

Does urbanization facilitate individual recognition of humans by house sparrows?

Ernő Vincze · Sándor Papp · Bálint Preiszner ·
Gábor Seress · András Liker · Veronika Bókony

Received: 29 January 2014/Revised: 10 July 2014/Accepted: 11 August 2014/Published online: 28 August 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract Wild animals living in proximity to humans may benefit from recognizing people individually and adjusting their behaviour to the potential risk or gain expected from each person. Although several urban-dwelling species exhibit such skills, it is unclear whether this is due to pre-existing advanced cognitive abilities of taxa predisposed for city life or arises specifically in urban populations either by selection or through ontogenetic changes facilitated by exposure to humans. To test these alternatives, we studied populations of house sparrows (*Passer domesticus*) along the urbanization gradient. We manipulated the birds' experience (hostile or not) associated with humans with different faces (masks) and measured their behavioural responses to the proximity of each person. Contrary to our expectations, we found that while rural birds showed less fear of the non-hostile than of the hostile or an unfamiliar person, urban birds made no distinction. These results indicate that house sparrows are less able to recognize individual humans or less willing to behaviourally respond to them in more urbanized habitats with high human population density. We propose several mechanisms that may explain this difference, including

reduced pay-off of discrimination due to a low chance of repeated interactions with city people, or a higher likelihood that city people will ignore them.

Keywords Urban–rural gradient · Avian cognition · Human disturbance · House sparrow

Introduction

Cities provide a complex and often challenging habitat for wild animals, and various behavioural adjustments seem important for successfully exploiting urbanized environments (Sol et al. 2013). One of the most characteristic aspects of urban environments is frequent proximity to humans, and animals' ability to cope with this extreme anthropogenic disturbance may play a key role in urban adaptations (Carrete and Tella 2011; Møller 2010; Sol et al. 2013). For example, animals in more urbanized habitats often show reduced fear reactions, e.g. flee at shorter distances from humans, but also adjust their activities in space and time to avoid disturbance by people (reviewed in Sol et al. 2013). Since humans may present both threat and opportunities such as food, a fine-tuned response to different persons is thought to be beneficial for urban-dwelling animals (Sol et al. 2013).

The ability to individually recognize humans has long been known in domestic animals such as dogs (Mongillo et al. 2010; Racca et al. 2010), sheep (Kendrick et al. 2001; Peirce et al. 2001), rabbits (Davis and Gibson 2000), and homing pigeons (Dittrich et al. 2010; Stephan et al. 2012); for example, the latter two respond differently to people who regularly feed them than to familiar or unfamiliar people who have never fed them before. Recent studies have also demonstrated such abilities in wild birds that live

Electronic supplementary material The online version of this article (doi:10.1007/s10071-014-0799-z) contains supplementary material, which is available to authorized users.

E. Vincze (✉) · S. Papp · B. Preiszner · G. Seress · A. Liker
Department of Limnology, University of Pannonia,
Pf. 158, Veszprém 8201, Hungary
e-mail: erno.vincze@gmail.com

V. Bókony
Lendület Evolutionary Ecology Research Group, Centre for
Agricultural Research, Plant Protection Institute, Hungarian
Academy of Sciences, Herman Ottó út 15, Budapest 1022,
Hungary

in urban areas. For example, feral pigeons delayed feeding when food was offered by a previously hostile human (Belguermi et al. 2011), and corvids and mockingbirds attacked persons who had previously captured them or approached their nests (Lee et al. 2011; Levey et al. 2009; Marzluff et al. 2010). Since anti-predatory behaviours such as vigilance and mobbing may entail high costs, of starvation and injury, respectively, individual recognition of humans as potential predators may be adaptive by increasing foraging efficiency and focusing mobbing on hostile persons. Such discrimination may be particularly beneficial for urban animals because higher human population density makes humans a more common as well as more relevant feature of the animals' environment, and we may also expect a broader range of behaviours from a higher number of people, with a greater possibility for both positive (e.g. bird feeding) and negative (e.g. harassment) actions towards urban wildlife.

Various mechanisms have been hypothesized to explain how the cognitive skills that are necessary for learning to discriminate between individual humans by wild animals may become especially prevalent in urban habitats. Firstly, species with larger brains and more flexible behaviour are believed to be pre-disposed for successfully exploiting urban environments (Carrete and Tella 2011; Maklakov et al. 2011; Snell-Rood and Wick 2013), and this pre-existing cognitive capacity may also promote individual recognition of humans once the species has colonized urban habitats (Lee et al. 2011; Levey et al. 2009; Marzluff et al. 2010; Sol et al. 2013). Secondly, species without superior cognitive abilities may also establish themselves in cities (Belguermi et al. 2011; Snell-Rood and Wick 2013) but once there, urbanized populations may undergo selection for cognitive skills and diverge from rural populations (Snell-Rood and Wick 2013). Thirdly, urban animals may develop distinct skills during ontogeny. For example, since animal–human encounters are more frequent in cities, this “pre-exposure to stimuli” throughout the individuals' life may facilitate their differentiation between relevant stimuli, i.e. to detect and learn the distinctive features of humans representing different levels of threat or benefit (Lee et al. 2011).

Either of the above mechanisms or any combination of them may result in a better ability of urban animals to individually recognize people. However, the different combinations of these mechanisms predict varying levels of individual human recognition within species across the urban gradient. If memorizing persons is part of a pre-existing cognitive arsenal of urban-invasive species without further microevolutionary or ontogenetic adaptation, then individuals of such species should be equally good at telling people apart regardless of the type of habitat they live in. In contrast, if this skill evolved or improved

specifically in urban populations or results from better learning due to pre-exposure to stimuli, then animals from habitats more densely populated by people should be better at recognizing humans than conspecifics from less populated rural habitats. Previous studies of individual human recognition by wild animals focused only on urban populations (Belguermi et al. 2011; Lee et al. 2011; Levey et al. 2009; Marzluff et al. 2010) and did not compare animals of the same species from differently urbanized habitats.

To test the prediction of the “pre-adaptation” hypothesis as opposed to the alternative scenarios, we studied house sparrows (*Passer domesticus*), a species with long history of commensalism with humans (Anderson 2006; Sætre et al. 2012). House sparrows often exhibit novel behaviours in the wild (Overington et al. 2009; Suárez-Rodríguez et al. 2013) and show remarkable learning skills in lab experiments (Porter 1904; Sasvári 1985), suggesting they may be good candidates for studies on cognition. We captured sparrows from several populations along the urbanization gradient, and tested experimentally whether they vary in the degree of recognition of and/or responsiveness to individual humans with whom they have different experiences.

Methods

The present study is part of a more general project that explores the causes and consequences of behavioural flexibility in birds, and the same set of individual birds was used in several experiments (Bókony et al. 2014). However, there is no overlap in the research questions and results between this study and Bókony et al. (2014). Methods shared by both studies are repeated here to make all relevant details readily available.

Study subjects and housing

We captured house sparrows with mist nets (Ecotone, Gdynia, Poland) from differently urbanized habitats in Hungary from January to March in 2012. We focused on capture sites from the two extremes of the urban gradient occupied by house sparrows, i.e. isolated small farms or edges of small villages and densely built inner city sites (Table S1). Over 8 weeks, we captured 10–14 birds in total each week from two sites of the same habitat type, alternating city sites and farm/village sites weekly. At capture, we measured each bird's body mass (± 0.1 g) and tarsus length (± 0.1 mm), and ringed them with an individually numbered metal ring. The birds were transported to Veszprém and housed indoors (for details, see Bókony et al. 2014).

A total number of 97 individuals participated in the experiment. One week after capture, birds were placed individually into $42 \times 30 \times 35$ cm cages, each containing two perches and a vertical plastic sheet hanging from the top of the cage as shelter. All cages were in one room, positioned on three 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, food (millet seeds) was constantly available to 26 birds, whereas 71 birds were deprived of food for half an hour before and after each training session (see below) as part of another study (Bókony et al. 2014); this food availability treatment was included in the statistical analyses but had no significant effect on the behaviours analysed in this study.

Quantifying habitat urbanization

Urbanization of the capture sites was quantified based on four habitat features: building density, vegetation cover, the presence of roads, and human population density. Firstly, the digital aerial photograph of each site was scored by a single observer (S.P.) using the method of Liker et al. (2008). We divided a 1-km² area around the site of capture into 10×10 cells, and each cell was assigned a score for the cover of vegetation (0: absent, 1: <50 %, 2: >50 %), density of buildings (0: absent, 1: <50 %, 2: >50 %), and the presence of paved roads (0: absent, 1: present). From these cell scores, we calculated five 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. For the two sites in Budapest, we used the data for the corresponding districts of the capital. For the three farm sites, we ascertained population density by either asking the residents (family farm at Szentgál) or consulting the website of the farms (Üllő-Dóramajor and Babat).

We then included the above five habitat characteristics and human population density in a principal component analysis (PCA), which resulted in a single axis with >1 eigenvalue that explained 92.75 % 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 ($r = 0.98$), number of cells with high building density ($r = 0.98$), number of cells with roads ($r = 0.98$), and human population density ($r = 0.86$). We refer to the scores along this axis as “urbanization score”. In one set of the analyses, we divided the capture sites into two groups (henceforth “urbanization category”): “urban” (positive urbanization score) and “rural” (negative urbanization score); these categories matched the administrative titles of all but one settlement in our sample (site Ajka is located in the suburbs of a small town and received a negative urbanization score).

Experimental protocol

To manipulate the experience of birds associated with different human faces, a single experimenter (E.V.) manipulated his appearance by wearing different latex masks (Fig. 1) while playing each of three different roles (henceforth: “mask treatment”) which represented different levels of threat to the birds, namely “hostile”, “non-hostile”, and “unfamiliar”. For each weekly group of birds (referred to as “cohorts” hereafter), a different combination of masks was used from a total of four masks, and we randomly distributed the masks between different treatments among the cohorts (Table S2); each mask was used for all kinds of treatment during the study. The experimenter did not change anything else (e.g. clothes) between the treatments on the same day.

The experiment started 1 week after capture. During the first 4 days of the experiment, there were 14 training sessions, 7 for non-hostile and 7 for hostile treatment. Each day, an equal number of non-hostile and hostile sessions



Fig. 1 Masks used for manipulating the experimenter’s appearance in the three treatments

were performed in randomized order (Table S2). In the non-hostile sessions, the experimenter came out from cover and stood 2 m away from the cages facing the birds for 5 min, so all the birds could see him. In the hostile sessions, he stood 2 m away from the cages for 1 min, then approached the cages and mimicked an attack against each bird of the cohort in randomized order for 20 s each by following the bird with his hand along the cage bars.

On the fifth day, there were three test sessions during which the experimenter stood 2 m away from the cages for 5 min wearing either the non-hostile mask, or the hostile mask, or a third unfamiliar mask (not seen by the birds before this session) in randomized order (Table S2). The test sessions were recorded by a video camera, mounted on a tripod about 2 m away from the cages.

Quantifying risk taking

The birds' behaviour during the three test sessions was analysed in detail from the video-recordings by E.V. using Solomon Coder (Péter 2013). The observer was blind to the birds' capture location and the mask treatment they received. For each bird, position and activity within the cage were recorded as follows. The position of bird was recorded continuously as "hiding" when at least its head was behind the shelter; it was in the "back" when it was not behind the shelter but in the back half of the cage, and in the "front" if it was in the front half of the cage. Activity was only recorded when the bird was not hiding, as "passive" if it did not move for at least 4 s, otherwise as "active". Because the videotaped sessions were slightly different in length, we coded only the first 305 s (i.e. the duration of the shortest recording) of each video record.

We quantified risk taking using the following five variables (higher values of each variable meaning higher level of risk taking): (1) Front: the time the bird spent in the cage's front part; (2) Not hiding: the time the bird spent outside the shelter (sum of front and back); (3) Flight latency: the time the bird spent in the cage's front from the beginning of the session until moving to the back of the cage or behind the shelter (0 for birds that were in the back of the cage or behind the shelter at the beginning of the session); (4) Hiding latency: the latency of the bird to go behind the shelter for the first time (0 for birds that were behind the shelter at the beginning of the session); (5) Passivity: the time the bird spent without moving for at least 4 s (excluding the time spent behind the shelter). We interpreted longer passivity as a higher level of risk taking because in our experiment passive birds were likely to be more relaxed than active birds, as most activity was fleeing behaviour. Passivity was also positively correlated with the other 4 measures of risk-taking behaviour (see "Results"). All variables were computed separately for the three test

sessions of each bird. Since all five response variables measured bold behaviour in the presence of a human, we rank-transformed them and calculated the mean of these rank scores to obtain a measure of the birds' average risk taking within a session (henceforth "risk taking").

To assess the repeatability of our behavioural measurements, a second observer (G. S.) also coded the behaviour of a subset of birds from the video recordings. We randomly chose ten 5-min sessions from each of the three treatments with at least one bird from each cohort, such that no individual was sampled more than once. For these 30 sessions, we calculated the risk-taking score as described above for both observers and expressed the repeatability between them by the intra-class correlation coefficient (ICC; Nakagawa and Schielzeth 2010).

Statistical analyses

Consistency of behavioural variables between the three test sessions and correlation of behavioural variables with each other were tested by Kendall's concordance tests (Legendre 2005). The effects of mask treatment and habitat were analysed using linear mixed-effects (LME) models with risk taking as dependent variable. Since there were three test sessions for each bird, and the stimulus was presented for all birds in a cohort at the same time, we used bird ID and cohort ID as nested random factors. We included the following explanatory variables in the initial model: mask treatment (i.e. hostile, non-hostile, or unfamiliar), urbanization category (urban, rural), cage position (vertical and horizontal), treatment order (i.e. order of the three treatments over the test day, e.g. non-hostile-hostile-unfamiliar, hostile-unfamiliar-non-hostile, etc.), session number (i.e. first, second, or third), mask ID, food availability (i.e. ad libitum or fasted), sex, and body condition. We quantified body condition as the scaled mass index proposed by Peig and Green (2009) using the equation of Bókony et al. (2012, 2014). We also included two relevant interactions in the initial model, namely the treatment \times urbanization interaction to test if the differences between responses to the three treatments were different in urban and rural birds, and the treatment order \times session number interaction to control for the possible effects of preceding treatments on the same day. From the initial model, non-significant ($P > 0.05$) terms (food availability, sex and body condition) were dropped stepwise, and we report the final model only. We also repeated this analysis by replacing urbanization category with either urbanization score or human population density. To test the pairwise differences of the interaction between mask treatment and urbanization category, we performed post hoc analyses by calculating linear contrasts and correcting their P values using the false discovery rate (FDR) method (Benjamini et al. 2001).

Table 1 Analysis of deviance tables of the final LME models of the risk-taking score, using three alternative measures of habitat urbanization (urbanization category, urbanization score and human population density; referred to as “urbanization” in the list of predictors)

Predictors	Urbanization category			Urbanization score			Human population density		
	χ^2	<i>df</i>	<i>P</i>	χ^2	<i>df</i>	<i>P</i>	χ^2	<i>df</i>	<i>P</i>
Intercept	65.81	1	<0.001	75.49	1	<0.001	65.11	1	<0.001
Mask treatment	0.12	2	0.940	8.38	2	0.015	14.81	2	0.001
Urbanization	0.08	1	0.779	1.26	1	0.263	0.88	1	0.348
Mask treatment × urbanization	11.93	2	0.003	13.63	2	0.001	10.43	2	0.005
Cage position—vertical	8.26	2	0.016	8.11	2	0.017	8.49	2	0.014
Cage position—horizontal	13.12	4	0.011	12.69	4	0.013	11.71	4	0.020
Mask ID	8.22	3	0.042	11.27	3	0.010	8.50	3	0.037
Treatment order	21.38	4	<0.001	23.27	4	<0.001	35.32	4	<0.001
Session number	1.53	1	0.216	3.14	1	0.076	0.36	1	0.548
Treatment order × session number	16.26	4	0.003	19.63	4	0.001	22.70	4	<0.001

The mask treatment × urbanization interaction, highlighted in bold, expresses the differences between birds from differently urbanized habitats in the extent to which they respond differently to the three persons

Results

The five risk-taking variables were significantly consistent within individuals across the three test sessions (Kendall’s concordance tests, not hiding: $W = 0.9$, $P < 0.001$; front: $W = 0.66$, $P < 0.001$; flight latency: $W = 0.52$, $P < 0.001$; hiding latency: $W = 0.68$, $P < 0.001$; passivity: $W = 0.65$, $P < 0.001$; $N = 97$ in all tests) and were positively correlated with each other ($W = 0.48$, $P < 0.001$). Risk taking was also significantly consistent within individuals over the three test sessions ($W = 0.79$, $P < 0.001$, $N = 97$). Between the two observers, risk taking showed high and significant repeatability (ICC = 0.913, $P < 0.001$, $N = 30$).

We found that sparrows responded differently to the three masks representing differently threatening persons, and the degree of this discrimination differed between urban and rural birds (mask treatment × habitat interaction; Table 1; Fig. 2). Rural birds behaved more boldly towards the familiar non-hostile person than the unfamiliar person (linear contrast, $P < 0.001$; $P = 0.002$ after FDR correction) and, to a lesser extent, they were also more bold towards the familiar non-hostile person than the familiar hostile person ($P = 0.012$; $P = 0.056$ after FDR correction); there was no difference between their response towards the hostile and the unfamiliar persons ($P = 0.219$; $P = 0.395$ after FDR correction). In contrast, urban birds’ risk taking did not differ significantly among the three treatments ($P > 0.371$ for all linear contrasts; $P > 0.446$ after FDR correction), whereas they tended to be bolder towards the unfamiliar person ($P = 0.042$; $P = 0.096$ after FDR correction) and less bold towards the non-hostile person ($P = 0.024$; $P = 0.072$ after FDR correction) than rural birds. These results are robust since we controlled for

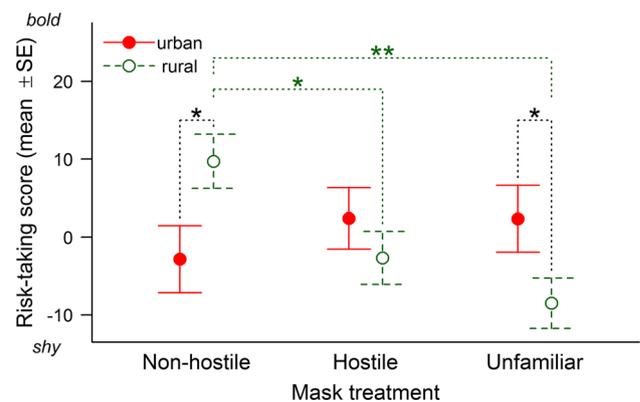


Fig. 2 Effects of mask treatment on urban ($N = 42$) and rural ($N = 55$) sparrows’ risk taking, shown as residuals controlled for confounding effects. Differences marked by asterisk were significant (** $P < 0.001$, after false discovery rate correction $P = 0.002$; * $P = 0.012$ – 0.042 , after false discovery rate correction $P = 0.056$ – 0.096)

several confounding variables in the analyses (Table 1) and the effect of mask treatment × habitat interaction on risk taking remained significant when we replaced the urbanization category of each capture site (urban or rural) by either the numeric urbanization score or human population density (Table 1; Fig. 3).

Birds were the least bold in the first test session and became bolder later during the day (Table 1); this diurnal change was greatest when they saw the familiar non-hostile mask in the first session (treatment order × session number interaction, Table 1). Birds on the top shelf were bolder than those on the lower shelves, and birds in the middle on each shelf (i.e. those facing the experimenter most directly) were the most fearful (Table 1). Overall, the birds behaved

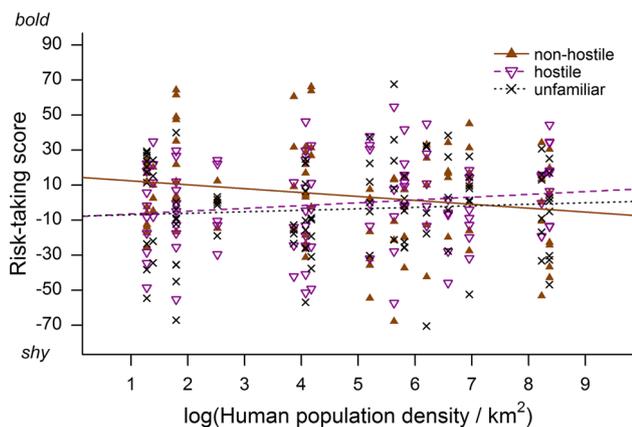


Fig. 3 Interactive effects of mask treatment and human population density (on logarithmic scale) on risk-taking (shown as residuals controlled for confounding effects). Lines are regression lines from the final LME model

more fearfully towards mask B than the other three masks (Table 1).

Discussion

Contrary to all hypotheses predicting better individual recognition of humans in urban animals, we found that house sparrows from more urbanized habitats were less discriminating than rural conspecifics in their responses towards persons from whom they had experienced consistently different behaviours. This suggests that urban sparrows either cannot tell persons apart by their faces, or they can but do not adjust their behaviour accordingly. We suggest that sparrows' discrimination of, or responsiveness to, individual humans may be constrained in highly urbanized habitats due to increased costs and/or reduced benefits.

Firstly, repeated encounters with the same person might be rare in big cities, so animals may have difficulties with and/or gain less advantage from memorizing individual people. Notably, other wild species that differentiated efficiently among persons (Belguermi et al. 2011; Lee et al. 2011; Levey et al. 2009; Marzluff et al. 2010) were tested mostly in university campuses where the human population, while numerous, might be more constant than at the busy bus/train stations we mostly sampled (Table S1). Nevertheless, in these studies, only a few negative experiences (Levey et al. 2009) or even a single one (Marzluff et al. 2010) was enough for the birds to efficiently recognize a hostile person, indicating that at least in those species repeated encounters may not be necessary for individual recognition of humans.

Secondly, in more urbanized habitats, the interactions between humans and birds might be less diverse, as people

may behave more neutrally towards birds, so memorizing different persons may be more rewarding in rural than in urban habitats. This idea is supported by recent studies indicating that both hostile and benevolent human behaviours towards birds are more common in less urbanized areas (Clucas and Marzluff 2012), a higher proportion of people engage in bird feeding at sites with low population density (Fuller et al. 2012), and people in rural areas are better at recognizing endangered birds (De Azevedo et al. 2012). Also, house sparrows are often treated as pests in the countryside due to their crop consumption and displacement of other birds (Anderson 2006). Thus, rural sparrows, while encountering fewer people overall, may encounter more who are actually worth remembering, both hostile and friendly.

Thirdly, sparrows in urban environments might face some cognitive constraint on learning. For example, pigeons can discriminate between less than a thousand images in an associative learning task (Cook et al. 2005), whereas human population density can exceed several thousands per square kilometre in cities (Table S1), so memory load might prevent urban birds from efficiently learning to recognize people and remembering their attitudes. Although urban species are thought to be cognitively superior (Lee et al. 2011; Levey et al. 2009; Marzluff et al. 2010; Sasvári 1985; Sol et al. 2013), little is known about differences in learning ability between urban and rural conspecifics. Even in species that generally perform well in cognitive tasks, urbanization might suppress the expression of behavioural flexibility by the above mechanisms. For example, a recent study found that cranial capacity, a proxy for brain size, tended to decrease over time in urban populations whereas it increased in rural populations of several mammalian species (Snell-Rood and Wick 2013), and smaller brain can result in limited cognitive abilities. Furthermore, another urban species, the Zenaida dove (*Zenaida aurita*) learned more slowly in a foraging task when human disturbance was high (Boogert et al. 2010).

Finally, urban and rural birds might use different cues to tell people apart. In our experiment, only the experimenter's head (face and hair) was manipulated by masks, his height, build, clothing, or movements were not. If urban birds pay less attention to the face than rural birds, this may have limited their performance. However, the face is typically a central cue for animals in interactions with humans (Racca et al. 2010; Stephan et al. 2012); for example, dogs prefer to interact with humans with faces oriented towards them and visible eyes (Gácsi et al. 2004) and they differentiate less between their owners and strangers when their heads are covered (Mongillo et al. 2010). Also, birds may view humans as potential predators, and in predator–prey interactions facial orientation and eye-gaze direction may provide vital information about the predator's intentions

for the prey (Carter et al. 2008; Hampton 1994). Accordingly, previous studies on birds found that face differences allow effective recognition of human individuals even for long periods (Marzluff et al. 2010) while clothing seems to be a less important cue (Belguermi et al. 2011; Lee et al. 2011; Levey et al. 2009).

Our study highlights the potential for urbanization, and particularly interactions between humans and wild animals, to have intricate effects on the evolution of animal cognition and behavioural flexibility. Differences not only in people's numbers but also the diversity and predictability of their behaviours towards animals may interplay in shaping the pay-offs and constraints of animals' behavioural responses to human disturbance, which is an exciting avenue for further research.

Acknowledgments We thank András Péter for providing Solomon Coder. Birds were housed at Veszprém Zoo. The research was financed by the Hungarian Scientific Research Fund (OTKA, K84132). During the study, A.L. was supported by a Marie Curie Intra-European Fellowship. During the preparation of the manuscript, we were supported by the European Union, with the co-funding of the European Social Fund (S.P., B.P., and E.V. by TÁMOP-4.2.2.A-11/1/KONV-2012-0064, and V.B. by TÁMOP-4.2.4.A/2-11/1-2012-0001 'National Excellence Program').

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All procedures were in accordance with Hungarian laws and licensed by the Middle Transdanubian Inspectorate for Environmental Protection, Natural Protection and Water Management (permission number: 31559/2011).

References

- Anderson TR (2006) Biology of the ubiquitous house sparrow: from genes to populations. Oxford University Press, New York
- Belguermi A, Bovet D, Pascal A, Prévot-Julliard A-C, Saint Jalme M, Rat-Fischer L, Leboucher G (2011) Pigeons discriminate between human feeders. *Anim Cogn* 14:909–914. doi:10.1007/s10071-011-0420-7
- Benjamini Y, Drai D, Elmer G, Kafkafi N, Golani I (2001) Controlling the false discovery rate in behavior genetics research. *Behav Brain Res* 125:279–284
- Bókony V, Kulcsár A, Liker A (2010) Does urbanization select for weak competitors in house sparrows? *Oikos* 119:437–444. doi:10.1111/j.1600-0706.2009.17848.x
- Bókony V, Seress G, Nagy S, Lendvai ÁZ, Liker A (2012) Multiple indices of body condition reveal no negative effect of urbanization in adult house sparrows. *Landsc Urban Plan* 104:75–84. doi:10.1016/j.landurbplan.2011.10.006
- Bókony V, Lendvai ÁZ, Vágási CI, Pátraş L, Pap PL, Németh J, Vincze E, Papp S, Preiszner B, Seress G, Liker A (2014) Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. *Behav Ecol* 25:124–135. doi:10.1093/beheco/art094
- Boogert NJ, Monceau K, Lefebvre L (2010) A field test of behavioural flexibility in Zenaida doves (*Zenaida aurita*). *Behav Processes* 85:135–141. doi:10.1016/j.beproc.2010.06.020
- Carrete M, Tella JL (2011) Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. *PLoS ONE* 6:e18859. doi:10.1371/journal.pone.0018859
- Carter J, Lyons NJ, Cole HL, Goldsmith AR (2008) Subtle cues of predation risk: starlings respond to a predator's direction of eye-gaze. *Proc R Soc B* 275:1709–1715. doi:10.1098/rspb.2008.0095
- Clucas B, Marzluff JM (2012) Attitudes and actions toward birds in urban areas: human cultural differences influence bird behavior. *Auk* 129:8–16. doi:10.1525/auk.2011.11121
- Cook RG, Levison DG, Gillett SR, Blaisdell AP (2005) Capacity and limits of associative memory in pigeons. *Psychon Bull Rev* 12:350–358
- Davis H, Gibson JA (2000) Can rabbits tell humans apart? Discrimination of individual humans and its implications for animal research. *Comp Med* 50:483–485
- De Azevedo CS, Silva KS, Ferraz JB, Tinoco HP, Young RJ, Rodrigues M (2012) Does people's knowledge about an endangered bird species differ between rural and urban communities? The case of the Greater Rhea (*Rhea americana*, Rheidae) in Minas Gerais, Brazil. *Rev Bras Ornitol* 20:8–18
- Dittrich L, Adam R, Unver E, Güntürkün O (2010) Pigeons identify individual humans but show no sign of recognizing them in photographs. *Behav Processes* 83:82–89. doi:10.1016/j.beproc.2009.10.006
- Fuller RA, Irvine KN, Davies ZG, Armsworth PR, Gaston KJ (2012) Interactions between people and birds in urban landscapes. In: Lepczyk CA, Warren PS (eds) *Urban Bird Ecol. Conserv.* University of California Press, Berkeley, pp 249–266
- Gácsi M, Miklósi A, Varga O, Topál J, Csányi V (2004) Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Anim Cogn* 7:144–153. doi:10.1007/s10071-003-0205-8
- Hampton R (1994) Sensitivity to information specifying the line of gaze of humans in sparrows (*Passer domesticus*). *Behaviour* 130:41–50
- Kendrick KM, da Costa AP, Leigh AE, Hinton MR, Peirce JW (2001) Sheep don't forget a face. *Nature* 414:165–166. doi:10.1038/35102669
- Lee WY, Lee S, Choe JC, Jablonski PG (2011) Wild birds recognize individual humans: experiments on magpies, *Pica pica*. *Anim Cogn* 14:817–825. doi:10.1007/s10071-011-0415-4
- Legendre P (2005) Species associations: the Kendall coefficient of concordance revisited. *J Agric Biol Environ Stat* 10:226–245. doi:10.1198/108571105X46642
- Levey DJ, Londoño GA, Ungvari-Martin J, Hiersoux MR, Jankowski JE, Poulsen JR, Stracey CM, Robinson SK (2009) Urban mockingbirds quickly learn to identify individual humans. *Proc Natl Acad Sci USA* 106:8959–8962. doi:10.1073/pnas.0811422106
- Liker A, Papp Z, Bókony V, Lendvai ÁZ (2008) Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. *J Anim Ecol* 77:789–795. doi:10.1111/j.1365-2656.2008.01402.x
- Maklakov AA, Immler S, Gonzalez-Voyer A, Rönn J, Kolm N (2011) Brains and the city: big-brained passerine birds succeed in urban environments. *Biol Lett* 7:730–732. doi:10.1098/rsbl.2011.0341
- Marzluff JM, Walls J, Cornell HN, Withey JC, Craig DP (2010) Lasting recognition of threatening people by wild American crows. *Anim Behav* 79:699–707. doi:10.1016/j.anbehav.2009.12.022

- Møller AP (2010) Interspecific variation in fear responses predicts urbanization in birds. *Behav Ecol* 21:365–371. doi:[10.1093/beheco/arp199](https://doi.org/10.1093/beheco/arp199)
- Mongillo P, Bono G, Regolin L, Marinelli L (2010) Selective attention to humans in companion dogs, *Canis familiaris*. *Anim Behav* 80:1057–1063. doi:[10.1016/j.anbehav.2010.09.014](https://doi.org/10.1016/j.anbehav.2010.09.014)
- Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev Camb Philos Soc* 85:935–956. doi:[10.1111/j.1469-185X.2010.00141.x](https://doi.org/10.1111/j.1469-185X.2010.00141.x)
- Overington SE, Morand-Ferron J, Boogert NJ, Lefebvre L (2009) Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Anim Behav* 78:1001–1010. doi:[10.1016/j.anbehav.2009.06.033](https://doi.org/10.1016/j.anbehav.2009.06.033)
- Peig J, Green AJ (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118:1883–1891. doi:[10.1111/j.1600-0706.2009.17643.x](https://doi.org/10.1111/j.1600-0706.2009.17643.x)
- Peirce JW, Leigh AE, DaCosta APC, Kendrick KM (2001) Human face recognition in sheep: lack of configurational coding and right hemisphere advantage. *Behav Processes* 55:13–26
- Péter A (2013) Solomon Coder: a simple and free solution for behavior coding. <http://www.solomoncoder.com>
- Porter JP (1904) A preliminary study of the psychology of the English sparrow. *Am J Psychol* 15:313–346
- Racca A, Amadei E, Ligout S, Guo K, Meints K, Mills D (2010) Discrimination of human and dog faces and inversion responses in domestic dogs (*Canis familiaris*). *Anim Cogn* 13:525–533. doi:[10.1007/s10071-009-0303-3](https://doi.org/10.1007/s10071-009-0303-3)
- Sætre G-P, Riyahi S, Aliabadian M, Hermansen JS, Hogner S, Olsson U, Gonzalez Rojas MF, Sæther SA, Trier CN, Elgvin TO (2012) Single origin of human commensalism in the house sparrow. *J Evol Biol* 25:788–796. doi:[10.1111/j.1420-9101.2012.02470.x](https://doi.org/10.1111/j.1420-9101.2012.02470.x)
- Sasvári L (1985) Keypeck conditioning with reinforcements in two different locations in thrush, tit and sparrow species. *Behav Processes* 11:245–252
- Snell-Rood EC, Wick N (2013) Anthropogenic environments exert variable selection on cranial capacity in mammals. *Proc R Soc B* 280:20131384. doi:[10.1098/rspb.2013.1384](https://doi.org/10.1098/rspb.2013.1384)
- Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city. *Anim Behav* 85:1101–1112. doi:[10.1016/j.anbehav.2013.01.023](https://doi.org/10.1016/j.anbehav.2013.01.023)
- Stephan C, Wilkinson A, Huber L (2012) Have we met before? Pigeons recognise familiar human faces. *Avian Biol Res* 5:75–80. doi:[10.3184/175815512X13350970204867](https://doi.org/10.3184/175815512X13350970204867)
- Suárez-Rodríguez M, López-Rull I, García CM (2013) Incorporation of cigarette butts into nests reduces nest ectoparasite load in urban birds: new ingredients for an old recipe? *Biol Lett* 9:20120931. doi:[10.1098/rsbl.2012.0931](https://doi.org/10.1098/rsbl.2012.0931)