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Author for correspondence:
Pizza Ka Yee Chow
e-mail: pizzachow@orn.mpg.de; kyc202.pc@gmail.com

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Characteristics of urban environments and novel problem-solving performance in Eurasian red squirrels

Pizza Ka Yee Chow[1,2,3], Kenta Uchida[2,4], Auguste M. P. von Bayern[1] and Itsuro Koizumi[2]

[1]Max Planck Institute for Ornithology, Eberhard-Gwinner-Strasse, 82319 Starnberg, Germany
[2]Division of Biosphere Science, Faculty of Environmental Earth Science, Hokkaido University, N10W5 Sapporo, Hokkaido 060-0810, Japan
[3]Department of Psychology, University of Exeter, Exeter EX4 4QG, UK
[4]Department of Ecology and Evolutionary Biology, University of California Los Angeles, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, USA

PKYC, 0000-0002-8208-592X; KU, 0000-0001-7998-1363; AMPvB, 0000-0002-0981-9456

Urban environments can be deemed 'harsh' for some wildlife species, but individuals frequently show behavioural flexibility to cope with challenges and demands posed by life in the city. For example, urban animals often show better performance in solving novel problems than rural conspecifics, which helps when using novel resources under human-modified environments. However, which characteristics of urban environments fine-tune novel problem-solving performance, and their relative importance, remain unclear. Here, we examined how four urban environmental characteristics (direct human disturbance, indirect human disturbance, size of green coverage and squirrel population size) may potentially influence novel problem-solving performance of a successful 'urban dweller', the Eurasian red squirrel, by presenting them with a novel food-extraction problem. We found that increased direct human disturbance, indirect human disturbance and a higher squirrel population size decreased the proportion of solving success at the population level. At the individual level, an increase in squirrel population size decreased the latency to successfully solve the novel problem the first time. More importantly, increased direct human disturbance, squirrel population size and experience with the novel problem decreased problem-solving time over time. These findings highlight that some urban environmental characteristics shape two phenotypic extremes in the behaviour-flexibility spectrum: individuals either demonstrated enhanced learning or they failed to solve the novel problem.

1. Introduction

Urban environments have unique landscapes that are different from most, if not all, types of natural environment. An urban area typically encompasses humans, buildings, traffic and fragmented green areas. Together, these characteristics of urban environments and the increased speed of environmental change may be considered 'harsh' for some species (e.g. [1–3]), analogous to other kinds of extreme environmental conditions such as extreme temperature or unpredictable food availability [4,5]. However, each of these characteristics may represent 'harshness' on its own such that it becomes a stressor, and may pose a different challenge to urban wildlife [6,7], which may ultimately determine whether a species thrives or declines. In responding to these challenges and stressors, urban wildlife has been reported to show behavioural flexibility, a phenotypic trait that is broadly conceived as the ability to adjust behaviours according to changes or demands in environments [8]. Although research about the behaviour of urban wildlife remains low [9], interests in understanding which and how urban environmental characteristics would affect behavioural flexibility is growing [10]. As of yet, the relative importance of different environmental characteristics necessitating flexible behaviour within urban environments remains largely unclear. Nevertheless, the significance of such investigations will allow us to understand how variation in behavioural responses may relate to a species's successful settlement, and the growth and decline of their population sizes in urban environments [11–16].

Despite the field still being in its infancy, an increasing number of studies have suggested that anthropogenic-dominated environments have selected for an ability to 'innovate', or to solve novel food-extraction problems [1,17–20]. In novel problem solving, behavioural flexibility can be demonstrated when individuals use pre-existing behaviours to solve a new problem [21,22]. Urban wildlife has been shown to be more proficient (i.e. more individuals succeed in extracting food) and more efficient (i.e. lower solving latency to reach a success) in solving novel or complex food-extraction problems than their rural counterparts [1,17–20]. Such an enhanced ability has been suggested to be driven by harsh urban environments as a whole [1,23]. However, novel problem-solving performance has also been shown to vary between populations in urban habitats [24], along urbanization gradients [20] and in proportion to distance from the city centre [25]. These findings suggest that urban environmental characteristics such as increased humans and conspecific density, increased infrastructures, and decreased greenness may affect novel problem-solving performance (and thus the displayed flexibility) and therefore represent 'harshness' within environments. Accordingly, understanding which environmental characteristics exert the most influence on novel problem-solving performance can highlight conditions that facilitate or suppress the emergence of flexible behaviour.

To investigate which environmental characteristics in urban habitats are potentially deemed to be harsh and which would affect novel problem-solving performance, a plausible first step would be selecting those characteristics that have impacts on survival [26] or are likely to be related to stressors for wildlife. Here, we examined four urban environmental characteristics (i.e. direct human disturbance, indirect human disturbance, size of green coverage and squirrel population size) that are potential stressors, and thus represent harshness for a successful urban dweller, the Eurasian red squirrel (*Sciurus vulgaris*) [27–29]. We examined and compared how these urban environmental characteristics affected the squirrels' solving performance in a novel food-extraction problem by quantifying three behavioural measures. We evaluated the proportion of squirrels in each urban site that successfully solved the novel problem, individuals' solving latency (time in seconds) on the first success and individuals' solving latencies over time (i.e. learning speed). Urban red squirrels rely on green coverage for food and safety [30], but they are food and habitat generalists that also use anthropogenic resources [28,30]. They have shown behavioural adjustments such as increased tolerance to human disturbance [31,32]. Moreover, another population of this species has demonstrated a wide variation in solving a novel problem when tested with the same problem [33]. These suggest that this squirrel species is a good study model to examine the impact of certain environmental characteristics on novel problem-solving performance.

Our general hypothesis was that the examined, potentially 'harsh' environmental characteristics would affect novel problem-solving performance. However, it is not straightforward to generate predictions because of the few studies to date, and each aspect of an environmental characteristic may relate to different aspects of problem-solving performance (e.g. outcome and latency of solving a problem) differently. This means that 'harshness' may promote or impede novel problem-solving performance. Nevertheless, the few available studies have suggested that some of these urban environmental characteristics would be key stressors, shedding light on which and how environmental characteristics affect the outcome of solving novel problems (i.e. success or failure in food extraction) at the population level:

(1) *Direct human disturbance*. A short intensive exposure to the presence of a human has been shown to decrease success in solving a novel problem in wild-caught temporary captive urban juvenile house finches, *Haemorhous mexicanus* [34]. Such a decrease in success may be related to the perception of humans as potential threats, causing interference with the ability to solve novel problems even though urban house finches are typically habituated to the presence of humans. Given that standard measures such as flight initiation distance from approaching humans have shown that this squirrel species appears to adapt to the presence of humans, but also retreats from approaching humans [31,32,35], we propose to measure the intensity of direct human disturbance, and predict that an increased number of humans would decrease the proportion of success in solving novel problems.
(2) *Indirect human disturbance*. An increased number of buildings (e.g. households, shops) may reflect an increase in human activity. Success in solving novel problems (using new resources) that are available within squirrels' habitat may increase as a result of minimizing exposures to humans (especially for species that may not be entirely habituated to humans, as in the case for this squirrel species), avoiding other risks such as road death [36] or human and vehicle traffic around the area [37]. Alternatively, an increased number of buildings may also decrease success as the necessity to solve novel problems decreases if buildings provide alternative, easily accessible food sources (e.g. anthropogenic food sources from open garbage) around that area [38–40].
(3) *Green coverage*. Green coverage could be defined as the area (m^2) covered by trees in a site, and the (relative) availability or absence of green coverage in urban habitats reflects habitat suitability (food availability and safety) for squirrels. A decrease of green coverage in a site may decrease success in solving novel problems as a result of increased exposure to predation risk [41,42]. However, decreased green coverage may well indicate insufficient food supply, and thus increase the proportion of success as a result of the need to seek alternative food sources via solving novel problems.
(4) *Squirrel population size*. Several wildlife species may share the same urban habitats [43], but areas with high population density of the same species would increase the number of conspecifics using the same resources. Individuals of this species of red squirrels compete for the same resources [44]. At the individual level, an increased

number of squirrels in the same habitat may drive some individuals to solve novel problems as a result of 'necessity drive' [45] in securing resources. However, it is likely that only a few individuals would be able to compete for alternative food sources, leading to a decrease in the proportion of success in solving novel problems at site (population) level.

A few relevant studies have either measured the solving latency on the first success [1,42] or showed the change of learning speed over time [46] at the individual level. Accordingly, we predicted that squirrels would solve novel problem more quickly (i.e. decrease in solving latency) when exposed to increased urban stressors (i.e. increase in direct and indirect human disturbance or conspecific density, and decrease in green coverage).

2. Material and methods

(a) Environmental characteristics of the study sites

We collected data on 71 squirrels at 11 urban sites in Obihiro, Hokkaido, Japan, between May 2018 and January 2019. To capture the diversity of urban environments, sites were selected based on sight of squirrels, distance of site from the city centre, and avoiding proximity to major roads (as road death is the primary cause of fatality of this species [47]). These sites were scattered in the city that included green areas in a university campus, different urban parks and urban forests (see electronic supplementary material, table S1A). Selected sites were at least 800 m apart to avoid sampling the same individuals. We used the satellite mode in Google Maps to note the geographical location of each site (map of study sites), the size of each site (total area in m^2), green coverage (total area in m^2 that included tree coverage) and the number of human-built structures (e.g. houses, restaurants and stores) within and 50 m surrounding each site (which covered the minimum routine movement of urban red squirrels [48], and presumably, captured the greatest human-induced disturbance such as noise pollution, traffic, household and other human activities, but also the opportunity to encounter anthropogenic food).

All sites typically had Korean pine (*Pinus koraiensis*) and Manchurian walnut (*Juglans mandshurica* var. *sachalinensis*) on which red squirrels predominantly fed. There were one or two artificial feeders (e.g. uncovered plastic bottles or covered wooden boxes connected with a lid) provided for squirrels, and to a lesser extent, for birds within all sites. The presence of artificial feeders suggested that the squirrels had experience approaching novel stimuli and retrieving food from artificial devices. The feeders were empty when we checked them before the start of the experiment each day and before we re-baited the apparatus each time. In two study sites, humans occasionally providing supplementary food (e.g. sunflower/pumpkins seeds) on tree trunks or at the base of a tree [35]. In all sites, non-human potential threats (e.g. raptors, foxes, domestic cats) to urban squirrels were rare and the number of threats appeared to be comparable [31–32,49] (see electronic supplementary material, note S1 and table S1A).

We recorded the number of humans in a site 4–5 times daily for an average of 38 observation days in each site regardless of weather condition (see electronic supplementary material, note S2). Daily records were taken before setting up the experiment, before or after re-bating the apparatus and when the experiment ended for the day. Each record was obtained either from in-site recording or using distance-based methods. In-site recordings consisted of walking around the site and counting each human that walked passed the experimenter; this allowed us to count the number of humans more accurately if a site had a large area of bushes. Distance-based records meant dividing a site into four roughly equal areas and counting the number of humans in each area at the centre of the site or at the outer edge of the site; this minimized double counting. We divided the total number of humans across the daily four to five checks in a site and across all observation days by the number of observation days to obtain the mean number of humans in a site per day.

The identity and the number of squirrels residing in each site were predominantly determined using the mark–recapture method. Following Chow *et al*. [33] who used frame-by-frame analysis in Adobe Premiere Pro CS6 software, individuals were 'marked' by their individual characteristics (e.g. sex, shape and colour of body and face) when they first appeared from video footage and noted as 'recaptured' when the same individual reappeared in the videos (see electronic supplementary material, note S3). We also used the 'mark–resight' method, a relatively reliable measure for us, to count the population size (see electronic supplementary material, table S1B). We 'marked' a squirrel using its characteristics when we were walking on pathways or standing still in bushes and among trees, and noted 'resight' when we saw the same squirrel. Together, these records appeared to reveal the maximum (or actual) number of squirrels residing in each site. Because squirrels from the same population have been shown to retreat from approaching humans [31,32,35], records from the mark–resight method may be affected by the presence of the experimenter. Accordingly, we used the number of squirrels obtained from the mark–recapture method for analyses. We divided the number of squirrels by the corresponding site size to obtain squirrel population density for each site.

(b) Novel food-extraction problem

To examine novel problem-solving performance, we presented the squirrels with an established artificial food-extraction problem (hereafter, the novel problem) [50]. The solutions to the problem were considered counterintuitive for the squirrels and thus required behavioural flexibility in changing the approach to solve the problem (see more below). The same problem had been shown to be successfully solved by 60% of another red squirrel population [33], which renders the ceiling and floor effects unlikely (i.e. minimal variation in performance because the problem was either too easy or too difficult for individuals). The problem consisted of a transparent cube-shaped top (length 25 × width 25 × height 25 cm) and a wooden and plastic pyramid-shaped bottom (figure 1). Each side of the top had ten horizontally, but not vertically, aligned holes (each 2 cm × 0.9 cm, width × height). These holes were roughly aligned with the holes on the opposite side so that ten levers (each 29.8 × 1.5 × 0.5 cm thickness) could be inserted horizontally across the box. Ten hazelnut kernels were placed on each side of the box without levers (for 2 × 2 h) in order to minimize the squirrels' neophobic response as well as habituate them to this new box. Once the squirrels obtained all the nuts, we inserted ten levers across the box for the main experiment. Each lever had a three-sided nut container (transparent back: 2 cm × 1.5 cm and opaque side: 1.5 cm × 1.5 cm) 2.5 cm away from one end of a lever positioned just inside the box. The transparent back of the containers allowed the squirrels to see if there was a nut in the containers when they were on the opposite side of the box. This set-up also left 2.5 cm of both lever-ends outside the holes, which meant the squirrels could use their nose, teeth and front paws to manipulate a lever-end. The thickness of each lever was made to be thinner than the height of the holes, allowing squirrels to smell, but not reach, the nut. Five levers contained hazelnuts and the other five levers were empty, to serve as controls. We randomized which levers contained a hazelnut and their facing direction across trials. The whole box was secured by six metal legs, creating a 3.5 cm gap between

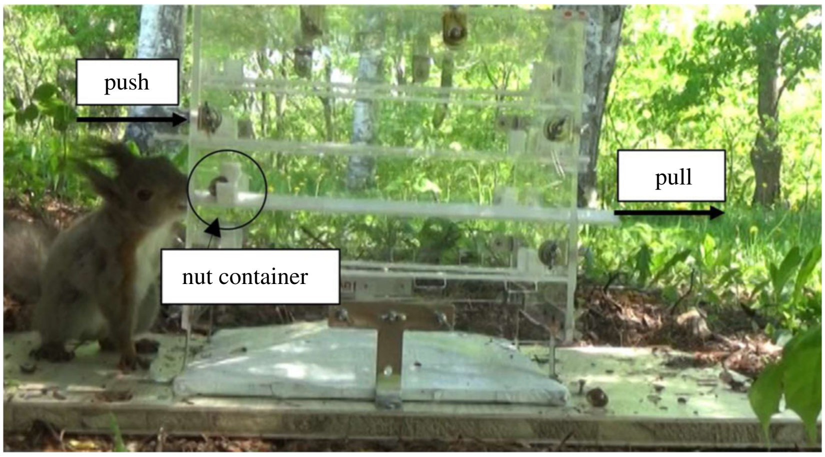

Figure 1. The novel food-extraction problem that was used to examine variation in behavioural flexibility. The solutions for this problem are counter-intuitive to squirrels in which a squirrel (demonstrated by Mario here; also see video 'PST' in the electronic supplementary material) has to push (instead of pull) a lever-end if it is close to a nut container, or pull (instead of push) the lever-end if it is far from the nut container so as to make a lever/nut drop (i.e. successful solving). (Online version in colour.)

the top and the bottom; the squirrels could obtain a nut upon successfully solving the problem, which meant they had to push (as opposed to pull) the near-end if they were close to a nut container, or pull (as opposed to push) the far-end if they were far from the nut container to make a lever/nut drop (see video).

The whole experiment, including the baiting and habituation, lasted at least two and a maximum of three weeks, depending on how quickly the squirrels could locate the baits in each site. This testing period allowed this food generalist species to explore the apparatus, and to recruit 'bold' and 'shy' individuals within each site to increase the participation rate (mean 90.7%, see electronic supplementary material, table S1). At each site, we chose a location (either close to a tree or inside bushes, and away from major roads) that could maximize the safety (e.g. avoid road kill and potential threats) for squirrels, and thus increased their comfort of visiting the apparatus. We baited the location with hazelnut kernels twice a day for 3–5 days prior to the experiment. Once we observed squirrels taking the nuts away from the location regularly (and checked the absence of nuts in the location), we set the apparatus at this baiting location. The performance was recorded by the video camera (placed 1 m away from the apparatus) that was also used to identify individuals. We followed the field protocol of Chow *et al.* [33], varying intertrial intervals between 45 min and 1.5 h (i.e. 3–4 times re-baiting every day from dawn to noon during squirrels' active period [28] regardless of weather conditions). This resulted in 4–5 instances of checking the apparatus per day, including setting it up at the location and collecting it when the experiment was completed on that day. As individual squirrels have slightly variable active times, such intertrial intervals maximized the chances of recording the performance of different individuals, while minimizing social interference or social learning (see electronic supplementary material, note S4). The start of the experiment at dawn (3.30 during the summer and 6.00 during the winter) also maximized the squirrels' participation rate because there were fewer human activities (e.g. morning exercises, dog walking) in a site. Because the squirrels were free to come and leave the task, the number of successes that a squirrel obtained varied in each trial and daily.

(c) Video analyses

We analysed novel problem-solving performance using frame-by-frame analysis in Adobe Premiere Pro CS6, following Chow *et al.* [33]. Two measurements were recorded for each manipulation, which was defined as when a squirrel touched a lever using any part of its body, until it stopped doing so. The first measurement was the solving outcome (success' or 'failure'). A 'success' was scored when a squirrel used any part of its body to cause a lever/nut drop (see video 'PST' in the electronic supplementary material), whereas a 'failure' was measured when the squirrel had manipulated any lever, but did not solve the problem throughout the course of this experiment. The second measure was solving latency (in seconds) of each manipulation (regardless of solving outcome), measured from when a squirrel started manipulating a lever using any part of its body, until either it stopped manipulating that lever (in the case of a failure) or until it made the lever/nut drop (in the case of a success).

Following Chow *et al.* [33], we classified individuals as 'problem solvers' or 'non-solvers'. Problem solvers were squirrels that successfully solved the task repeatedly (more than once regardless of whether successes occurred within a trial or between trials), whereas non-solvers were those that solved the task only once but could not repeat the success or could not solve the task throughout the course of this study. We obtained the proportion of successful individuals by counting the number of problem solvers divided by the total number of squirrels that participated in this problem for each site. Given that problem solvers could manipulate levers with and without rewards or made several unsuccessful manipulations in different trials before a success occurred, we obtained the latency on the first success for each problem solver by summing the durations of all unsuccessful manipulations until the first success occurred. We further examined whether environmental characteristics affected the learning speed of solving this problem over time. To do so, we employed the method of Chow *et al.* [33], who showed that another population of red squirrels tested on the same problem required about 40 successes (accounting for successes occurring both within a trial and between trials) for reaching asymptotic performance. We assessed learning performance over time from a broader perspective in relation to increased experience by taking the mean of every five latencies to success that a problem solver made on different occasions as a 'block' (thus, resulting in eight success blocks). We then examined their learning performance across success blocks.

(d) Data analyses

Data were analysed using R v. 3.5.2 (R Development Core Team) and SPSS v. 25 (IBM Inc.). We avoid multicollinearity before and after running a model using Pearson's correlation (r) and VIF, respectively (see electronic supplementary material, note S5). Subsequent analyses excluded any variables that had moderate

Table 1. Four selected environmental characteristics as predictors for (*a*) proportion of success at the population level ($n = 11$) and (*b*) individuals' solving latency on the first success in the novel problem ($n = 38$). Each model includes four standardized variables: (i) direct human disturbance, measured as mean number of humans in each site per day (i.e. the total number of humans from the daily 4–5 times of checks per day and across all observation days divided by the number of observation days in each site); (ii) indirect human disturbance, measured as the number of human-built structures such as household or shops within and 50 m surrounding a site; (iii) green coverage, measured as the area (m^2) covered by trees in a site; and (iv) squirrel population size, measured as the number of squirrels residing in each site. This table includes standardized estimates (Est), standard errors (s.e.), *Z*- and *p*-values for each model. Bold values indicate $p \leq 0.05$.

	(*a*) the proportion of success				(*b*) solving latency on first success			
predictors	Est	s.e.	*Z*	*p*	Est	s.e.	*Z*	*p*
direct human disturbance	−1.17	0.26	−4.50	**<0.001**	−0.12	0.16	−0.08	0.941
indirect human disturbance	−0.61	0.23	−2.70	**0.007**	−0.26	0.18	−1.42	0.155
green coverage	−0.35	0.22	−1.61	0.108	−0.02	0.16	−0.10	0.923
squirrel population size	−0.77	0.23	−3.38	**<0.001**	−0.51	0.17	−3.00	**0.003**

to high correlation ($r \geq 0.5$) [51] (electronic supplementary material, tables S2–S4). Because sites varied in size, which may affect the number of buildings surrounding a site or the number of humans present and the green coverage (i.e. tree-covered space) within a site, we scaled all variables relative to the size of a site. However, one or more of the scaled variables were moderately to highly correlated with other variables but not among the original variables (electronic supplementary material, tables S2–S4). While the scaling by the site size did not essentially change the results (electronic supplementary material, tables S2–S4), we were required to drop one or more variables of interest in models when examining the research questions. Accordingly, subsequent analyses included the original variables, which allowed us to examine all environmental characteristics of interests in relation to novel problem-solving performance (but see electronic supplementary material, tables S2–S4 for additional analyses). Unless otherwise specified, all the models included four fixed factors, namely the number of buildings, the mean number of humans in a site per day, green coverage (m^2) and squirrel population size. Prior to all model testing, we standardized all the variables so as to compare the effect size of variables on the same scale. We checked the randomness of error distribution in each model. We report pseudo R^2 for each model using package 'MuMIn' [52], the original values (mean ± standard error) in the results and figures. We considered a significant two-tailed test when $\alpha \leq 0.05$.

We examined the predictors for the proportion of success at site (population) level using beta regression in the package 'betareg' [53]. We examined the predictors for individuals' solving latency on the first success (and included squirrel identity as a random variable) using a generalized linear mixed model (GLMM) with gamma log link function to accommodate the positively skewed continuous response variables in package 'glmmTMB' [54]. A GLMM model with gamma log link function was also used to examine the predictors for the solving latency across eight success blocks (i.e. learning performance over time), with success block number, individual identity and their interaction as random variables. In this model, we dropped the variable of the number of buildings, because it was highly correlated with another two variables (see electronic supplementary material, note S6) and we were more interested in the environmental characteristics within than outside a site in relation to novel problem-solving performance (but also see electronic supplementary material, table S5 for additional analyses). We first examined which and how these environmental variables (mean number of humans in a site per day, green coverage and population size), alongside success block number, affected the overall learning performance (solving latency across eight success blocks). We then broke down the learning performance into the initial learning phase (1st–4th success blocks) and later learning phase (5th–8th success blocks) in order to examine whether the environmental characteristics continue to affect problem solvers' performance when the learning process is optimized.

3. Results

(a) Predictors of first success in solving the novel problem

We recorded 79 squirrels across 11 sites, and 71 (90%) squirrels participated in the novel problem. These squirrels mostly (greater than or equal to 99%) manipulated levers with food, indicating their behaviour was food-oriented regardless of site. However, of these 71 squirrels, only 38 (53.5%) were problem solvers who successfully extracted food or caused a lever to drop more than once. The model of the four environmental characteristics for the proportion of first success was pseudo $R^2 = 0.77$. At the population level, we found that increased proportion of first success in the novel problem was related to the decreased mean number of humans presented in a site per day (beta regression: $\chi^2_1 = 20.21$, $p < 0.001$), the number of buildings ($\chi^2_1 = 7.26$, $p = 0.007$), and squirrel population size ($\chi^2_1 = 11.39$, $p < 0.001$; table 1*a*; electronic supplementary material, figure S1). The mean number of humans present in a site per day had the highest effect among the significant variables, followed by squirrel population size (table 1*a*). Problem solvers took 13.41 ± 2.11 s (mean ± s.d.) to reach their first success. The model for the solving latency on the first success was pseudo $R^2 = 0.22$. Squirrel population size was the only significant factor (GLMM: $\chi^2_1 = 9.01$, $p = 0.003$; table 1*b*; electronic supplementary material, figure S2) affecting the solving latency on the first success; individuals residing in sites with increased squirrel population size had lower solving latency of the first success.

(b) Predictors for solving latency across successes

Nine (out of 38) problem solvers completed eight success blocks (i.e. solved the problem 40 times), and we analysed their learning performance. The overall solving latency across success blocks was predicted by the mean number

Table 2. This table contains standardized estimates (Est), standard errors (s.e.), *Z*- and *p*-values for the effects of success block and environmental characteristics on learning performance (solving latency across success blocks) broken down by (*a*) across all eight success blocks, (*b*) initial learning (1st–4th success blocks) and (*c*) later learning (5th–8th success blocks) ($n = 9$ squirrels from seven sites). Measurement of the environmental characteristics include: (i) direct human disturbance, measured as mean number of humans in each site per day (i.e. the total number of humans from the daily 4–5 times of checks per day and across all observation days divided by the number of observation days in each site); (ii) green coverage, measured as the areas (m^2) covered by tree canopies in a site; and (iii) squirrel population size, measured as the number of squirrels residing in each site. Bold values indicate $p \leq 0.05$.

response	predictors	Est	s.e.	*Z*	*p*
(*a*) solving latency across eight success blocks	direct human disturbance	−0.15	0.06	−2.45	**0.014**
	green coverage	−0.11	0.06	−1.89	0.059
	squirrel population size	−0.13	0.05	−2.32	**0.020**
	success block number				
	success block number 2	−0.50	0.20	−2.55	**0.011**
	success block number 3	−0.97	0.17	−5.54	**<0.001**
	success block number 4	−1.43	0.14	−10.00	**<0.001**
	success block number 5	−1.12	0.12	−10.47	**<0.001**
	success block number 6	−1.35	0.16	−8.42	**<0.001**
	success block number 7	−1.55	0.19	−8.02	**<0.001**
	success block number 8	−1.61	0.13	−12.39	**<0.001**
(*b*) solving latency in initial learning (i.e. 1st–4th success blocks)	direct human disturbance	−0.28	0.07	−3.87	**<0.001**
	green coverage	−0.14	0.07	−2.06	**0.039**
	squirrel population size	0.02	0.07	0.34	0.735
	success block number				
	success block number 2	−0.50	0.23	−2.16	**0.031**
	success block number 3	−0.97	0.16	−5.89	**<0.001**
	success block number 4	−1.43	0.12	−12.14	**<0.001**
(*c*) solving latency in later learning (i.e. 5th–8th success blocks)	direct human disturbance	−0.08	0.07	−1.15	0.250
	green coverage	−0.13	0.07	−1.16	0.101
	squirrel population size	−0.26	0.07	−3.65	**<0.001**
	success block number				
	success block number 2	−0.11	0.15	−0.69	0.488
	success block number 3	−0.31	0.20	−1.53	0.125
	success block number 4	−0.37	0.12	−3.03	**0.002**

of humans in a site per day (GLMM: $\chi^2_1 = 6.01$, $p = 0.014$), squirrel population size ($\chi^2_1 = 5.40$, $p = 0.020$) and success block number ($\chi^2_7 = 226.10$, $p < 0.001$; table 2*a*; electronic supplementary material, figure S3). This model showed a pseudo $R^2 = 0.87$. To examine whether problem solvers were flexibly responding to humans, we ran an additional model by including the mean number of humans in a site corresponding to each success block, success block number and their interaction, whereas success block, individual identity and their interaction as random variables. This model showed a pseudo $R^2 = 0.96$, with decreased solving latency across blocks was predicted by the increased mean number of humans in a site corresponding to each success block ($\chi^2_1 = 8.01$, $p = 0.005$), success block number ($\chi^2_7 = 299.68$, $p < 0.001$) and their interaction ($\chi^2_7 = 16.81$, $p = 0.019$). That is to say, squirrels solved the novel problem quicker with increased human exposures and successful solving experience.

Regarding performance in the initial and later learning phase, the problem solvers decreased their solving latency in both learning phases (initial: $\chi^2_3 = 153.56$, $p < 0.001$; later: $\chi^2_3 = 10.10$, $p = 0.018$). The model for the initial learning phase showed a pseudo $R^2 = 0.88$. Decreased solving latency across blocks was predicted by increased mean number of humans in a site per day ($\chi^2_1 = 14.98$, $p < 0.001$) and green coverage ($\chi^2_1 = 4.26$, $p = 0.039$). The number of humans in a site per day had a greater effect than green coverage (table 2*b*). Performance in later learning was affected by squirrel population size (pseudo $R^2 = 0.84$, $\chi^2_1 = 13.32$, $p < 0.001$; table 2*c*).

4. Discussion

By narrowing down urban environments as a whole to specific environmental characteristics within and around a site, we focused on four characteristics that potentially symbolize 'harshness' for urban species. We show the relative importance of these characteristics in relation to solving a novel food-extraction problem. Among the environmental characteristics of interest, the mean number of humans in a site per day and squirrel population size play a relatively important role. Our measurement of each environmental characteristic further provides some insights as to which aspect of a stressor may affect flexible behaviour in urban environments. Together, these results reveal some of the potential selective pressures exerted by urban environments in varying behavioural flexibility, which in turn contributes to the understanding of how this evolutionarily favourable trait emerges and develops.

Our first environmental characteristic of interest was direct human disturbance, measured as the mean number of humans in a site per day. Increased direct human disturbance directly decreased the proportion of first success in solving this novel problem at the population level, and thus confirms our prediction. This result is in line with the finding in temporarily captive house finches [34], for which the presence of a human represents a notable stressor for the birds to achieve problem-solving success, and therefore can be considered as a 'harsh' environmental characteristic in urban habitats. Likewise, our results reflect that the problem solvers are sensitive to humans, and suggest the presence of humans has inhibited their novel problem-solving ability, especially when the successful solutions are unknown to them. Interestingly, at the individual level, such disturbances led some individuals to fail to innovate, but enhanced the learning speed in others that had successfully solving the novel problem (table 2*a*), particularly in the initial learning phase (table 2*b*). An enhanced learning speed in relation to areas with high human disturbance may reflect the pressure to solve the problem quickly in case a human approaches. The bi-directional outcome within the population may reflect two equally adaptive strategies that could increase foraging efficiency in urban environments; non-problem solvers may gain time to use familiar resources over investing time to learn solving novel problems, whereas problem solvers can promptly deploy the learned successful solutions to increase foraging efficiency.

Our results indicate that increased indirect human disturbance, reflected by the increased number of human-built structures within and closely around a site, decreases the proportion of success in solving the novel problem at the population level. An increased number of buildings (e.g. households) may have provided alternative food sources (e.g. anthropogenic or processed food from garbage [38–40]) for many wildlife species, including this squirrel species, and in turn decreases the necessity for them to solve novel problems. However, this explanation is unlikely as accessing artificial processed food around buildings is difficult in Hokkaido, a prefecture where streets are without bins, and food waste is only allowed to be placed on the designated location on a specific collection time [55]. Alternatively, the low proportion of success may be explained by the fact that indirect human disturbance is related to buildings and roads themselves [56], in that increased human activities and traffic at peak traffic hours has led many wildlife species (including this species of squirrel) to remain within their habitats in order to minimize the risk of road deaths [48,57]. Logically, this may encourage this food generalist squirrel species to exploit novel resources like our apparatus that is placed within their habitats, and thus increase novel problem-solving success. However, there appears to have been other factors at play in lowering the proportion of success. One possible factor could be the trade-offs between remaining within the habitat and intra-conspecific competition on the same food sources, which is suggested by the number of buildings positively associated with squirrel population size (see below). Another possible factor could be related to the solutions of the novel problem itself; the time invested to seek unknown solutions may lower foraging efficiency, leading some individuals to forage elsewhere after several failed attempts, thus decreasing the proportion of success overall.

In contrast to our prediction, we found that the size of green coverage in a site does not predict the proportion of success at population level as well as individuals' solving latency on their first success of the novel problem (table 1). Seemingly, these non-significant results may suggest that neither the availability of food sources nor that of shelters matters in regard to novel problem-solving performance, or that green coverage should not be considered as one of the characteristics that would induce harshness at all. However, our results are more appropriately explained by our procedure, in which the apparatus was placed in a location that had maximized safety for squirrels. Nevertheless, the result that decreased green coverage significantly slows down initial learning (table 2*b*) may reflect that limited green coverage is a stressor, as it may increase the exposure to potential threats; it has been shown in urban great and blue tits that green coverage reflects safety and increases problem-solving success [42].

The fact that squirrel population size (the number of squirrels in a site) is positively correlated with squirrel population density (the number of squirrels in a site divided by the site size; electronic supplementary material, tables S2–S4) allows us to evaluate our prediction that an increased squirrel population density would decrease the proportion of success at population level and solving latency on the first success at the individual level. Indeed, these predictions can be confirmed and the results highlight another outstanding stressor in urban environments that can affect novel problem-solving performance. A high squirrel population size may imply an increase in intra-conspecific competition on the same resources, especially for this scatter-hoarding squirrel species that has to maximize opportunities to store food for later consumption [44]. Such competition in a high population density area probably leads to a few competent individuals being able to secure most resources, resulting in a decrease of success at the population level. The fact that squirrel population size continues to exert forces on sharpening later learning efficiency suggests the problem solvers maximize efficiency to obtain rewards as a result of competition (table 2*b*).

To this end, we have highlighted that human disturbance and population size are two of the many environmental characteristics that play an important role in affecting behavioural flexibility, measured as the performances in solving a novel problem shown in this species. Because such performance involves cognition [58,59] and some cognitive processes are interrelated (e.g. memory for solving the same problem after an extended period or generalization as in solving a similar but different problem), investigations into what and how these environmental characteristics would carry on to affect other cognitive processes could reveal the driving forces in urban environments that select for behavioural flexibility. A related noteworthy point is that increasing the magnitude of any of these harsh environmental characteristics appears to have enhanced the learning speed of some individuals, but also impaired some individuals in showing flexibility. These results may reveal the adaptive advantages of solving novel problems in urban environments. Together, our results contribute to understanding within-species variation in novel problem-solving performance, thus behavioural flexibility in adapting to urban environments and the evolutionary drivers that shape the underlying cognitive processes.

Ethics. This study did not involve any invasive methods—individuals were identified by software, Adobe Premiere Pro CS6, on their characteristics. The field experiment did not involve any punishment—individuals visited and left the task volunteerily during their active period. This study was approved by the Institutional Animal Care and Use Committee of National University Corporation Hokkaido University (ethics number: 606) and obtained permission from Obihiro University.

Data accessibility. All dataset and supplementary video are now uploaded to Open Science Framework, open to public: doi:10.17605/OSF.IO/DVGXQ.

Authors' contributions. P.K.Y.C. designed the experiments, conducted the field work, analysed the data and wrote the first draft of the manuscript. K.U. supported fieldwork logistics. K.U., A.M.P.v.B. and I.K. contributed to the manuscript and approved the final submitted version.

Competing interests. We declare we have no competing interests.

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