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Urban living predicts behavioural response in a neotropical raptor

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ABSTRACT

Behaviour is expected to be one of the most important factors driving urban living of bird species because it largely determines how animals interact with their environments. The contribution of different behavioural traits as facilitators of contemporary process of bird colonization of urban environments, however, is still unclear. Here we examined the differences in three behavioural traits: neophobia (avoidance of a new object) and solving success and solving latency of a problem solving test related to obtain food, in rural and urban living individuals of a common diurnal Neotropical raptor, the chimango caracara (*Phalcoboenus chimango*). Moreover, for solving success and solving latency behaviours, we tested the plasticity (i.e., habituation) in birds. Urban and rural chimangos showed similar neophobia of a new object. All chimangos showed an improvement in their output in problem-solving test as the five-day testing passed but urban chimangos showed higher solving capabilities than rural conspecifics as they were more successful in solving the problem test. More, urban birds shown lower solving latency than rural, as they were able to improve their test performance by opening doors in less time as the day passed; in rural birds this relation was not so abrupt. In addition, those individuals that opened more doors, opened these faster too. Lastly, both solving success and latency showed very low individual consistency (repeatability < 0.275). Our results provide evidence of plasticity in solving capabilities of chimango caracaras which reveal that a habituation process in these behavioural traits could be associated to establishment of birds in urban environments.

1. Introduction

Human activities cause environmental changes that may involve accelerated evolutionary processes of animals inhabiting these environments (Palumbi, 2001). These new, human modified scenarios may be a challenge for wild species and the ability to cope with these changes may make the difference between survival and death (Sol et al., 2011). Urban development is one of the most important causes of habitat transformation and a severe threat for biodiversity (McKinney, 2006; Sol et al., 2014). The response by species to urbanization and replacement of native habitats is not always uniform. Some species can thrive in slightly urbanised environments due to reduced predation risk by native predators and an increase in food availability promoted by disturbance (McKinney, 2002; Møller, 2009; Rebolo-Ifrán et al., 2017; Shochat et al., 2006). These advantages could be exploited only by those species that are able to adapt their behaviour to these novel environments (Boal and Mannan, 1999; Gilroy and Sutherland, 2007; Sih et al., 2011; Sol et al., 2014). In this context, behavioural flexibility plays an important role in species persistence and success in human modified environments (Colles et al., 2009; Sih et al., 2011; Sol et al., 2002; Sol and Lefebvre, 2000) allowing animals to respond rapidly to cope with the changes imposed by these habitats (Sol and Lefebvre, 2000). Thus, low neophobia (aversion towards approaching to new food item, object or place (Greenberg, 2003)) and innovation and learning capabilities are among the behavioural traits usually exhibited among urban dwelling birds, allowing individuals to enter a new situation and readily develop novel behaviours to confront it and storing new responses in their behavioural repertoire (Sol et al., 2011; Sol and Lefebvre, 2000). In this context of urbanization and in experimental conditions with birds, it has been shown that urban birds have greater ability to problem-solving related to food than rural individuals (Audet et al., 2016; Cook et al., 2017; Preiszner et al., 2017).

Determining which individuals become urban dwellers while others remain in less human-disturbed habitats requires the study of

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behavioural and physiological traits associated with individual-based habitat selection (Audet et al., 2016; Rebolo-Ifrán et al., 2015; Sol et al., 2011). Recent studies have highlighted the importance of examining differences between rural and urban birds but also on the consistency of individual expression of traits potentially related to successful urban living as a way to identify the most important drivers of individuals' settlement in urban environments. In this sense, two hypothesis have been proposed to aim to explain the differential occupation of environments with different human perturbation degree: the first proposes that a habituation process would lead to a reduction of the response to a stimulus when it is repeatedly showed to individual (Blumstein, 2016). The second, the non-random or disturbance-induced habitat selection hypothesis proposes that if a behavioural trait has a strong and invariable individual component (low variability), then this trait will be exposed to a selective process that will result in an individual and unequal distribution among urban and rural sites depending on their susceptibility to human disturbance (Carrete and Tella, 2010). Although these hypotheses have been studied in birds from a fear ecology perspective (Vincze et al., 2016), it is possible that the same can be studied in the innovation and learning context due to the individual variability or consistency of these behaviours.

In the raptor bird group, the above two hypothesis have been tested in relation to fear of human of burrowing owl (*Athene cunicularia*) finding foundation both to habituation (Cavalli et al., 2018) and for habitat selection hypothesis (Carrete and Tella, 2010). However, although urban burrowing owls have been shown to be more explorative than their rural counterparts (which can be advantageous in exploiting of novel resources in urbanised environments) (Carrete and Tella, 2017), a selective or habituation process of other behavioural traits of urban dwelling birds has not been tested, such as neophobia, problem-solving and learning capabilities. If individuals from urban and rural environments show strong individual consistency in these behaviours, then it is expected that such traits could be potentially involved in a process of phenotypic selection in which the individual's problem-solving and learning capabilities would allow them to confront these new environments. For its part, if both urban and rural individuals show high behavioural plasticity in a trait that would allow urban living, then a habituation process could be happening in these individuals.

The chimango caracara (*Phalcoboenus chimango*) is the most common bird of prey in southern South America and stands out from other raptors for its ecological ability to occupy different environments, particularly those severely modified by humans such as urban habitats (Biondi et al., 2013, 2005; Carrete et al., 2009; Carrete and Tella, 2011; Guido et al., 2017). The chimango caracara is a facultative scavenger with a generalist diet (Biondi et al., 2005) that can usually be seen feeding from antropogenic food sources as garbage (Fig. 1). Experimental studies have demonstrated the species' ability to obtain food in innovative ways (Biondi et al., 2008). This particular trait has been suggested as one of the factors that allows individuals to establish themselves in human altered environments (Biondi et al., 2013). However, neither differences nor individual consistencies on neophobia and problem-solving capabilities between urban and rural living individuals have yet been assessed for chimango caracaras.

Here we tested the general predictions that urban living chimango caracaras will show enhanced problem-solving skills (i.e. solving success and solving latency of a problem solving test related to obtain food) in comparison with rural conspecifics. Furthermore, because the low neophobia would be beneficial to birds in urban territories (Biondi et al., 2010a), we predict that urban individuals will be less neophobic than rural birds. In addition, we examined the consistency through time of solving success and solving latency of chimangos in both rural and urban habitats with the aim of assessing whether or not these behavioural traits could be involved in selective process that could determine that only those individuals with more problem-solving capabilities may become urban dwellers.

Fig. 1. A banded chimango caracara looking for food at an outdoor trash container in the urban area considered in this study. Photo credit: Arkaitz Pedrajas Etxebarria.

2. Materials and methods

2.1. Study area

Experimental tests were carried out on birds inhabiting in two different habitats in central Argentina. The first area, the urban, comprised a moderately urbanised habitat (two houses for hectare approximately) that included a residential area around Santa Rosa city in La Pampa province, Argentina (36° 43′ S 64° 16′ W). This area has a strong human presence due to stay-at-home residents, pedestrians and vehicular traffic around the colony of chimango caracaras. The second area comprised a rural zone localized ~20 km from Santa Rosa (36° 34′ S 64° 08′ W). This was a zone of agricultural activities including crops and cattle and sheep raising. In this habitat, human presence is lower than in the urban area and is limited to a ranch with a single house. In both urbanised and rural habitats, chimango caracaras lived in colonies in reproductive and non-reproductive season.

2.2. Bird trapping and captivity conditions

We used walk-in traps (Bloom et al., 2007) to capture chimango caracaras in urban and rural environments during 2012 and 2013. Even though some sampling methods could generate a bias in samples of animals (Biro, 2013) and considering that walk-in trap require that chimangos explore the trap to be able to walk in, then this trapping methods could have facilitated the capture of more explorative personalities. However, it is known that explorative behaviours not correlate with neophofia level and problem-solving performance in chimango caracara (Biondi et al., 2010a), therefore, this bias in samples could not affect our results. Trapping was carried out during the non-breeding period between April and August (Solaro and Sarasola, 2015). Traps were baited with meat and bones and set close to the area comprising the breeding colony where chimangos remained all year round (Solaro, unpub. data). Traps were activated early in the morning (8:00-9:00 a.m.) and checked every one hour until afternoon, removing the birds captured at every visit (Solaro and Sarasola, 2017a). We used tarsi and cere colours and moult stage to establish age of trapped birds (Ferguson-Lees and Christie, 2001; Sarasola et al., 2010). Because of the potential dispersal movements of post-fledging birds (Solaro and

Sarasola, 2017b), which precluded assigning birds as definitively settled in a particular area during such life stages, only adult chimango caracaras (> 2 years old) were selected for this study obtaining 18 chimango caracaras that were suitable. This restriction led to an unbalanced sample size between rural and urban populations (six rural vs 12 urban individuals). But considering that these experiment in captivity are strictly necessary to carry out in non-reproductive period in order not to affect the reproductive behaviour of studied populations and because in non-reproductive period it is much more difficult to capture chimango caracaras than in other seasons (Solaro and Sarasola, 2017a), our sample size seemed appropriate to the species studied and the logistic difficulties that we faced. Moreover, each individual studied was an experimental unit independent from rest even though they belonged to the same capture site. Lastly, our sample size, its distribution and independence of individuals accords with samples used by others authors that have worked in the same conditions with chimango caracara and that have highlighted on behavioural aspects of this species (Biondi et al., 2010a, 2008).

Birds were banded with aluminium and PVC rings and transported to the Universidad Nacional de La Pampa campus where they were housed in individual cages (100 × 100 x 100 cm) visually, but not acoustically, isolated from each other. Cages were placed in an empty room to avoid any distress due to odd noises, persons or objects. Before experimental tests, birds were subject to an acclimation period during which they were provided food and water *at libitum*. This period was maintained until birds ate and drank comfortably from the source provided (3–5 days).

For all individuals, the captivity period lasted less than 12 days. An individual arrived to laboratory in day one, then it was 3–5 days of acclimation, then it was six days of experiments and in the last day of experiment each bird was released at their site of initial capture. Capture and experimental tests were performed in accordance to and under permits for the use of wild animals in research awarded by Dirección de Recursos Naturales, Ministerio de la Producción, Gobierno de La Pampa.

2.3. Experimental test

Neophobia and problem-solving capabilities of urban and rural chimango caracaras were examined by confronting birds with experimental tests involving obtaining food in innovative ways. Tests involved exposing birds once per day to a compartmented transparent acrylic box with four doors (Fig. 2) following the same experimental procedure employed by Biondi et al (Biondi et al., 2008). After acclimation period, and with the aim to avoid inter-individual differences in the motivation feed, all birds were deprived of food for 24 h before being tested. Each test was video recorded using D-Link DCS-2121 camera and video monitored from a neighbour room. The resolution tests allowed access to food (approximately eight g of meat) inside four compartments of the box (Biondi et al., 2008; Webster and Lefebvre, 2001) with doors that opened in different ways: push to slide door, push inwards to open door, raise the door, or pull the door outward (Fig. 2). Tests were performed over six consecutive days. During the first day (day zero), the box was exposed with the four compartment doors opened while for the following five days (one to five) the box was exposed to birds with all the doors closed. The individual tests lasted a maximum of 35 min or until the four compartments were reached and the food eaten by the bird.

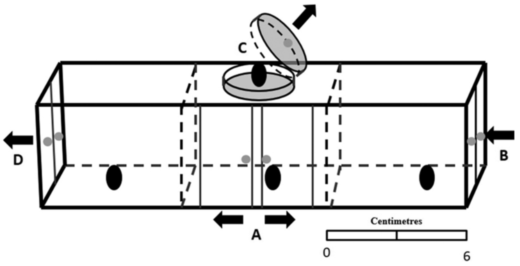

Fig. 2. Diagram of transparent acrylic box used in experimental test. Acrylic box design was taken from previous study (Biondi et al., 2008). Black dots represents pieces of meat inside each compartment. Grey dots represents handles that could be used to open doors. The doors opening in different ways are represented by A: push to slide door, B: push inwards to open door, C: raise the door and D: or pull the door outward.

2.3.1. Neophobia

This test was performed in each individual in the first day test (day zero) when the four doors of box were opened and the meat was inside each compartment and accessible to bird without having to open one door. In this test, we recorded the latency time to access the first piece of food as a measure of neophobia of each individual to novel object. This measure was taken in 17 chimango caracaras due to video recording failed in an urban individual experimental session.

2.3.2. Solving success

Cognitive capacity of birds to solve an unusual and subsistence problem related to acquisition of food was measured as the success of each bird in opening doors box and eating what was inside. In this sense, we recorded the number of doors opened per individual in each experimental session, obtaining in total five measures each (one measure per day).

2.3.3. Solving latency

In five subsequent experimental sessions after day zero (when the box was exposed with four doors closed) we recorded the latency time to open each door of box. Learning include the acquisition of learned behaviours to devise solutions to problems related to subsistence (Sol et al., 2013). Thus, latency time was considered as a measure of individual learning capability because a reduction in this time as five days goes by indicates that the individual learned in first days and then, in subsequent days, gets the meat faster (and it could improve its subsistence). A non-reduction or an increase in this time could mean less or non-existent learning by that individual. Latency time for the first door was defined as at the time from presentation of the box until the first compartment door was opened and for the remaining doors latency time was the interval between opening two consecutive doors.

2.4. Statistical analysis

With the aim of evaluate if the neophobia varied according to bird's original environment, we used Linear Models (LMs) to assess the effect of environment (i.e., rural or urban) on the latency to reach the first piece of food in the zero-test day. Because of lack of normality, latency time was transformed to natural logarithms before being including in the models and then the normality of residuals of model was checked with Shapiro-Wilk normality test.

Generalized Linear Mixed Models (GLMMs) using a Poisson error distribution and a log link function were performed to investigate the effects of environment (i.e., rural or urban) and test day on the total number of doors opened by individuals in each experimental test. We used the environment as an explanatory variable with the purpose of assessing whether the cognitive capacity for problem-solving varied with the degree of urbanisation present in each individual's environment (Sol et al., 2011). Test day, ranging from one to five, was included in the models as numeric covariate with the aim of examining learning capability of chimango caracaras. Through this analysis we examined any change or improvement through time on individuals performance in solving the test (Biondi et al., 2010a, 2010b). We tested the interaction between environment and test day too. Individual identity of birds was included in the models as a random term.

To test for differences in solving latency, we analysed the variation in the latency to open each of doors of the testing apparatus (in the last five days of experiment) as a function of environment (urban vs rural), test day (day one to five), the type of door opening (push, raise or pull outward) and number of doors oppened using Linear Mixed Effects (LMEs) models. Because of lack of normality, latency time was transformed to natural logarithms before being including in the models and then the normality of residuals of models was checked with Shapiro-Wilk normality test. Because opening each door represents a different level of difficulty, the explanatory variable type of door opening was included in the models. This variable had three level that included four door type because we grouped two door aperture modes with similar complexity to be opened (push to slide door and push inwards to open door) in a single level named push and then the other two levels of door opening with different complexities (raise and pull outward) represented each a single door type. Although *a priori* we could considerer that push is easier than raise and that raise is easier than pull outward, the incorporation of this variable in our model allowed us to prove a potential effect posed by the difficulty to open each door type. We tested the interaction between environment and test day too. More, number of doors opened was included in the models to the aim to control latency time for solver capacity (i.e. a bird that opened one or few doors but very quick could be considered as a fast solver to solving latency models, however this bird is a poor solver for the doors that didn't open). Last, individual identity was also included as a random term in the models.

Since chimango caracara is a species with low sexual dimorphism, without sexual differentiation in parental care (Gallego et al., 2018) and with similar exploratory behaviour between sexes (Biondi et al., 2013), the variable "sex" was not considered in models to evaluate variation in neophobia, solving success and solving latency.

Due to more than one explanatory variable being included in GLMM and LMEs models, we did a variables selection following a backward-stepwise procedure, by removing non-significant predictors until only significant ones remained (Crawley, 2015). The significance of the predictors was tested using likelihood ratio tests comparing the model with and without the predictor. Significant outcomes were considered when $p < 0.05$, marginally significant outcomes were considered when $0.05 < p < 0.1$ and no significant outcomes were considered when $p > 0.1$. Finally, in the LME model case, we readjusted the selected model using Restricted Maximum Likelihood (REML).

Repeatability of both number of doors opened and latency time were calculated with the aim of quantifying the individual consistency in these two traits (Nakagawa and Schielzeth, 2010). In both cases we used the *rpt* function ("Repeatability Estimation for Gaussian and Non-Gaussian Data", included in *rptR* package (Stoffel et al., 2017)). Repeatability was calculated separately for rural and urban population.

All tests were performed using the software R (R Core Team, 2016).

3. Results

3.1. Neophobia

The latency time to eat the first meat piece in the day zero when all doors were opened was 1.28 ± 1.51 min. The latency time in the day 0 was not affected by the environment (Table 1). Residuals of this model were normally distributed ($W = 0.96$, $p = 0.70$).

3.2. Solving success

During the problem-solving tests, all individuals opened at least one door of the box to reach food on at least one day of the five-day experiment (Table 2). In the first session, 16 of 18 individuals (88.9%) succeeded in opening at least one door and five birds (27.7%) opened all four doors of the box in their first session. During the last day of experiments, all individuals opened at least one door, and nine birds (50.0%) opened all four doors. Test day was marginally significant in models examining the number of doors opened by birds during the experimental tests (Table 1). In this sense chimangos tended to increase the number of doors they opened as the 5-day experiment progressed (Fig. 3). Environment was significant in GLMM model with individuals from urban environments opening more doors than individuals from rural areas (Table 1, Fig. 3). However, the total number of doors opened was not affected by interaction between environment and test day (Table 1).

The values of repeatability in number of doors opened measures were low, both rural ($r = 0.273 \pm 0.175$) and urban ($r = 0 \pm 0.035$) birds.

3.3. Solving latency

The mean latency time to open each door was 3.89 ± 5.95 min. Even if the estimated slope to test day was near to cero, this variable significantly affected latency time (Table 1). Even more, the effect of test day on latency time was more notorious specifically in interaction with environment (Table 1, Fig. 4). In this sense, the 12 urban chimangos decreased the latency time through the 5-day experiment while

Table 1

Model analysis showing the effect of different explanatory variables over the variability in neophobia (latency time day zero), problem-solving (number of doors opened) and learning capabilities (latency time) for chimango caracaras.

Analysis	Dependent	Explanatory variable	Estimate	SE	χ^2	df	P
Neophobia: LM	Log(Latency time day zero)	Environment			14.0793	16	0.5928
Problem-solving capability: GLMM	Number of doors opened	Intercept	0.8504	0.1736			
		Test day	0.0789	0.0462	2.9167	1	0.0876 *
		Environment (Urban)	0.5478	0.1843	7.7504	1	0.0053
		Test day : Environment			0.1372	1	0.7111
Learning capability: LME	Log(Latency time)	Intercept	1.9634	0.6231			
		Environment			0.5868	1	0.4436
		Day	0.0657	0.1196	8.5342	1	0.0034
		Number of doors opened	−0.2667	0.1285	4.3045	1	0.0380
		Type of door opening	−0.7726 −	0.2634	11.4191	2	0.0033
		(Raise)	0.7471	0.2309			
		(Push)					
		Test day : Environment (Urban)	−0.3302	0.1377	5.7470	1	0.0165

Estimate and SE are showed only for intercept and significant or marginally significant terms.
Significant results are presented in bold.
Marginal significance is indicated with asterisk (*).
When categorical variables (environment and type of door opening) were significant, the reference category was included in the intercept and compared with the category shown between brackets.

Table 2
Number of times birds accessed food (in 0 day testing) and number of times birds accessed food after opening doors (in 1–5 day testing) for each individual in sequence of six-day testing according to bird's environment. Day 0 (when the four doors were opened) was reported in this table but was not considered in problem-solving analysis.

	Day testing					
Individual for environment	**0**	**1**	**2**	**3**	**4**	**5**
Urban						
S12670	3	3	3	4	3	3
T10498	2	1	3	3	4	4
T10924	3	0	0	4	3	3
T11095	3	3	3	4	3	3
T11609	4	2	3	4	3	4
T12055	4	4	2	4	3	4
T12321	4	1	2	1	2	2
T12388	3	0	0	4	2	4
T12526	2	4	4	4	4	3
T12684	4	3	4	4	4	4
T13155	4	4	4	4	4	4
T13156	4	4	2	4	4	4
Rural						
T12197	4	3	0	0	0	1
T12305	4	2	1	1	1	4
T12306	3	3	1	2	1	3
T12527	3	4	3	3	4	4
T12528	4	1	0	0	1	1
T13154	4	1	3	2	1	3

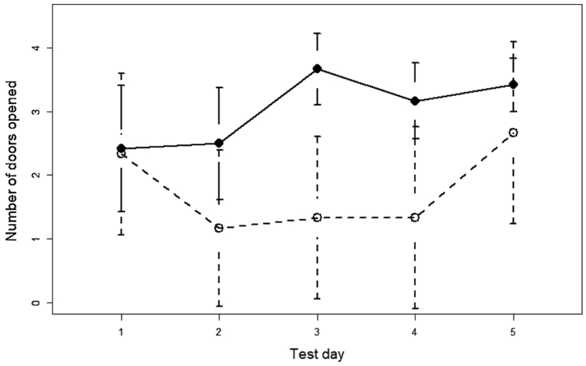

Fig. 3. Variation on the number of doors/compartments (mean ± 95% CI) of the acrylic box opened by chimango caracaras in sequence of five-day of testing according to environment. Solid line and black points shown urban individuals and dashed line and open points shown rural individuals.

the six rural individuals did show an increase in latency time when the 5-day experiment progressed (Fig. 4). Finally, latency time varied significantly depending on type of door opening (Table 1, Fig. 5), with a lesser latency times to open doors by pushing (3.16 ± 4.35 min) or raising (3.30 ± 5.76 min) both being much less than opening doors by pulling outward (6.98 ± 8.85 min). Solving latency was significantly and negatively related to number of doors opened (Table 1, Fig. 6). Residuals of model were normally distributed (W = 0.99, p = 0.30).

The values of repeatability in latency time measures were low, both rural (r = 0.275 ± 0.161) and urban (r = 0.198 ± 0.088) birds.

4. Discussion

Differences in problem solving capacities between urban vs rural individuals have been verified in several bird species (Audet et al., 2016; Cook et al., 2017; Ducatez et al., 2016; Preiszner et al., 2017), however this topic had not been studied in raptorial birds living un urbanized habitats so far. Our results reveal that two behavioural processes related to problem-solving and learning, differ between rural and urban individuals of a very common Neotropical raptor bird, the chimango caracara. Furthermore, these traits show a low individual consistency when in general they enhance its performance in an experimental test of five days.

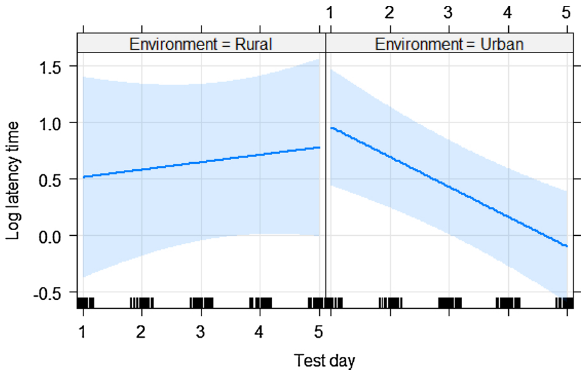

Fig. 4. Tendency estimated for LME model in logarithm of latency time to open doors of compartments to get food by chimango caracaras through sequence of five-days of testing for rural and urban individuals. See methods for definition of latency time.

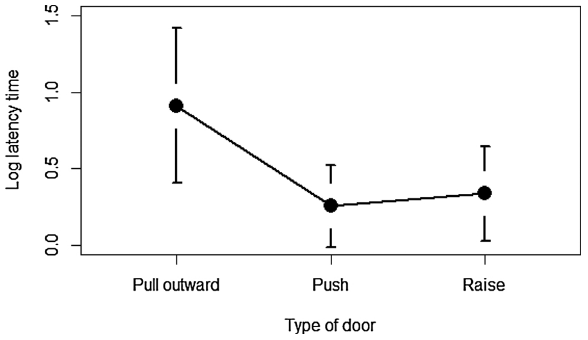

Fig. 5. Variation in logarithm of latency time (± 95% CI) to open doors of compartments to get food by chimango caracaras according to type of door opened. See methods for definition of latency time.

Neophobia can protect birds from potential dangers such as toxic food or predators (Greenberg, 2003). Hence high neophobia might be advantageous in urban habitats where there is a stable food source but the probability of encounter with novel and dangerous situations is higher (Miranda et al., 2013). But, on the other hand, low neophobia may be advantageous to birds in urbanised habitats because they could take advantage of novel resource opportunities (Sol et al., 2011). Then, low neophobia could be an important trait for a generalist and opportunistic raptor as the chimango caracara to obtain the ecological success that now it has even in urbanised habitats (Biondi et al., 2010a). However, we cannot verify our prediction that urban birds would be less neophobic than rural chimango caracaras since both populations shown similar neophobia. Neophobia, then would be inherent to the species rather than to individuals confronting with different degree of human stressors.

Behavioural plasticity is hence a key aspect determining the success of species in new environments (Sol et al., 2002). Behavioural plasticity is closely linked with learning capabilities as these may result in the expression of innovative behaviours usually exhibited by urban individuals when confronting novel food sources and potential predators (Sih et al., 2011; Sol et al., 2013). In our problem-solving experiments, both urban and rural chimango caracaras were capable of obtaining food in an innovative manner. However, urban individuals appeared more efficient (opening more doors) than rural birds. In addition, although marginally significant, both experimental groups improved their performance in problem-solving through time in the five days that the experiment lasted. The mean number of doors opened by rural chimangos at the end of the experiment was similar to the initial mean

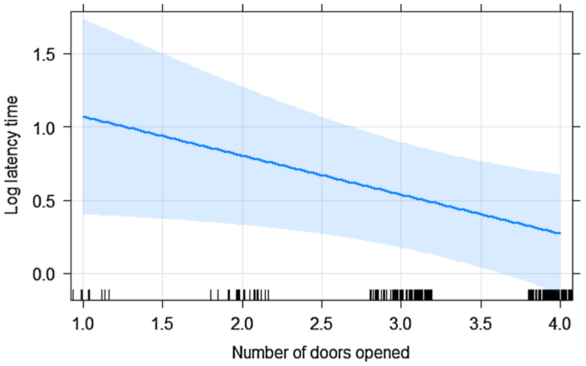

Fig. 6. Variation in logarithm of latency time (± 95% CI) to open doors of compartments to get food by chimango caracaras in function of type of doors opened. See methods for definition of latency time.

value of doors opened by urban chimangos (i.e. first experiment day, Fig. 3). Considering this trend and the verified learning skills of the species, it would be expected that the performance of rural birds finally match that of urban birds.

Learning is one of the most important behavioural traits allowing survival in urban environments (Møller, 2009). Through this cognitive process urban individuals may store vital experiences promoting survival in these environments, such as identifying and avoiding new predators and threats or by recognizing and localizing novel food sources and suitable habitats (Sol et al., 2013). In our study, solving latency of chimango caracaras were related to the environment from which they came, showing rural and urban chimango caracaras differences in the time to find and open the doors of box. Further, latency time was affected by the type of door, which could indicate that each door presented a different degree of difficulty (Fig. 4). Last, latency time was affected by the number of doors opened too, showing the more successful to open doors individuals the lowest solving latencies. Although it has been reported that chimango caracara has learning ability (Biondi et al., 2010a, 2010b, 2008), this trait had not been examined in the context of birds living in contrasting environments such as rural vs. urban habitats.

It is known that exploratory behaviour of chimango caracara is not influenced by sex (Biondi et al., 2013) and that chimango caracaras is social raptor bird that show similar and symmetrical parental investment of both sexes in the reproductive stage (Gallego et al., 2018). Following this line, it is not difficult to think that both males and females could have similar problem solving behaviour because both sexes are subjected to the same environmental pressures of each habitat and to the same demands of offspring during the reproductive season. However, it is important to highlight that more studies should be done to clarify if sex has some effect on the differential problem solving behaviour in habitats different human perturbation degree.

Models showed an improvement in the performance of chimangos during the experimental tests (increase in the number of doors opened through 5-day testing and diminution in latency time to open the doors and obtain food), however urban individuals lowered the latency time to open doors over the successive days of the experiment in a more abrupt way than rural individuals with a negative urban slope and a positive or near to zero rural slope (Fig. 4). Although individuals of both populations showed habituation and low consistency in learning and innovative behaviours ($r < 0.275$), this habituation was higher in urban chimangos than in their rural conspecifics. Assuming that urban birds are less affected by human disturbance due to habituation process (Cook et al., 2017) and that habituation involves behavioural flexibility (Vincze et al., 2016), urban could be more flexible than rural chimangos.

The learning capabilities and behavioural adjustments exhibited by chimango caracaras denote the plasticity of the species to adapt to new and challenging situations. This could indicate that solving success and solving latency are involved in a habituation process rather than in phenotypic selection process in urban individuals as has been proposed for other traits (e.g., fear of humans) under the habitat-matching dispersal hypothesis. Although problem-solving and learning capabilities may be potentially important in facilitating resource use, the observed behavioural plasticity in solving success and solving latency for chimango caracaras would leave little margin for environmental selection pressures to act on those more innovative individuals that could ultimately become urban dwellers. Although this is somewhat speculative, problem-solving and learning behaviours may allow success in urban environments for those individuals selected by other behavioural traits that do not vary on time and that have a strong individual component, as might potentially be the case of fear of humans following the disturbance-induced habitat selection hypothesis (Carrete and Tella, 2010).

5. Conclusions

Our results show that two behavioural traits of chimango caracara associated with urban living – solving success and solving latency – have different responses depending on the degree of urbanization present in the habitat where they live. While solving success and solving latency improved for urban living birds when compared with rural conspecifics, neophobia did not differ. These traits enhancing in solving success and solving latency in urban population could be the behavioural response of these individuals faced with the routine new feeding opportunities presents in more human modified environment such as urbanised habitats. Further research is needed to examine individual consistency or variability in other behavioural traits such as fear of humans in chimango caracaras, physiological (e.g., stress and hormonal responses) and demographic (e.g., survival and fitness) studies that could contribute to a better understanding of why some individuals of this species can cope with urbanization while others cannot.

Declaration of Competing Interest

None.

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