The Behavioral Responses of the Chiguanco Thrush to Urbanization in a Neotropical City Comes From Preadapted Behavioral Traits

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Several animal species can survive within cities by changing their behavior; such changes could be the result of evolutionary adaptation, epigenetic effects, or come from preadapted traits through phenotypic plasticity or non-random dispersal. Exploring whether behavioral preadapted traits are present in non-urbanized populations could improve our understanding of the processes that allow animals to cope with urbanization. We compared the boldness, neophobia, and solving-test skills of adult individuals of the Chiguanco Thrush (*Turdus chiguanco*) between urban and extra-urban habitats in La Paz (Bolivia), a high-altitude Neotropical city. The urban Chiguanco Thrushes were bolder, less neophobic, and performed better in problem-solving tests. Extra-urban individuals varied significantly more among them in boldness and neophobia, and although a smaller proportion of individuals were able to solve the simplest problem-solving test, they did so in the same way as the urban ones. This evidence suggests that the behavioral responses of the Chiguanco Thrush to urbanization in La Paz come from preadapted traits.

Keywords: urban ecology, evolution, *Turdus*, FID, neophobia, problem-solving

INTRODUCTION

Urbanization is an intense global phenomenon that is affecting the biota in several ways, therefore understanding how the biota responds to urbanization has applications from ecological and evolutionary theory to sustainable urban planning (McDonnell and Hahs, 2015; Alberti et al., 2017a; Johnson and Munshi-South, 2017). The phenotypic changes in the behavior of animals that allow them to colonize and survive within cities are among the most described responses (Sol et al., 2013, 2020; Alberti et al., 2017b; Miranda, 2017). They may come from preadapted characters present before urbanization in non-urbanized populations, from epigenetic changes, or from evolutionary adaptation to urban conditions through natural selection (Partecke, 2014; McDonnell and Hahs, 2015).

Preadapted learning and innovation skills could allow urban colonizing populations to adjust their behaviors quickly through phenotypic plasticity (Snell-Rood, 2013; Sol et al., 2013). But also, there are several evidences of genetic divergences in behavioral responses between urban

and non-urban populations suggesting adaptive evolutionary processes after urban colonization (e.g., Partecke et al., 2006; Partecke and Gwinner, 2007; Miranda et al., 2013; Mueller et al., 2013; Costantini et al., 2014). However, genetic divergences between urban and non-urban populations can also be explained by non-random dispersal (Edelaar and Bolnick, 2012) or immigrant selection (Partecke, 2014), a sorting process of subsampling in that only non-urban individuals with the appropriate preadapted behaviors would be those who could colonize and establish in urban settings.

Therefore, it is of special interest for the better understanding of the processes that allow the animals to adjust their behaviors to the urbanization, to explore whether the behavioral patterns conductive to colonizing and surviving in cities are present in non-urbanized populations. Our objective is to compare some behaviors between urban and non-urban populations of a same species, exploring the existence of preadapted behavioral responses to urbanization in the natural variations of non-urbanized populations. We selected the Chiguanco Thrush (*Turdus chiguanco*), an Andean bird species reported as one of the most ubiquitous, frequent, and abundant inhabitants from the hardest urban core to the rural areas of La Paz (Bolivia), a high-altitude tropical city of South America (Villegas and Garitano-Zavala, 2010).

Studying species of the genus *Turdus* also allows comparing behavioral responses to urbanization with congeneric species, since this genus has a worldwide distribution, many species are in contact with people in cities and suburbs around the world (Evans et al., 2010), and there are several studies on behavioral responses to urbanization for various species. Between them, for example, tolerance to humans (e.g., Møller, 2010; Carrete and Tella, 2011; Møller and Liang, 2012; Díaz et al., 2013; Mikula et al., 2014; Møller and Tryjanowski, 2014; Piratelli et al., 2015), and neophobia and neophilia (Miranda et al., 2013; Batisteli et al., 2022).

We compared the boldness, neophobia and innovation of adult individuals that inhabit the hardest urban core of the city with individuals from extra-urban habitats. For the boldness, we measured flight initiation distance (FID), and for innovation and neophobia we worked with individuals captured temporarily who were subjected to experimental behavioral tests. We focus special attention to differences in intra-population variations. We hypothesize that urban individuals will have a shorter FID, spend less time approaching a novel object, and solve problem-solving tests in less time compared to their extra-urban counterparts. In addition, we hypothesize that the range of intra-populational variation in behavioral responses in urban individuals will be less wide and part of the intra-population variation of the extra-urban Chiguanco Thrushes, such that those responses could come from preadapted traits.

MATERIALS AND METHODS

Study Area
The city of La Paz is the administrative capital of Bolivia (**Figure 1**). The urban limits ranges from 16°26′ to 16°33′ S,

68°02′ to 68°10′ W, and 3,300 to 4,100 m. The climate is predominantly dry and cold, with a long arid season (March-October) and a short rainy season (November-February) that corresponds to the breeding season of the birds.

The city was founded as a Spanish colonial city in the mid-16th century on a pre-Hispanic agrarian settlement located in an inter-Andean valley. It experienced a very low expansion for three centuries maintaining the surroundings as agro-ecosystems. From the mid-twentieth century to the present, La Paz is a sprawling city reaching an urbanized area of 80 km² with more than 835 thousand inhabitants (United Nations, 2020). Although urban sprawl is recent, the current effect of urbanization on the erosion of native bird species richness is the most severe compared to other cities in South America (Leveau et al., 2017).

For this study, we used the definitions of urban-gradient habitat types proposed by Marzluff et al. (2001) and MacGregor-Fors (2011). We selected the two extremes of the urban gradient, the most urbanized urban core and the extra-urban environment, hereafter called "zones." Various landscape and demographic parameters could describe the level of urbanization, in our case, the quantification of the level of urbanization does not require a high level of precision or the conjunction of several parameters. We select the percentage of impervious surface as the only parameter, which includes the total surface covered by any human infrastructure (houses, buildings, roads and cemented surfaces). For the estimation of the impervious surface estimation of each of the study sites, we used free Google Earth satellite images corresponding to the period in which we obtained the behavior data, and with good contrast between the vegetation and the impervious surfaces (end of the rainy season in March 2014). We evaluated the impervious surface for each study site in areas of 1 km² (100 hectares), for this we located a central point for each site and delimited a square of 1000 × 1000 m, with a superimposed grid of 100 squares of 1 ha (**Supplementary Figures 1**, **2**). We visually estimated the proportion of impervious surface in each 1-ha square in four discrete ranges: 0–25%, 26–50%, 51–75%, and 76–100%, and for quantification, we assigned the mean value for each range (12.5, 37.5, 62.5, and 87.5, respectively). We obtained the value for each plot of 1 km² by the average of the 100 values of the plots of one-hectare.

Our sites in the urban zone had high values of impervious surface (more than 75%, see **Supplementary Table 1**), high rates of pedestrian and vehicle traffic, multi-family houses, multi-story buildings, and small and scarce public and private green areas dominated by exotic species of trees, shrubs, and herbs. Our sites in the extra-urban zone had less than 20% of impervious surface (**Supplementary Table 1**), dominated by a matrix of secondary shrub vegetation of native species, mixed with small crops and exotic trees.

Boldness Measurement
We studied the boldness of the Chiguanco Thrush using the Flight Initiation Distance (FID) method in two different events in the non-reproductive period. For the first, we selected six study sites, three for the urban zone (U1, U2, U3) and three for the extra-urban zone (E1, E2, E3) (**Figure 1**), evaluated in the mornings (06:45 to10:00), between March and June of 2012
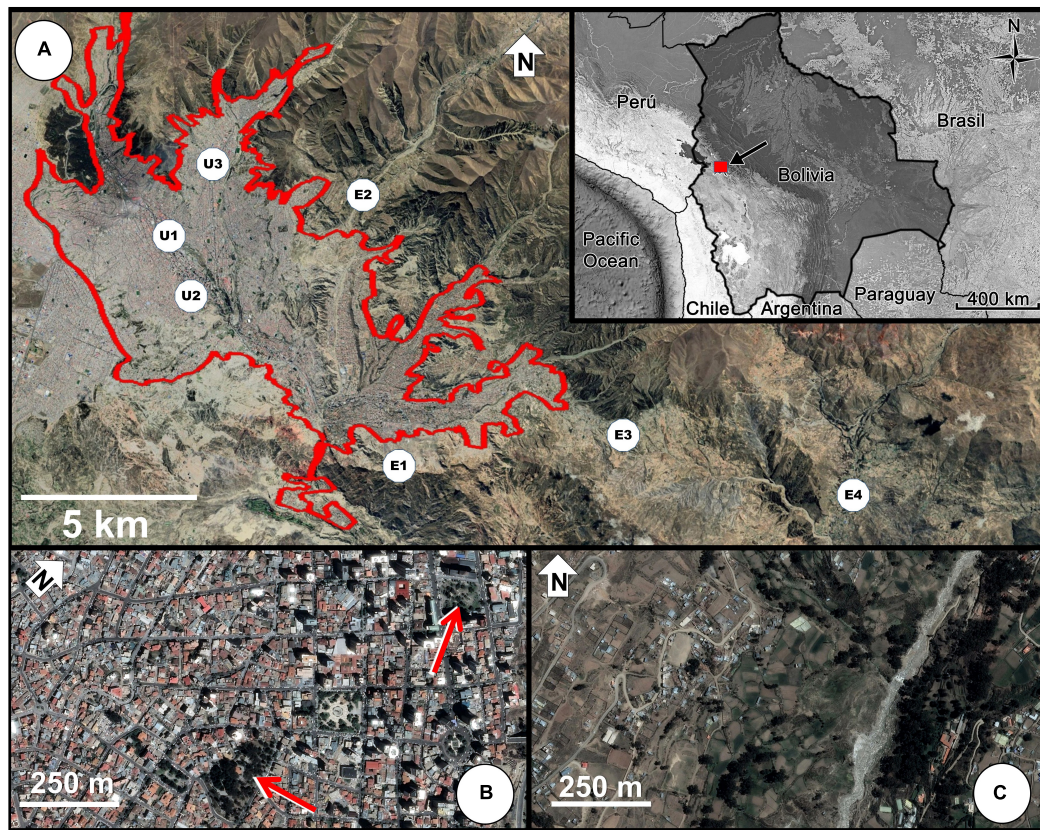
FIGURE 1 | Location of the study sites for behavioral studies of the Chiguanco Thrush in the city of La Paz (Bolivia). In **(A)** the city of La Paz with the limits of the urban fringe in November 2013 (red polygon), the upper right square details the position of the study area in the Bolivian Andes (solid red square); the position of the study sites is marked with white circles, U1 to U3 for the urban zone, and E1 to E4 for the extra-urban zone. Urban site U2 **(B)** and extra-urban site E2 **(C)** are shown in detail as examples of general landscapes. The red arrows in **(B)** mark the urban capture places for adult individuals. Satellite images from Google Earth Pro 7.3.2, 2019, (11/10/2013).
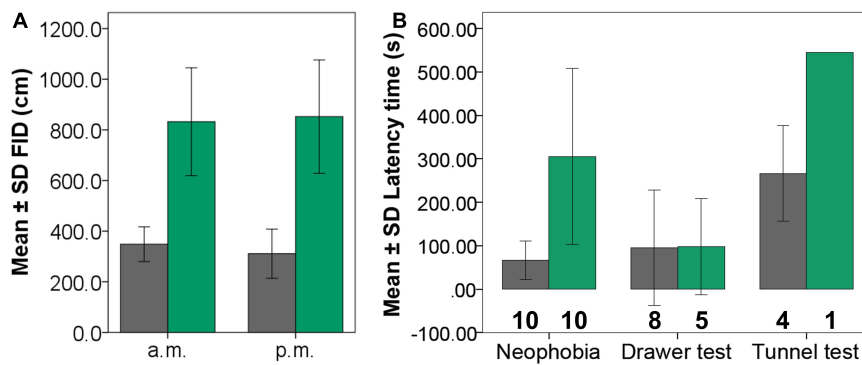

FIGURE 2 | Comparison between urban (gray bars) and extra-urban (green bars) individuals of Chiguanco Thrush in the city of Paz for flight initiation distance (FID) **(A)** and for performance in the neophobia test and two problem-solving tests (drawer test and tunnel test) **(B)**. In **(A)** the comparison between the morning (a.m.) and the afternoon (p.m.) is included, and in **(B)** the numbers below the bars show the total number of individuals who were able to solve the tests (out of a total of ten per zone).

and 2013. In order to compare the possible daily variations, we carried out a second measurement event in two urban sites (U1, U2) and two extra-urban sites (E1, E4) (**Figure 1**), between July and November 2016, in the afternoons (16:30 to

19:00). At each site, we used one or more linear-transects that summed approximately 1.5 km, traveled in one direction to avoid measuring the same individuals, and were repeated at each site three to five times with an interval of at least six weeks

between them to avoid the habituation of birds. The home range reported for the species of the genus *Turdus* is from 2 to 10 ha (Ferry et al., 1981; Calegaro-Marques and Amato, 2014; Moraes et al., 2018); in our study, the linear distance between the central points (see **Supplementary Material**), the linear transects, and the capture sites (see next section), was at least 500 m with respect to the urban fringe, so we consider that the probability of movement of individuals between urban and extra-urban zones was very low.

To avoid factors that could alter the consistency of the results such as level of alertness, previous activities, number of human observers, flock size or starting distance (Blumstein et al., 2015), we performed FID measurements considering only single adult individuals (without gender distinction), observed relaxed and not vigilant on the ground at least 30 m from the observer. Throughout the study period, which includes the dry season and the transition to the wet season, herbaceous vegetation cover at ground level is short in both urban and extra-urban zones, which does not compromise the FID measurements. One of us, wearing in all cases the same clothing, approached the bird in a straight line, without interception of vegetation, at a constant speed (0.5–1.0 m/s) taking care that initially the bird was undisturbed by the presence of the observer or other external factors, such as the presence of dogs or sudden sounds. We measured the FID in centimeters when the bird flew, from the observer's position to the exact starting point of the bird with a tape measure, we did not consider escapes by walking or jumping.

In the city of La Paz and its surroundings another species of the genus *Turdus* is present, the Great Thrush (*T. fuscater*), but is less abundant and frequent than the Chiguanco Thrush (Villegas and Garitano-Zavala, 2010). Although both species are very similar, it is possible to distinguish them because the Great Thrush is larger, with a longer tail, a darker blackish color on the back and a brighter eye-ring (Fjeldså and Krabbe, 1990; Collar, 2005). We excluded any individual observed with the combination of these morphological characters.

Neophobia and Problem-Solving Abilities Measurement

Captures and Captivity Conditions

For the experimental tests of neophobia and problem solving, we captured with mist nets a total of 20 adult individuals of Chiguanco Thrush without distinction of gender, ten in two urban places and ten in two extra-urban places. The urban places were two squares within site U2, the first extra-urban place was within site E1, and the other in site E4 (**Figure 1**, **Supplementary Figures 1,2** and **Supplementary Table 2**). We opened the mist nets in the mornings (07:00–11:00), and in the afternoons (16:00–19:00); one of us, an expert in bird handling, untangled the bird from the net without causing any damage, placed it in a fabric bag and immediately transported it to the captivity facilities on the campus of the Universidad Mayor de San Andrés. The birds were housed in individual metal mesh covered aviaries (4.60 m

length × 1.40 m width × 1.7 m height), with natural vegetation and soil.

The individuals were visually but not acoustically isolated from each other, the enclosures were surrounded by outdoors located in a natural area without human disturbance. We cleaned and disinfected the enclosures before and after the entry of a new bird. We kept each individual in captivity for only four days; on the fourth day, we released individuals in the same place where they were caught, with a temporary mark on the leg (nail polish), to avoid recapture. No individual died or showed any obvious signs of weakness or illness after captivity. We carried out the captures and tests before the birds entered the breeding season, between August and November 2016. The General Direction of Biodiversity and Protected Areas of the Bolivian Government (administrative resolution 026/09 and technical report 0214/2016) approved the captures and all the procedures.

We consider that our outdoor aviary would replicate the conditions of the Chiguanco Thrush natural habitat, so the responses would be more similar to those found in nature. However, we gave two days of adaptation before behavioral testing began as suggested by Audet et al. (2016). During these days, we fed the birds *ad libitum* with birdseed, fresh fruits (apple, grapes and oranges) and bread on a dish, there was always water available in another dish. Because non-urbanized birds may be less likely to eat from feeders (Tryjanowski et al., 2016), we pay particular attention to the feeding of the captured individuals. All the birds after two days' adaptation fed adequately with no obvious signs of stress. On the third and fourth day, we carried out the behavioral tests in the mornings starting at 09:00. The day before the behavioral tests, we starved the birds overnight from 18:00 to increase their motivation when they faced the tests. After each test, the birds were fed again *ad libitum* until the next food deprivation.

Running the Tests

We used two different problem boxes, the "drawer test" and the "tunnel test" (**Supplementary Figure 3**), similar to those used by Audet et al. (2016), made of translucent white plastic. Our drawer test (7 cm height × 7 cm width × 7 cm length) had a hook in one side; the birds had to realize that to access the food they had to pull out the drawer by pulling the hook. Our tunnel test (5 cm height × 5 cm width × 20 cm length), had an opening on one side, inside the tunnel was a wooden stick (25cm) with a hook attached to the end that was outside the tunnel, we placed the food on the other end of the stick, the one that was inside the tunnel. The birds needed to realize that the only way to reach the food was by pulling the stick with their beak using the hook.

For the evaluation of neophobia, we presented the drawer test as a novel object on the third day, in the same place where we normally provided food *ad libitum*, placing fresh bread inside as a reward (determined as a favorite food based on previous observations). We did this as recommended by Greenberg and Mettke-Hofmann (2001) to exclude neophilic responses since the willingness to feed would compete with the

phobia toward the new object. Looking behind the enclosure door through a hole, we measured the bird's latency (seconds) to approach and peck at the object from the moment the bird entered the enclosure.

After the first approach and pecking, the bird had the opportunity to access the food by pulling the drawer; this was the first problem solving test. We measured from the first peck if each bird was able to solve it or not and the latency time (seconds). On the fourth day, we presented the tunnel test as a second problem; we also measured from the first peck if each bird was able to solve it or not, and the latency time (seconds). We gave a maximum of 20 min to solve each test, after that we considered that the birds were unable to solve it. Additionally, we videotaped the tests with a GoPro HERO camera and then re-analyzed them to make sure the data was collected correctly. A video of an urban individual solving the tunnel test is included in the **Supplementary Material**.

Data Analysis

The data on FID, neophobia and problem-solving abilities were continuous in nature and normally distributed (**Supplementary Table 3**). For the evaluation of the FID, we applied a two-factor general lineal model taking as factors the zone (urban and extra-urban) and the time of day (morning and afternoon), appealing to the robustness of the test with respect to heteroscedasticity. Subsequently, we compared between urban and extra-urban zones (independently for mornings and afternoons in the case of FID), differences in deviation using Lavene's test, and differences between means using Welch's *t*-test (because we obtained significant differences in deviations for most of cases). We correlated latency times for neophobia and problem solving for individuals who were able to solve the tests using Pearson's correlation test. We performed all the statistical analysis and

graphs with IBM SPSS Statistics v 23 (IBM Corporation, 2015), considering a significance threshold value of 0.05.

RESULTS

Urban individuals of Chiguanco Thrush showed a significantly shorter distance to initiate flight escape behavior compared to their extra-urban counterparts ($F_{1,99} = 281.377$, $p < 0.001$), with no variation between mornings and afternoons ($F_{1,99} = 0.080$, $p = 0.778$) and without interaction between factors ($F_{1,99} = 0.894$, $p = 0.347$). In the extra-urban zone, there was a significantly greater interindividual variation, but only the upper part of the urban population data range is part of the extra-urban population data range, both for the measurements of the first event carried out in the mornings, and in the second one carried out in the afternoons (**Figure 2A**, **Table 1**).
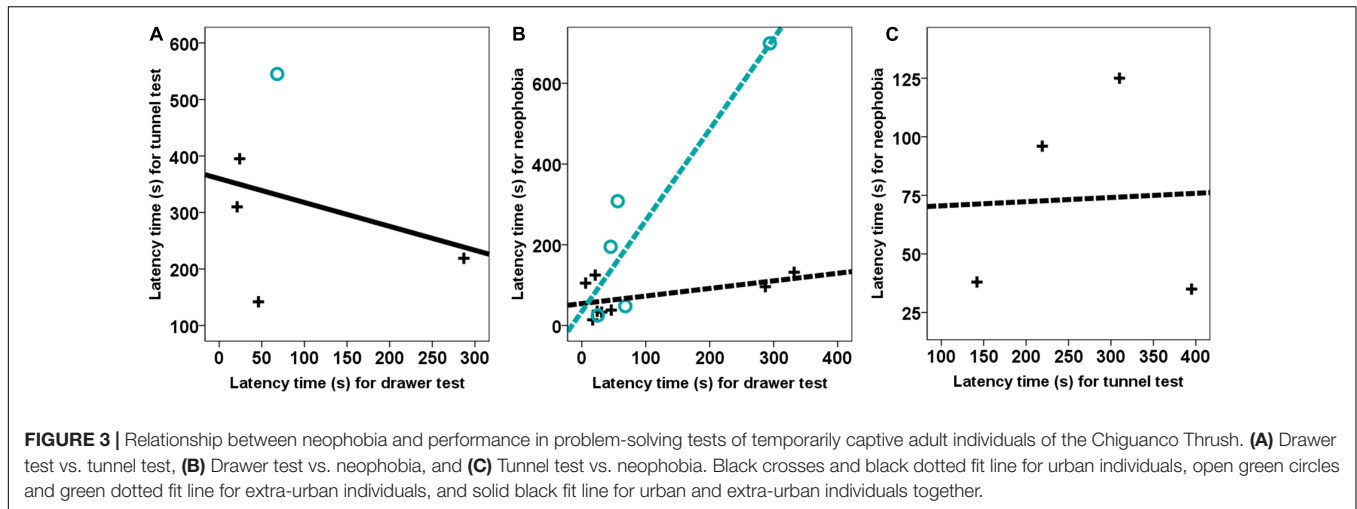
All captured urban and extra-urban individuals of Chiguanco Thrush who faced the drawer test as a novel object, came to explore and peck at it, but the urban individuals did so on average approximately 4.5 times faster than their extra-urban counterparts (**Table 1**). As reported for FID, the extra-urban individuals showed a significantly greater variation among them in neophobia (**Figure 2B**, **Table 1**), and the urban population data range falls in the lower part of the extra-urban population data range.

After scanning, not all individuals could solve the drawer test, 80% of urban individuals did and only 50% of extra-urban ones. Interestingly, the extra-urban individuals who solved the drawer test did so in the same latency time and with the same interindividual variation as their urban counterparts (**Table 1**). The tunnel test was more difficult to solve, only 40% of urban and 10% of extra-urban individuals did, the only extra-urban spent twice the average time of urban ones (**Figure 2**, **Table 1**). All

TABLE 1 | Characteristics of the behavioral performance in boldness, neophobia and two problem- solving tests carried out with individuals of Chiguanco Thrush from urban (U) and extra-urban (Eu) zones of the city of La Paz.

Task	Zone	N	FID ± SD; (min-max) (cm)	Lavene's test (*p*-value)	Welch's *t*-test (*p*-value)
Boldness (FID)					
Morning	U	38	348.61 ± 68.66; (185.8–602.2)	16.353	−9.647
	E-u	19	832.17 ± 213.02; (537.2–1345.7)	(< 0.001)	(< 0.001)
Afternoon	U	25	311.08 ± 96.99; (121.0–454.0)	7.878	−10.301
	E-u	21	852.43 ± 233.81; (340.0–1326.0)	(= 0.007)	(< 0.001)

	Zone	N	Latency time ± SD; (min-max) (s)	Lavene's test (*p*-value)	Welch's *t*-test (*p*-value)
Neophobia	U	10	66.80 ± 44.62; (14–132)	8.885	−3.642
	E-u	10	305.70 ± 202.56; (25–699)	(= 0.008)	(= 0.005)
Drawer test	U	8	95.50 ± 133.12; (6–332)	0.539	−0.029
	E-u	5	97.60 ± 110.92; (25–294)	(= 0.478)	(= 0.977)
Tunnel test	U	4	266.50 ± 109.79; (142–395)		−5.073
	E-u	1	545.00		(= 0.015)

Mean values and deviations of the flight initiation distance (FID) and latency time of neophobia, drawer-test and tunnel-test. The number of events measured for FID or individuals that responded the tests (N), as well as the values of the tests for deviations (Lavene) and means (Welch's t) are included.

FIGURE 3 | Relationship between neophobia and performance in problem-solving tests of temporarily captive adult individuals of the Chiguanco Thrush. **(A)** Drawer test vs. tunnel test, **(B)** Drawer test vs. neophobia, and **(C)** Tunnel test vs. neophobia. Black crosses and black dotted fit line for urban individuals, open green circles and green dotted fit line for extra-urban individuals, and solid black fit line for urban and extra-urban individuals together.

individuals who successfully completed the tunnel test solved the drawer test previously, but there was no correlation in latency times ($r = -0.302$, $p = 0.621$) (**Figure 3A**). Less neophobic urban individuals were not necessarily capable or faster in solving the drawer test ($r = 0.531$; $p = 0.175$) or the tunnel test ($r = 0.044$; $p = 0.956$) (**Figures 3B,C**), but the five extra-urban individuals who solved the drawer test showed a significant positive correlation between the latency time of the neophobia test and the drawer test ($r = 0.914$; $p = 0.030$) (**Figure 3B**).

DISCUSSION

Urban Chiguanco Thrush individuals responded to urbanization in La Paz with a significantly shorter FID, they were also less neophobic and more innovative, spent significantly less time approaching and exploring a novel object and more individuals solved the problem-solving tests. Although we did not assess learning skills directly, the fact that 50% of urban individuals who solved the simplest test were able to solve the most complex test the next day suggests that they probably have better learning abilities as well.

The decrease of FID was reported as an urbanization response for a broad spectrum of bird species (Evans et al., 2010; Sol et al., 2013; Miranda, 2017; Samia et al., 2017), as well as for all other species of the genus *Turdus* studied to date on all continents (Cooke, 1980; Wang et al., 2004; Møller, 2010; Carrete and Tella, 2011; Clucas and Marzluff, 2012; Díaz et al., 2013; Møller and Tryjanowski, 2014; Piratelli et al., 2015). There is also relative consistency between studies to show that urban bird populations have better capacities for innovation and problem solving (Møller, 2009; Sol et al., 2013; Griffin et al., 2017; Sayol et al., 2020). Although no other urban-gradient studies on innovation and problem-solving abilities were conducted for other species of the genus *Turdus*, innovation skills were previously reported. It is the case of novel foraging strategies (reviewed in Lefebvre et al., 1997), the use of novel nesting sites (Batisteli et al., 2022), true use of tools (reviewed in Bentley-Condit and Smith, 2010),

faster habituation to experimental situations (Walasz, 1990), and the exploration and consumption of novel foods sources and opportunities (Marples et al., 1998; Lafleur et al., 2007; Møller et al., 2014).

Unlike the behaviors mentioned above, the results on the variations of neophobia and neophilia in the urban-gradient with different species of birds are far from consistent (Griffin et al., 2017; Sol et al., 2020). Precisely, Miranda et al. (2013) reported contradictory to our results that hand-reared Eurasian Blackbirds (*Turdus merula*) from urban areas were more neophobic and seasonally less neophilic compared to individuals from rural areas. Although it was suggested that the different responses reported in the literature arose in the difficulties to disentangle between neophobic and neophilic measures (Greenberg and Mettke-Hofmann, 2001), is it most probable that neophobic responses depend on the conditions of each city, because they vary widely in predictability, complexity and predation pressures (Griffin et al., 2017).

The less neophobic extra-urban Chiguanco Thrushes were at the same time the most innovative. Batisteli et al. (2022) reported a similar situation for peri-urban females of the Pale-breasted Thrush (*Turdus leucomelas*), the most innovative capable of nesting in human buildings were also less neophobic compared to tree-nesting females. Curiously, in the urban Chiguanco Thrushes, innovation and neophilia were decoupled; Riyahi et al. (2017) described the same pattern in Great Tit (*Parus major*) and suggest that it is a sign of the process to better cope with the more variable urban habitat, an interesting subject to explore in the future.

The variance of the FID of the Chiguanco Thrush in the urban core of the city of La Paz was significantly lower, and the range of urban population data overlaps only with the lower part of the range of extra-urban population data, a situation that is also temporarily stable. Following Møller (2010), it is possible to interpret that in La Paz the mean urban FID values represent the lowest subset of escape behaviors previously present in extra-urban populations before the colonization process and that currently, urban individuals are capable of responding even more boldly. Our results on neophobia and problem-solving skills with

Chiguanco Thrush also suggest that a specific subset of previous behaviors found in the extra-urban populations colonized the city. Individuals from extra-urban sites showed more inter-individual variation in their motivation to explore novel objects, and the few individuals who were able to solve the simplest test performed it in the same average time as the urban ones.

To our knowledge, no previous study simultaneously explored such a broad spectrum of behavioral responses to urbanization in a single species. Our results with the Chiguanco Thrush in La Paz, consistently support that the behavioral responses to urbanization studied here are not the result of an adaptive process, but rather correspond to preadaptation processes or adaptedness (McDonnell and Hahs, 2015) because the observed responses to urbanization were part of the interindividual variation and the natural mechanisms of extra-urban populations.

Although we do not have evidence of genetic differences between urban and extra-urban populations of the Chiguanco Thrush, there is evidence of this in the Eurasian Blackbird in relation to migratory parameters (Partecke and Gwinner, 2007), neophilic and neophobic behaviors (Miranda et al., 2013), SERT gene polymorphism (Mueller et al., 2013), response to acute stress (Partecke et al., 2006), and blood oxidative response to chronic stress (Costantini et al., 2014). A mechanism that could reconcile the evidence of genetic differences between urban and non-urban populations with preadaptation is "Non-random dispersal" (Edelaar and Bolnick, 2012) or "Immigrant selection" (Partecke, 2014), a sorting process of subsampling of the original genetic pool, which could explain that only non-urban individuals with the appropriate preadapted behaviors would be the ones who could colonize and establish in urban environments. To asses this possibility, future studies with the Chiguanco Thrush could focus on genetic differences between urban and extra-urban populations, intra-individual and inter-individual behavioral variations, as well as the inheritance of these traits.

Studies in the Southern Hemisphere, and particularly the Neotropics where the urbanization process is still in early stages, are very scarce (Evans et al., 2010; Marzluff, 2016; Lepczyk et al., 2017; Miranda, 2017; Blumstein, 2019), offering interesting opportunities to explore the processes that allow the emergence of the behavioral responses to urbanization (e.g., Tryjanowski et al., 2020).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by General Direction of Biodiversity and Protected Areas of the Bolivian Government (administrative resolution 026/09 and technical report 0214/2016).

AUTHOR CONTRIBUTIONS

ÁG-Z, RC, and GE-H designed the study. RC obtained FID data in 2012 and 2013. GE-H obtained FID data in 2016, built the problem- solving boxes, and recorded latency times from direct observations and videotapes. ÁG-Z performed the statistical analysis. All authors participated in the writing of the manuscript and approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.830902/full#supplementary-material

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