

Cognitive flexibility in a generalist raptor: a comparative analysis along an urbanization
gradient

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Abstract:

In this study, we analyzed the variation in cognitive flexibility in the Chimango Caracara (*Milvago chimango*), across areas with different levels of urbanization. To assess this, we utilized the reversal learning assay which measures the ability to adapt behavior in response to changes in environmental contingencies. We also investigated the impact of neophobia on this variation. All chimangos studied succeeded in acquiring a color-reward association and reverting this learned association when the contingencies changed. Urban chimangos were faster than their rural and suburban counterparts during the initial discrimination and reversal phases. The reversal phase proved to be the most challenging task. The analysis of the errors made during this phase revealed that acquiring a new association (i.e., regressive errors) was challenging for the individuals studied, in comparison to inhibiting a previously learned one (i.e., perseverative errors). Neophobia was found to be lower in urban individuals compared to suburban and rural raptors. Moreover, neophobia showed a correlation with regressive errors during the reversal phase among rural and suburban chimangos, while no such correlation was observed among city-dwelling chimangos. We suggest that neophobia acted as a regulating factor of cognitive flexibility, mainly for individuals expressing relatively high levels of this personality trait.

Keywords: *behavioral flexibility, reversal learning, raptors, urbanization, neophobia.*

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Background

Humans have modified natural habitats through fragmentation, deforestation, and urbanization (Sih et al. 2011; Tuomainen and Candolin 2011). These modifications generally alter the interactions between species and differentially affect their survival and reproductive success, causing changes in biodiversity and ranges of distribution (Jackson and Sax 2010; Sih et al. 2011). Human-induced rapid environmental changes can lead some species to decrease their abundance or even become extinct (Thomas et al. 2004; Jackson and Sax 2010), while others may be favored by these changes (Rahman and Candolin 2022). In this sense, it has been observed that populations that survive sudden changes in the environment are those capable of rapidly adjusting their behavior to these new resulting conditions, that is, those who show behavioral flexibility (Price et al. 2003; Kinnison and Hairston 2007).

Urban-dwelling animals confront an array of environmental changes characterized by unprecedented rates of spatial and temporal fluctuations (Shochat et al. 2006; Alberti et al. 2017). Coping with these changes becomes crucial for species as they strive to capitalize on anthropogenic novel food sources, identify suitable breeding grounds, and contend with challenges such as noise and chemical pollution, traffic, and human presence (Legagneux and Ducatez 2013; Potvin 2017; Goumas et al. 2020). In this context, extreme novel environments, like cities, favor the selection for behavioral flexibility (Snell-Rood and Ehlman 2021) that enable animals to take advantage of emerging opportunities while responding adeptly to evolving threats (Wright et al. 2010; Sol et al. 2013; Ducatez et al. 2020b). Urban environments are also considered structurally more complex than rural or natural areas (Sol et al. 2002; Shochat et al. 2006; Møller 2008), a characteristic known to be one factor influencing learning evolution and flexibility (e.g., Møller 2008, Dridi and Lehmann 2015). The complexity of the urban landscape arises from the amalgamation of built surfaces and green spaces, such as parks and gardens. This integration gives rise to a spatially heterogeneous configuration, impacting resource distribution and habitat structure (Faeth et

al. 2005; Cadenasso et al. 2007). In turn, it is considered that urban areas can sustain superabundant and predictable sources of food compared to rural or natural environments, especially for organisms that feed at community feeders and food dumps (Oro et al. 2013) (Oro et al. 2013). However, for those whose diet is based on anthropogenic waste found opportunistically (e.g., in dumpsters, trash cans, loose litter left in parks, restaurants, etc.), these food sources can be more variable and less predictably distributed than those found in rural areas (Tryjanowski et al. 2015, 2016). This is because the emergence dynamics of such trophic resources depend on human activity (Shochat et al. 2006; Federspiel et al. 2017), and animals must rely on their ability to learn cues associated with such human-related activities to rapidly locate such resources. Therefore, novel, complex, and variable environments, such as urban areas, are a selective force that favors flexible behavioral phenotypes (Shochat et al. 2006, Lee and Thornton 2021, Snell-Rood and Ehlman 2021).

Animals that live in urban environments should have the ability to respond quickly and effectively to novel changes in their environment, being better prepared to find alternative “solutions” to the difficulties they encounter (Griffin et al. 2017). In this way, the organisms that inhabit these environments would benefit from the development of advanced cognitive skills, concerning the information acquisition processes, learning, memory, and decision-making (Shettleworth 2009). Behavioral flexibility has been observed to play a key role in the success of biological invasions (Sol et al. 2002; Sol et al. 2005), in the way organisms cope with changes in their environments (Liker and Bokony 2009), in the successful use of urban areas (Sol et al. 2013), and some of the basic ecological differences between populations of the same species (Greenberg 1983; Greenberg 2003). Particularly in environments that experience frequent modifications, individuals should be able to modify learned associations and establish new ones quickly and flexibly. Thus, the learning process increases the survival probability mainly in those individuals living in changing and moderately predictable environments (Boogert et al. 2010; Kotrschal and Taborsky 2010).

Differences in behavioral flexibility have frequently been studied using the variation in the frequency of anecdotal reports of novel trophic behaviors (behavioral innovation; Lefebvre and Sol 2008; Lefebvre et al. 2013) and the variation in innovative problem-solving ability (e.g., Benson-Amram and Holekamp 2012; Griffin and Guez 2014; Audet et al. 2016; Chow et al. 2016; Cook et al. 2017; Biondi et al. 2022; Muller and Pillay 2023; Harrington et al. 2023). In this context, behavioral flexibility has been seen as a phenotypic expression of the cognitive ability to adjust behavior in the face of changes in ecological conditions (Lefebvre et al. 2013). Another way to experimentally measure the flexibility of behavior is through the reversal learning paradigm, a standard learning psychological test used to measure the propensity to change behavior when the environment changes, or cognitive flexibility (e.g., Bond et al. 2007; Guillette et al. 2011; Logan 2016; Izquierdo et al. 2017). In the initial phase of this test, an instrumental conditioning task (aka discrimination learning) is presented, where the individual chooses the rewarded clue or stimulus over the unrewarded one. As soon as the individual discriminates between both clues, the contingencies are reversed (Shettleworth 2009). The speed at which the new environmental contingency is acquired provides an indicator of an individual's propensity to adjust their behavior to changes in the environment. As reversal learning requires adapting to a new reward contingency and inhibiting learned responses to previously rewarded stimuli, it is considered a measure of cognitive flexibility (Bond et al. 2007, Izquierdo et al. 2017). While the reverse learning paradigm has been applied to a wide range of taxa, it has only recently been used to explore cognitive flexibility in an ecological context (Izquierdo et al. 2017; Guillette et al. 2011; Aljadef and Lotem 2017; Audet and Lefebvre 2017). In this sense, it has been employed to determine whether populations that inhabit environments with different anthropogenic disturbances differ in their propensity to respond to changes in the previously learned contingencies (e.g., Guillette et al. 2011; Griffin et al. 2013; Audet et al. 2016; Federspiel et al. 2017).

Moreover, personality traits have been hypothesized to be related to differences in behavioral flexibility and cognition (Sih and Del Giudice 2012; Griffin et al. 2015). Animal personality is defined as consistent individual differences in behavior across time and/or contexts (Dal et al. 2004; Wolf and Weissing 2012) and has been most characterized along five behavioral axes: shyness–boldness, exploratory behavior (in which neophobia/neophilia is also included), activity, aggressiveness, and sociability (Réale et al. 2007). These behavioral traits can be correlated with each other, forming behavioral syndromes (Sih et al. 2004). This concept of behavioral syndromes has extended to include cognition, regarding a consistent cognitive style that is related to personality (Sih and Del Giudice 2012). Cognitive styles refer to the individual's specific strategy for acquiring, processing, storing, and acting on information, which is independent of its cognitive ability per se (Gruszka et al. 2009), and these strategies can vary across a speed-accuracy/flexibility trade-off. According to Sih and Del Giudice (2012), those individuals with fast and proactive behavioral types (i.e., more bold, aggressive, active, and novelty-seekers) learn a particular contingency in their environment faster but they behave with less accuracy or flexibility in response to changes than individuals with a slow and reactive behavioral type (i.e., Verbeek et al. 1994; Guillette et al. 2011). One hypothesized reason for this is that proactive individuals are less sensitive to modifications in their surroundings (their responses are guided by intrinsic information) and exhibit a higher proclivity for forming behavioral routines (resulting in less capacity for inhibiting previously learned behaviors) than reactive ones (Sih and Del Giudice 2012). On the contrary, reactive individuals might exhibit slower learning of new associations as they rely heavily on environmental stimuli and persistently explore their surroundings to gather comprehensive and precise information. However, their heightened sensitivity enables them to rapidly detect alterations in environmental conditions. Consequently, they respond faster and more accurately to these changes compared to fast and proactive animals. Although there has been some initial support for these predictions, currently there are a broad number of empiric studies showing contrasting results about this relationship between personality traits and cognitive performance/flexibility, which can vary between species and, also,

intraspecifically, between different populations on different environmental contexts (Dougherty and Guillette 2018).

The Chimango Caracara, *Milvago chimango* (hereafter: chimango), can be considered an interesting study case to understand the role of cognitive flexibility in coping with urbanization. This is a generalist Neotropical raptor with notable ecological plasticity and environmental tolerance (Ferguson-Lees and Christie 2001; Biondi et al. 2005; Biondi et al. 2010a; Biondi 2021). In Argentina, the chimango is the only raptor species whose abundance is positively correlated with the level of human disturbance (Carrete et al. 2009). Their generalist and opportunistic feeding habits (Biondi et al. 2005), along with their relatively high tolerance for human presence (Biondi et al. 2020) have allowed them to benefit from the resources generated by different human activities, such as the use of domestic trash containers and urban waste sites (Biondi et al. 2005; Biondi et al. 2008). In experiments performed with individuals from suburban populations, it was observed that chimangos have a remarkable ability to solve novel feeding problems, a high tendency to intrinsic exploration, a low level of neophobia, and the capacity for social learning of novel behaviors (Audet and Lefebvre. 2017; Biondi et al. 2010a; Biondi et al. 2008; Biondi et al. 2010b; Biondi et al. 2013), attributes considered correlates of behavioral flexibility in animals (Reader and Laland 2003). In addition, a series of recent studies showed that urban populations of this raptor were bolder in human presence, less neophobic, and more explorative in front of novel objects (Biondi et al. 2020), as well as were quicker solving a novel feeding problem than less urban populations (Solaro and Sarasola 2019; Biondi et al. 2022). The difference between urban and rural chimangos in solving performance was directly explained by variation in novelty response (i.e., neophobia, exploration), as well as indirectly through the influence of neophobia and exploratory behavior on persistence, motor flexibility, and solving effectiveness (Biondi et al. 2022). Moreover, in a previous study about chimangos' cognitive flexibility, we observed that the level of neophobia negatively correlated with reversal learning velocity in suburban individuals (Guido et al. 2017), which

contradicts the expected higher flexibility in more reactive and neophobic individuals (Groothuis and Carere 2005). Thus, considering that the effect of neophobia on other behavioral traits depends on the environmental context in which this species is immersed (e.g., Biondi et al. 2020), it would be necessary to expand this analysis and include and compare chimangos' populations living in different urbanization levels. This would be paramount to understand the effect of urban settings on the way the chimangos cope and learn about changes in clue-reward contingencies and the differential effect of neophobia on this ability. Thus, this work would provide the first information about the importance of cognitive flexibility and its relationship with personality as key factors explaining adaptation to urbanization in this species, and raptors in general.

Methods

Study area

The study area included urban, suburban, and rural habitats in the southwestern Pampas region of Argentina. The urban habitat was represented by Mar del Plata City (38° 00' S 57° 33' W), the largest coastal city of Argentina with > 682.605 year-round residents and about 3 million tourists during the summer (EMTUR, 2022). The suburban habitat included two locations represented by small localities of less than 1000 inhabitants each: Balneario Parque Mar Chiquita (37°40'40"S 57°30'00"W), located 34 km north of Mar del Plata city, and Playa Los Lobos (38°09'22"S 57°37'34"W), located 22 km south from the city. The rural habitat was represented by private lands with agriculture and livestock activities, located approximately 36 km west of Mar del Plata City (37° 47' 07.9" S 57 °35' 09.3" W). The available data on the daily movement of this raptor species indicate that it ranges from approximately 0.5 km² to 21 km² (Morrison and Phillips 2000; Solaro 2014). With the additional data from 5 years of records including direct observations and citizen science contributions (Biondi in prep.), of banded birds in each of the habitats included in this study, we are confident that the individuals trapped for this study belong to the specific habitat type from which the capture was made.

Subjects and housing

We trapped twenty-six adult chimangos (10 urban, 8 rural, and 8 suburban) with baited walk-in traps between March and August (non-breeding period). Immediately after capture, we weighed and housed the individuals in outdoor aviaries (1.5 x 1.5 x 1.2 m) following housing and care conditions described by Aprile and Bertonatti (1996). Aviaries were visually isolated from one another by black synthetic fabric, ensuring that individuals performed on their own, without social motivation (Biondi et al. 2010a). All individuals were identified with a plastic ring on their tarsus and then released at their capture sites at the end of the experimental tests.

We gave the birds at least 5 days to become habituated to captivity, during which we fed them once a day from a dish containing beef and chicken meat (40–60 g approximately: 15 % of the individual weight; Arent 2007), and water was provided ad libitum. We considered the birds habituated to captivity when they were comfortable enough to feed shortly after the food presentation by the researcher. This period also allowed us to ensure that all individuals were equally habituated not only to captivity but also to the continuous presence of a researcher before the start of the experiments. All individuals were tested for object neophobia and 24 hours later, for reversal learning performance. During all tests, the subjects were video-recorded for later analysis of behavioral variables with a Sony Hdr-cx440 camcorder placed at 5 m from the aviaries (and zooming).

Object neophobia test

Twenty-four hours after the last habituation day, we presented to each bird a standard experimental protocol already used in previous studies to assess the neophobia level in this raptor species (e.g., Biondi et al. 2010a; Audet and Lefebvre. 2017; Biondi et al. 2022). This test occurred during a single session. We first offered each bird a dish containing pieces of meat (40 g in total). Immediately after the bird approached and consumed the first piece of meat (approximately 5 g), a researcher interrupted the feeding, approached the bird, and placed a novel object (Fig. 1) next to the remaining food. We constructed this object using a

mix of materials, including plastic, wood, and cardboard, all in bright colors. Additionally, we incorporated movable elements, such as small cardboard circles hanging from strings. Our decision to create such an object was driven by the fact that the chimango is a highly generalist bird, often foraging for food among garbage left by people, even in rural areas. Hence, we aimed to create a unique stimulus that would elicit a genuine novelty response during the neophobia test (Biondi et al. 2010, 2020, 2022). We gave each bird 600 seconds to return to the dish. If a bird did not eat within this time, we recorded a 600-s maximum latency. We used the difference between the latency to consume in the presence of the novel object and the consumption latency in its absence as a measure of its neophobia level.

Reversal learning test

Test apparatus and pre-training

The test apparatus comprised a 55 cm² square Plexiglas white plate (6 cm in height) with 9 wells of 5 cm diameter each, which were organized in 3 rows of 3 wells (Fig. 1). Two of the wells were covered with plastic discs of 6 cm in diameter. Each disc had a central hook from which chimangos could hold and lift to uncover the reward. This pre-training period served also to habituate the birds to feed from the Plexiglas plate, thus avoiding the effect of neophobia on the experimental apparatus during the learning tests, as well as to the continuous approaching of the researchers during each trial.

In our study, we employed a method of successive approximations to train chimangos in extracting hidden food from a specialized apparatus. Each step of the training procedure mirrored the ultimate task. Our approach involved daily sessions consisting of 5 consecutive trials lasting 3 minutes each (or until two food pieces were retrieved), with roughly 1-minute inter-trial periods. During these inter-trial periods, researchers cleaned and refilled the plate with food in different wells, distinct from the previous trial. Initially, we introduced the chimangos to the apparatus with all the wells uncovered. Two of them were filled with 1 g of meat each (hereafter: reward). Subsequently, we gradually covered the rewarded wells with white plastic discs in subsequent steps, progressing to complete coverage. Advancement to

the next step required five successful retrievals in a row within a maximum of 6 sessions. Subjects were not deprived of food, though testing occurred before their regular feeding time.

Learning tests

The learning tests consisted of a color discrimination learning phase (first discrimination phase) followed by a reversion of such color-reward association (reversion phase), and ended with a second color discrimination phase, using different color stimuli (second discrimination phase). The order in which the birds were tested each day was randomized. In the initial color discrimination phase, we trained the birds to discriminate between two stimuli: two wells were covered by a plastic disc of two colors (green and yellow) but only one color was rewarded with 1 g piece of meat. Half of the subjects of each habitat type were tested with green as a rewarded stimulus and the other half with yellow. The two covered wells were fixed across trials, though we alternated the location of the color discs between these two positions in a pseudo-random manner, thus avoiding repeating in more than two consecutive trials the location of the two discs. Despite caracara raptors having a poorly developed olfaction sense (Ferguson-Lees and Christie 2001), to prevent any possibility of chimangos guiding their choice based on the rewarded odor, we concealed a second piece of meat inside the non-rewarded well, covered by an opaque white cardboard sheet, making it not visible to the chimangos during each trial.

The learning criteria employed in this study entailed the individuals performing six consecutive correct trials, which involved lifting the rewarded disc. We gave the chimangos as much time as they needed to reach this criterium. However, we put a maximum of 20 consecutive trials per day so that, if an individual reached the criteria during the same day, they would still have enough motivation to continue searching for food in the next phase (Guido et al. 2017). We implement a 30-second intertrial period if individuals initially choose the rewarded disks. However, if this initial choice results in an error, we implement a 2-minute penalty period so that individuals must wait longer to receive the next rewarded trial.

Once the chimangos met this criterion, they entered the reversal phase on the next trial. In this phase, the procedure was the same as before except the contingency of reinforcement was reversed between the two discs. Twenty-four hours after subjects reached the learning criterium of the reversion phase, they moved to a second color discrimination phase. The goal of this second discrimination phase was to analyze whether these birds showed the ability to acquire learning rules about how the experimental set worked. The experimental procedure and learning criteria were the same as the initial discrimination, though the discs had two different colors (orange and light blue) and were presented in two different locations than in the previous phases (Fig. 1).

In each learning phase, we recorded the number of trials needed and errors made before reaching the learning criteria. Moreover, only for the reversal phase, in addition to the total quantity of errors, we analyzed the response perseveration of the individuals (e.g., Audet and Lefebvre 2017). Perseveration errors occurred when individuals continued to choose the color that was rewarded in the previous discrimination phase and was operationally defined as opening the incorrect well for three or more trials in consecutive blocks of four trials each (Ragozzino et al. 2002). Once a bird had made fewer than three errors in a block for the first time, all subsequent errors were counted as regressive errors. In this way, we were able to measure the ability to learn and maintain a new choice after initially shifting away from the previously correct choice.

Data analysis

All statistical analyses were conducted using the program R v. 4.3.1. All tests were two-tailed, and the significance level was set to $\alpha = 0.05$.

To analyze the effect of habitat type and learning phase, as well as its interaction, on the number of trials needed to reach the learning criterium we use a generalized linear mixed model (GLMM) including chimangos' identity as a random factor. We also run a GLMM to compare the number of two error types made during the reversal phase, perseverative and regressive errors, as well as the interaction of habitat type on this comparison. In these two

models, we use a Poisson error structure with a log link function. We examined the significance of the full models as compared to their corresponding null models (containing only the intercept and random effect) using a likelihood ratio test (R function 'anova' with argument test 'x2' [Schielzeth and Forstmeier 2009]). If the models were significant, we used the 'Anova' function on these GLMMs to obtain the significance of each fixed factor and its interaction. Finally, we use the lsmeans function (emmeans R package) to run the contrasts between factor levels. Model fits were assessed visually for the assumption of normality and homoscedasticity.

A GLM was implemented to compare the neophobia level of the chimangos coming from the three habitats. A gamma distribution with an inverse link function was used in this analysis. Finally, we used Spearman Rank Order Correlations to analyze the relation between neophobia and learning speed in each phase (number of errors made before criterium) and between neophobia and the number of perseverative and regressive errors registered during the reversal phase. In this study, we also chose to analyze these correlations between neophobia and learning separately within each habitat, as previous studies have found clear differences between rural and urban chimango in the correlations between various behavioral and cognitive traits (Biondi et al. 2020, Biondi et al. 2022). Due to the limited capture of males (2 urban, 1 suburban, 1 rural, totaling 4), and in alignment with prior research indicating no observed sex differences in cognition and personality traits among chimangos (e.g., Biondi et al. 2013, Biondi et al. 2020), we opted to exclude gender as a factor in our analyses.

Results

All individuals were able to reach the learning criteria in the three learning phases. The GLMM including habitat type, learning phase, and its interaction, as well as the individual ID as a random factor, was statistically different from the reduced model (Chisq = 220.5, df = 8, $p < 0.0001$). When we ran this full model, we found a significant effect of habitat type (Chisq = 10.3, df = 2, $p = 0.006$), learning phase (Chisq = 196.1, df = 2, $p < 0.001$), and its

interaction (Chisq = 15.4, df = 4, p = 0.004). During the initial discrimination and reversal phases, we found that urban birds were faster reaching the learning criterium than rural and suburban birds (Fig. 2, Table 1). Regarding the second discrimination phase, our study revealed no discernible difference among habitats in the number of trials required to achieve the learning criteria (Fig. 2, table 1).

The reversal phase represented the most difficult task for the chimangos from all three habitats analyzed, which was indicated by a higher number of errors and trials needed to reach the criterium registered during reversal compared to those needed in the first and second discrimination phases (Table 1, Fig. 2). Furthermore, we found that learning times of the chimangos from the three habitats did not change significantly between the initial and the second discrimination task (Table 1, Fig. 2).

The GLMM comparing the error types (perseverative vs. regressive) made during the reversal phase and its interaction with habitat type, with individual ID as a random factor, was significant compared to the reduced model (Chisq = 64.9, df = 5, p < 0.0001). We observed a significant difference between the two error types in all the chimangos (Chisq = 37.72, df = 1, p < 0.001). We also found a significant interaction between habitat type and error type (Chisq = 18.41, df = 2, p < 0.001). In rural chimangos, the number of regressive errors was higher than perseverative errors (Perseverative vs regressive: $\beta = -1.07$, $z = -5.32$, p < 0.001), as well as in suburban chimangos (Perseverative vs regressive: $\beta = -0.84$, $z = -4.92$, p < 0.001). However, in urban raptors, we did not find any significant difference between the number of perseverative and regressive errors (Perseverative vs regressive: $\beta = -0.03$, $z = -0.18$, p < 0.859). (Fig. 3). It was in these regressive errors that we observed the only differences among habitats, with rural and suburban individuals making more regressive errors on average than chimangos from the city (Fig.3, Table 2).

Neophobia levels differed among habitat types (GLM, urban vs. rural: $\beta = -1.48$, $t = -4.25$, p < 0.001; suburban vs. rural: $\beta = -0.85$, $t = -2.32$, p = 0.029; suburban vs. urban: $\beta = 0.63$, $t = 1.88$, p = 0.063); it appears to follow an urbanization gradient, with the highest values of

neophobia observed in rural chimangos, intermediate values in suburban individuals, and the lowest levels in city-dwelling chimangos (Fig. 4). Furthermore, upon analyzing the complete dataset, we identified a significant and positive correlation between neophobia, and the number of errors committed until meeting the learning criterion, during the reversal phase (Initial discrimination: $r = 0.21$, $p = 0.301$, $CI = -0.12-0.49$; reversal: $r = 0.59$, $p < 0.001$, $CI = 0.33-0.78$; second discrimination: $r = -0.16$, $p = 0.436$, $CI = -0.51-0.15$; Fig. 5). Neophobia was also positively correlated with regressive errors but showed no significant correlation with perseverative errors in the reversal phase (Regressive: $r = 0.63$, $p < 0.001$, $CI = 0.41-0.79$; perseverative: $r = 0.26$, $p = 0.194$, $CI = 0.04-0.59$; Fig. 5). When we analyzed these relationships separately within each habitat, we only found a positive correlation between neophobia and the total of errors made during reversal in both rural and suburban chimangos, but not in urban raptors (Table 3). Particularly, in chimangos from these two habitat types, we found a positive correlation between neophobia and the number of regressive errors (Table 3). None of the correlations we ran in urban chimangos resulted in statistical significance (Table 3).

Discussion

Urban habitats are associated with novel challenges for wildlife, which can differ substantially from those found in their natural habitats (Sol et al. 2013). This includes challenges involved in exploiting novel and/or artificial food, avoiding the risk of traffic and buildings (Sol et al. 2020), or feeding on anthropogenic items (Federspiel et al. 2017). Even for ecologically generalist animals, like the chimango, with a more relaxed phenotype-environment match, these novel urban characteristics can result in challenges (Lee and Thornton 2021). In this context, learning allows animals to flexibly adjust their behavior in response to the novel opportunities and threats found in urban environments (Griffin et al. 2017). The empirical support for this hypothesis is mixed, however (Sol et al. 2020; Lee and

Thornton 2021). Some studies have indeed found a higher learning speed during different associative and non-associative learning tests in individuals from urbanized areas compared to rural or natural habitats (i.e., Vincz et al. 2016; Federspiel et al. 2017; Kozlovsky et al. 2017), while others have found non-significant differences (i.e., Audet et al. 2016; Kang et al. 2018) (for a recent review see Sol et al. 2020; Lee and Thornton 2021). In theory, learning and plasticity should be favored in complex and variable environments (Dridi and Lehmann 2016; Snell-Rood and Steck 2019), features that are commonly considered to be present in urban habitats. However, not all organisms are confronted with or perceive the variability and complexity of their surroundings in the same way, which might lead to a difference in the benefits of learning and plasticity (Snell-Rood and Steck 2019). In the present work, all the chimangos studied succeeded during the three learning phases, though the reversal phase was the most difficult task for chimangos from all habitats studied, matching the results from previous studies on this (Guido et al. 2017) and several vertebrate species (e.g., Pagani et al. 2005; Chadman et al. 2006; Titulaer et al. 2012; Bond et al. 2007). Also, chimangos coming from the city were faster acquiring a stimulus-reward association and reverting this previously learned response when the stimulus-reward contingency changed than rural and suburban individuals, thus supporting the idea that high levels of urbanization favor faster and more flexible learning in these generalist animals. In this sense, chimangos and other birds in highly urbanized habitats must frequently cope with variations in the value of the cues used, for example, to find relevant resources. This is particularly true for those species using food sources whose variation is conditioned to human behavior (i.e., generalist species that feed on human waste or supplemented food) (Federspiel et al. 2017). Consequently, it would be an advantage to species like the chimango to be able to quickly detect this variation and adjust their behavior to changes in the signaling value of these environmental cues.

During the second discrimination phase, however, we could not find any significant difference among chimangos from the three habitats. Also, we expected to find an improvement in the performance between the first and the second color-stimulus acquisition, due to a learning set phenomenon or because chimangos confronted with extra discrimination training could quickly abandon the inefficient responses. In several individuals of each population, the trials needed to reach the criterion were lower for the second discrimination phase. However, this tendency was not strong enough to find a significant difference with the initial discrimination. In general, the experimental protocol for evaluating learning set formation includes more than 2 repetitions of the learning task (e.g., several discrimination learning tasks with their reversals) (Shettleworth 2009, Thomas 2019, Caglayan et al. 2021), a protocol that we were not able to follow here, since it would require the birds to spend more days in captivity than recommended to avoid their loss of muscle mass. Additionally, the discs that we used during the second discrimination task were not only represented by two novel colors but also, they were in two new positions on the board, which could interfere in the rule formation process. Further works focusing on how fast an individual can learn and what they are learning during the tasks should clarify the tendency observed here.

A reversal learning task requires subjects to first learn a new stimulus-reward association, but then, in the reversal phase, the task may require subjects to notice that a change has occurred, inhibit attraction to the previously rewarding stimulus, overcome aversion to the previously nonrewarding stimulus, and learn the new association (Aljadeff and Lotem 2021). By analyzing the types of errors made during the reversal phase, one can dissect two of these main processes, i.e., the ability to inhibit responding to previously rewarded stimuli when they are no longer rewarded, and the ability to learn new associations involving previously unrewarded stimuli (Ragozzino et al. 2002, Guido et al. 2017). Thus, we found that during the reversal phase, urban raptors did not differ in the types of errors they made,

whereas suburban and rural birds made more reversal errors than perseverative errors. This result suggests that in these less urbanized raptors it was more difficult to acquire a novel association than to inhibit a previously learned one (Dias et al. 1996; Clark et al. 2004), which directly influenced their ability to flexibly change their response. Also, comparing the two error types across habitats revealed a significant difference only in these reversal errors, so the slower reversal speed observed in suburban and rural chimangos compared to urban chimangos was most likely caused by the greater difficulty of forming a new color-reward association with the previously unrewarded stimulus in these less urban chimangos.

Previous studies evaluating the variation of neophobia in chimangos from contrasting habitats evidenced higher values of this personality trait in individuals coming from rural areas compared with those from more urban areas (Biondi et al. 2020; Biondi et al. 2022). The results from our work match with these previous findings, with city chimangos showing less neophobia compared with less urban individuals. In this sense, several behavioral shifts observed between urban and rural animals have been attributed to three independents but not necessarily exclusive mechanisms: local evolution by divergent natural selection, phenotypic plasticity, and differential colonization process (Sol et al. 2013). Regardless of the specific mechanisms, animals in urbanized environments tend to be adept at coping with novelty. In chimangos, this adaptability allows them to explore and learn about new resource opportunities without expending unnecessary time and energy on avoiding potential risks associated with these new settings (Ducatez et al. 2017; Samia et al. 2017). Moreover, when we related this personality trait with cognition, we observed that neophobia level correlated with learning performance only during the most difficult task, that is, during the reversal phase. This aligns with the results from studies in other bird species (e.g., Titulaer et al. 2012; Zidar et al. 2018) and is consistent with our previous work in a suburban population of this raptor species (Guido et al. 2017). In the present study, however, we obtained new information about the neophobia-reversal learning relationship. First, we detected a

correlation between these two attributes in rural and suburban chimangos, but not in urban birds. It appears that neophobia at low levels, such as those observed in city-dwelling chimangos, does not have a significant effect on cognitive flexibility. This result aligns with our previous research on the relationship between innovative problem-solving ability and neophobia in chimangos from rural and urban habitats (Biondi et al. 2022). Second, the relationship between speed in reversal learning and the level of neophobia observed in the less urban individuals aligns with the pattern observed for this species (Guido et al. 2017), though it contradicted the expected tendency according to the relation between proactive-reactive behavioral types and the speed-accuracy trade-off (Sih and Del Giudice 2012). Thus, in this work, suburban and rural individuals that showed greater neophobia were those with less cognitive flexibility, or higher difficulty in forming a new stimulus-reward association when the previously learned association is no longer rewarded (i.e., regressive errors). In previous studies in which we analyzed the relationship between neophobia and explorative behavior in the chimango (Biondi et al. 2010a; Biondi et al. 2020), we observed a similar tendency, i.e., individuals with high neophobia were slower initiating the exploration of novel stimuli in their surroundings and dedicated less time to their investigation (more superficial exploration) compared to less neophobic ones, which is also not in line with the predicted direction of the relationship between the two proactive-reactive and bold-shy behavioral axes (Verbeek et al. 1994; Sih et al. 2004). Scales and collaborators (2011) observed a group of house sparrows in which individuals displaying moderate levels of fearfulness towards a novel object exhibited more thorough exploration compared to individuals at the extremes of the shy-bold spectrum, labeling this personality type as "inquisitive." In our study, chimangos from less urban habitats seem to follow this behavioral profile, since high neophobia is related to low exploratory behavior (Biondi et al. 2020), and low ability (i.e., low speed) to respond to changes in the environmental contingencies (this work). Thus, this study serves as another example wherein analyzing the correlation between cognition and personality in distinct populations of the same species has yielded divergent findings, revealing contradictory and mixed trends regarding the intricate interplay between cognitive styles and

environmental factors (Liedtke and Fromhage 2019). We propose that a combination of factors such as increased predatory pressure, and elevated risks associated with novel objects and situations (such as trapping, poisoning, etc.) for chimangos residing in less urban environments, serves as one of the driving factors behind the observed relationship between behavioral and cognitive styles in this bird of prey. Moreover, there is an additional factor, namely social behavior, which has not been considered in this analysis but needs further attention because it could significantly influence the dynamics between personality and cognition. In this sense, chimangos are highly gregarious during feeding, resting, and breeding. Observations of intraspecific interactions along an urbanization gradient indicated that the size and frequency of group formation are more notable in suburban and rural areas compared to the city (Biondi, In prep.). So, the role of social behavior (i.e., any kind of social learning), which is considered most relevant for neophobic individuals (Smit and van Oers 2019), could compensate for their relatively lower learning speed when the situation still requires it.

In conclusion, the results from this study evidenced a general capacity of chimangos to swiftly modify learned responses in the face of changing circumstances, which can be crucial for their survival and success (Ducatez et al. 2015). We also know that it can be of great advantage for a generalist species to exhibit the propensity for risk-taking behaviors when confronted with situations that can potentially lead to the discovery of novel resources. Notwithstanding, in chimangos, this propensity seems to vary according to the potential risks of the local environmental characteristics (i.e., predation pressure, trapping or poisoning risks, etc.). This is important considering that in our study, neophobia acted as a regulator of behavioral flexibility, especially for individuals expressing relatively high levels of this personality trait (e.g., those living in less urbanized habitats). For chimangos living in cities, cognitive flexibility was not affected by neophobia and was higher than in rural and suburban raptors, which can be of greater advantage as they tend to depend more on food sources

that do not experience typical seasonal fluctuations but are influenced by human activity schemes (e.g., organic waste). In this sense, given that these food sources can undergo both prolonged stability and sudden, unpredictable changes due to human interventions, it becomes crucial for chimangos, to possess the ability to rapidly adjust their learned behavioral routines when confronted with such resource fluctuations. Thus, we suggest that the observed behavioral adaptability of chimangos, particularly those inhabiting urban habitats, highlights the significance of their capacity to flexibly modify their responses to effectively navigate and exploit the ever-changing resource dynamics within their environment.

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Figure 1: a) Experimental plate used in the reversal learning test; b) Novel object presented to individuals during the neophobia test to assess their response to a novel stimulus.

Figure 2: Graphic showing the trials (a) needed and errors made (b) until learning meeting the criterium during the initial discrimination (dis1), the second discrimination (dis2), and reversal (rev) phases by chimangos from rural (rur), suburban (sub) and urban (urb) areas. Boxplots show the median and the interquartile range from the 25th to the 75th percentiles. Whiskers indicate the 1.5 interquartile range of the data. Circles represent outliers.

Figure 3: Graphic showing the number of perseverative (p) and regressive (r) errors made by chimangos from rural (rur), suburban (sub) and urban (urb) areas during the reversal phase. Boxplots show the median and the interquartile range from the 25th to the 75th percentiles. Whiskers indicate the 1.5 interquartile range of the data. Circles represent outliers.

Figure 4: Graphic showing the neophobia level shown by chimangos from rural (rur), suburban (sub) and urban (urb) areas during the reversal phase. Boxplots show the median and the interquartile range from the 25th to the 75th percentiles. Whiskers indicate the 1.5 interquartile range of the data. Circles represent row data.

Figure 5: Graphic showing the relationships between Neophobia level and total errors made during reversal phase (A), perseverative errors (B), and regressive errors (C) also committed during reversal phase by all chimangos.

Table 1: Results from the GLMM comparing the number of trials needed before reaching the learning criterium a) between the three habitats (Urban: urb, Suburban: sub, Rural: rur) in each learning phase; b) between the reversal learning phases (Initial discrimination: Dis1; Reversal: Rev; Second discrimination: D2) in each habitat type. To get the contrasts shown we used *lsmeans* function.

a) Factor: phase	Contrasts	Estimate	SE	z value	p
Initial discrimination	sub vs rur	0.01	0.21	0.02	0.986
	urb vs rur	-0.74	0.22	-3.45	0.001
	sub vs urb	0.75	0.21	3.59	<0.001
Reversion	sub vs rur	-0.14	0.20	-0.69	0.490
	urb vs rur	-0.56	0.19	-2.93	0.003
	sub vs urb	0.42	0.19	2.28	0.022
Second discrimination	sub vs rur	0.15	0.22	0.69	0.492
	urb vs rur	-0.14	0.21	-0.68	0.496
	sub vs urb	0.29	0.20	1.46	0.145
b) Factor: habitat	Contrast	Estimate	SE	z value	p
Rural	Rev vs Dis1	0.72	0.30	2.39	0.017
	Rev vs Dis2	0.91	0.31	2.97	0.003
	Dis2 vs Dis1	-0.18	0.31	-0.59	0.555
Suburban	Rev vs Dis1	0.58	0.28	2.05	0.040
	Rev vs Dis2	0.62	0.28	2.19	0.029
	Dis2 vs Dis1	-0.04	0.29	-0.13	0.893
Urban	Rev vs Dis1	0.91	0.27	3.40	0.001
	Rev vs Dis2	0.49	0.26	1.99	0.041
	Dis2 vs Dis1	0.42	0.27	1.53	0.125

Table 2: Contrasts resulted from the GLMM analysing of the effect of habitat (Urban: urb; Suburban: sub; Rural: rur), error type (perseverative and regressive) and its interaction on the quantity of errors made during reversal phase. To get these contrasts we used *lsmeans* function (Error type | habitat).

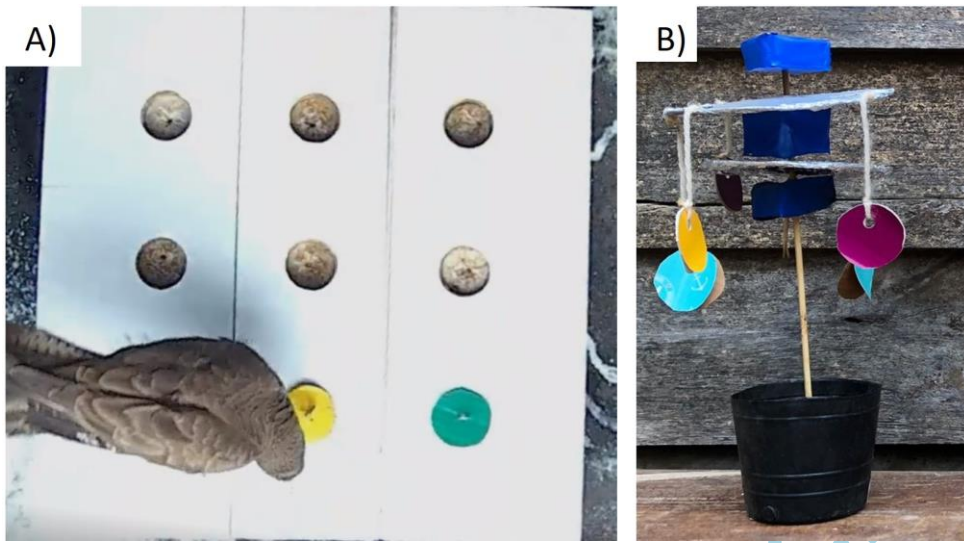
Error type	Contrast	Estimate	SE	z ratio	Pr(> z)
Perseverative	Rur vs Sub	-0.24	0.29	-0.85	0.673
	Rur vs Urb	-0.27	0.27	-0.99	0.582
	Sub vs Urb	-0.03	0.25	-0.11	0.993
Regressive	Rur vs Sub	-0.02	0.23	-0.09	0.996
	Rur vs Urb	0.76	0.23	3.26	0.003
	Sub vs Urb	0.78	0.22	3.46	0.002

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Table 3: Results from Spearman correlations between neophobia level and the three learning phases: initial and second discrimination and reversal, as well as the correlation of neophobia with the two types of errors made during the reversal phase, for chimangos from the three habitats sampled (Urban, Suburban and Rural).

Initial discrimination			
Habitat	<i>rho</i>	CI (84 %)	<i>p</i>
Urban	0.18	-0,36 - 0.67	0.623
Suburban	-0.49	-0.81 - 0.05	0.213
Rural	0.53	0.01 - 0.87	0.171
Second discrimination			
Habitat	<i>rho</i>	CI (84 %)	<i>p</i>
Urban	-0.01	-0.59 - 0.53	0.967
Suburban	-0.41	-0.98 - 0.18	0.307
Rural	0.17	-0.38 - 0.71	0.686
Reversal			
Habitat	<i>rho</i>	CI (84 %)	<i>p</i>
Urban	0.18	-0.39 - 0.69	0.602
Suburban	0.69	0.19 - 1.01	0.046
Rural	0.84	0.48 - 1.01	0.009
Perseverative errors			
Habitat	<i>rho</i>	CI (84 %)	<i>p</i>
Urban	0.45	-0.06 - 0.84	0.189
Suburban	0.38	-0.19 - 0.81	0.352
Rural	-0.06	-0.72 - 0.58	0.888
Regressive errors			
Habitat	<i>rho</i>	CI (84 %)	<i>p</i>
Urban	-0.05	-0.69 - 0.51	0.871
Suburban	0.82	0.34 - 0.98	0.012
Rural	0.77	0.29 - 1.00	0.024

Figure 1



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Figure 2

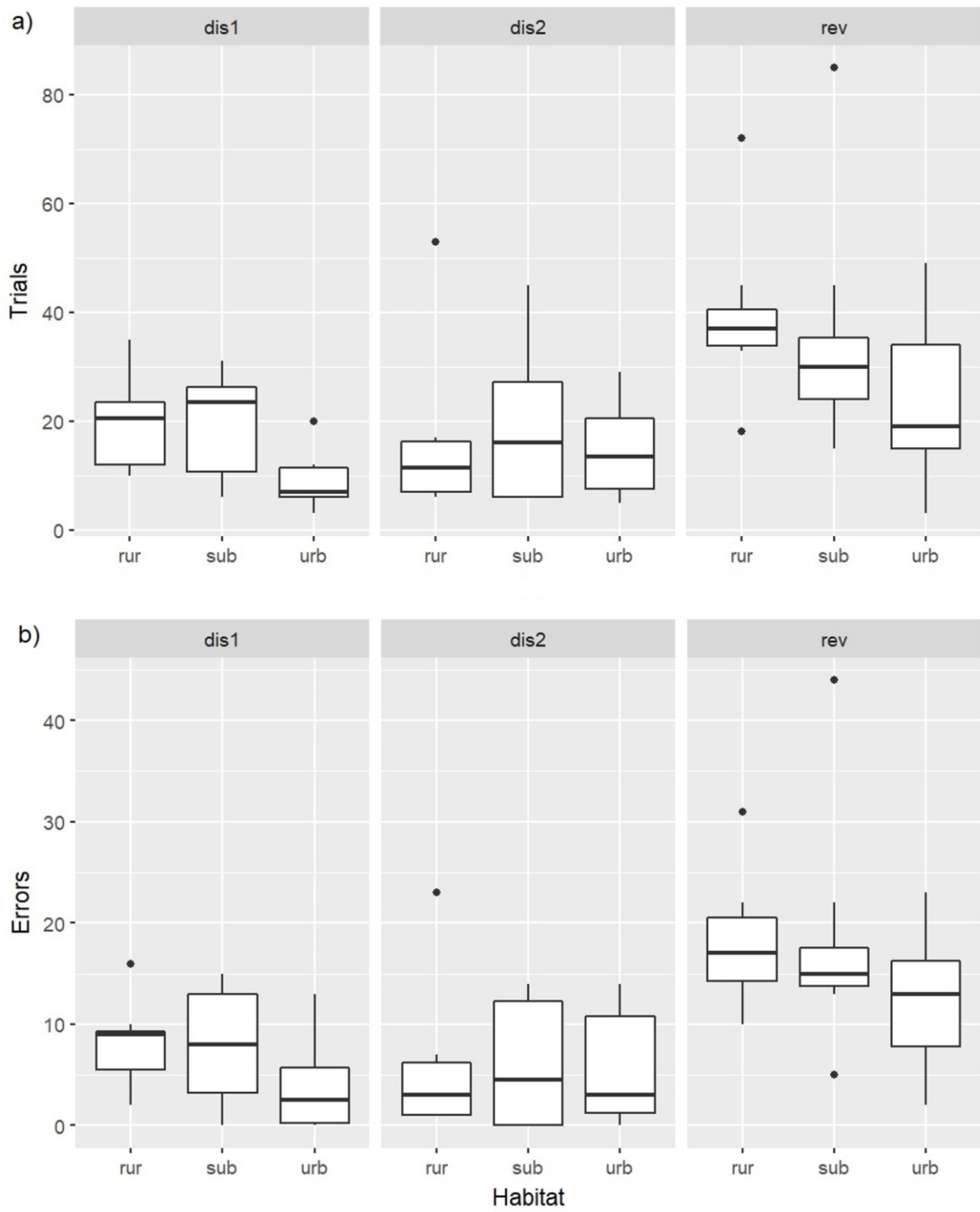
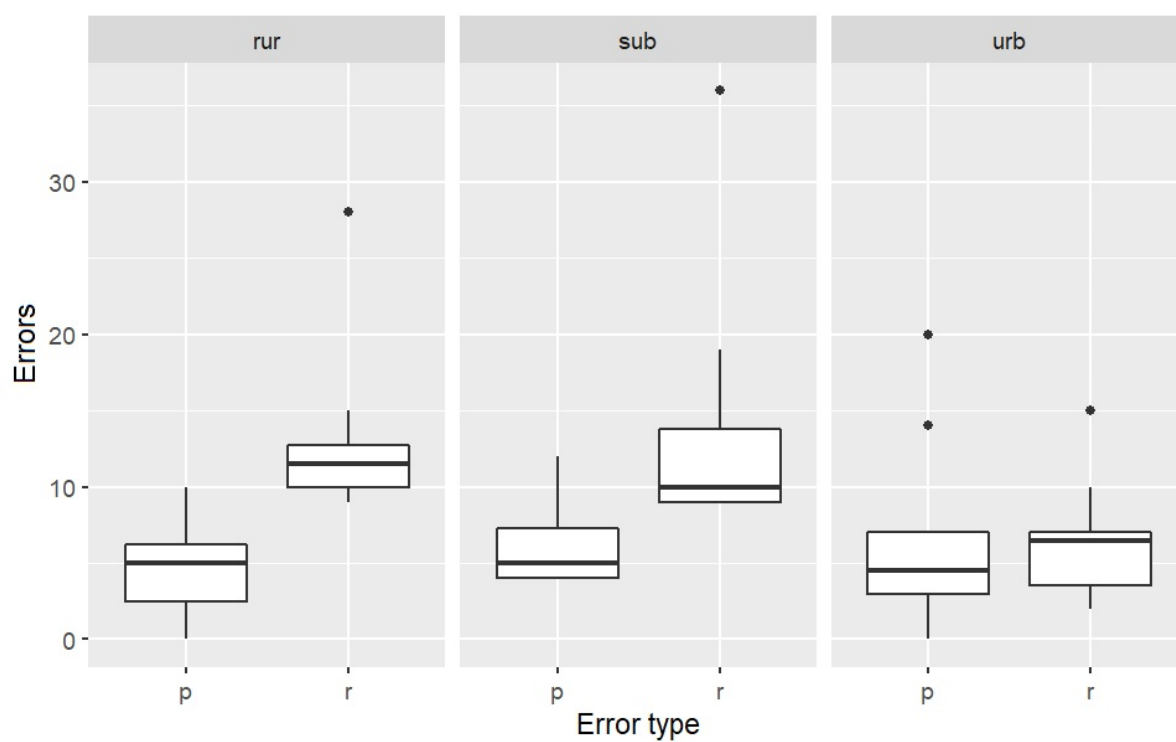
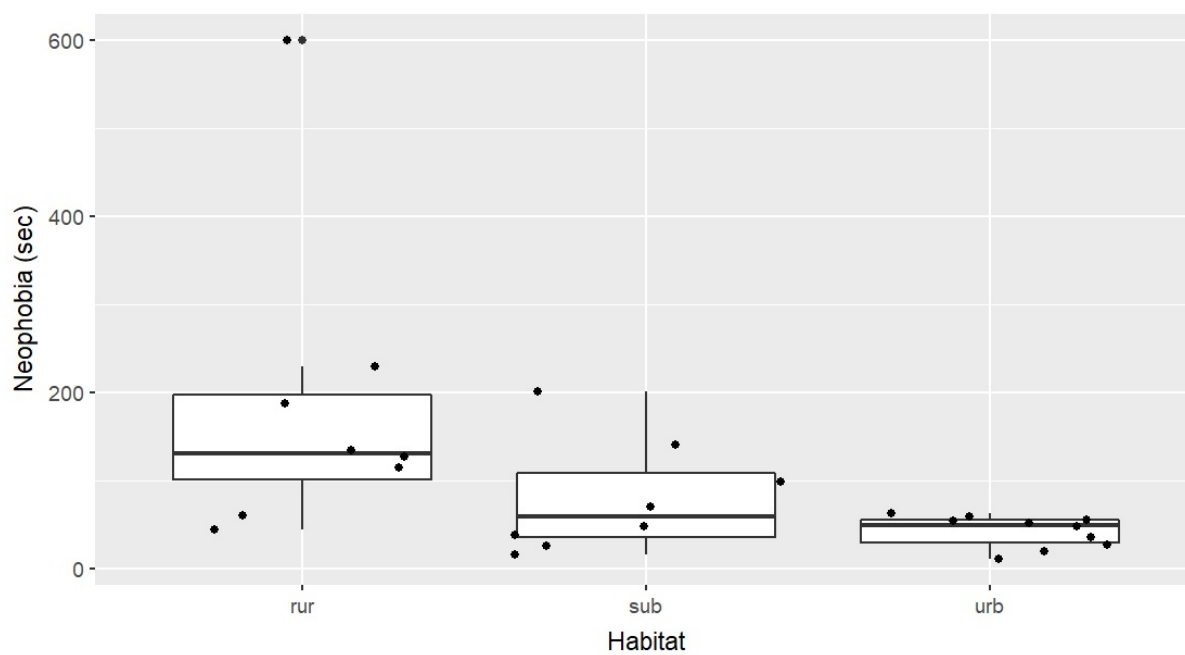


Figure 3



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Figure 4



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Figure 5

