

Differential risk perception of rural and urban Burrowing Owls exposed to humans and dogs



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ABSTRACT

Urban areas expose wildlife to an array of novel predators, amongst which, humans and dogs are highly frequent. Thus, wild animals living in urban areas are forced to invest more time and energy in defence behaviours, which depend on how the risk is perceived and assessed. We experimentally tested whether Burrowing owls coming from rural and urban habitats showed differences in behavioural responses when facing humans and domestic dogs. We measured flight initiation distances (FIDs), nest returning, and aggressiveness level when owls faced a human and a human with a dog walking towards them. Our results showed that urban owls recognise a human with a dog as a greater threat than a human alone, thus indicating that fear of domestic animals should be considered as affecting owls' settlement in cities and towns. On the other hand, rural owls perceived human and dogs as similar threats, but showed higher FIDs, less aggressiveness, and lower tendency to return to the nest than urban owls in both treatments. These findings emphasize the importance of modified habitats in modelling the response of urban and rural owls to predators and represent another step in the explanation of how wild animals assess and respond to threats associated with living in urbanized environments.

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1. Introduction

Human activities often have negative impacts on wildlife. Effects are diverse, ranging from local extinction to changes in behaviour, life history traits, and physiology (Ditchkoff et al., 2006; Møller, 2008; Partecke et al., 2006; Tuomainen and Candolin, 2011). The capacity of animals to survive in human disturbed habitat depends on their abilities to cope with and adapt to the resulting new conditions (Carroll et al., 2007). One of the main consequences of human population growth is the increase of urbanized areas (Vitousek et al., 1997). Urban development has significant effects on wildlife density, distribution and behaviour (Palmer, 2003; Shanahan et al., 2014). While a great number of local species reduce their abundance and occurrence in response to increasing urbanization, a smaller number can survive in these highly disturbed areas. Thus, wildlife in urban habitats are usually tolerant species that are able to cope and adapt to high levels of human stimuli (Samia et al., 2015).

The capacity to live in urbanized areas has been widely studied in several bird species (e.g. Mikula, 2014; Partecke et al., 2006; Sol et al., 2013). Such studies show that these species perceive urban habitats as ecological opportunities, which allow them to proliferate and expand their distributions (Sol et al., 2013). Usually modification of behaviour (i.e. by learning) is the first response to habitat changes. Thus, the ability to adjust their behavioural repertoire rapidly to changing conditions (i.e. altered habitat selection, changes on vigilance rate, and changes on resource use) ultimately prevents individuals from suffering fitness losses (Sih et al., 2010; Sol et al., 2013; Tuomainen and Candolin, 2011).

Since species living in cities and towns are regularly confronted by humans, risk perception is an important aspect of their behaviour, given that human represents a form of predation risk (Frid and Dill, 2002; Jiménez et al., 2013). However, human presence might be also perceived as nonthreatening if a species can habituate to frequent harmless confrontations reducing their responses through a learning process (Rankin et al., 2009). Alternatively, a growing body of literature suggests that, within a population, only those individuals that are preconditioned to be tolerant to novel settings and thus capable of dealing with their challenges (e.g. constant human presence), succeed and thrive in

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habitats with high human influence (Carrete and Tella, 2010, 2013; Sih et al., 2012; Sol et al., 2013). However, most behaviour is determined by a mixture of both innate (genetically fixed) and learned features and the combination that best tracks and cope with environmental changes will result in the optimal behaviour phenotype (Brown, 2012).

In addition to increased human density, urban landscapes show considerable variation in assemblages of predators compared to rural and native landscapes (Møller and Ibáñez-Alamo, 2012). While urban habitats contain a high density of domestic animals that prey on wildlife [e.g. cats (*Felis catus*) and dogs (*Canis lupus familiaris*)]; Møller and Ibáñez-Alamo, 2012; Randler, 2006], rural habitats hold a larger diversity of native predators (Shanahan et al., 2014) such as carnivores and raptors (Ditchkoff et al., 2006; Møller and Ibáñez-Alamo, 2012). The change in predator assemblages between rural and urban areas could have important consequences for the development of anti-predatory behaviours (Mikula, 2014; Møller and Ibáñez-Alamo, 2012). In this sense, animals should be able to recognise if novel predators are real or potential threats and only display an anti-predatory behaviour when it is appropriate to do so to avoid energetic losses (Lima and Dill, 1990).

Birds usually react to predators by adopting escape behaviours (Blumstein, 2014; Møller and Ibáñez-Alamo, 2012), and such behaviours provide insight about species risk-perception. Flight initiation distance (FID), which is defined as the distance at which a bird flies due to the presence of an approaching stimulus, provides a standardized estimate of the risk that an individual is willing to take when facing a real or potential predator (Blumstein, 2006). This kind of stress response is costly if it is elicited frequently. For that reason, if human and domestic animals are perceived as a threat and prompt birds to fly whenever they are detected, living in urban areas might become energetically too costly and urban environments might attract individuals with reduced sensitivity to frequent stressors (Kenney and Knight, 1992). Thus, the study of the variations in risk perception measured as FID provides information about the ability of animals to adapt to changing environmental conditions such as those emerging in urban environments (Blumstein, 2006; Møller, 2008).

The Burrowing owl (*Athene cunicularia*) is a ground nesting raptor that can be found across American open landscapes such as treeless plains, grasslands, prairies, savannah, golf courses, road verges, airports, and vacant lots on residential and periurban areas (Poulin et al., 2011). This owl, at its southernmost distribution in central Argentina, is a year-round resident and excavates its own burrows (Marks et al., 1994). Mating pairs are territorial, highly conspicuous in the daylight and are easily located near their nests (Marks et al., 1994). The behavioural response of this owl to a predator stimulus can be easily measured by assessing an array of stereotyped behaviours, such as retreating underground in the burrow, flying away, making alarm calls, adopting threatening postures, diving attacks (Coulombe, 1971; Fisher et al., 2004; Thomsen, 1971). The analysis of the behavioural response to predators by Burrowing owls inhabiting urban and rural areas might provide valuable information to help understand the success of this species dwelling in urban habitats.

Although humans and dogs can be both perceived as threats for wildlife, it has been argued that most human activities represent potential, non-threatening stimuli (Ditchkoff et al., 2006; Steven et al., 2011), whereas dogs may represent a real threat with negative effects on birds (Banks and Bryant, 2007; Mainini et al., 1993). We hypothesize that the ability of the Burrowing owl to succeed in urban habitats is explained in part by its capacity to discriminate between real and potential threats. To test this, we designed a study to assess the effect of the type of predator (pedestrian and dog) on risk perception (i.e. estimated by their behavioural response) of Burrowing owl's individuals coming from rural and urban habitats.

We predict that if owls are able to differentiate between frequent stressors and turn down their response (habituation hypothesis) then urban owls, which are exposed to a higher encounter rate of potential and real predators, would have lower responses (i.e., shorter FIDs, less aggressiveness) compared to rural owls. Alternatively, if owls living in urban habitats are the result of a selection process, then a fixed phenotype would be observed (i.e. shorter FIDs, higher aggressiveness levels). In addition, since predator type may be translated into the type of behavioural response elicited, we predict that the anti-predatory responses by Burrowing Owl will vary depending on the predation risk perception that each predator stimulus represents.

2. Material and methods

2.1. Study area

The study was conducted in urban and rural habitats in the southeastern Pampas region from Argentina. Different urban localities and rural areas were sampled between Mar Chiquita village ($37^{\circ} 44.6' S$; $57^{\circ} 25.7' W$) and Mar del Plata city ($38^{\circ} 00.8' S$; $57^{\circ} 33.1' W$). This area, dominated in the past by dunes, wetlands and grasslands, is nowadays a mosaic of different land-uses where agroecosystems (grazing fields, croplands, and pasturelands) and urbanizations dominate the landscape (Pedrana et al., 2008). The urban area encompasses 7950 ha and holds more than half a million inhabitants (366.6 habitants per km²). During summer months (December–March), the study area receives between 2 and 3 million tourists (Bouvet et al., 2005), thus being the most populated coastal area in Argentina (Juárez and Mantobani, 2006). The climate of this region is mesothermal with the lowest monthly temperature in July (mean = $6.7^{\circ} C$) and the highest in January (mean = $21.1^{\circ} C$). Maximum rainfall occurs in January (mean = 124.2 mm) and minimum in June (mean = 21.5 mm) (Servicio Meteorológico Nacional). In this area, Burrowing owls inhabit rural habitats, sand dunes, and urban habitats (Cavalli et al., 2014a; Pedrana et al., 2008). In our study, we defined urban habitats as built-up areas where owls will regularly encounter humans. We consider as urban those owls which nests were surrounded by more than 35 houses in a radius of 200 m. Rural habitat comprised open farmlands, grazing fields, pastures, and croplands. Distance from owl nests to houses in rural habitats was always greater than 1 km. Thus, the rate of encounter with humans is greater for urban owls.

2.2. Sampling design and data collection

Sampling was carried out from late September to mid-October of 2012 and 2014. Prior to data collection, we located Burrowing owl nests by travelling the areas on foot or vehicle and visually detecting adult birds on their burrows in rural and urban habitats, and by on-line censuses (Cavalli et al., 2014b; Conway et al., 2008).

We monitored 17 nests (8 at rural and 9 at urban habitats) in 2012 and 19 nests (6 at rural and 13 at urban habitats) in 2014. We considered a nest occupied by owls if we saw either an owl or a sign of an owl (e.g. whitewash, pellets, manure, or other lining materials) at the nest burrow entrance. Rural nests were located in large extensions of grazing fields, pasturelands or croplands where human presence is extremely low since most areas belong to private properties and pedestrian are not allowed to walk freely through these fields. Urban nests were located in private and public gardens and parks where human presence is frequent.

We measured different behavioural indicators of nest defence: FIDs, escaping distance (the distance at which the owl flies away), owl nest returning (whether the owl returns to the nest), and aggressiveness of defence. We obtain FIDs measurements by walk-

ing along a straight line towards male Burrowing owls that were standing alone outside their nest, distances were recorded by counting the number of steps between the observer and the owl at the moment the owl flew away. After nest approaching ended, the pedestrian hid at a blind and recorded whether owls returned to the nest after a maximum waiting time of 10 min (owl nest returning).

To assess aggressiveness of defence, we described all owl behaviours in a digital voice recorder while approaching to each owl and later classified them according to aggressiveness level. We ranked behavioural responses from less to more aggressive (adapted from Fisher et al., 2004), (0) flies away or enters to the nest, (1) bows and/or vocalizes, (2) owl raises feathers and spreads wings in order to appear larger, (3) hovers overhead and, (4) performs dive attacks. The same procedure was followed at both habitats (urban and rural). To perform statistical analyses we used the most aggressive response during the observational period.

All data collected were of male individuals to reduce bias based on sex differences. Males and females at our study sites were previously captured and banded to make identification easier. For those nests where banded owls were not present, males were distinguished from females by their lighter plumage coloration (Baladrón et al., 2015). We adhered to guidelines for the use of animals in research and to the legal requirements of Argentina (permit numbers: 2145–14331 and 22500–24871).

Two treatments were repeated to the same owls: (1) pedestrian with dog (PD), that involved a person walking with a domestic dog in leash following a straight line and at constant speed of 5 km/h towards Burrowing owl nest, and (2) pedestrian (P), in which a person alone walked to each nest in a straight line and at a constant speed of 5 km/h. Both treatments were developed by the same person (AVB) and the same dog (an adult middle-sized brown fur male). Since Burrowing owls are usually resting on the ground in their nests, we established a starting distance of 200 m for all nests, thus avoiding variability in behaviour variables associated with varying starting distances (Carrete and Tella, 2010; Rodríguez-Prieto et al., 2009). Treatments for the same nest were separated by 5 days to avoid possible habituation to the researcher. The initial treatment at each nest was determined randomly. All approaches were made during the morning (0800–12.00 h) to reduce bias due to time of day. We controlled for weather conditions by testing defence behaviour only on days under favourable environmental conditions (i.e. low wind, no rain, no fog; Andersen, 1990; Sproat and Ritchison, 1993).

To control for the effect of the number of predators approaching to owls (one person or a person and a dog), we performed a third experiment that consisted in two treatments: (1) having a person walking towards a male owl that was standing outside its nest, and (2) having two people walking towards a male owl that was standing outside its nest. In both treatments we recorded FIDs, escaping distance, owl nest returning, and aggressiveness of defence as explained above. The same group of owls was used to perform both of these treatments. To perform this control treatments we used a set of owls ($n=19$) different from P and PD treatments.

2.3. Statistical analysis

Firstly, we performed preliminary analyses to determine the relationships between sampling years and amongst behavioural variables. Since values of variables did not differ significantly between years (Wilcoxon rank test, all P values >0.05), we used pooled data of 2012 and 2014 for further analyses. In addition, we decided to exclude escape distance from further analyses, since it was correlated with FIDs in rural habitats (Spearman rank order test: $r_s = 0.674$, $P < 0.05$). Thus, the data set included the variable FIDs (continuous, in metre), owl nest returning (bimodal: returns

or non returns to the nest within the 10 min of waiting), aggressiveness of the defence behaviour (categorical, ordinal), treatment (categorical, P and PD) and habitat type (categorical; urban and rural).

We performed Linear mixed effects models (lme function) to test the effect of habitat and treatment (explanatory variables) or both (contrasts) on FID (response variable, log transformed) (Crawley, 2007; Zuur et al., 2009) with a Gaussian error distribution and identity link function (package nlme; Pinheiro and Bates, 2000). Male identity ($n=36$) was included as a random term (~1 | male identity) specifying a random intercept model since a random slope for each individual in each situation (random intercept and slope model) did not result in a better model according to AIC values (Zuur et al., 2009).

In order to evaluate if owl nest returning (response variable, bimodal) depends on habitat type and treatment (categorical explanatory variables, two levels) or both (contrasts), 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).

A cumulative link mixed model (clmm function) was run to test the effect of habitat and treatment (explanatory variables) or both (contrasts) on Burrowing owl aggressiveness behaviour (ordinal response variable). Male identity was included as a random term

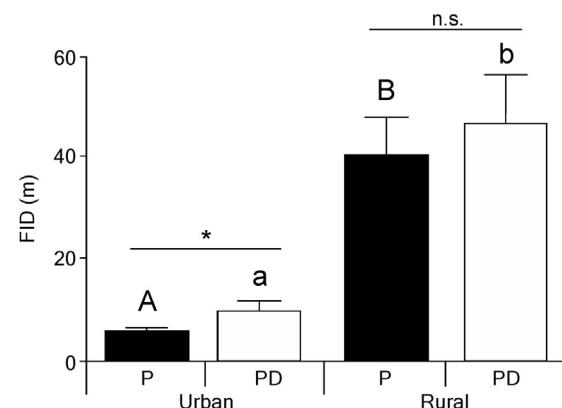


Fig. 1. Burrowing owls Flight initiation distances (FIDs). FIDs of male Burrowing owls compared between Pedestrian (P, black bars) and Pedestrian with Dog (PD, white bars) treatments and between habitats (rural, urban). Whiskers represent standard error (SE). Asterisks indicate differences among treatments within habitats and letters indicate differences between habitats for the same treatment (after performing linear mixed effects models, lme).

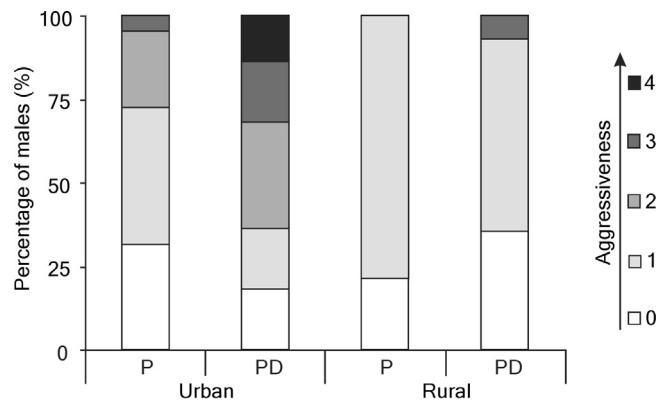


Fig. 2. Burrowing owls' aggressiveness level. Percentage of urban and rural Burrowing owls males that exhibit different aggressiveness level (0: flies away or enters to the nest, 1: bows and/or vocalizes, 2: owl raises feathers and spreads wings in order to appear larger, 3: hovers overhead and, 4: performs dive attacks). P: Pedestrian, PD: Pedestrian with Dog.

Table 1

Fixed factors contrasts resulted from linear mixed effects models, mixed effect models and cumulative link mixed models testing the effect of the interactions between (a) treatments (P: Pedestrian alone, PD: Pedestrian with Dog) and (b) habitats (rural, urban) on male Burrowing owls' FIDs. Male identity was included in models as a random factor. Text in bold denotes significant results.

General	FID			Nest return			Aggressiveness		
	β	t	P	β	z	P	β	z	P
Urban vs. rural	-1.77	-8.78	<0.001	1.80	3.33	0.000	0.80	2.28	0.022
P vs. PD	-0.35	-2.14	0.041	0.28	0.53	0.591	-0.67	-2.44	0.014
Contrasts between factors									
Within treatment between habitats									
P: urban vs. rural	-1.64	-6.17	<0.001	3.30	3.40	0.000	0.23	0.51	0.605
PD: urban vs. rural	-1.90	-7.16	<0.001	0.78	1.10	0.270	1.48	3.02	0.002
Within habitat between treatments									
Urban: P vs. PD	-0.45	-2.13	0.040	1.57	1.77	0.076	-1.20	-3.24	0.001
Rural: P vs PD	-0.19	-0.71	0.479	-0.94	-1.18	0.237	0.04	0.11	0.909

(1) male identity) 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).

We performed similar analyses for the control group, including FIDs, nest returning latency and aggressiveness behaviour as response variables in each model and treatment (one person vs. two people) as explanatory variable. Owl identity was included as a random term.

Model adjustments were assessed by plot inspection assessing normality distribution (qqplot) and homoscedasticity (plot fitted values vs. residuals of the model). All statistical analyses were carried out using R software, Version 3.0.1 (R Development Core Team, 2015). Values are reported as mean \pm SE except where noted. All tests were two-tailed, and differences were considered significant at $P < 0.05$.

3. Results

We did not find an effect of the number of people (one or two) approaching to male owls in FIDs ($\beta = 0.209$, $t_{19} = 1.411$, $P = 0.174$), owls nest returning ($\beta = 0.030$, $Z_{11} = 0.003$, $P = 0.998$) and aggressiveness ($\beta = -0.1261$, $Z_{11} = -0.259$, $P = 0.795$). Consequently we used the data from one person treatment to perform the remaining analyses.

Overall, we made P and PD approaches to 36 nests (14 at rural and 22 at urban habitats). Model explaining FIDs variability showed an effect of habitat and treatment (Table 1). On one hand, burrowing owls' responses to treatment (PD and P) differed between habitats. Males from rural habitats exhibited longer FIDs compared to urban males in both treatments (Table 1, Fig. 1). On the other hand, the response to treatments was different within each habitat type (Table 1). Urban males showed longer FIDs in response to PD treatment compared to P treatment, while no differences were detected between treatments for rural males (Fig. 1).

Burrowing owls returned more frequently to the nest in urban compared to those at rural habitats (Table 1). Overall, in urban habitats 79.5% of male owls returned to their nest after treatments while nest returning percentage was 39.2% for rural owls. We did not find an effect of the treatment within habitats (see Table 1). During P treatment urban owls tended to return more to their nest than rural owls (90.91% vs. 28.57% respectively, see Table 1).

Aggressiveness level exhibited by Burrowing owls at urban habitat was higher than that at rural habitats ($\beta = 0.802$, $Z = 2.287$, $P = 0.022$). Urban owls showed a similar aggressive level than rural owls (P treatment) but showed more aggressive behaviours when they were exposed to PD treatments (Table 1). We found that urban males were more aggressive when exposed to PD treatment compared to pedestrian alone ($\beta = 1.207$, $Z = 3.246$, $P = 0.001$), while no

differences were detected in this variable between P and PD in rural habitats ($\beta = 0.048$, $Z = 0.429$, $P = 0.909$, Fig. 2).

4. Discussion

Burrowing owls risk perception differed between urban and rural habitats. We found that urban owls were more aggressive, had shorter FIDs, and returned to their nests more frequently than their rural counterparts when faced to an approaching human and a domestic dog. We had predicted that urban owls, which are exposed to a higher encounter rate of potential and real predators, would have lower responses than rural owls if they were able to turn down their response after recognizing frequent stressors. This prediction was partially supported by our results, since even though FIDs were shorter at urban habitats, aggressiveness level was always more intense. In addition, we found that different predator types elicited different responses in urban Burrowing owls, which were characterized by longer FIDs and increased aggressiveness in front of a PD treatment than in P treatment. These results indicate that, at least for urban owls, the risk perception was higher at dog presence than during the confrontation of a pedestrian alone.

We found that nest returning behaviour was different between owls from rural and urban habitats, with urban owls returning more to their nest than rural ones. Such differences might be due to the recovery time after risky stimuli are perceived. That is, rural owls take longer to return to their normal behaviour after a stressful situation (P and PD approaches) than urban owls. Stress response is mediated by hormonal adjustments, mainly by the modulation of adrenocortical system (Atwell et al., 2012; Partecke et al., 2006). Rural owls might be undergoing a more intense release of corticosterone compared to urban owls which could be related to a higher risk perception when facing a same stimulus. Another aspect to be considered is the time needed to turn-off the stress response and resume to a normal behaviour, aspect that has been shown to vary between individuals within a same species in mammals (Neufeld-Cohen et al., 2010).

Burrowing owls responded differently to both treatments (P and PD) according to the habitat used for nesting. This finding indicates that owls living at urban habitats may tolerate humans' presence near the nest, but when a critical approaching distance is exceeded an aggressive response is triggered. Rural owls, in contrast, show a different strategy avoiding aggressive encounters by flying earlier when a potential predator is detected and non aggressive behaviours were dominant. The strategy followed by rural owls would be associated with the risk perception and predator avoidance, since they might perceive P and PD in similar way, as real predators, and then the best strategy might be to avoid revealing nest position by flying earlier, regardless of predator type. On the other hand, urban owls may have the capacity to respond differen-

tially in front of human alone or with a dog. In this sense, there is evidence indicating that some urban birds have the ability to discriminate even between different people and their approaching. This has been related to a high general cognitive ability and/or rapid learning capacity in these individuals (Levey et al., 2009; Marzluff et al., 2010), feature that has been linked to their success colonizing urban habitats (Sih et al., 2010; Sol et al., 2013).

Human and dog presence in rural habitats is low since most of the sampled area belong to private properties with restricted access. However, given that animals rarely have perfect information about their predators, they are expected to overestimate rather than underestimate predation risk to maximise fitness (Frid and Dill, 2002). This seems to be another plausible explanation of the lack of difference in owls' response between treatments in rural habitats. On the other hand, human presence is much higher in urban than in rural habitats, hence fleeing from each human that pass by walking might represent a cost too high for urban owls. In this sense, stressful situations such as exposure to predator represents a trade-off that would favour the ability to distinguish stimulus with different threat level, eliciting stress when a stimulus is reliable enough to warrant the costs associated with hormonal activation. Thus, urban owls should learn to distinguish between real or potential predator and reduce its sensitivity to frequently occurring stressors such as humans (Møller, 2008; Marzluff et al., 2010) while remaining alert to real predators such as domestic dogs. Considering this, previous studies have suggested that repeated exposure to novel stressors allow animals to acquire and retain information regarding its relevance (i.e. riskiness). This means that while response to stressors is enhanced when represents a risk, it can also wane if they are experienced repeatedly without being associated with a real risk, (Brown et al., 2015).

Dogs have negative effects on wildlife (Ditchkoff et al., 2006) and they also resemble foxes, which are typical predators of native and rural habitats of the Pampas (Redford and Eisenberg, 1992). Considering that animals have evolved generalised anti-predator responses to similar threatening stimuli (Frid and Dill, 2002), owls might show an innate recognition to dogs as predators, which would trigger long FIDs responses. However, this behaviour can be modified as a result of experience (i.e. learning) during ontogeny to produce an optimal response specific to more local conditions (Brown, 2012). For example, Brown et al. (2013) found that fear response to novel predator cues is determined by exposure to fearful situation during critical juvenile periods in fishes. Similarly, in urban birds early exposure to frequent and harmless human presence could favour the development of a lower response to them (shorter FIDs).

From our sampling we are not able to state which is the mechanism underlying behavioural differences (i.e. personality, behavioural plasticity via learning processes) between urban and rural owls in response to treatments; though a clear pattern of individuals differing in their behaviour phenotype is emerging and becoming evident at each habitat. Urbanization might be acting as a selective force and only more tolerant individuals would be able to dwell and succeed on urban areas (i.e. phenotypic habitat-selection hypothesis, Carrete and Tella, 2010). FIDs also have been considered a consistent trait in Burrowing owls lifespan (Carrete and Tella, 2013), indicating that personality and not just habituation alone might be causing flight distance to decrease rapidly with increasing exposure to humans. However, depending on the degree that an environment is stable and predictable through space and time, animals can learn to recognise which stimuli are associated to danger and which are not and act in consequence by performing shorter or longer FIDS and different intensity of aggressiveness. However, since most environments are variable, a certain phenotype would not always be optimal and some degree of phenotypic plasticity would be required (Brown, 2012), especially in changing

habitats such as urban areas (Sol et al., 2013). According to this, urban environments might be selecting for individuals that are less fearful of humans and more aggressive in front to predators than rural environments, though the continuous exposition to the harmless and frequently occurring human presence could reduce their sensitivity to this stressors through learning.

In conclusion, we found that the anti-predatory behaviour of Burrowing owls differs according to habitat and predator type. Urban owls recognise human with dogs as a greater threat than a human alone, indicating that fear of domestic animals should be considered as one of the possible mechanisms contributing to whether birds settle in cities and towns or not. On the other hand, human and dogs seem to represent similar threats for rural owls but greater than that perceived by urban owls, evidenced by the early anti-predatory response. Our findings emphasises the importance of modified habitats in modelling the response of owls to potential and real predators, and represents another step in the explanation of how wild animals perceive and respond to potential and real risks associated with living in urbanized environments. Further research would contribute to the understanding of how urbanization may influence selection on personalities and what is the role of learning and its interplay with personality traits in animals faced to novel environmental challenges.

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