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Original Article

Habituation to human disturbance is faster in urban than rural house sparrows

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Animals living in urbanized habitats often show reduced fear responses to humans compared with their rural conspecifics. This is usually assumed to be the result of habituation, but may also be explained by differential colonization or local adaptation. To contrast these hypotheses, we studied the fear responses of urban and rural house sparrows (*Passer domesticus*) to humans, by measuring flight initiation distances (FID) in free-living flocks and observing the hiding behavior of wild-caught individuals in response to repeated human disturbance in captivity. We found that although sparrows had shorter FID at urban compared with rural sites, sparrows from both habitat types were equally likely to hide when they were disturbed for the first time in the new captive situation. Both urban and rural sparrows decreased their time spent hiding over the course of 8 trials, but the decrease was faster in urban sparrows. This difference was primarily due to a decrease in the sparrows' immediate response (reactivity) to the disturbance, whereas the speed of recovery after disturbance increased similarly over trials in urban and rural birds. These results demonstrate that urban individuals habituate faster to human disturbance than their rural conspecifics. Our findings suggest that the reduced fear of urban animals is the result of behavioral plasticity, whereas we found no evidence for their higher intrinsic boldness as predicted by differential colonization and local adaptation.

Key words: fear responses to humans, flight initiation distance, habituation, house sparrow, urbanization.

INTRODUCTION

In urban habitats, animals are frequently exposed to the presence and various actions of humans. Due to their evolutionary background, wild animals often perceive humans as potential predators and respond to their presence with flight (Blumstein 2014). However, antipredator behaviors are costly because they take time and energy from other behaviors such as feeding and parental care that are important components of fitness (Lima 1998). Because people rarely pose real threat to urban wildlife such as birds (Clucas and Marzluff 2012), animals that live in urban habitats may benefit from decreasing their fear responses to humans. This idea is well supported by studies showing that animals in habitats with frequent human disturbance flee from humans at shorter distances (Metcalf et al. 2000; Møller 2008; McCleery 2009; Rodriguez-Prieto et al. 2009; Carrete and Tella 2011; Engelhardt and Weladji 2011;

Keeley and Bechard 2011; Scales et al. 2011; Chapman et al. 2012; Clucas and Marzluff 2012; van Dongen et al. 2015; Cavalli et al. 2016).

Usually, the decreased fear response by urban animals is assumed to be a result of habituation to humans (Metcalf et al. 2000; McCleery 2009; Rodriguez-Prieto et al. 2009; Chapman et al. 2012). Habituation is defined as a reduced behavioral response to a repeated, neutral stimulus (Whittaker and Knight 1998; Blumstein 2014); therefore, it is a form of behavioral plasticity and implies a learning process. However, 2 alternative mechanisms may also account for the reduced fearfulness of urban animals. First, if fearfulness varies greatly between but little within individuals, the less fearful individuals are expected to move to and settle in cities more often than the more fearful individuals; this theory is referred to as differential colonization hypothesis (Møller 2010), or sometimes habitat selection hypothesis (Carrete and Tella 2010) or differential recruitment hypothesis (Blumstein 2014). For example, a study of flight initiation distances (FID; a frequently used proxy for wild animals' fear from humans) found that species with the highest

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interindividual variance in FID at their original, rural habitats are the most successful in colonizing cities (Carrete and Tella 2011). Second, bold urban phenotypes may also result from selection in urban habitats that allows individuals with low intrinsic fearfulness to realize high fitness; this theory is known as local adaptation hypothesis (Møller 2008). In contrast to habituation, which involves behavioral plasticity, both the differential colonization and local adaptation hypotheses assume that fearfulness from humans varies consistently among individuals, a core concept of animal personality (Dingemanse et al. 2010). Such individual consistency in tolerance of human proximity has been found in several species (Carrete and Tella 2010; Evans et al. 2010; Scales et al. 2011; Végvári et al. 2011). Some studies suggest genetic differences underlying fear behaviors between urban and rural populations, which supports the differential colonization and/or local adaptation hypotheses (Mueller et al. 2013; van Dongen et al. 2015).

The above 3 mechanisms are nonexclusive, and there may also be selection for individuals with higher behavioral plasticity and better habituation ability, instead of a certain behavioral type

(Dingemanse et al. 2010). Very few studies have specifically investigated whether individuals of wild animals differ in their rate of habituation to human disturbance, but they all found significant interindividual variation (Runyan and Blumstein 2004; Ellenberg et al. 2009; Carrete and Tella 2010). Such variation may be the basis of selection for better habituation abilities in urban habitats, but whether urban individuals indeed habituate faster to human disturbance than their rural conspecifics has not yet been demonstrated. Furthermore, habituation may come about by decreasing reactivity (i.e., the initial response to a specific disturbance event) or by speeding up recovery (i.e., the time during which the response persists after the disturbance has ended) over the course of repeated disturbance events (Figure 1); these 2 aspects of coping with disturbance do not necessarily covary (Linden et al. 1997).

In this study, our aim was to examine whether fearfulness from humans and the rate of habituation to human disturbance differ between urban and rural individuals in the house sparrow (*Passer domesticus*) that is a common species in anthropogenic habitats (Anderson 2006). After quantifying the sparrows' fear response to

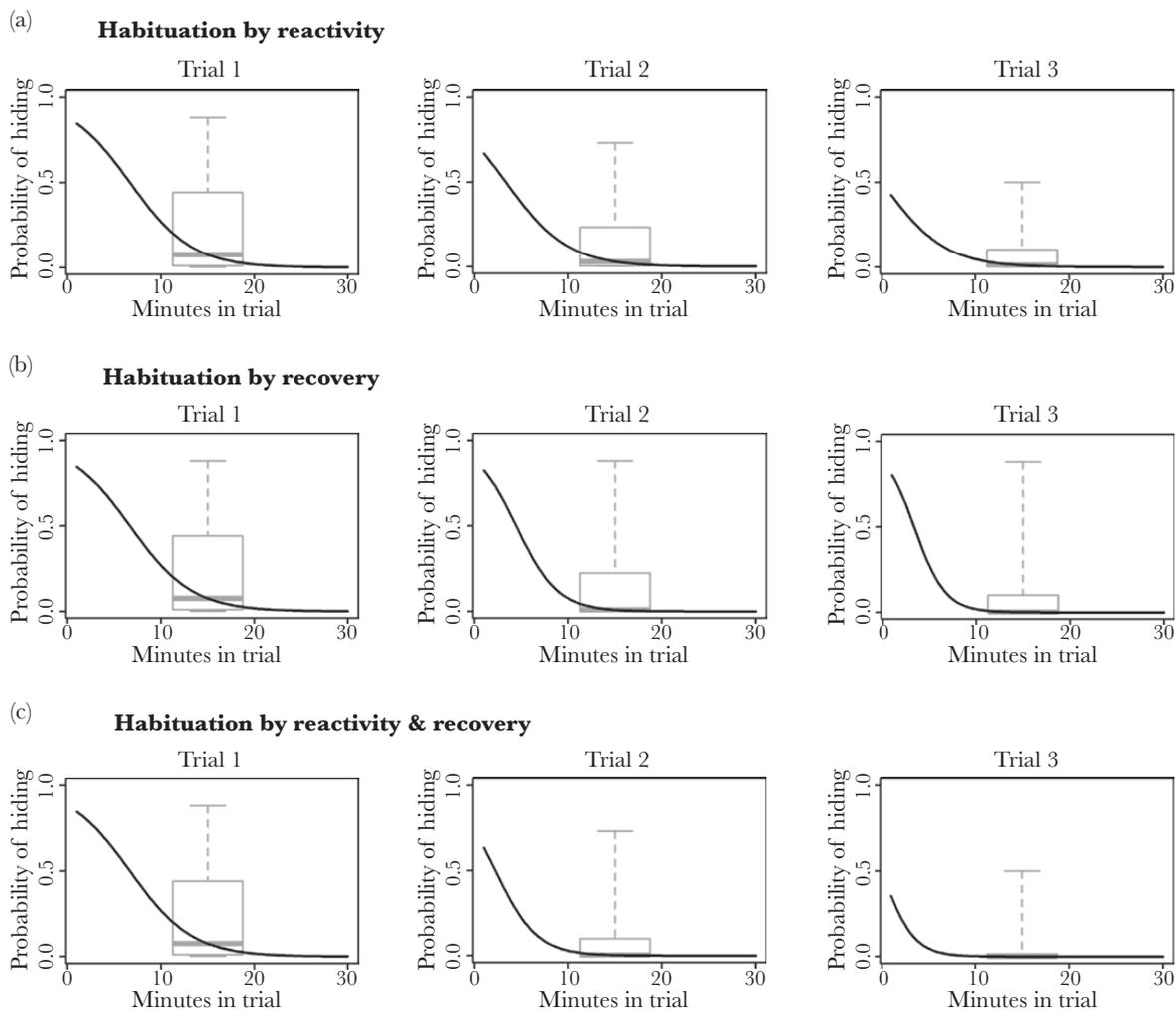


Figure 1

Illustration of 3 hypothetical cases of habituation over 3 disturbance trials. For each trial, the boxplot shows the among-individual variation in the proportion of records in which the bird was hiding (“hiding frequency”) during the trial. The black curves show the average response of the birds in each trial (among-individual variation would be represented by several different curves on the same graph; these are omitted for clarity). For each curve, the intercept expresses the probability at which the birds were hiding at the beginning of the trial (“reactivity”), whereas the slope expresses the speed of decrease in the probability of hiding within the trial (“recovery”). We refer to hiding behavior in the first trial as “intrinsic boldness” and to the across-trial change of behavior as “habituation.” The latter can occur by decreasing (a) reactivity, (b) recovery, or (c) both across the trials; all resulting in reduced hiding frequency.

humans in the field, we placed both urban and rural birds in an unfamiliar situation and observed their habituation to repeated human disturbance by looking at the changes in their reactivity, recovery, and overall fearfulness (which encompasses both reactivity and recovery). We predicted that urban birds should show faster habituation (i.e., faster change across trials in their reactivity and/or recovery, Figure 1) if this type of behavioral plasticity is mainly responsible for the reduced fearfulness of urban individuals. In contrast, if differential colonization or local adaptation for bolder behavior play a major role, then urban birds are expected to show less fear from humans (i.e., lower reactivity and/or faster recovery following the disturbance events) than rural birds overall, even at the first encounter with the novel disturbance.

METHODS

Study sites

We studied house sparrows in 15 differently urbanized habitats in Hungary (Supplementary Table S1). We focused on sites from the 2 extremes of the urbanization gradient occupied by the species, that is, remote farms or edges of small villages and densely built inner city centers. To verify our choice of sites, we quantified the urbanization of the capture sites based on 4 habitat features: building density, vegetation cover, presence of roads, and human population density. First, we scored the digital aerial photograph of each site using the *UrbanizationScore* image-analysis software (Seress et al. 2014) based on the methods of Líker et al. (2008). A 1-km² area around the site of capture was divided into 10 × 10 cells, and each cell was assigned a score for vegetation cover (0: absent, 1: <50%, 2: >50%), density of buildings (0: absent, 1: <50%, 2: >50%), and presence of paved roads (0: absent, 1: present). From these cell scores, we calculated 5 habitat characteristics for each site (mean vegetation density, mean building density, number of cells with roads, and number of cells with >50% vegetation and buildings, respectively). Then, following Bókony et al. (2010), we collected data on the density of residential human population for each settlement from the Hungarian Central Statistical Office; for the 2 sites in Budapest, we used the data for the respective districts of the capital. For 3 farm sites, we ascertained population density by either asking the residents (family farm at Szentgál) or consulting the web site of the farms (Üllő-Dóramajor and Babat). Then, we included the above 5 habitat characteristics and log₁₀-transformed human population density in a Principal component analysis, which resulted in a single axis with >1 eigenvalue that explained 93.4% of total variance, and correlated strongly negatively with mean vegetation density ($r = -0.98$) and number of cells with high vegetation density ($r = -0.99$), and strongly positively with mean building density ($r = 0.99$), number of cells with high building density ($r = 0.97$), number of cells with roads ($r = 0.99$), and human population density ($r = 0.88$). We refer to the scores along this axis as “urbanization score.” Based on these scores, we divided the capture sites into 2 groups (henceforth “urbanization category”): “urban” (positive urbanization score) and “rural” (negative urbanization score); these categories matched our initial, subjective categorization of urban and rural sites in all cases (see Supplementary Table S1 for further details). This categorization also clearly separated sites with high and low human population density (182–4315.5 residents/km² for urban sites, 3.6–64.9 residents/km² for rural sites). We used the urbanization categories in the analyses because this approach involves fewer statistical assumptions (i.e., it is not known if human population density and/or landscape composition adequately

reflect the fine-scale between-site variation in those conditions that are most relevant for house sparrows’ fearfulness). Nevertheless, we repeated all analyses by replacing urbanization category with urbanization score, and our results were qualitatively unchanged (available from the authors on request).

FID in the field

FID were measured by a single observer (S.P.) at each of the 15 sites between December 2011 and March 2012. Whenever the observer spotted either a single house sparrow or a flock while searching for them along random transects, he walked toward them in a straight line at a constant speed with constant pace length (0.75 m), noting his starting distance (mean ± standard deviation [SD] = 11.72 ± 8.17 m), as it may significantly affect the FID (Blumstein 2003; Rodriguez-Prieto et al. 2009; Atwell et al. 2012). Because sparrows are gregarious and seldom feed alone, we included both flocks and single individuals. The distances at which the first and the last individual of a flock fled, respectively, were recorded in all cases (because in 46% of the flocks, the birds did not take off at the same time) by counting the number of paces. We also recorded the following variables that may influence the birds’ perception of threat: time of day, flock size (the estimated number of sparrows in the flock), the presence or absence of other bird species in the flock, and flock position (i.e., whether the birds were on the ground or perching on a bush or a fence). We included off-ground FID because sparrows were more often found perching instead of on the ground (88.4% in our FID records); note however that the proportion of ground and off-ground FID was very similar at our urban and rural sites (89.2% and 87.4%; χ^2 test: $\chi^2_1 = 0.10$, $P = 0.748$). FID is often measured off-ground in species that spend a considerable amount of time perching (Metcalf et al. 2000; Blumstein 2003; Valcarcel and Fernández-Juricic 2009; Scales et al. 2011), and perching birds do not always have a shorter FID than those on the ground (Blumstein et al. 2004). Because the birds were unmarked, different flocks measured at the same site may contain the same individuals; to reduce the potential for pseudoreplication, the observer walked for at least 15 min between consecutive measures. Note that wintering flocks of sparrows normally have home ranges of several hundred meters (Líker et al. 2009). A moderate degree of pseudoreplication did not qualitatively affect the results of analyses examining the relationship between FID and other variables in another study (Runyan and Blumstein 2004).

Observations where the flock got startled from another source of disturbance (such as another human, a dog or a car) instead of the observer were excluded from the analysis. At each site, we took 8–16 (mean ± SD = 10.9 ± 2.4) measures over the course of up to 9 days (mean ± SD = 3.9 ± 2.0 days), with up to 10 measures per day (mean ± SD = 2.8 ± 1.8), resulting in FID records from 156 flocks’ first and last individuals and 7 single birds that were treated as first individuals (Supplementary Table S1).

Habituation in captivity

We captured house sparrows with mist nets (Ecotone, Gdynia, Poland) between January and March 2012 from the same sites where we measured FID. Over 8 weeks, we captured 10–14 birds each week from 2 sites of the same urbanization category, alternating urban and rural sites weekly. At capture, we measured each bird’s tarsus length (±0.1 mm) and ringed them with an individually numbered metal ring. Then, the birds were transported to Veszprém and housed indoors, where they participated in a series of studies as part of a more general project (Bókony et al. 2014;

Papp et al. 2015; Preiszner et al. 2015; Vincze et al. 2015). Methods shared by the present study and the previously published ones are repeated here to make all relevant details readily available; however, note that each study had different a priori research questions and separate analyses.

Each weekly set of birds (henceforth “cohort”) was captured over 2 days (days 1–2) and spent the following 3 days in individual cages while participating in a behavioral experiment (Papp et al. 2015), during which they were exposed to little disturbance, that is, briefly approached by a human (different from the experimenter in the current study) 2 times per day, in contrast with the 12 daily approaches in the habituation regime (see below). On day 5 in the afternoon, we weighed the birds (± 0.1 g) and moved them into a new room used for the present study where they were allowed to acclimate without disturbance for 2 days (days 6–7). Then, the birds were observed in 8 trials involving human disturbance over 2 days (days 8–9) as described below. After the present study, the birds participated in further experiments, and then, they were released as detailed elsewhere (Preiszner et al. 2015; Vincze et al. 2015).

The birds were housed individually in $42 \times 30 \times 35$ cm cages, each containing 2 perches and a vertical plastic sheet hanging from the top of the cage as shelter. All cages were in 1 room, positioned on 3 shelves and visually separated from each other with opaque plastic boards. About 2.5 m away from the cages, there was a curtain behind which the experimenter could hide. During the study, water was provided ad libitum, amended by multivitamin droplets. Food (millet seeds) was constantly available to 26 birds in a transparent plastic dish (7.5-cm diameter, 3.5-cm high), whereas 71 birds were fasted for an hour before each trial as part of another study (Preiszner et al. 2015). The latter birds received their food in a white plastic box ($8.5 \times 8.5 \times 2.5$ cm) with a lid on the top which had to be opened up to access the seeds; this feeding method was unfamiliar for all 71 birds in the first trial, but 73% of them (52 birds) learned to use it by the end of the 8th trial (Papp et al. 2015). Between-individual variation in food availability and within-individual variation in feeder-opening success were taken into account as confounding variables in the statistical analyses (see below).

On days 8–9, the birds were observed in 4 trials each day as follows. Each trial started after a 60-min resting period (during which the 71 birds with the openable feeder were fasted), consisted of a circa 5-min disturbance phase and a 30-min observation period, and was followed by a 15-min feeding period. At the end of the resting period, the experimenter (E.V.) approached the cages in randomized order and disturbed each bird by placing an openable feeder in the cage of the fasted birds and replacing the feeder dish of the nonfasted birds with an identical dish. Then, the experimenter hid behind the curtain and observed the birds through a 1-way window by scanning the birds and recording their behavior every 3 min as 1 or more of the following categories: hiding behind the shelter, resting nonhidden in the cage, hopping, flapping, perching on or next to the feeder, attempting to feed (i.e., manipulating the feeder with the beak), feeding, drinking, preening, and engaging in stereotypical movements (this occurred in only 3% of records). Thereby, 10 records of each bird’s behavior were collected in each trial. After 30 min of observation, the experimenter fixed the feeder lids in open position in all of the cages, and then left the birds undisturbed for 15 min so that all of them could feed. Finally, following this feeding period, the openable feeders were removed from the cages while the dishes were replaced in randomized order, as above, and the next 60-min resting period started. The 4 trials were distributed evenly within each day between 8:00 and 16:00; lights

were on from 7:00 till 17:00, allowing the birds to feed freely for 1 h each before the first fasting and after the last trial. Although this general protocol was continued on days 10–12, here we analyzed the data from days 8–9 only because some aspects of the protocol varied among birds in the last 3 days as part of another study (Preiszner et al. 2015).

Data analysis

To see if FID varied consistently among study sites, we calculated the site-specific repeatability of FID following Lessells and Boag (1987). The effects of urbanization and other factors on FID were analyzed with a linear mixed-effects model that allowed the response variable to have different variance in urban and rural habitats. We included the following explanatory variables in the initial model: urbanization category, starting distance, flock size, flock position (ground or perching), date (expressed as the number of days since 1 December 2011), time of day (expressed as the number of minutes since 6:00 AM), the presence of other species, flight order (i.e., if the FID was of the first or the last individual in the flock), and the interaction between urbanization category and flight order (to test whether the habitat effect depends on the type of measurement, i.e., first- or last-fleeing flock members). We included study site and flock ID as nested random factors (i.e., the first and last individuals of the same flock were treated as repeated measures).

In the captive birds, to quantify fearfulness and its decrease over time (i.e., habituation), we focused on hiding behavior because sparrows often responded to the approach of the experimenter by hiding behind the shelter in their cages. Although hiding behavior in captivity is not the exact equivalent of FID in the wild, both forms of behavior are related to fear from humans and therefore may be influenced by similar underlying mechanisms. For each bird in each trial, we estimated the proportion of time spent in shelter (henceforth “hiding frequency”) as the proportion of records (out of all 10 records per trial) when the bird was observed hiding behind the shelter. Because sometimes both hiding and one or more other behaviors were observed in the same record (e.g., if the bird was coming out from behind the shelter and started to engage in another activity, then both behaviors were recorded), hiding frequency was corrected for the total number of behaviors observed in the 10 records (e.g., if a bird was seen hiding in 1 out of 10 records, then it got a hiding frequency score of 0.1 if it was observed fully hiding within the record, but 0.05 if it was coming out of the shelter and engaging in another behavior).

First, we compared urban and rural birds’ fearfulness in the first trial as a proxy for intrinsic boldness. We used hiding frequency as response variable in a generalized linear mixed-effects model with quasi-binomial error distribution and logit link function, and cohort ID as random factor to control for the nonindependence of birds tested together (i.e., in the same week). We included the following explanatory variables in the initial model: urbanization category, vertical and horizontal position of the cage, sex, food treatment (fasted or not), and body condition calculated as the scaled mass index proposed by Peig and Green (2009) using the equation: $\text{body mass} \times (19/\text{tarsus length})^{1.71}$ (Bókony, Seress, et al. 2012).

Then, we investigated the rate of habituation in 2 sets of analyses. The first analysis used the same modeling framework as the analysis of hiding frequency in the first trial, but here we used the data of all 8 trials, and added trial number and its interaction with urbanization as explanatory variables. To be able to express the rate of habituation as the decrease of hiding time over consecutive

trials, we used trial number as a continuous variable (thus assuming a linear change over time). The initial model included cohort ID and bird ID as nested random factors, and the same potentially confounding variables as listed above. In addition, we controlled for variation in access to food, that is, whether or not in each trial the individual could access the food in its feeder (“yes” for nonfasted birds and for those fasted birds that had learnt to open the feeder in previous trials, “no” for fasted birds that had not yet used the feeder before), by including it as an additional term in our models.

To examine the change of hiding behavior in more detail, we conducted a second set of analyses in which we considered changes not only across trials but also within trials, to separately investigate the 2 aspects of habituation: reactivity, that is, the immediate response to disturbance at the beginning of a trial, and recovery, that is, the rate of calming down after the disturbance within a trial (Figure 1). To do so, we modeled the temporal change in the occurrence of hiding over the 30-min trial for each bird. First, for each of the 8 trials, we built a generalized linear mixed-effects model with quasi-binomial error and random intercepts and random slopes for each individual, with the occurrence of hiding (i.e., whether hiding behavior occurred or not in each scan sample, either by itself or together with other behaviors) as the response variable and time of sampling (i.e., order of the 3-min records) within trial as the explanatory variable. From these models we extracted, for each individual in each trial, the intercept and slope estimates. Then, we used the intercepts as an estimate of the birds’ reactivity to human disturbance (i.e., the probability of hiding at the start of the trial). The slopes, on the other hand, provide an estimate of the speed by which the fear response decreased within the trial, that is, the rate of recovery. However, the slopes are not independent from the intercepts because the individuals that were less fearful at the start had less steep slopes (Spearman rank correlation: $r_s = -0.73$, $P < 0.001$). Therefore, we estimated the recovery rates by calculating the residuals of a standardized major axis regression that included the slope estimates of the previous model as response variable and the intercept estimates as the explanatory variable. Thus, these residuals express how fast the individual recovered relative to how strongly it reacted initially; larger negative values mean faster recovery rate. Then, we analyzed how reactivity and recovery rate changed across the trials in urban and rural birds

in 2 respective linear mixed-effect models that included trial number as a continuous variable, and its interaction with urbanization category. Both initial models included vertical and horizontal position of the cage, sex, food treatment, access to food, and body condition as potentially confounding variables and cohort ID and bird ID as nested random factors.

In each analysis, we removed nonsignificant terms stepwise until only $P < 0.05$ terms remained, except that we never omitted urbanization because this was the effect we aimed to test specifically. In the analyses of habituation rates, we always retained trial number because it was necessary for quantifying the rates of habituation. In the analysis of FID, we retained the interaction between flight order and urbanization, and used linear contrasts with correction for false discovery rate (Benjamini et al. 2001) to test if habitat difference is present in both the first- and last-fleeing individuals of the flocks. We also present our full initial models, with both significant and nonsignificant terms, in Supplementary Table S2. All analyses were run in R 3.0.2, using the “nlme” and “multcomp” packages.

RESULTS

FID in the field

FID varied consistently among the study sites, as shown by its high repeatability ($R = 0.795$, $F_{14,304} = 41.6$, $P < 0.001$). On average, FID was about 4 m longer at rural sites than at urban sites (Table 1, Figure 2). The difference between urban and rural FID was slightly larger in the first-fleeing individuals than in the last-fleeing individuals (Table 1, Figure 2), but post hoc tests revealed that the habitat difference was highly significant among the first and last birds alike (linear contrasts, urban–rural difference in the first-fleeing birds: -4.44 ± 0.92 m, in the last-fleeing birds: -3.75 ± 0.92 m, both $P < 0.001$). Birds on the ground and in larger flocks fled from greater distances than perching birds and those in smaller flocks; FID also increased with starting distance and decreased with calendar date (Table 1).

Habituation in captivity

In the first trial, hiding frequency did not differ significantly between urban and rural birds (Table 2, Figure 3). Over the 8

Table 1
FID in wild house sparrows in relation to habitat type, flight order (first or last fleeing), and other variables

	$b \pm SE$	df	t	P
Intercept (urban, last fleeing, ground) ^a	1.155 ± 1.234	154	0.936	0.358
Habitat (rural vs. urban) ^b	3.750 ± 0.918	13	4.086	0.001
Flight order (first vs. last) ^b	0.680 ± 0.138	154	4.917	<0.001
Habitat \times flight order ^c	0.691 ± 0.367	154	1.884	0.062
Starting distance ^d	0.433 ± 0.044	144	9.807	<0.001
Flock size ^d	0.099 ± 0.031	144	3.183	0.002
Position (perching vs. ground) ^b	-2.894 ± 0.760	144	-3.809	<0.001
Date ^d	-0.032 ± 0.013	144	-2.436	0.016

Parameter estimates (b) of the final linear mixed-effects model are shown. df, degrees of freedom; SE, standard error.

^aIn this and the following tables, the parameter estimate (b) for the intercept shows the average value of the dependent variable in the reference category, which is defined in brackets following “Intercept.”

^bFor categorical variables (fixed factors), b for each category shows the difference (in the average value of the dependent variable) of that category from the intercept (e.g., perching flocks had 2.89 m shorter FID than flocks on the ground). If the factor is in interaction with another factor, the parameter estimate refers to the difference between the categories of this factor, when the other factor is at the intercept value (e.g., rural FID were 3.75 m longer than urban FID in the case of last-fleeing flock members).

^cInteraction terms express how the difference between 2 categories of 1 factor differs between 2 categories of another factor (e.g., the difference between first- and last-fleeing flock members, which is 0.68 m in urban birds, is by 0.691 m larger in rural birds; similarly, the difference between urban and rural birds is by 0.691 m larger in the first-fleeing birds than in last-fleeing birds).

^dFor numeric predictors, b shows the slope of the regression line (e.g., if the starting distance increases by 1 m, FID increases by 0.433 m on average).

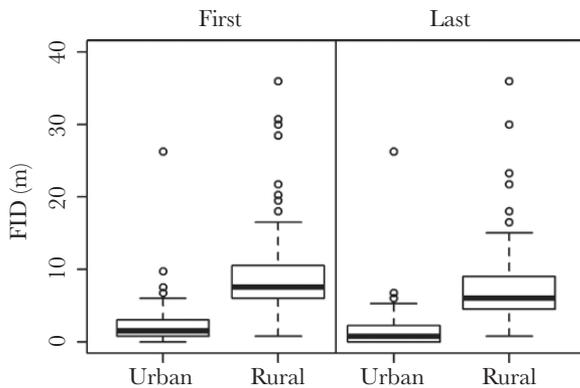


Figure 2

FID of the first- and last-fleeing members of house sparrow flocks at urban and rural sites. Boxplots show the median and the upper and lower quartiles, with the whiskers representing data within the $1.5 \times$ interquartile range.

Table 2

Hiding frequency in captive house sparrows in the first trial of the experiment in relation to habitat type

	$b \pm SE$	df	t	P
Intercept (urban, top shelf)	-2.486 ± 0.600	87	-4.141	<0.001
Habitat (rural vs. urban)	0.965 ± 0.777	6	1.242	0.261
Position (middle shelf vs. top shelf)	-0.025 ± 0.337	87	-0.074	0.942
Position (bottom shelf vs. top shelf)	0.696 ± 0.325	87	2.145	0.035

Parameter estimates (b) of the final generalized linear mixed-effect are shown; higher values mean that the bird spent more time hiding during the trial. The error distribution of the model was quasi-binomial; the interpretation of parameter estimates (as described in the footnotes of Table 1) applies to the logit-transformed values of the dependent variable. df, degrees of freedom; SE, standard error.

trials, hiding frequency decreased significantly, and the rate of this decrease was faster in urban than rural birds (Table 3, Figure 3).

Within trials, the occurrence of hiding was highest at the start of the trial and then decreased over the 30 min (Figure 4). Reactivity decreased across trials, meaning that the birds were less likely to hide at the start of later trials than at the start of earlier trials (Table 4, Figure 4). In the very first trial, the proportion of individuals that were hiding in the first 3 min did not differ significantly between urban (55.1%) and rural birds (70.8%; χ^2 test: $\chi^2_1 = 1.94$, $P = 0.164$; see also Table 4). However, we found a significant interaction between habitat type and trial number, that is, the decrease in reactivity across trials was less steep in rural birds (Table 4, Figure 4). Recovery rate also showed a trend of getting faster (i.e., larger negative slope values) after the first trial (Table 5, Figure 4); however, there was no significant interaction between habitat type and trial number ($P = 0.916$), that is, urban and rural birds showed similar change in recovery rate across trials. Furthermore, the difference between urban and rural birds' recovery rates was not significant (Table 5).

Birds on the bottom shelf spent more time hiding and had less steep recovery rates than those on the top and middle shelves (Tables 2 and 4); vertical cage position had no significant effect on reactivity. Food treatment and access to food had significant effects on reactivity: Birds that were fasted before the test, and those that knew how to open the feeder, were less likely to hide in the beginning of the trial than either nonfasted birds or those that were

unable to access their food (Table 4). Horizontal cage position, sex, and body condition did not have significant effect on any response variable and were omitted from the final models.

DISCUSSION

Our results show that, despite urban house sparrows showing much shorter FID in the field than rural conspecifics, birds of both habitat types responded similarly to human disturbance in captivity when they encountered the test situation for the first time. Although individuals from both habitat types showed habituation during repeated exposure to the same disturbance, urban individuals habituated significantly faster than rural individuals, and they did so by decreasing their immediate response (reactivity) to the disturbance. Although the few days of pretest captivity may have influenced the behavior of birds, this is not likely to explain the similarity of the birds' initial response because faster habituation by urban individuals should intensify, not reduce, any pre-existing fear differences. Taken together, these results support the hypothesis that habituation to humans can play a significant role in the tameness of urban animals.

The shorter FID we found in urban house sparrow populations compared with rural ones is in line with what several other studies found, that is, individuals from habitats with higher human disturbance flee from closer distances than those from less disturbed habitats in most species (Blumstein 2014), including house sparrows (Clucas and Marzluff 2012). Both the first- and last-fleeing members of the house sparrow flocks in our study showed a significant difference between urban and rural habitats. Other studies that measured the FID of a random individual of the flock (Carrete and Tella 2011) or the closest individual to the observer (Rodríguez-Prieto et al. 2009) also found shorter FID in habitats with more human disturbance, which suggests that this effect is robust regardless of the method of selecting focal individuals. However, when birds from the same populations in which we found FID differences were subjected to a novel kind of human disturbance in captivity, we found no strong difference between urban and rural birds in their initial fear responses. The same lack of difference was also reported by other studies that compared the behavior of urban and rural birds under standardized captive conditions; for example, in the "control tests" of personality assays where the birds were exposed to brief human disturbance, neither house sparrows (Bókony, Kulcsár, et al. 2012) nor blackbirds (*Turdus merula*) (Miranda et al. 2013) showed a habitat difference in their risk-taking behavior. These findings do not support that urban individuals have increased intrinsic boldness in general or to humans in specific.

The similar intrinsic boldness of urban and rural birds implies that differential colonization and local adaptation may play a less important role in the lower fearfulness of urban individuals. Even if increased boldness to humans has a selective advantage in urban habitats, fear from humans might be part of a behavioral syndrome, in which different behavioral traits are linked by a common underlying (e.g., genetic) cause (Sih et al. 2004). For example, some urban birds seem to be more fearful of novel situations (Echeverría and Vassallo 2008; Bókony, Kulcsár, et al. 2012; Miranda et al. 2013) and of predators (Seress et al. 2011) than their rural conspecifics, both of which suggest selection for a more fearful behavioral type in cities. Thus, if fear from humans is proximally linked with fear from predators and/or novelty, this might constrain their adaptation to opposing selection pressures (Geffroy et al. 2015). Although behavioral syndromes may break down in urban habitats (Scales

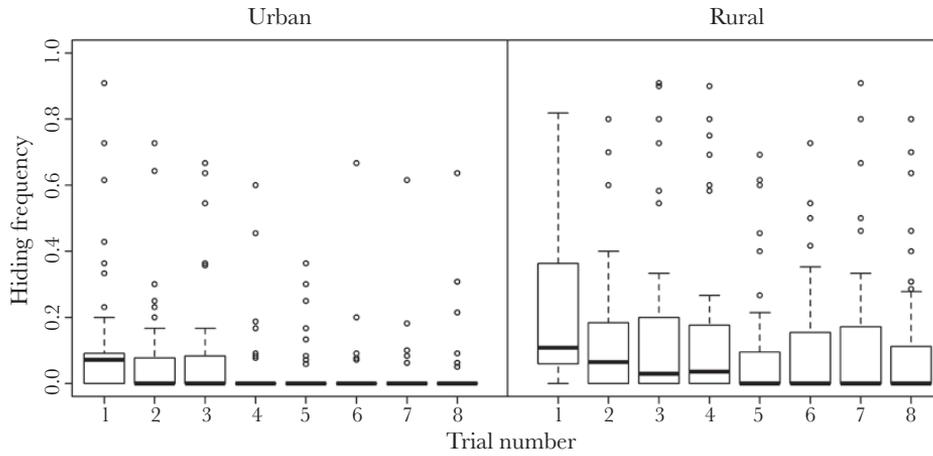


Figure 3 Hiding frequency of urban and rural birds in the 8 trials (see Figure 2 for the interpretation of boxplots).

Table 3 Change in hiding frequency in captive house sparrows over 8 trials in relation to habitat type

	$b \pm SE$	df	t	P
Intercept (urban, top shelf, first trial)	-2.605 ± 0.489	677	-5.327	<0.001
Trial number	-0.333 ± 0.040	677	-8.270	<0.001
Habitat (rural vs. urban)	0.488 ± 0.608	6	0.804	0.452
Trial number \times habitat	0.171 ± 0.048	677	3.569	<0.001
Position (middle shelf vs. top shelf)	-0.169 ± 0.376	87	-0.451	0.653
Position (bottom shelf vs. top shelf)	1.044 ± 0.383	87	2.724	0.008

Parameter estimates (b) of the final generalized linear mixed-effect are shown; higher values mean that the bird spent more time hiding during the trial. The error distribution of the model was quasi-binomial; the interpretation of parameter estimates (as described in the footnotes of Table 1) applies to the logit-transformed values of the dependent variable. df, degrees of freedom; SE, standard error.

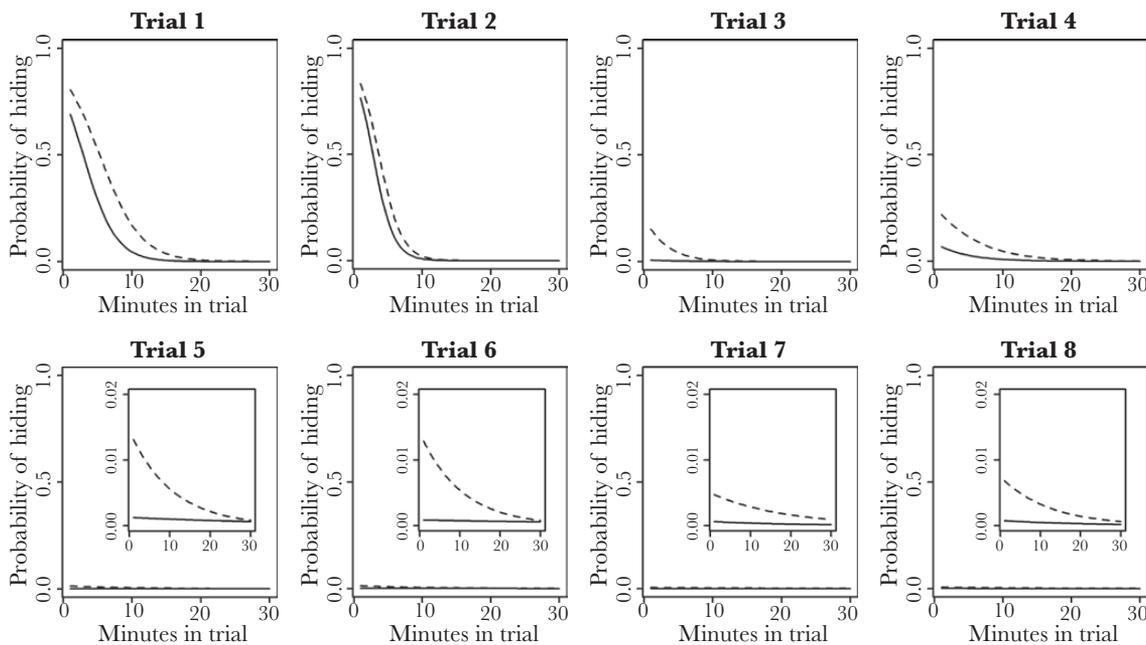


Figure 4 Changes in the probability of hiding over 30min after human disturbance for urban (solid line) and rural (dashed line) birds within each trial, as predicted from the models in Tables 4 and 5. The inset plots for trials 5–8 show the data with the range of the y axis set to 0–0.02, to facilitate within-trial comparison of urban and rural birds.

et al. 2011), we found little evidence for this in house sparrows (Bókony, Kulcsár, et al. 2012). Because failing to show antipredatory response when it is needed is costly (Rödl et al. 2007), urban

populations may be selected to maintain a general fear response but fine-tune it within each individual’s life through behavioral plasticity. In line with this idea, some studies found that animals

Table 4**Change in reactivity to human disturbance in captive house sparrows (i.e., the occurrence of hiding at the start of the trial) over 8 trials in relation to habitat type**

	$b \pm SE$	df	t	P
Intercept (urban, not fasted, can access food, first trial)	2.458 \pm 0.825	676	2.980	0.003
Trial number	-1.314 \pm 0.080	676	-16.452	<0.001
Habitat (rural vs. urban)	0.825 \pm 1.044	6	0.791	0.459
Trial number \times habitat	0.249 \pm 0.107	676	2.325	0.020
Treatment group (fasted vs. not fasted)	-1.417 \pm 0.549	88	-2.578	0.012
Access to food (no vs. yes)	1.015 \pm 0.408	676	2.488	0.013

Parameter estimates (b) of the final linear mixed-effects model are shown; higher values mean that the bird was more likely to hide at the beginning of the trial (see the footnotes of Table 1). df, degrees of freedom; SE, standard error.

Table 5**Change in recovery rate (i.e., speed of calming down within a trial) in captive house sparrows over 8 trials in relation to habitat type**

	$b \pm SE$	df	t	P
Intercept (urban, top shelf, first trial)	-0.455 \pm 0.044	678	-10.451	<0.001
Trial number	-0.004 \pm 0.002	678	-1.772	0.077
Habitat (rural vs. urban)	0.089 \pm 0.053	6	1.652	0.150
Position (middle shelf vs. top shelf)	-0.006 \pm 0.033	87	-0.180	0.857
Position (bottom shelf vs. top shelf)	0.100 \pm 0.035	87	2.892	0.005

Parameter estimates (b) of the final linear mixed-effects model are shown; lower (i.e., more negative) values mean that the bird's recovery was more rapid (i.e., probability of hiding decreased faster) within the trial (see the footnotes of Table 1). df, degrees of freedom; SE, standard error.

have enhanced predator discrimination in populations habituated to humans (Coleman et al. 2008; Carrasco and Blumstein 2012; Cavalli et al. 2016).

In line with this behavioral-plasticity hypothesis, we found that although both urban and rural birds habituated to repeated disturbance by decreasing their hiding response, this habituation was faster in the urban sparrows than in their rural conspecifics. The difference in the habituation potential of urban and rural animals is also supported indirectly by a study on fox squirrels (*Sciurus niger*), where young urban individuals had similar FID and were similarly vigilant as old rural individuals, whereas old urban individuals had shorter FID and were less vigilant, suggesting that urban animals habituated over their lifetime (McCleery 2009). Our analyses showed that the habitat difference in habituation rate is primarily due to reactivity (i.e., the initial response to humans), whereas the recovery rate (i.e., calming down after the disturbance) was similar in urban and rural sparrows. Interestingly, in the only other study we know of that quantified both reactivity and recovery to human disturbance (Ellenberg et al. 2009), the initial heart-rate response of yellow-eyed penguins (*Megadyptes antipodes*) did not change but their recovery times decreased after a habituation period. This suggests that the ways by which animals cope with human disturbance may differ among species.

Habituation is a form of behavioral plasticity; thus, it is possible that the faster habituation we found in urban birds is the result of their more flexible behavior. Indeed, it is often assumed that urbanization is accompanied by increased behavioral flexibility (Sih 2013; Sol et al. 2013), a notion that appears notoriously difficult to validate due to controversial empirical evidence and inconsistent interpretations of the term "behavioral flexibility" (for an overview, see Papp et al. 2015). For example, behavioral flexibility is frequently approximated by foraging innovations (Kark et al. 2007; Møller 2009), but when we measured the problem-solving performance of the same sparrows that were tested for habituation in this article, we found little difference between urban and rural

birds' innovativeness (Papp et al. 2015). This might indicate that behavioral flexibility is context dependent, such that flexibility in fear responses may not necessarily be linked to flexibility in other behaviors such as foraging techniques.

Several features of urban habitats may contribute to the faster habituation of urban animals. For example, weaker fear response to humans has been found when there were no alternative habitats to flee to (Gill et al. 2001; Gill 2007) or when animals had less access to food resources (Beale and Monaghan 2004). The distribution of shelter and/or food may be scattered in cities, as suggested by the constrained home range behavior of house sparrows (Vangestel et al. 2010); this might make flight from humans more costly and thus higher tolerance of human disturbance more beneficial. Flock size may also differ between urban and rural habitats, which may then influence behavioral responses to risk (Valcarcel and Fernández-Juricic 2009), for example, by larger flocks spotting the predator from greater distance. It would be interesting to repeat our experiment with birds housed in small flocks to see if we find the same patterns as in the individually housed birds. Predation risk may also vary along the urban-rural gradient, which may further influence fearfulness; however, no consistent differences were found in house sparrows' fear response to sparrowhawks between rural and urban populations (Seress et al. 2011; Bókony, Kulcsár, et al. 2012), not supporting that the slower habituation of the rural birds in the present study was due to habitat differences in predation pressure.

Overall, our results suggest that the weaker fear responses to humans by urban house sparrows are likely to be the result of behavioral plasticity in the form of habituation, whereas we found no evidence for reduced intrinsic boldness. A possible direction for future research is to infer the role of selection and/or differential colonization by separating genetic and environmental effects, that is, testing whether the differences between urban and rural conspecifics in their behavioral plasticity is due to selection in urban habitats favoring individuals that are intrinsically more flexible in their responses to humans or due to the animals growing up in habitats

with different levels of human disturbance. Recent common garden experiments have started to reveal behavioral differences between urban and rural populations that likely represent genetically based adaptations (Atwell et al. 2012; Miranda et al. 2013); this approach could also be applied to studying behavioral reaction norms (Dingemanse et al. 2010) such as habituation.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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