

Problem-solving performance and reproductive success of great tits in urban and forest habitats

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Abstract Success in problem solving, a form of innovativeness, can help animals exploit their environments, and recent research suggests that it may correlate with reproductive success. Innovativeness has been proposed to be especially beneficial in urbanized habitats, as suggested by superior problem-solving performance of urban individuals in some species. If there is stronger selection for innovativeness in cities than in natural habitats, we expect problem-solving performance to have a greater positive effect on fitness in more urbanized habitats. We tested this idea in great tits (*Parus major*) breeding at two urban sites and two forests by measuring their problem-solving performance in an obstacle-removal task and a food-acquisition task. Urban pairs were significantly faster problem-solvers in both tasks. Solving speed in the obstacle-removal task was

positively correlated with hatching success and the number of fledglings, whereas performance in the food-acquisition task did not correlate with reproductive success. These relationships did not differ between urban and forest habitats. Neophobia, sensitivity to human disturbance, and risk taking in the presence of a predator did not explain the relationships of problem-solving performance either with habitat type or with reproductive success. Our results suggest that the benefit of innovativeness in terms of reproductive success is similar in urban and natural habitats, implying that problem-solving skills may be enhanced in urban populations by some other benefits (e.g. increased survival) or reduced costs (e.g. more opportunities to gain practice with challenging tasks).

Keywords Innovation · Urbanization · Breeding success · Birds · Behaviour

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Introduction

Innovations are defined as novel behaviours whereby animals solve new problems, or apply them to solve familiar tasks in novel ways (Reader and Laland 2003). Such behaviours have become a central topic in the past decade, given their vast potential to facilitate adaptation to novel or changing environments (Griffin and Guez 2014; Reader et al. 2016). Studying animal innovations is appealing also because it may offer a way to understand the ecological significance of cognitive skills by which the information from the environment is acquired, processed, stored, and acted upon (Shettleworth 2010). While innovative problem-solving performance does not necessarily reflect cognitive capacity (Rowe and Healy 2014; Thornton et al. 2014), several cognitive processes have been suggested to

be associated with animal innovations; for example, empirical work on mechanisms has implicated operant conditioning (Overington et al. 2011) and inhibitory control (Thornton and Samson 2012), whereas other studies have discussed the potential role of insight (Bird and Emery 2009) and classifying the encountered stimulus as novel (Greggor et al. 2015). Therefore, problem-solving ability has been put forward as a candidate cognitive trait (Morand-Ferron et al. 2015). A recent review found that the three most consistent predictors of problem solving were learning speed, motor skill diversity, and perseverance, and that problem-solving performance is a reliable measure of innovativeness (Griffin and Guez 2014).

Recently, there has been an increasing interest in assessing the strength of selection on cognitive traits in the wild (Rowe and Healy 2014; Morand-Ferron and Quinn 2015). Research focusing on innovative behaviour is increasingly revealing that problem solving can enhance individuals' fitness by increasing reproductive success. For example, better problem-solving performance is associated with higher mating success in male satin bowerbirds *Ptilonorhynchus violaceus* (Keagy et al. 2011), with plumage traits that are attractive in mate choice in male siskins *Carduelis spinus* (Mateos-Gonzalez et al. 2011) and with larger brood size in great tits *Parus major* (Cauchard et al. 2013). However, the correlation between innovativeness and specific components of fitness varies between species (Keagy et al. 2011; Isden et al. 2013), between populations of the same species (Cole et al. 2012; Cauchard et al. 2013), and among different components of fitness in the same population (Cole et al. 2012). The reasons for this heterogeneity are not known.

The benefits of innovative behaviour may vary between habitat types, and selection may favour an innovative phenotype in more challenging environments more strongly. For example, in chickadees (*Poecile spp.*), individuals living in harsher environments have enhanced spatial memory and better problem-solving performance compared to conspecifics living under milder conditions; this difference has been attributed to the importance of food caching, and the cognitive skills required for it, which is necessary for survival in harsh habitats (reviewed in Pravosudov and Roth 2013). Along a similar logic, innovativeness may be particularly important in urban environments, because urban animals are exposed to several kinds of novel or variable stimuli such as fragmented landscapes, noise and light pollution, disturbance by domestic animals and humans, and new food resources such as garbage (Sol et al. 2013). Accordingly, individuals from more urbanized habitats were found to be more successful in certain problem-solving tasks in three avian species (Liker and Bókonyi 2009; Sol et al. 2011; Audet et al. 2015), although the relationship between urbanization

and innovativeness is equivocal (Audet et al. 2015; Papp et al. 2015). Consequently, if innovativeness is particularly relevant in urban habitats, we may expect that it has a stronger effect on fitness than in non-urbanized habitats.

We tested this idea in the great tit, which is one of the most common breeding birds in both urban areas and natural forests in Europe (Burfield and van Bommel 2004). We measured innovativeness in urbanized and forest-dwelling breeding pairs in two different problem-solving situations, an obstacle-removal task and a food-acquisition task, and monitored their breeding success. We investigated whether (1) urban pairs outperform their forest-dwelling conspecifics in the speed of problem-solving, (2) individuals with superior problem-solving performance have higher breeding success within their habitats, and (3) the relationship between problem-solving performance and breeding success is more pronounced in urban habitats than in forests. Furthermore, we examined whether any of the above relationships is mediated or confounded by differences in three behavioural traits that have been found to be related to problem-solving performance as well as to urbanization in several species: neophobia (Sol et al. 2011; Miranda et al. 2013; Cauchard et al. 2013), sensitivity to predation risk (Seress et al. 2011; Cole et al. 2012), and sensitivity to human disturbance (Cole et al. 2012; Vincze et al. 2016).

Methods

We tested 55 wild great tit pairs nesting in artificial nest boxes in 2 urban and 2 forest habitats in 2013. The urban study sites are located in Veszprém (47°05'17"N, 17°54'29"E) and Balatonfüred (46°57'30"N, 17°53'34"E), whereas the forest study sites are a downy oak (*Quercus pubescens*) and south European flowering ash (*Fraxinus ornus*) forest at Vilma-puszta (47°05'02"N, 17°52'01"E) and a beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*) forest near Szentgál (47°06'39"N, 17°41'17"E) in Hungary.

Throughout the breeding season, we checked the nest boxes twice a week and recorded the number of eggs and/or chicks at each visit. The experimental protocol began by catching one of the parents (excepting a few pairs where one or both parents had already been ringed) using a nest box trap when the chicks were 5–9 (mean \pm SE = 6.18 \pm 0.16) days old, considering the day of hatching of the first chick as day 1. Upon capture we ringed the birds with a unique combination of a metal ring and 3 plastic colour rings, and we recorded their age class (2nd calendar year or older) and sex, both based on plumage characteristics (Svensson 1992). Ringing one of the parents before the behavioural tests ensured that the sex of the parents could be recognized

unambiguously during all observations, as it was not always possible to sex the birds by plumage from the videos (see below). We trapped only one parent before the tests to minimize stress and the risk of nest desertion. Between days 6 and 16 of chick age, we conducted five behavioural tests at each nest as detailed below; then we trapped and ringed the other parent (if it had not been ringed earlier) following the last test, so that individuals could be identified in later breeding episodes. Because trapping might have affected the birds' behaviour (Schlicht and Kempenaers 2015), the trapping status of each individual (i.e. trapped a few days before the tests or not) and each pair (i.e. one or no parent trapped a few days before the tests) was taken into account in the analyses (see below). At the age of 13–17 (mean \pm SE = 15.07 ± 0.12) days, we ringed the chicks and measured their body mass and tarsus length.

Behavioural tests

First, we assayed the parents' neophobia between days 6–10 (mean \pm SE = 7.98 ± 0.16) of chick age. After 30 min of baseline observation, we fixed a small rubber ball with adhesive putty on the platform next to the entrance of the nest box (Fig. S1) and observed the nest box until both parents entered the nest, or for 30 min. We assessed the neophobia of each parent by measuring the latency to enter the nest box after the observer had placed the ball and left the vicinity of the nest.

The next two tests were designed to assay problem-solving performance. First, all pairs were tested in an obstacle-removal task between 7 and 11 (mean \pm SE = 9.15 ± 0.15 ; mean difference between forest and urban pairs: 0.19 ± 0.31) days of chick age. Before the test, during a 30-min period of baseline observation, there was a ca. 3×7 cm grey feather fixed with adhesive putty on the platform near the entrance. The birds had been familiarized with this situation because we had put a similar feather near the entrance upon the start of egg laying, and replaced it with another feather at every nest check (whether or not it was removed by the birds between the successive nest checks) until the obstacle-removal test. In most cases, these feathers had been removed by the birds between the successive nest checks, but we kept no record whether or when it happened. At the start of the test, we blocked the entrance by fixing a similar grey feather in front of it using magnetic tape and observed the nest box until one of the parents removed the feather and entered the nest, or for 30 min. To remove the feather, the bird had to grab it with the beak or a foot to pull it off (Online Resources, Video S1).

In the second problem-solving test, the parents were tested in a food-acquisition task between 8 and 13 (mean \pm SE = 10.35 ± 0.19 ; mean difference between forest and urban pairs: 0.56 ± 0.37) days of chick age. During the 30 min of baseline observation before the test,

we provided the birds with 3 mealworms (*Tenebrio molitor* larvae) in a well on the platform near the entrance of the nest box. This situation was familiar for the birds because we provided 3 mealworms in the same well upon every nest check from the start of egg laying. At the start of the test, we topped up the number of mealworms in the well to 3, and we covered the well by a transparent plastic lid that was fixed at its two ends by sticking small pieces of toothpicks into prepared holes. In order to reach the mealworms, the birds had to remove at least one toothpick and move the lid, or lift the lid off from the toothpicks by pulling it upwards (Online Resources, Video S2). We observed the nest box until one of the parents removed the lid and took out at least one mealworm, or for 30 min.

After the first 3 tests, when the chicks were 9–16 (mean \pm SE = 12.81 ± 0.14) days old, each pair was observed in two more behavioural assays, the order of which was randomly chosen at each nest. These two tests were designed to assess the birds' sensitivity to predation risk and to human disturbance. At the beginning of the predation risk test, we placed a ca. 1-m-high tripod on the ground, setting up the top end 3 m from the nest box entrance. The observation started when the experimenter left the vicinity of the nest. After 15 min of baseline observation, we fixed a taxidermally mounted Eurasian collared dove (*Streptopelia decaocto*) on the tripod for 10 min, then removed the dove and conducted an additional 10-min observation. After this, a taxidermally mounted Eurasian sparrowhawk (*Accipiter nisus*) was fixed on the tripod for 10 min, and after the removal of the sparrowhawk the observations were carried out for a further 10 min. Thus, the entire test was 55 min long. We measured the number of visits (i.e. entering the nest box) per minute (henceforth visit rate) by both parents in each 10-min interval; then, we quantified their response to predation risk as visit rate recorded in the 10 min after the removal of the sparrowhawk minus the visit rate recorded in the 10 min after the removal of the dove.

The human disturbance test followed a similar design as the predation-risk test, but no tripod was placed near the nest. Again, the observation started when the experimenter left the vicinity of the nest. After the first 15-min baseline observation, a person stood under the nest box for 10 min. After the person had left, we observed the nest for a further 10 min, and thus the entire test was 35 min long. We measured the number of visits per minute by both parents in each interval; then, we quantified their response to human disturbance as visit rate in the 10 min after the person had left minus the visit rate in the 15 min before the arrival of the person to the nest box.

Each test was conducted on a different day. All observations were made using a small ($98 \times 58 \times 34$ mm) camera hidden in a plastic box that was permanently

Table 1 Number of solver, non-solver, non-measured, and non-participating birds in two types of habitat in the two problem-solving tasks (the first test per task of each pair)

	Forest habitat				Urban habitat				χ^2	P
	Solver	Non-solver ^a	Non-measured ^b	Non-participating ^c	Solver	Non-solver	Non-measured	Non-participating		
Obstacle-removal task										
Pairs ($N = 52$)	11	12	0	0	22	7	0	0	4.35	0.037
Males ($N = 23$)	2	11	9	1	3	7	19	0	0.71	0.400
Females ($N = 46$)	9	12	2	0	19	6	3	1	5.26	0.022
Food-acquisition task										
Pairs ($N = 48$)	7	14	0	0	18	9	0	0	5.26	0.022
Males ($N = 34$)	5	13	2	1	7	9	11	0	0.95	0.331
Females ($N = 36$)	2	14	5	0	11	9	7	0	6.96	0.008

The χ^2 and *P* values stand for χ^2 tests comparing the proportion of solvers and non-solvers between habitats

^a Birds that landed on the nest box at least once during the 30 min of the test but did not solve

^b Individuals whose mate solved the given task were treated as non-measured because their performance could not be quantified

^c Birds that did not visit the nest box during the 30 min of the test

attached to the nest box ca. 15 cm from the entrance (Fig. S1). All tests began with a few-minute period that supposedly attracted the attention of the parent birds (i.e. the experimenter walked into their territory and installed the camera on the nest box and the other devices needed for the test); since the parents could hide in the canopy when approaching the nest boxes, it was not possible to ascertain when they became aware of the stimuli. The 5 behavioural tests were repeated with the same protocol in later breeding episodes in the same breeding season (2013) for a subset of the same pairs in order to test individual consistency in problem-solving performance.

Data analyses

In the problem-solving tests, we measured solving latency as the time the solving parent took to remove the feather in the obstacle-removal task or open the well in the food-acquisition task after it first landed at the entrance. We used the criterion of landing at the entrance because proximity to the task was necessary for starting to attempt problem solving. Hence, time spent potentially visually inspecting the task at close range was included in the problem-solving latency. In contrast, during neophobia tests, birds typically entered the nest box very soon after landing. In this case, although birds occasionally spent considerable time inspecting the novel object from a greater distance, this time could not be quantified given our reliance on close-up video. If a bird landed on the nest box at least once during the 30 min of the test but did not solve, we considered it as a non-solver. Birds that did not visit the nest box during the 30 min of the test

were treated as non-participating. Individuals whose mate solved the given task were treated as non-measured because their performance could not be quantified (i.e. the test ended when one of the parents solved, so it is unknown whether the other parent would have been a solver, a non-solver, or non-participating if it had had 30 min). Non-measured and non-participating birds were excluded from all individual-level analyses (Table 1). Non-solvers were assigned the maximal latency (1860s, i.e. the duration of the test plus 1 min). To analyse whether problem-solving latency is individually consistent, we used the data of 26 pairs that were tested in 2 consecutive breeding episodes within the season. Within each task, we correlated the latencies between their first and second tests if the solver individual was the same in both tests or if none of the parents solved in one or both tests. In all other analyses (detailed below), we used only the data collected during the rearing of the first brood of the year for each pair.

To analyse the effects of habitat type and potential confounder variables on problem-solving performance, we used Cox's proportional hazards models with solving latency of the respective task as dependent variable, treating maximal latencies as censored observations. Initial models contained habitat type (urban vs. forest), provisioning rate (the number of visits of the parents during the baseline observation of the respective test divided by the number of nestlings alive on the day of the respective test), date of the test (number of days since 1st of May), age of nestlings on the day of the test, time of day at the start of the test (number of minutes since 7:00), and the parents' age class and trapping status (as explained below).

To measure breeding success, we calculated the following variables: clutch size (i.e. the maximum number of eggs observed in the nest); hatching success (i.e. the proportion of eggs that hatched); number of fledglings (i.e. number of nestlings alive at the age of ringing); proportion of chicks fledged (i.e. the proportion of hatchlings that survived to ringing age); mean tarsus length (± 0.1 mm), and mean body mass (± 0.1 g) of fledglings measured at ringing. Linear mixed-effects models were used with study site as random factor to investigate whether each measure of breeding success is predicted by solving latency in the two problem-solving tasks. In the models of hatching success and proportion of chicks fledged, we used quasibinomial error distribution with logit link function. Solving latency of the respective test, habitat type, hatching date of the first chick, parents' age class, and trapping status (see below) was included in the initial models as predictors, along with the solving latency \times habitat type interaction to test whether the effect of solving latency differs between urban and forest pairs.

In all analyses, we also tested the effects of neophobia, response to predation risk, response to human disturbance, and their interactions with habitat type by adding each to the initial models separately (we did not include all potential confounders into one model to avoid over-parameterization). Each initial model was then reduced by omitting the term associated with the largest P value stepwise, except that we always retained the predictor that we were primarily interested in, i.e., habitat type in the Cox's analyses and problem-solving latency in the mixed models, regardless of their significance level, to estimate their effects even if they were not significant. Also, we always kept habitat type in the mixed models to control for the difference between urban and forest breeding parameters (Solonen 2001; Bailly et al. 2015). Other predictors and interactions were omitted if they had $P > 0.05$.

We used two approaches throughout the analyses: in one set we used pairs as the units of analysis, while in the other set we used the data of individuals. This dual approach was necessary because we had only one solver individual per pair, so the confounding variables can be calculated in two equally relevant ways. First, when analysing pairs, we considered that breeding success may depend on the traits of both parents, thus we coded the parents' age class and trapping status as whether or not the pair contained at least one individual that was older than second calendar year and had been trapped before the behavioural tests, respectively, and we expressed neophobia, response to predation risk, and response to human disturbance as the average of the two parents' values. Second, when analysing individuals, we focused on the traits of the solving parent (this could not be done in the analyses of pairs because there was no solving parent in the unsuccessful pairs). Thus, in the

analyses of females, we compared the data of solver females to non-solver pairs (i.e. non-solver females), omitting those pairs in which the male was the solver because in these latter cases we could not measure female performance. Similarly, in the analyses of males, we used the data of solver males and non-solver pairs and omitted the pairs in which the female was the solver (note that this could not be done in the obstacle-removal task with reasonable power because there were only 5 successful males; thus, this task was analysed only by using pair and female performance). In these individual-level analyses, we used the solver parent's age class, trapping status, neophobia, response to predation risk, and response to human disturbance as predictors.

Results

Individual consistency of problem-solving performance

Individuals that were tested in two consecutive breeding episodes of the same year in the obstacle-removal task showed a strong correlation between the two repeated measurements (Spearman rank correlation, all birds: $r_s = 0.73$, $P < 0.001$, $N = 18$; females: $r_s = 0.72$, $P = 0.001$, $N = 17$; Fig. S2). Their solving time decreased from 13.36 ± 2.84 min in the first test to 7.68 ± 2.91 min in the second test (Fig. S2; paired t test, all birds: $t_{17} = 4.87$, $P < 0.001$; females: $t_{16} = 4.50$, $P < 0.001$, solver females only: $t_{12} = 5.71$, $P < 0.001$). In the food-acquisition task, 10 out of 14 pairs were unsuccessful in both the first and the second test; one female was successful in the first but not the second test, while one male and two females solved both tests within 2 min (Fisher's test for the 2×2 contingency table of the occurrence of success in the first and second food-acquisition test: $P = 0.011$). Solving latency did not correlate between the obstacle-removal task and the food-acquisition task (all birds: $r_s = -0.15$, $P = 0.345$, $N = 43$; females: $r_s = -0.29$, $P = 0.155$, $N = 25$; males: $r_s = 0.29$, $P = 0.264$, $N = 18$).

Urbanization and problem-solving performance

When tested for the first time in each task, urban pairs solved both tasks significantly more often (Table 1) and faster than forest-dwelling pairs (Table 2; Fig. 1). When we analysed the sexes separately, females showed the same habitat difference in both tasks, while there was no difference between urban and forest males in either task (Table 2; note that sample sizes were smaller for males than females in both tests, and effect sizes were similar for

Table 2 Effects of habitat urbanization and other traits on problem-solving latencies

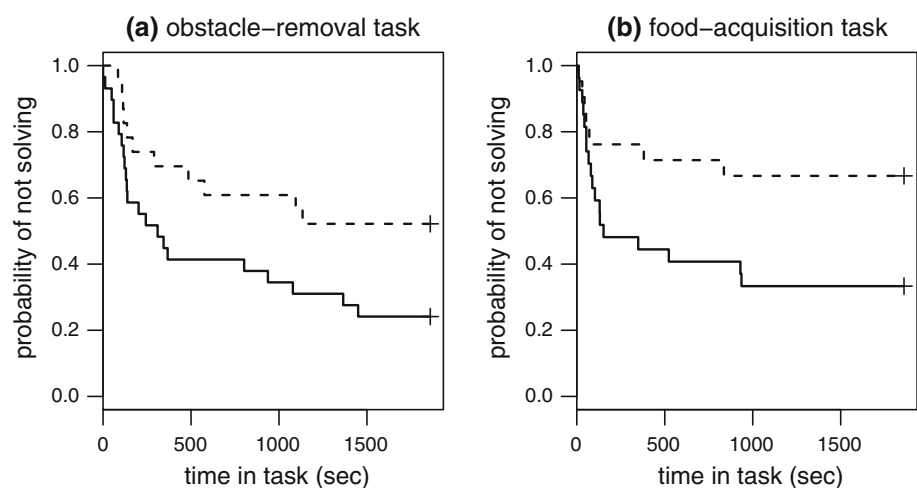
Model	Predictor variables	$b \pm SE$	Z	P	e^b [95 % CI]
Obstacle-removal task					
Pairs ($N = 52$)	Habitat ^a	1.27 ± 0.41	3.12	0.002	3.55 [1.60; 7.85]
	Total provisioning rate ^b	-0.91 ± 0.37	-2.43	0.015	0.40 [0.19; 0.84]
Females ($N = 46$)	Habitat	0.95 ± 0.41	2.33	0.020	2.58 [1.16; 5.73]
Males ($N = 23$)	Habitat	0.69 ± 0.91	0.76	0.448	2.00 [0.33; 11.98]
Food-acquisition task					
Pairs ($N = 48$)	Habitat	0.90 ± 0.45	2.01	0.044	2.46 [1.02; 5.92]
Females ($N = 36$)	Habitat	1.78 ± 0.77	2.31	0.021	5.95 [1.31; 26.94]
Males ($N = 34$)	Habitat	0.48 ± 0.59	0.82	0.411	1.62 [0.51; 5.11]

Table shows the results of the final Cox's proportional hazards models. Positive parameter estimates (b) indicate positive effect on solving speed (i.e. shorter latencies). Exponentially transformed parameter estimates (e^b) show the proportional change in hazard ratio in response to unit change of predictors

^a Urban compared to forest

^b Sum of visits of both parents in the 30-min pretest observation, divided by the number of chicks

Fig. 1 Problem-solving latency in the two tasks in forests (dashed line) and urban habitats (solid line). The figures show the change over test time in the probability of not solving; a steeper decrease in probability indicates faster problem solving



the sexes in the obstacle-removal task). Pairs with higher provisioning rate had shorter solving latency in the obstacle-removal task, but there was no such effect in the analyses of individuals or in the food-acquisition task (Table 2). No other investigated variable had statistically significant effect on solving latency in either task.

Breeding success and problem-solving performance

In the obstacle-removal task (Table 3), faster pairs had higher hatching success (Fig. 2b) and more fledglings (Fig. 2c), but clutch size (Fig. 2a), proportion of chicks fledged (Fig. 2d), and fledglings' mean body mass or tarsus length (Fig. 2e, f) did not correlate with problem-solving latency. Clutch size, the number of fledglings, and mean fledgling mass were lower in urban than forest habitats (Table 3). The interaction between solving latency and habitat type was not significant in any analysis (Table S1). None of the variables describing breeding success was related to neophobia, response to

predation risk, or response to human disturbance, and their interactions with habitat type. All these results were qualitatively the same when we analysed females instead of pairs (the details of all non-significant results are available from the authors upon request).

In the food-acquisition task, solving latency was not related to any measure of breeding success (Table S2; Fig. S3) regardless the unit of the analysis (pairs, males, or females), and the interaction between solving latency and habitat type was also not significant in any analysis (Table S3).

Discussion

In this study, we tested the innovative problem-solving performance of urban and forest-dwelling great tits in two tasks. In both tasks, we found that pairs in urban habitats were more successful (i.e. had lower latencies to solve, and

Table 3 Effects of problem-solving latency in the obstacle-removal task and habitat urbanization on breeding success ($N = 52$ pairs)

Dependent variable	Predictor variables	$b \pm SE$	df	t	P
Clutch size	Intercept	12.32 ± 0.40	47	30.83	<0.001
	Latency ^a	-0.02 ± 0.01	47	-1.13	0.265
	Habitat ^b	-3.15 ± 0.39	2	-8.08	0.015
Hatching success	Intercept	3.78 ± 0.57	47	6.61	<0.001
	Latency	-0.04 ± 0.02	47	-2.14	0.038
	Habitat	-0.95 ± 0.48	2	-1.98	0.187
Number of fledglings	Intercept	12.26 ± 0.67	47	18.36	0.000
	Latency	-0.05 ± 0.02	47	-2.45	0.018
	Habitat	-4.87 ± 0.76	2	-6.45	0.023
Proportion of chicks fledged	Intercept	5.97 ± 1.46	47	4.08	<0.001
	Latency	-0.02 ± 0.02	47	-0.97	0.336
	Habitat	-3.95 ± 1.43	2	-2.77	0.110
Fledgling body mass	Intercept	18.35 ± 0.81	45	22.58	<0.001
	Latency	-0.01 ± 0.02	45	-0.50	0.622
	Habitat	-3.37 ± 0.47	2	-7.10	0.019
	Hatching date ^c	0.11 ± 0.03	45	4.25	<0.001
	Trapping status ^d	-1.70 ± 0.57	45	-2.98	0.005
Fledgling tarsus length	Intercept	20.09 ± 0.29	45	70.04	<0.001
	Latency	0.01 ± 0.01	45	1.07	0.290
	Habitat	-0.70 ± 0.19	2	-3.63	0.068
	Hatching date	0.02 ± 0.01	45	2.63	0.012
	Trapping status	-0.58 ± 0.19	45	-3.00	0.004

The table shows the results of final mixed models (with study site as random factor; quasi-binomial error for hatching success and proportion of chicks fledged)

^a Problem-solving latency in minutes

^b Urban compared to forest

^c Number of days since 1st of May

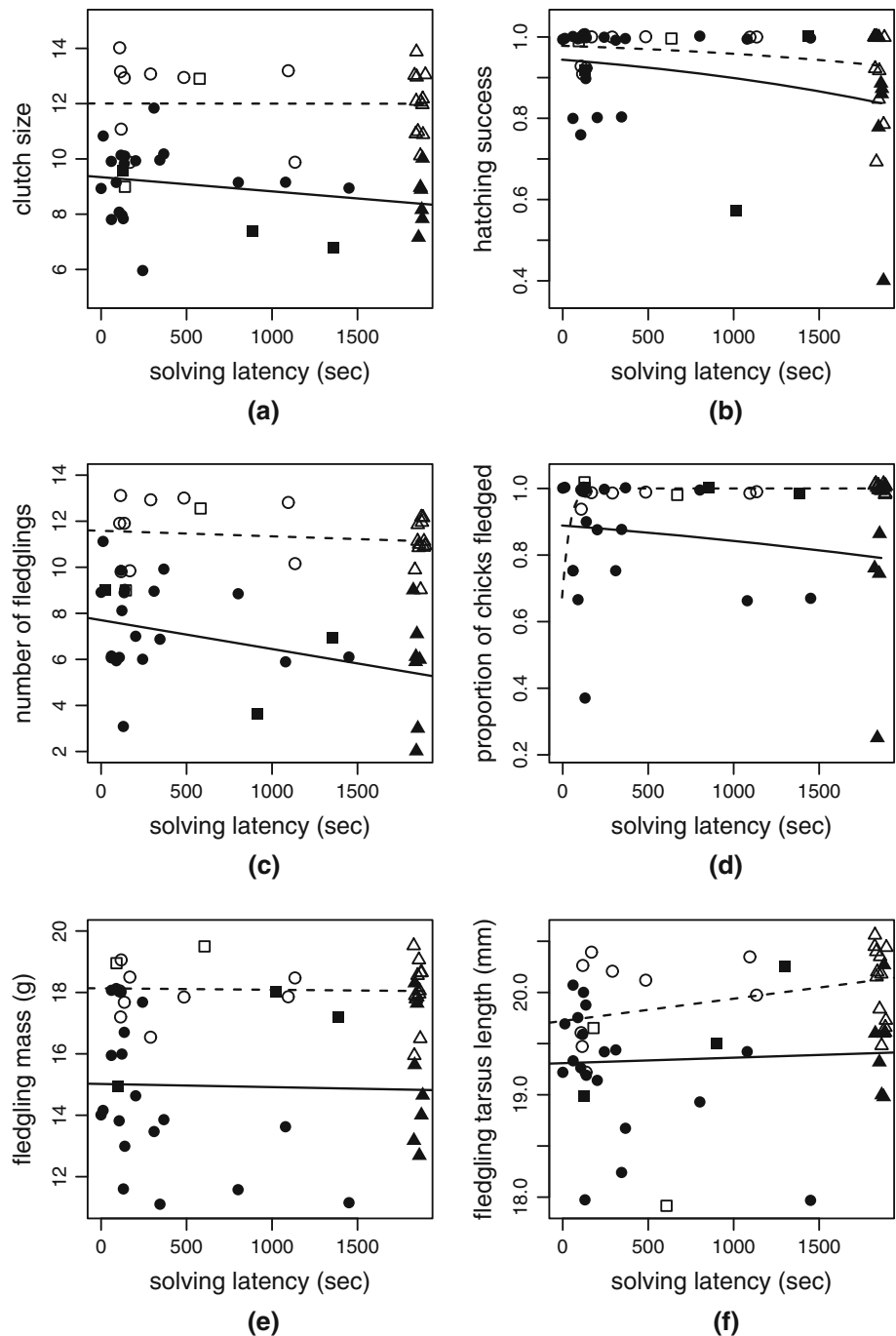
^d At least one versus none of the parents trapped

higher proportion of solving) than pairs breeding in forests. Similar differences were found in food-extracting tasks in common mynas *Acridotheres tristis* (Sol et al. 2011), Barbados bullfinches *Loxigilla barbadensis* (Audet et al. 2015), and house sparrows *Passer domesticus* (Liker and Bókonyi 2009), although the habitat effect seems to vary with task type and/or difficulty (Audet et al. 2015; Papp et al. 2015). In our present study, the habitat difference was significant in females but not in males. One possible explanation for this is that the tasks may have been more motivating for females than for males, because the reward in both situations was related to parental care, i.e., the access to the chicks in the obstacle-removal task and access to chick food in the food-acquisition task. Although urbanization may select for better problem-solving skills in birds, males may be less motivated to use those skills in a parental care context because their confidence of paternity can be lower due to extra-pair matings. On average, ca. one third of the broods in great tit populations have been found to contain extra-pair offspring (reviewed by García-Navas et al. 2015), and female promiscuity occurs at all 4 of our

study sites (unpubl. data). Alternatively, the sex difference we found might be attributable to the lower statistical power for males due to smaller sample sizes, at least in the obstacle-removal test in which the estimated size of habitat effect was similar for the two sexes.

When looking at the relationships between problem-solving latencies and aspects of breeding success, we found no correlation with performance in the food-acquisition task, whereas performance in the obstacle-removal task correlated positively with hatching success and the number of fledglings, but not with the proportion of chicks that fledged or fledgling size. These results partially mirror and confirm further the findings of two similar studies on great tits in forest habitats (Cole et al. 2012; Cauchard et al. 2013). Measuring problem-solving performance in a lever-pulling foraging task prior to breeding, Cole et al. (2012) found that solver females had larger clutch sizes and more but not heavier fledglings than non-solver females, while the effect of male performance was much weaker. Cole et al. (2012) interpreted these findings as a result of solvers' more efficient foraging during the early stages of breeding

Fig. 2 Relationship of breeding success with solving latency in the obstacle-removal task in forests (*dashed lines, open symbols*) and urban habitats (*solid lines, filled symbols*). The lines were fitted from linear mixed models containing the interaction between habitat and solving latency. *Circles, squares, and triangles* denote pairs in which the solver was the female, the male, or none of the parents, respectively; overlapping data points were jittered



when food is not yet abundant. Solvers had shorter working days and smaller foraging ranges which may have allowed them to invest more time to nest attendance (Cole et al. 2012). This may also explain the higher hatching success of solver females in our study. In another population, Cauchard et al. (2013) measured great tits' performance in a string-pulling obstacle-removal task during breeding and found that pair performance positively correlated with clutch size, hatching success and also nestling survival. This difference between populations might be due to fine-

scale variation along environmental gradients in the pay-offs of problem-solving skills (Morand-Ferron et al. 2015).

Despite their superior problem-solving performance, urban pairs had significantly reduced breeding success compared to forest pairs in terms of clutch size and the number and weight of fledglings. These results are in line with findings on several avian species, indicating that urban birds face difficulties with obtaining the resources for egg production and chick feeding (Chamberlain et al. 2009; Seress et al. 2012; Bailly et al. 2015). We expected that,

given such difficult conditions, superior problem-solving skills would confer disproportionately greater benefits to urban birds during reproduction than to forest birds. Surprisingly, however, we found no interaction between the effects of habitat type and problem-solving performance in either of our tests for any measure of breeding success. This was not due to any confounding effect of the birds' neophobia and sensitivity to predation risk or human disturbance, because none of these traits were correlated with either problem-solving performance or any measure of breeding success. Thus, our study revealed no strong difference between forests and urban habitats in the relationship between problem-solving and breeding success, providing no support for the idea that urbanization selects for enhanced innovativeness. A potential explanation is that increased benefits of solvers may be negated by increased costs in urban habitats. For example, individuals with better problem-solving performance were found to be less competent in agonistic interactions (Cole and Quinn 2012; Kozlovsky et al. 2014, 2015) or attacked more frequently by their flock mates (Preisner et al. 2015), although the relationship between problem solving and competitiveness is not unequivocal (reviewed by Griffin and Guez 2014; Preisner et al. 2015; Quinn et al. 2016). Thus, stronger competition for food during breeding in urban habitats (Foltz et al. 2015) might reduce the reproductive payoffs of problem-solving skills. Also, solvers can be more prone to desert their broods in response to disturbance (Cole et al. 2012), which might reduce their success in habitats with frequent disturbance by humans and nest predators. Our present results, however, did not reveal any relationship between sensitivity either to predation risk or to human disturbance and problem-solving performance; moreover, nest desertion after trapping occurred at only one urban nest in our study.

Despite significant individual consistency (at least in the obstacle-removal test where the data enabled meaningful analysis), individual performance did not correlate between the two tasks. This result is in accordance with the cautionary views that single problem-solving tests cannot be assumed to measure an overall (or any) cognitive capacity without studying the underlying mechanisms (Rowe and Healy 2014; Thornton et al. 2014; Griffin 2016; Reader et al. 2016), and with other findings that problem-solving performance can vary across task types and contexts (reviewed by Thornton and Lukas 2012). In our study, the inconsistency between tasks could have arisen from motivational differences, i.e., solving the obstacle-removal task was imperative to provision the chicks, whereas solving the food-acquisition task merely offered extra food items. Alternatively or additionally, the two tests may have assayed at least partially different traits. In the obstacle-removal task, removing the feather usually required few

attempts, suggesting that no great physical force or dexterity was needed, but fast solving might have relied on the perception of object permanence, i.e., recognizing that the entrance is still in its original place despite being invisible (Etienne 1984; Emery 2006). In contrast, solving the food-acquisition task required a combination of motor actions and probably the inhibition of ineffective actions such as pecking at the centre of the lid, as in other foraging tasks where performance relies on motor diversity (Griffin et al. 2014; Diquelou et al. 2015), perseverance and/or paying attention to movement cues (Overington et al. 2011; Thornton and Samson 2012; Audet et al. 2015). A further factor that may have influenced solving performance in our tests is motivation due to variation in the demand for parental care, e.g., in the levels of chicks' hunger. This could explain why solving speed was faster when the parents' total provisioning rate before the test was lower. Furthermore, motivation may be greater if the parents have more chicks to feed; thereby, the relationship we found between solving speed and the number of fledglings might mean that the latter was influencing the former and not vice versa. The causality of this relationship can only be ascertained by brood-size manipulation experiments; nevertheless, we can speculate that motivational differences are not likely to be the main source of our results, for two reasons. First, forest pairs had significantly larger broods than urban pairs, yet the latter were much more successful in problem solving. Second, apart from the correlation between the pair's solving speed and their total provisioning rate, we found no evidence for motivational effects: the pretest provisioning rate of the solver individuals did not correlate with their problem-solving speed nor did any other variable such as time of day or chick age which probably reflect the chicks' need. However, motivation is very difficult to quantify or control for in correlational studies (Griffin and Guez 2016). Since our study was not designed to test the role of motivation or other proximate mechanisms underlying performance in the tasks, future experiments could clarify whether urban birds were better solvers due to higher motivation or better spatial cognition or more diverse motor skills.

In sum, we found that better problem-solving performance is associated with higher success in some aspects of breeding, but this relationship did not differ between urban and forest habitats, despite faster solving in the former. If there is no greater net benefit of innovativeness in terms of breeding success in cities than in forests, why are urban birds better solvers? We propose two non-exclusive explanations for this. Firstly, the enhanced benefits of innovativeness for urban birds might manifest in increased juvenile/adult survival. Although Cole et al. (2012) found no difference between solver and non-solver great tits' survival rates in a forest habitat, no systematic study has yet tested whether innovativeness is related to survival in

urbanized habitats and whether this effect varies along the urban–rural gradient (Morand-Ferron and Quinn 2015). Secondly, urban birds might be less constrained by the trade-offs that have been implicated between innovativeness and other fitness-related traits, i.e., it is possible that some of the costs of problem-solving are actually lower in urban environments. For example, risk sensitivity might be reduced by habituation to humans (Geffroy et al. 2015), whereas being less competitive might be less costly in cities due to altered distribution and abundance of food sources such as bird feeders (Shochat et al. 2006; Tryjanowski et al. 2015), although the latter hypothesis received little empirical support so far (Bókonyi et al. 2010). A further proposed cost of cognitive skills is the development and maintenance of energetically expensive brain tissue (Kotrschal et al. 2013, 2015); urban birds might afford not paying some of these costs if instead they have more opportunities to explore and learn about their environment and practice various tasks. It has been suggested that experience with diverse foraging substrates in urban habitats enhances motor diversity and thereby problem-solving performance (Diquelou et al. 2015). Exploring how these constraints and trade-offs contribute to innovativeness and the underlying cognitive and other mechanisms in various habitats will further our understanding about how animals succeed in exploiting their environments in our urbanizing world.

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Compliance with ethical standards

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).

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