban environments (Carrete and Tella 2010, 2013).

Defence behaviour is expected to vary between habitats and also over the breeding season since the relative importance of offspring to the inclusive fitness of parents increases from laying to the fledging of young. Thus the risk that the parents take to defend offspring could be expected to increase with the age of their offspring (Andersson *et al*. 1980). Furthermore, defence behaviour in response to threats has been shown to vary among habitats (Sih *et al*. 2011; Møller and Ibáñez-Álamo 2012). In this sense, elevated levels of aggression and increased boldness towards humans and conspecifics are characteristics of urban individuals, a phenomenon recognised as an 'urban wildlife syndrome' (Warren *et al*. 2006; Evans *et al*. 2010). Consequently, we expect urban Owls to be more aggressive than rural birds independently of their breeding state.

The aim of this study was to compare variation in nest-defence behaviour of Burrowing Owls between urban and rural habitats throughout the breeding season. Because the perception of risk and nest-defence have been linked to reproductive success in breeding birds (Lima 2009) and, considering differences in types and densities of predators in urban and rural habitats (Sih *et al*. 2011; Møller and Ibáñez- Álamo 2012), we expected to find differences in nest-defence behaviour between urban and rural Owls, specifically shorter flight-initiation distance (FID) and higher levels of aggression in nest-defence by Owls breeding in urban areas compared with Owls breeding in rural areas. Further, because nest-defence increases the probability of successful breeding (Andersson *et al*. 1980), we also expected levels of aggression in nest-defence to increase and FID to decrease as the breeding season progressed. The results of this work may increase understanding of which behavioural patterns are significant in the expansion and establishment of Burrowing Owls in urban habitats and how habitat modification modulates the behaviour of this species.

Methods

Study area

The study was conducted in rural and urban habitats in the south-eastern Pampas region of Argentina, between Mar Chiquita village (37°49′59″S, 57°30′46″W) and the city of Mar del Plata (38°00′08″S, 57°33′27″W). The landscape formerly comprised mainly sand-dunes, wetlands and grasslands but is now a mosaic of land-uses dominated by agroecosystems (i.e. rural habitats: grazing fields, pastureland, cropland and other open faming land) and urban areas (Pedrana *et al*. 2008). In the study area, Burrowing Owls are found in rural and urban habitats and the remaining sand-dunes (Pedrana *et al*. 2008; Cavalli *et al*. 2014). We defined urban breeding as nests with >35 houses in a radius of 200 m (from personal observation, this is approximately the area that Burrowing Owls live and forage within); in rural habitats, the distance between nests and houses was always >1 km. Thus, the rate of human encounters by Owls is greater in urban areas.

Study design and data collection

Sampling was carried out during the austral breeding seasons (September–February) of 2012 and 2014. We located nests of Burrowing Owls by walking or driving through rural and urban habitats and searching for adult birds atop their nesting burrows.

We monitored 58 nests (21 in rural habitats, 37 in urban habitat) in the 2012 breeding season and 47 nests (17 rural, 30 urban) during the 2014 breeding season. We visited all occupied nests every 1–14 days until eggs were found in the nest. We considered a nest occupied if we saw either an adult Owl or signs of occupation at the entrance to the nesting burrow, such as mammal manure (which the Owls use to line the entrance to their burrows), regurgitated pellets or nest-lining. We assessed the stage of nesting by checking each nest using a night-vision security camera (LYD Color Night Vision Infrared Waterproof Camera, model 802c) connected to a computer. This methodology has proven not to harm the species (García and Conway 2009). We divided the breeding cycle into three breeding stages: (1) incubation, which extended from detection of the first eggs to hatching; (2) the period after hatching when nestlings remain inside the nesting burrow (Ch1); and (3) the period when chicks are first seen outside the burrow (~10 days old) until they are around 25 days old and start doing venturing flights around the nest (Ch2). It is worth noting that nestlings remain associated with the parental nest almost until the following breeding season (M. Cavalli, unpubl. data).

To simplify identification of study birds, nesting Owls were captured using bal-chatri traps, bow-nets or noose carpets placed at the entrances to the nesting burrows (Bub 1991; Bloom *et al*. 2007) and then banded with numbered plastic bands. (The band colour was distinguishable using the naked eye and the number could be read using binoculars.) In 2012, we had 7 banded males and 16 banded females, and in 2014, 9 males and 11 females. Of the 58 nests in 2012, 19 had at least 1 banded adult, and of 47 nests in 2014, 16 had at least 1 banded adult. For the nests at which neither adult was banded (39 nests in 2012, 31 nests in 2014), males were distinguished by their paler plumage (Baladrón *et al*. 2015). We collected data from males only to avoid biasing data during incubation when females are rarely seen outside the nest.

We measured levels of nest-defence by Burrowing Owls at each of the three stages of breeding. Trials consisted of a person walking in a straight line at a constant speed (0.5 m/s) towards a male Burrowing Owl that was standing outside its nest. All trials started ~200 m from the nest to avoid variation in responses by Owls associated with starting distance (Rodriguez- Prieto *et al*. 2009) and all trials were conducted in the morning (0700–1145 hours). Trials were not conducted during rain, fog or high winds (Andersen 1990; Sproat and Ritchison 1993).

During each trial we measured FID, escape distance, return to the nest, and aggressiveness of nest-defence. FID was measured as the distance between the observer and the point from which an Owl flew when approached. (The measurement was taken at the end of each trial, after waiting 10 min to see whether the Owl returned to the nest. The observer marked their position at the moment the Owl flew with a coloured marker and then measured the distance between it and the Owl's initial position.) *Escape distance* was measured as the distance between the Owl's initial position and the point where it landed after flying. *Nest-return:* after the approach to the nest ended (i.e. after the coloured marker had been placed on the ground), the observer retreated to hide behind tall vegetation or a building, or lay on the ground and covered themselves with a camouflage net, and recorded the elapsed time before the Owl returned to the nest; the maximum time was 10 min. *Aggressiveness of defence* was recorded using a digital voice-recorder as the observer walked towards each nest and classified into five categories (adapted from Galeotti *et al.* 2000; Fisher *et al*. 2004): 0, the Owl flies away or enters the nest; 1, an Owl bows or vocalises, or both; 2, an Owl raises its feathers and spreads its wings in order to appear larger in a distraction display; 3, an Owl performs threat flights, in which it flies in a circle around the intruder, maintaining a height of 10–20 m from the ground; and 4, an Owl performs dive attacks, in which it dives at the intruder from behind in order to startle it (see Martin 1973). Only the most aggressive response during each trial was used for statistical analyses. Nests were checked every week to assess breeding stage; one trial was conducted per nest per stage of the breeding cycle.

Statistical analysis

We first analysed the relationship between sampling years. We found no significant differences in variables between years (Wilcoxon rank test, all $P > 0.05$), so used pooled data for 2012 and 2014 for further analyses. We also performed a Spearman rank order test to explore correlation among variables, and excluded escape distance because it showed a significant correlation with FID ($rs = 0.68$, $P < 0.05$).

Nest-defence behaviour

All statistical analyses were carried out using R version 3.0.1 (R Development Core Team 2015). We tested the effect of habitat type (categorical explanatory variable with two levels: urban and rural), nesting stage (categorical explanatory variables with three levels: Incubation, Ch1, Ch2) and their interaction on FID, the probability of returning to the nest within 10 min, and level of aggressiveness. For FID (continuous response variable, log-transformed) we used linear mixed effects models (lme function) with a Gaussian error distribution and identity link function (package nlme; Pinheiro and Bates 2000). Male identity was included as a random term. For nest-return (bimodal response variable) we fitted a mixed effect model using the lmer function in the lme4 package with a binomial error distribution and including male identity as a random term (Bates *et al*. 2014). For aggressiveness (ordinal response variable) we fitted a cumulative link mixed model (clmm function). Male identity was included as a random term with probit link function (package ordinal) and equidistant threshold parameters. Cumulative link mixed models are models for ordinal response variables and are fitted with the Laplace approximation (Christensen 2012).

Model adjustment was assessed by plot inspection assessing normality distribution (qqplot) and homoscedasticity (plot fitted values vs residuals of the model). Values are reported as means s.e., except where noted. All tests were two-tailed, and differences were considered significant at $P < 0.05$.

Results

Rates of abandonment and predation of nests and adult Owls were high and our final sample size for the two seasons was reduced to observations of males from 17 successful nests in rural habitat and 55 in urban habitat (from 38 and 67, respectively). To determine if our dataset was biased by analysing data from successful nests only, we compared FID of successful nests with FID from nests that did not survive until the young had fledged. We considered FID during incubation stage to make this comparison. FID did not differ significantly between successful and unsuccessful nests in rural habitat (t-test: $t = 1.622$, d.f. = 36, $P = 0.114$) or urban habitat (t-test: $t = 0.452$, d.f. = 63, $P = 0.653$). We have assumed our data for the other variables is similarly unbiased.

The FID of male Burrowing Owls in rural habitat was longer than that of males in urban habitat during all stages of nesting (Table 1, Fig. 1). An effect of nesting stage was observed in males in urban habitat, which had shorter FIDs in the second nestling

Table 1. Fixed factor contrasts from mixed effects models testing the effect of the interactions between breeding stage and habitat type on the behavioural responses of male Burrowing Owls (FID, nest-return behaviour, aggressiveness of nest-defence)

In each model, male identity was included as a random factor. Breeding stage: Inc., incubation; Ch1, nestlings in burrow; Ch2, nestlings from time seen outside the burrow until they fly. FID, flight-initiation distance; s.e., standard error. Text in bold denotes significant results

	FID				Nest-return behaviour				Aggressiveness of defence			
	β	s.e.	*t*	*P*	β	s.e.	*z*	*P*	β	s.e.	*z*	*P*
Habitat	–1.79	0.28	–6.29	**<0.001**	2.77	0.75	3.71	**<0.001**	0.48	0.34	1.40	0.16
Breeding stage												
Inc. vs Ch1	0.08	0.29	0.28	0.78	–0.41	0.73	–0.56	0.57	0.76	0.37	2.07	**0.04**
Inc. vs Ch2	–0.13	0.29	–0.47	0.64	–0.71	0.75	–0.95	0.34	0.99	0.37	2.66	**0.01**
Ch1 vs Ch2	–0.05	0.28	–0.19	0.84	0.29	0.75	0.39	0.69	–0.22	0.36	–0.63	0.52
Within habitat between breeding stage												
Rural habitat												
Inc. vs Ch1	0.08	0.29	0.28	0.78	–0.41	0.73	–0.56	0.57	0.76	0.37	2.07	**0.03**
Inc. vs Ch2	–0.05	0.28	–0.19	0.85	–0.71	0.75	–0.95	0.34	0.99	0.37	2.66	**0.01**
Ch1 vs Ch2	0.13	0.29	0.47	0.64	0.29	0.75	0.39	0.69	–0.22	0.36	–0.63	0.52
Urban habitat												
Inc. vs Ch1	–0.26	0.16	–1.58	0.12	–0.19	0.68	–0.27	0.78	0.57	0.20	2.80	**<0.01**
Inc. vs Ch2	–0.38	0.16	–2.33	**0.02**	–0.5	0.65	–0.82	0.41	0.49	0.20	2.39	**0.01**
Ch1 vs Ch2	0.12	0.16	0.74	0.46	0.35	0.61	0.56	0.57	0.08	0.19	0.43	0.67

stage (Ch2) compared with Incubation. FID of males in rural habitat did not change over the breeding cycle (Fig. 1, Table 1).

Males in rural habitat were less likely to return to their nest within 10 min of disturbance than males in urban habitat (Table 1). The percentage of male Owls that returned to their nest within 10 min was 86.1% for urban habitat and 36% for rural habitat. We did not find an effect of stage of nesting on nest-returning behaviour (see Table 1). The aggressiveness of nest-defence was similar for Owls in urban and rural habitat, and increased throughout breeding stages in both habitats (Fig. 2, Table 1).

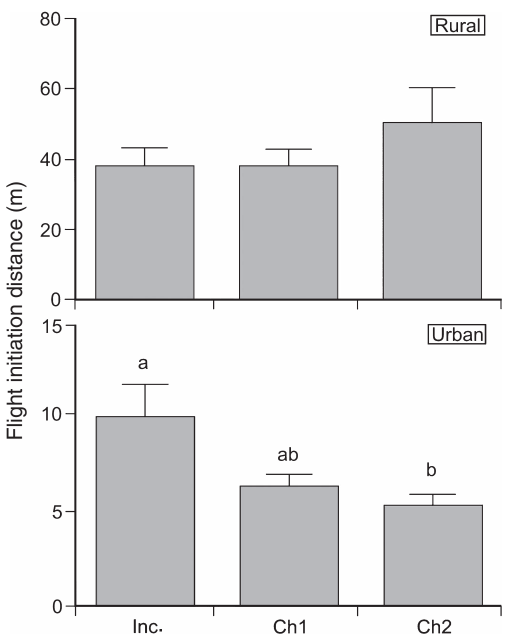

Fig. 1. Flight-initiation distance ~~(FID)~~ of male Burrowing Owls during three stages of the breeding season in urban and rural habitats. Inc., Incubation; Ch1, nestling in burrow; Ch2, nestling from first leaving nest until first flight. Letters indicate significant differences ($P < 0.05$) between breeding stages within the same habitat (linear mixed effects models). Whiskers show standard error.

Discussion

The process of urbanisation creates new habitats and may lead to behavioural differentiation between urban bird populations and natural, rural and other populations (Partecke *et al*. 2006; Møller 2009). In this study, we showed that some aspects of the nest-defence behaviour of Burrowing Owls differed between urban and rural habitats and at different stages of their breeding period.

We found that male Burrowing Owls nesting in urban habitat had shorter FID than those nesting in rural habitat. Nests in urban habitat are commonly approached and disturbed by humans and flight whenever a human approaches would be energetically costly, especially as most human disturbance does not represent a threat. Responses to threat stimuli, such as a human or a predator, can be the result of experience acquired during early stages in life (Brown *et al*. 2015). For example, it has been argued that habituation, a form of learning characterised by a progressive decrease in responsiveness to a repeated event that has proven to be irrelevant (see Rankin *et al*. 2009), contributes to differences in FID between areas with different level of disturbance (Rodríguez-Prieto *et al*. 2009). However, recent studies have shown that FID remains constant throughout the adult lifespan of Burrowing Owls, suggesting a heritable component (Carrete and Tella 2013). This might indicate that the shorter FID we observed in male Owls in urban habitat (compared with rural habitat) may be a result not only of learning the distance at which a human can approach before being considered a threat, but also of selection for certain successful phenotypes in this habitat. Other traits have been suggested to explain the success of Burrowing Owls in urban habitats, including a generalist diet and opportunistic hunting behaviour (Cavalli *et al*. 2014), tolerance to human presence (Carrete and Tella 2010, 2011), a monogamous reproductive strategy, which is maintained despite the increased density of Burrowing Owls in urban habitats (Rodriguez-Martínez *et al*. 2014), similar baseline levels of stress hormone in natural and urban habitats (Rebolo-Ifrán *et al*. 2015), and a reduced dependency on particular habitat types (Poulin *et al*. 2005).

We also found that Burrowing Owls nesting in urban habitat returned to their nests more rapidly than Owls nesting in rural

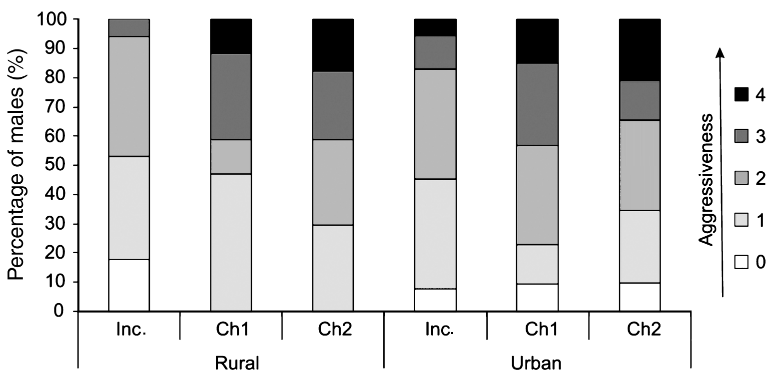

Fig. 2. Defence behaviour of male Burrowing Owls in urban and rural habitats in three stages of the breeding season. 0, Owl flies away or enters the nest; 1, Owl bows or vocalises, or both; 2, Owl raises feathers and spreads wings, which is usually meant to distract a predator from a nest; 3, Owl performs threat flights; and 4, Owl performs dive attacks. Inc., Incubation; Ch1, nestling in burrow; Ch2, nestling from first leaving nest until first flight.

habitat after human disturbance, which accords with previous findings for this species outside the breeding period (Cavalli *et al*. 2016). The decision to return immediately or not after a potential threat might be associated with the time a stimulus ceases to be perceived as dangerous as well as the time needed to turn-off the stress response associated with such threatening stimuli and to resume to a normal behaviour (e.g. Neufeld-Cohen *et al.* 2010). Moreover, nest-return behaviour was not influenced by breeding stage suggesting that the factors underlying this behavioural response were consistent through the breeding season.

Given that animals in urban habitats are often noticeably bolder or tamer in the presence of humans compared with populations in natural habitats (Evans *et al*. 2010) we had predicted Owls nesting in urban habitat would be more aggressive than Owls nesting in rural habitat. However, our results did not support this prediction. Owls in urban habitat had similar levels of aggression in response to an approaching human as Owls nesting in rural habitat, as had been observed during the non-breeding period (Cavalli *et al*. 2016). However, aggressiveness of nest-defence increased through the breeding period in both rural and urban habitats, which can be explained by the increasing fitness benefits of parental care when chicks became older (Montgomerie and Weatherhead 1988). Fitness gains can also explain the change in FID in urban males over the breeding period (a significant decrease in FID from hatching to fledging), a pattern not observed in males breeding in rural habitat, which showed no change in FID over the breeding season. These results suggest that Owls breeding in urban and rural habitats could be adopting different strategies in response to a predator-like stimuli (i.e. a human) over the duration of the breeding season. In urban habitat, Owls remain on their nest longer, let humans approach closer and become more aggressive as breeding progresses. In contrast, in rural habitat, Owls did not change FID over the breeding period, but did increase their level of aggression as breeding progressed.

It is worth noting that the rate of predation and abandonment of nests for Owls breeding in rural habitat (55%) was much higher than that observed in urban areas (18%). Urban areas represent a challenge for animals willing to live there, but also provide refuge from native predators, destruction of nests and fumigation. Indeed, these last features are characteristics of rural habitats and may explain the high proportion of nests lost, and which seems to be consistent throughout the study area (Martínez 2013; M. Cavalli, pers. obs.). Thus, the nesting success of Owls in rural habitats might not only be the result of anti-predator strategies, but also a result of nesting failures owing to other causes, which may be random and are less common in urban habitats.

In conclusion, although we expected consistency in FID between rural and urban habitats, based on previous studies (Møller 2008*b*; Carrete and Tella 2010, 2011, 2013), we observed that FID varied throughout the breeding season, especially in urban habitats. This demonstrates that traits constituting the individual personality of an animal (e.g. FID, levels of aggression) can be adaptively modified in response to breeding demands. It also shows that Owls breeding in urban habitats may have greater plasticity in behavioural strategies than Owls breeding in rural habitats. The consistency of FID throughout the breeding season for Owls breeding in rural habitat could indicate that phenotypic plasticity is more restricted in these populations than for Owls breeding in urban habitat. Our findings provide a novel insight on the role of behaviour in explaining the ability of Burrowing owls to live in a variety of habitats and highlight the importance of considering breeding stage when assessing the behaviour that allows Owls to inhabit and be successful in urban habitats.

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