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Quesada, J.

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Bold or shy? Examining the risk-taking behavior and neophobia of invasive and non-invasive house sparrows

J. Quesada, C. A. Chávez–Zichinelli, M. García–Arroyo, P. J. Yeh, R. Guevara, J. Izquierdo–Palma, I. MacGregor–Fors

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Abstract

Bold or shy? Examining the risk-taking behavior and neophobia of invasive and non-invasive house sparrows. Behavior provides a useful framework for understanding specialization, with animal personality aiding our understanding of the invasiveness of birds. Invasions imply dispersion into unknown areas and could require changes in behavior or spatial clustering based on personality. Reduced neophobia and increased exploring behavior could allow individuals to colonize new areas as they test and use non-familiar resources. Here, we hypothesized that house sparrow (*Passer domesticus*) individuals from invasive populations would exhibit bolder behavior than in non-invasive populations. We assessed risk taking and neophobia in male house sparrows in Barcelona (where it is considered native) and in Mexico City (where it has become widely invasive), captured in two different habitats, urban and non-urban. We assessed latency to enter an experimental cage and to explore it, and latency to feed and feeding time in the presence of a novel object. We found that sparrows from Mexico City, both from urban and non-urban areas, were quicker to enter the experimental cage than the sparrows from Barcelona. The time it took the birds to start exploring the cage gave a similar result. We found no differences between cities or habitats in the latency to feed and feeding time while exposed to a novel object. Our results partially support the view that the invader populations from Mexico City are bolder than those from Barcelona. Behavior is an important component of plasticity and its variability may have an important effect on adaptation to local situations. Future studies should disentangle the underlying mechanisms that explain the different personalities found in populations of different regions, contrasting populations of different densities, and taking different food availability scenarios into account.

Key words: Experimental, Exotic, Native, *Passer domesticus*, Personality, Urban ecology

Resumen

¿Audaz o tímido? Examinando el comportamiento de toma de riesgo y neofobia de los gorriones comunes invasivos y no invasivos. Dado que el comportamiento proporciona un marco útil para comprender la especialización, la personalidad animal puede ayudar a explicar la capacidad invasiva de las aves. La invasión implica la dispersión por áreas desconocidas y podría requerir cambios en el comportamiento o agrupaciones espaciales basadas en la personalidad. La reducción de la neofobia y el aumento del comportamiento de exploración podrían permitir a los individuos colonizar nuevas áreas a medida que prueban y utilizan recursos que no les son familiares. En este trabajo suponemos que los individuos de gorrión común (*Passer domesticus*) mostrarán un comportamiento más audaz en las poblaciones invasivas que en las poblaciones no invasivas. En este estudio evaluamos la toma de riesgo y la neofobia en machos de gorrión común de Barcelona (donde se considera nativo) y de Ciudad de México (donde es invasivo) capturados en dos hábitats diferentes (urbano y no urbano). Evaluamos la latencia para entrar en la jaula experimental y para explorarla, así como la latencia para alimentarse y el tiempo de alimentación en presencia de un objeto extraño. Encontramos que los gorriones de Ciudad de México, tanto de hábitats urbanos como no urbanos, entraron más rápido en la jaula experimental que los gorriones de Barcelona. El resultado fue similar para el tiempo que les tomó comenzar a explorar la jaula. No encontramos diferencias entre ciudades y hábitats en cuanto a la latencia para alimentarse y el tiempo



que les tomó alimentarse en presencia de un objeto extraño. Nuestros resultados apoyan parcialmente la idea de que las poblaciones invasivas de Ciudad de México son más atrevidas que las de Barcelona. El comportamiento es un componente importante de la plasticidad y su variabilidad puede tener un efecto importante en la adaptación a situaciones locales. Se deberían llevar a cabo otros estudios para desentrañar los mecanismos que explican las diferencias de personalidad que se encuentran entre poblaciones de distintos orígenes, así como comparando poblaciones con diferente densidad demográfica y teniendo en cuenta diferentes contextos de disponibilidad de alimentos.

Palabras clave: Experimental, Exótico, Nativo, *Passer domesticus*, Personalidad, Ecología urbana

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Javier Quesada, Jaume Izquierdo–Palma, Departament de Vertebrats, Museu de Ciències Naturals de Barcelona, Barcelona, Catalonia, Spain.– Carlos A. Chávez–Zichinelli, El Colegio de Puebla, Puebla, Mexico.– Michelle García–Arroyo, Ian MacGregor–Fors, Ecosystems and Environment Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Niemenkatu 73, FI–15140, Lahti, Finland.– Pamela J. Yeh, Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, USA; Santa Fe Institute, Santa Fe, NM, USA.– Roger Guevara, Red de Biología Evolutiva, Instituto de Ecología A.C., Xalapa, Veracruz, Mexico.– Jaume Izquierdo–Palma, Laboratorio de Ecología, UBIPRO, Facultad de Estudios Superiores de Iztacala, Universidad Nacional Autónoma de México, Tlanepantla de Baz, Estado de México, Mexico.

Corresponding author: Ian MacGregor–Fors. E–mail: ian.macgregor@helsinki.fi

ORCID ID: J. Quesada: 0000-0002-6010-8473; M. García–Arroyo: 0000-0002-9167-4777;
P. J. Yeh: 0000-0002-7264-9509; R. Guevara: 0000-0003-0768-3580;
J. Izquierdo–Palma: 0000-0003-2420-3825; I. MacGregor–Fors: 0000-0003-3198-7322

Introduction

The success of exotic bird species may be explained by several traits (Candolin and Wong, 2012; Weis and Sol, 2016). Classical studies have focused on population dynamics while other important aspects such as behavior have received less attention (Sol and Maspons, 2016). Recently, behavior has been identified as a key element to explain successful invasion of new areas (Evans, 2010; González-Lagos and Quesada, 2017). Studies have highlighted the role of behavior in understanding specialization in species' use of movement and space with niche specialization (Spiegel et al., 2017; Schirmer et al., 2019). Because invasion of new environments implies dispersion into unknown areas and thus implies unknown dangers, one could expect that individuals with certain behavioral traits are more prone to successfully invade new areas (Chapple et al., 2012; Wolf and Weissing, 2012; Myles-Gonzalez et al., 2015). Not surprisingly, it has been shown that these behavioral traits can be subjected to selective pressures (Canestrelli et al., 2016).

Animals have systematic and structured within-population differences regarding their behavioral tendencies. Such tendencies have been shown to be stable over time when exposed to the same situation or context, a phenomenon that has been called personality (Wolf and Weissing, 2012). Personality traits may be identified and quantified through antagonistic behaviors that are observable among the individuals in a group or population, always under the same scenario (Réale et al., 2007). The personality traits most widely studied in the past are boldness–shyness, exploration, activity, aggressiveness, and sociability (Réale et al., 2007).

When an invasion process starts, individuals need a set of capabilities, including boldness, to explore new environments or use novel resources (Chapple et al., 2012; Weis and Sol, 2016). This topic has been studied in fish and reptile species, but evidence in bird species is still scarce (Dingemans et al., 2007; Herczeg et al., 2009; Myles-Gonzalez et al., 2015; Lapiedra et al., 2017). Specifically, how personality might contribute to species invasiveness is a relatively unexplored area of research in birds. Here we hypothesized that within the same species (house sparrow *Passer domesticus*), individuals from populations in non-native areas where they are highly invasive would exhibit bolder behavior than individuals from a region where they are considered native. Since different personality traits are often correlated (Réale et al., 2007), individuals from non-native and invasive populations could also present bolder, more exploratory and less neophobic behaviors.

The house sparrow is a good biological model to test this hypothesis as it represents a well-known example of a successful invasive species worldwide (Anderson, 2006). Specifically, the North American population was introduced into northeastern USA during the mid–18th century as the result of several independent events. Afterwards, it invaded most of the USA and Mexico, presumably at the beginning of the 20th century (Wagner, 1959; Robbins, 1973; Anderson, 2006; Peña-Peniche et al., 2021). Unlike most bird species, house sparrows tend to increase their densities in urban areas when

conditions are favorable, yet their body condition, which has shown to be stable across urban land-uses, can be compromised in heavily-industrialized sites, for instance (Chávez-Zichinelli et al., 2010; Bókony et al., 2012b; Bonier, 2012). This sparrow has shown high plasticity in an extensive set of behaviors. These include the use of a wide variety of nest cavities and nest substrates (Kimball, 1997; Nhlane, 2000; Peach et al., 2008; Hoi et al., 2011), an extensive array of foraging behaviors (Guillory and Deshotels, 1981; Kötél, 1984; Flux and Thompson, 1986; Anderson, 2006), and adaptation to an omnivorous diet in urban environments, ranging from seeds to nectar, insects, and even discarded human-food leftovers (Stidolph, 1974; Gavett and Wakeley, 1986; Clergeau, 1990; Moulton and Ferris, 1991; Leveau, 2008). The species is not migrant (with the exception of a plesiomorphic population; i.e., Bactrianus; Sætre et al., 2012), and it has a small range in established populations (~5 km; Anderson, 2006). Its invasibility is thus not explained by population-based processes like migration and could perhaps be the result of an individual decision-making process based on personality. Thus, its behavioral flexibility (low levels of neophobia and high levels of exploratory behavior) could allow individuals to colonize new areas through their ability to recognize and use of non-familiar resources (Webster and Lefebvre 2001; Sol et al., 2002; Wright et al., 2010).

The house sparrow is a human commensal species. It has been hypothesized to have evolved along with human agriculture (Anderson, 2006), with only the Bactrianus population lacking association with human settlements (Sætre et al., 2012). Its relationship is so closely tied to humans across most of its distribution that local populations tend to become extinct when human settlements are abandoned (Anderson, 2006; Summers-Smith, 2010). Furthermore, this sparrow has learned to use humans as cues to find sites with large amounts of food resources in the form of human food waste (Fernández-Juricic, 2001), although this has been recorded only at intermediate levels of human presence (Fernández-Juricic et al., 2003).

Here, we studied risk taking and neophobia, assessed through boldness, in male house sparrows in two cities; one where the species is non-invasive and considered to be native (Barcelona, Spain), and another where it is invasive (Mexico City, Mexico). We acknowledge that the sparrow populations in Barcelona may have been the result of range-expansion together with that of the human species because the house sparrow originated in the Middle East (Anderson, 2006). We thus consider the Barcelona populations as well-settled (> 5,500 years; Ravinet et al., 2018) that arrived as a human commensal species through indirect human assistance (Anderson, 2006) in comparison with the more recently introduced (< 100 years) and settled populations in Mexico City (Peña-Peniche et al., 2021).

For this study, we focused on house sparrows from two habitats, urban and non-urban (mainly agricultural), from each city. We performed two experiments where we evaluated potential differences in (i) risk-taking (latency to enter the experimental

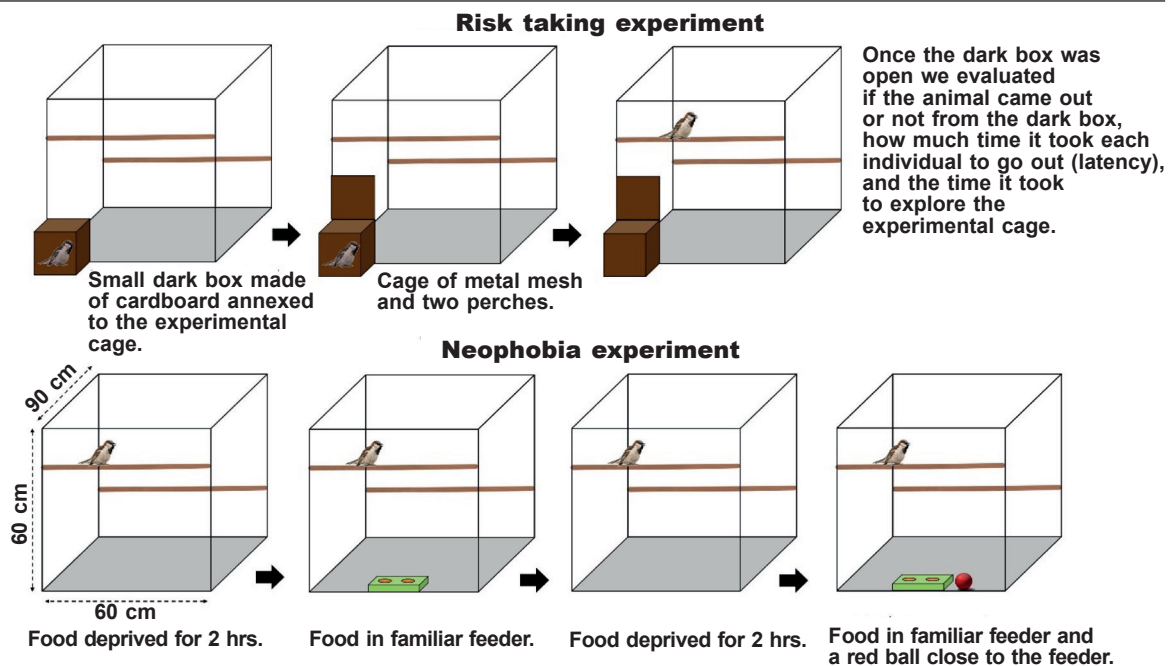


Fig. 1. Experimental design of risk-taking and neophobia.

Fig. 1. Diseño experimental de toma de riesgos y neofobia.

cage and latency to explore the experimental cage) and (ii) neophobia (latency to feed and feeding time in the presence of a novel object). Given that previous studies have shown that house sparrows can be bolder when exotic and invasive (Martin and Fitzgerald, 2005; MacGregor-Fors et al., 2010, 2019), we predicted that sparrows from Mexico City would be bolder than those from Barcelona in both experiments. Furthermore, given that urban birds have shown to be bolder than their non-urban relatives (Liker and Bókony, 2009; Bókony et al., 2012a; Riyahi et al., 2017), we expected urban individuals to be bolder than their non-urban counterparts, regardless of their native or non-native status.

Material and methods

Study area and fieldwork

We performed this study in two cities: Barcelona (Spain) and Mexico City (Mexico). Barcelona, located in the northeastern region of the Iberian Peninsula (41° 23' 30" N, 2° 10' 25" E), representing the second most populated urban center in Spain (1.6 million inhabitants), with its metropolitan area consisting of 3.2 million residents (AMB, 2021). Mexico City, located in the Valley of Mexico (19° 25' 56" N, 99° 7' 59" W), is the most populated urban center in Mexico (22 million residents; INEGI, 2020), and one of the most populated worldwide (United Nations, 2018).

We captured male adult house sparrows from September through December of 2014. We used mist nets that were open from dawn (6:00 h) to noon (12:00 h). In Mexico City, we captured 16 male house sparrows in the urban area (i.e., Ciudad Universitaria, UNAM) and 16 at the non-urban site (i.e., Milpa Alta). In Barcelona, we captured 20 male house sparrows in the urban area (Parc de la Ciutadella) and 22 at the non-urban site (Parc Agrari del Baix Llobregat, Gavà). We released all sparrows at the sites of capture after the trials were completed.

Experimental trials

Birds were housed in individual cages for at least 10 days in order to reduce the stress of captivity (Quesada et al., 2013). They were fed ad libitum with a mixture made for granivorous and insectivorous birds, complemented with vitamins (Moreno-Rueda and Soler, 2002; Bókony et al., 2012b). During the first three days we supplied an anti-parasite solution in the water so that a minimized condition was not a constraint that could mask the results of the experiment (Quesada et al., 2013).

We performed two personality tests: one of risk taking and one of neophobia. To evaluate risk-taking behavior, we put the sparrows individually inside a small dark box made of cardboard that was annexed to the experimental cage (made of metal mesh with two perches). After the observer was stationed behind the blinds, the door of the dark boxes was opened

Table 1. Generalized linear models assessing the proportion of individuals, the time that male house sparrows from Mexico City and Barcelona took to come out of the dark box and to enter the experimental box, and the time to start exploring the experimental cage.

Tabla 1. Modelos lineales generalizados que muestran la proporción de individuos, el tiempo que tardaron los gorriones machos de Ciudad de México y de Barcelona en salir de la caja oscura y entrar en la jaula experimental y el tiempo que tardaron en comenzar a explorar la jaula experimental.

	Df	Deviance Residuals	Df	Residual Deviance	P
Number of individuals that entered the experimental cage					
City	1	2.98	72	43.35	0.08
City/habitat	2	1.43	70	41.91	0.48
Latency to enter the experimental cage					
City	1	18.57	65	18.95	< 0.001
City/habitat	2	0.38	63	18.56	0.50
Latency to start exploring the cage					
City	1	0.39	64	4.02	0.01
City/habitat	2	0.03	62	4.00	0.79

from a distance by means of a string system. We then evaluated whether the animal came out or not (as several animals did not leave the box) and how long each individual took to go out (latency to enter to the cage). Once the bird came out, we measured the time it took for the individual to begin exploring the experimental cage (latency to explore the cage).

For the neophobia experiment we examined the individual behavioral response to an unknown (novel) object. After the first experiment (described above), the birds that came out from the experimental box were maintained in the experimental cage for two hours and food-deprived in order to assure that they were motivated when food was presented in the cage (Quesada et al., 2013). After the deprivation period, we introduced a feeder for 30 min, similar to the one from which they had been fed in the captivity cages so that they could quickly recognize that there was food. We then deprived the sparrows of food again for two hours and repeated the same protocol, but in this case, we introduced a red ball (novel object) close to the feeder. We recorded whether or not the birds approached the feeder, and measured the time it took them to approach and the length of time they fed (fig. 1).

Statistical analyses

For the latency to enter the experimental cage, we performed two analyses. First, as some individuals did not enter the experimental cage in the 120 min of the trial, we assessed the number of birds that came out of the box using a generalized linear model (GLM; binomial distribution), considering a nested scenario of city and habitat as independent variables (i.e., city/habitat). Second, for those individuals that did come out of the box, we performed two additional GLMs

(Gamma distribution, given the distribution of the dependent variables), one to assess the time they took to leave the box (latency to enter to the cage) and another to relate the time they took to explore the cage (i.e., latency to explore the cage).

For the latency to feed and feeding time in the presence of a novel object, we used a generalized linear mixed model (GLMM; Gamma distribution) for time to feed and a linear mixed model (LMM) for feeding time given the distribution of the data. For this test, using only the birds that came out of the box, we considered the nested scenario of city and habitat as independent variables (i.e., city/habitat), the experiment variables (foreign object, habitat) as a fixed factor, and the identity of the individual as random factor given that we used the same individual twice (with and without the novel object).

Results

The proportion of male sparrows that came out of the box to explore the experimental cages was not related to habitat, but there was a non-significant trend for differences between cities (table 1). A higher proportion of house sparrows from Mexico City left the dark box ($n = 31$; 96.7%) than those from Barcelona ($n = 35$; 85.4%). For those individuals that left the dark box, sparrows from Mexico City showed faster times than those from Barcelona, showing no interaction with habitat (Mx_{urb} : $7.20 \pm SE 0.97$ secs; Mx_{agr} : $30.06 \pm SE 4.53$ secs; Bcn_{urb} : 967.65 ± 55.45 secs; Bcn_{agr} : 862.53 ± 41.75 secs, table 1). A similar pattern occurred for the time individuals took to start exploring the experimental cage (Mx_{urb} : $32.93 \pm SE 2.25$ secs; Mx_{agr} : $53.38 \pm SE 5.32$ secs; Bcn_{urb} : 79.82 ± 6.18 secs;

Table 2. Mixed models assessing the latency to feed and feeding time in the presence of a novel object (NO) of male house sparrows that came out of the box.

Tabla 2. Modelos mixtos que muestran la relación entre la latencia para alimentarse y el tiempo que tardaron los gorriones macho que salieron de la caja en alimentarse en presencia de un objeto extraño (NO).

	χ^2	Df	P
Time to feed			
Intercept	118.23	1	< 0.001
NO	0.02	1	0.88
City	0.04	1	0.83
NO × City	0.05	1	0.82
NO × City / habitat	1.35	4	0.85
Feeding time			
Intercept	172.45	1	< 0.001
NO	1.22	1	0.26
City	0.07	1	0.79
NO × City	0.61	1	0.44
NO × City / habitat	4.10	4	0.39

Bcn_{agr} : 74.47 ± 3.10 secs, table 1). For the neophobia trials, we found no differences in city or habitat regarding the time to feed and feeding time, or for the presence–absence of the novel object (table 2).

Discussion

Invasiveness has traditionally been explained by life history traits, where some species have thrived in urban environments because they have a set of pre-existent behavioral, morphological, or physiological traits that are the consequence of their evolutionary history (Partecke, 2014). However, behavior can also be a key factor related to the invasiveness of some species that a priori do not fit as candidates to thrive in urban habitats (González-Lagos and Quesada, 2017). Indeed, behavior is an important component of plasticity, whether as a consequence of genetic expression or plasticity-based learning processes (Snell-Rood, 2013), and it can have an important impact on population dynamics (Pelletier and Garant, 2012). This variability may have a notable effect on generating new strategies to thrive in a new environment as a product of phenotypic variance, beyond what would be expected by natural selection alone. However, this variance in behavior can be associated with behavioral syndromes (i.e., the way in which the personality traits are combined)

that result in different personalities (Drent et al., 2003; Sih et al., 2004).

In this study we tested the hypothesis that personality is associated with the invasiveness of the house sparrow from Mexico City when compared to those from Barcelona by analyzing two basic personality traits (risk taking and neophobia) in a bold–to–shy spectrum (Canestrelli et al., 2016). Our results partially support the view that invasive populations from Mexico City are bolder than those from Barcelona. The populations from Mexico City, urban and non–urban, took more risk in exploring new areas than those from Barcelona. However, none of the studied populations showed differences regarding fear to new objects. This is not surprising given the plasticity of a species that is so well adapted to urban and agricultural scenarios where they tend to be exposed to novel objects on a regular basis.

Personality may play an important role in spatial ecology (Spiegel et al., 2017) given that in certain ecological contexts a selective regime may favor some particular personalities (Myles–Gonzalez et al., 2015). When the invasive process starts, the individuals need a set of capabilities for exploration and boldness to facilitate resource use, to cope with disturbances, and to enhance communication in new and unknown environments. Bolder personalities are thus candidates to thrive in areas outside their original range of distribution, given that explorers and bolder individuals tend to disperse farther (Canestrelli et al., 2016). Our results suggest that this variation in personality may be used to adapt to local situations. The house sparrows from the invasive population (Mexico) appeared to be bolder than the Barcelona population, at least in terms of risk taking (i.e., the time it took them to leave the experimental box and explore the cage).

Interestingly, dispersion ability, a key factor for invasiveness, is mediated by decision–taking processes that imply assuming the risk to explore (or not) new habitats, given that exploration implies the assumption of some cost in term of fitness (Chaine and Clobert, 2012; Gonzalez–Lagos and Quesada, 2017). Our results agree with several experimental studies that have been carried out in similar approaches of risk–taking. For instance, several studies have shown how birds of the same species express different risk–taking behaviors (i.e., flight initiation distance) when they invade a new environment (Scales et al., 2011; Tryjanowski et al., 2016; Ducatez et al., 2017). One common example is the comparison of non–typical urban species invading urban areas. In most cases, urban populations take more risks than populations from the non–urban areas. This finding applies to the house sparrows; as Seress et al. (2011) showed. They observed that young urban house sparrows were bolder than non–urban birds of any age group in Hungary, where the species is considered to be native, although older urban birds were less bold. In addition, studies have demonstrated that more exploratory birds disperse larger distances than less exploratory birds according to theoretical (Spiegel et al., 2017) and empirical approaches (Dingemanse et al., 2003; Korsten et al., 2013; Botero–Delgadillo

et al., 2020; Jablonszky et al., 2020), supporting the hypothesis that personality may play a significant role in the success of bird invasions.

MacGregor–Fors et al. (2019) recently showed that house sparrows are bolder—in terms of alert distances—where it is exotic, invasive, and abundant, suggesting a density–dependent process in urban areas. Given that house sparrow densities in Mexico City are greater than those in Barcelona (MacGregor–Fors et al., 2017), our results could also be influenced by a density–dependent process. Thus, broadening the number of populations from a wider spectrum of the sparrow's distribution could help to confirm whether our result is generalizable or not.

We recorded no differences for the neophobia experiment. Many studies have shown that birds adapted to new situations (i.e., urban birds) are less neophobic than those that remain in known conditions (Møller, 2008). A study carried out in house sparrows in Hungary in different intensities of urbanization did not find significant differences between personality traits (e.g., neophobia, predatory risk–taking, level of activity) or behavioral syndromes (Bókonyi et al., 2012a). In contrast, Cohen and Dor (2018) found that the southernmost range–expanding population of house sparrows in Israel had the fewest neophobic individuals, although this could be because the authors compared two different geographic populations (i.e., *Biblicus*, *Indicus*). Martin and Fitzgerald (2005) also compared neophobia in two invasive populations, one in Panama and the other in New Jersey (USA), at different stages of establishment. They found that the newer population (in Panama) approached and consumed novel food resources at faster rates. Altogether, these results suggest that differences in neophobia between invasive populations are detected when invasion is in its initial stages, but not when invasion has reached a temporal threshold as observed in the population of house sparrows in Mexico.

Regarding the selective mechanisms behind changes in the personality of invasive and non–invasive populations of one same species, we consider that a crucial question is: are these differences between populations a consequence of the selection factors of individuals with particular personalities (bold or shy personalities) or is this a consequence of learning processes, such as habituation or behavioral syndrome change? The time since colonization of both populations could shed some light on this question. Sparrows from Barcelona presumably range–expanded to the European Mediterranean region during the expansion of human agriculture, while they were intentionally translocated to North America (Anderson, 2006). Hence, the populations in Barcelona, generally considered native as they have been part of the avifauna of the region for millennia, appear to be the consequence of bold individuals, or groups that range–expanded to the European Mediterranean Basin as human commensals. The case of recent introductions in North America represents random samples of individuals (in terms of behavioral personality) that arrived to North America and underwent further selection processes to become bolder phenotypes, and then expanded

their distribution down to Panama, becoming established in central Mexico less than 100 years ago (Peña–Peniche et al., 2021). Although differences in the selection pressure that occurred in both cases could explain differences in current behaviors, we consider that time since settling as viable populations is a key factor to explain this difference. The time of settlement has been important to explain differences in other personality traits related to boldness (Martin and Fitzgerald, 2005; but see Cohen and Dor, 2018). Regardless of the mechanism behind the differences in risk–taking in invasive and non–invasive populations, our results reinforce recent studies that have highlighted the role of personality in understanding specialization in movement and use of space in avian species with niche specialization (Spiegel et al., 2017; Schirmer et al., 2019) and potential invasions (Sol and Maspons, 2016).

Another question yet to be answered is the role of group size in the interactions of populations (Liker and Bókonyi, 2009; Ducatez et al., 2017; MacGregor–Fors et al., 2019). In our experiments, we tested individuals separately; yet large groups may cope more effectively with unfamiliar situations through faster innovations of new solutions by some group members with favorable traits (Bókonyi et al., 2012a). This supposition agrees with a recent paper that emphasized the role of house sparrow density to explain the risk–taking of flight initiation distance (MacGregor–Fors et al., 2019). Thus we consider that future studies should explore the mechanisms underlying the different personalities found in invasive and non–invasive populations by contrasting populations of different densities, considering a wider spectrum of populations across the species' distribution, and taking into account different food availability scenarios.

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