‘Ripple effects’ of urban environmental characteristics on cognitive processes in Eurasian red squirrels.

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Abstract

Urban environmental characteristics such as direct human disturbance have been shown to create a double-edged sword effect on wildlife's ability to solve novel problems (1). However, these characteristics would continue to affect related cognitive processes (the 'ripple effect hypothesis'). Here, we demonstrate this in urban Eurasian red squirrels who have previously learned a successful solution for a food-extraction problem (the innovators) by using two established food-extraction problems. One of the problems assesses the generalisation process (applying the learned solution when solving a similar but novel problem) and another problem examining memory for the learned solution of the original problem. The innovators significantly improve their solving latency on their 3rd success, and efficiently solve the generalisation problem from the 5th success onward. They also quickly recall the learned solution for the original problem in the memory test. While urban environmental characteristics do not affect the innovators' ability to solve either problem, characteristics like direct human disturbance enhance the innovators' learning speed for the generalisation problem, first recall and recall speed in the memory test. Path analyses show that direct human disturbance and to a lesser extent, area of green coverage are the major variables affecting cognitive performance. Our results highlight that some urban environmental characteristics can induce a far-reaching impact on shaping cognitive performance, as well as provide direct evidence for better understanding the mechanism that supports wildlife in adapting to urban environments.

Keywords: urbanisation, human-induced rapid environmental change, phenotypic traits, behavioural flexibility, positive transfer, urban ecology, cognitive ecology, urban wildlife

Introduction

Urban areas are growing exponentially, leading more wildlife species to reside in urban environments as their alternative habitats. Mounting evidence has shown that urban environments have changed wildlife's fitness-related traits ranging from physiology (2) to morphology (3, 4), and not least behaviour (5–10). As of yet, investigations are still in infancy regarding how urban environments shape cognition (11, 12), a crucial fitness-related trait that can be considered as the process of acquiring, storing, utilising and reacting to their environment (13). As cognition is tightly related to behaviour, cognition is expected to play a significant role in facilitating wildlife to adapt to urban environments (8, 14). Consequently, investigation efforts in this area not only would highlight the role of urban environments in shaping cognition, but also help us better understand the mechanisms that support wildlife species thrive or decline in urban environments (14).

Urban environments appear to favour the ability to solve novel food-extraction problems (or innovation) (15–20), but recent evidence has shown that such ability is varied by environmental characteristics in urban habitats. For example, the presence of a human decreased the success rate in solving a novel food-extraction problem in House finches (*Haemorhous mexicanus*) (21), or the mean number of humans in a site per day led some Eurasian red squirrels (*Sciurus vulgaris*) to fail while other squirrels enhance learning speed when solving a novel problem (1). However, two major reasons indicate that this evidence is likely revealing the tip of an iceberg regarding the role of urban environmental characteristics in shaping cognition. The first reason being that a cognitive ability like problem solving entails many cognitive processes that are related to other cognitive abilities such as memory (22). For example, learned solutions to solve a novel food-extraction problem can be related to solving a similar but novel problem that has the same solving solutions (i.e., generalisation), or recalling these solutions when encountering the same problem (i.e., memory). Such interconnections of cognitive processes may seem obvious, but evidence for such far-reaching impacts of urban environmental characteristics on cognitive processes is missing. Consequently, these two reasons bring us to propose the 'ripple effect hypothesis'. This hypothesis states that if some urban environmental characteristics have shaped a cognitive ability, then these environmental characteristics are likely creating a 'ripple' effect on related cognitive processes (Fig. 1A). The second reason is related to the fact that environmental characteristics are interacting with each other (23). While the direct effects of some urban environmental characteristics on problem-solving performance have been highlighted (1, 21), investigating both direct and indirect effects of these characteristics on performance is crucial to build a comprehensive picture regarding the evolution of cognition in urban environments. Such investigations will highlight specific urban environmental characteristics that exert pressures on cognitive performance.

Two main objectives of this study: the first objective was to test the ripple effect hypothesis (Fig. 1A) by relating identified environmental characteristics (direct human disturbance, indirect human disturbance, squirrel population size and area of green coverage) (1) to cognitive processes (generalisation and memory) of novel problem solving. The second objective was to obtain a comprehensive picture of how the urban environmental characteristics directly and indirectly affect problem-solving performance. To achieve these objectives, we conducted a field experiment in a successful urban-dwelling species, the Eurasian red squirrels, in 11 urban areas that varied in their environmental characteristics. In these sites, 38 squirrels (hereafter, the innovators) had previously successfully solved a novel food-extraction problem (hereafter, the original problem) (SV1). To assess the innovators' generalisation performance, we adopted an established design (24) that contained the successful solutions of the original problem but presented them in a novel apparatus (Fig. 1B). We used the original problem to assess the innovators' memory of learned solutions (Fig. 1C). We quantified cognitive performance in three aspects: the proportion of success at site level, solving latency on the first success and across success of each innovator. These performances were then related to the urban environmental characteristics to test the ripple effect hypothesis. For the second objective, we used path analyses to examine all possible direct and indirect effects among the urban environmental characteristics on solving performance (Fig. 2A).

Results

28 (out of 38, 74%) innovators who had previously successfully solved the original problem participated in the generalisation problem. Participation rate in this problem decreased with higher squirrels population size (χ^2_1 = 3.83, P = 0.050, Table S1A), but none of the environmental characteristics affected success rate and the first generalisation latency (Table 1Aa-b). When the innovators first attempted to solve the generalisation problem, 19 (68%) of them were successful (SV1). 23 (82.1%) of them from 10 sites eventually solved the problem

in the first or subsequent visits more than once (i.e., repeated innovators). These repeated innovators' first generalisation latency was significantly longer than their last innovation latency (Z = -2.29, P = 0.022), and comparable to their first innovation latency in the original problem (Z = 1.86, P = 0.062, Fig. 1D). They decreased their generalisation latency across successes (χ^2_1 = 13.08, P < 0.001, Fig. 1E). Their first significant improvement was on the 3rd success (Z = -2.36, P = 0.018) and remained a low latency to solve the problem from the 5th success onward (Note S1), which suggests the repeated innovators were still learning the solution before the 5th success. Accordingly, we separated the generalisation latency across successes into early (1st-5th) and late (6-10th) learning when examining how urban environmental characteristics may affect their learning speed. Less green space lowered solving latency in early learning (χ^2_1 = 4.31, P = 0.038, Table 1Ac) whereas increased direct and indirect human disturbance lowered latency in later learning (direct: χ^2_1 = 4.25, P = 0.039; indirect: χ^2_1 = 3.83, P = 0.050, Table 1Ad). Green space (0.17) and direct human disturbance (0.14) were influential on early learning, whereas direct human disturbance (-0.32) continued to affect later learning (Fig. 2B-C, Table 1A, Table S2-S3 for full results).

For the memory test, increased direct and indirect human disturbance significantly lowered the participation rate at site level (direct: χ^2_1 = 8.03, P = 0.005; indirect: χ^2_1 = 4.98, P = 0.026, Table S6B). Despite this, 20 (out of 38, 53%) innovators from 9 sites returned to the memory test. Of these 20 innovators, 14 (70%) of them repeatedly solved the same problem. The repeated innovators' first memory latency (M = 6.8 ± 1.85s) was significantly lower than their first innovation latency (Z = 2.34, P = 0.019) and comparable to their last innovation latency (Z = -1.15, P = 0.249, Fig. 1F). None of the four environmental characteristics predicted the proportion of success at site level (Table 1Ba), but increased direct human disturbance significantly decreased the repeated innovators' first memory latency (χ^2_1 = 5.28, P = 0.022, Table 1Bb). Their memory latency to each success remained low across successes (χ^2_4 = 6.25, P = 0.182, Fig. 1G). However, those residing in sites with increased direct human disturbance (χ^2_1 = 12.53, P < 0.001) and lower squirrels population size (χ^2_1 = 7.10, P = 0.008) showed lower latency across successes (Table 1Bc). Direct human disturbance has the highest total effect on the first memory latency (-0.45) and memory latency across successes (-0.42) (Fig. 2D-E, Table 1Bb-c, Table S4-S5 for full results).

Discussion

Our results support the proposed 'ripple effect hypothesis'; some urban environmental characteristics (e.g., direct and indirect human disturbance) that have affected novel problem-solving ability continue to affect related cognitive processes (e.g., generalisation and memory). Thus showing that the impacts of urban environmental characteristics on cognitive processes are far reaching. The results of both food-extraction problems show a consistent pattern in that urban environmental characteristics do not affect generalisation or memory ability. However, one or more of these environmental characteristics shape learning and recall speed. Path analyses indicate that direct human disturbance and, to a lesser extent, green coverage are some of the influential urban environmental characteristics that shape these cognitive processes.

Recent findings have shown that urban environmental characteristics affect novel problem-solving performance (1, 21). In both tasks, direct human disturbance stands out as a significant variable, and thus it appears to be a major selective force in urban environments that vary cognitive performance. This may not be surprising given urban environments are predominantly occupied by humans. However, 'disturbance' entails many aspects (e.g., intensity, types of activity, distance toward humans) (29) and studies including ours so far have only examined a few aspects (e.g., human presence (21) and the mean number of humans in a site (1)). Accordingly, we urge future studies to examine different aspects of human-related factors in relation to cognitive performance, which will advance our understanding about this factor in the evolution of cognition in urban environments.

Contrary to the findings in the original problem (1), a decrease (instead of an increase) in squirrel population size enhanced recall speed when the innovators re-experienced the same problem. Squirrel population size is recorded as the number of squirrels in a site that reflects intra-conspecific competition (1). The opposite effect of squirrel population size in the original problem and the memory test both relate to intra-conspecific competition, but in different ways. In the original problem, increased squirrel population size reflects more squirrels were competing on the same resources. Since slightly more than half of the squirrels have solved the original problem repeatedly, these innovators demonstrate their comparable competitive ability. On their return to the memory test, these innovators were likely competing with fewer but competitive conspecifics, resulting in enhanced efficiency in securing the food sources among conspecifics before another competitive innovator arrived, which can be supported by the scatter-hoarding life history of this squirrel species (25).

Despite the costs associated with exploring and learning to solve novel problems, diet and habitat generalists such as this species of squirrel (26) may benefit from securing food sources by exploring novel resources or solving novel problems (27). The fact that most innovators have participated in the two food-extraction problems suggest the use of learned information when the problem recurs, reappears after an extended period or appears in a similar but novel context may increase foraging efficiency, which has been shown in Eastern grey squirrel (*S. carolinensis*) (24, 28). While comparable performance of the first generalisation latency and the first innovation latency suggests the innovators show minimal generalisation on their first success, they quickly recall the solutions for the generalisation problem was the same as the original problem. The innovators quickly improve their solving latency and remain efficient to reach successes early on. Moreover, they quickly recall relevant information for the original problem on their first and subsequent solvings. These results suggest that related cognitive processes like those that have demonstrated here may bring advantages for adaptation in urban environments.

Our proposed ripple effect hypothesis demonstrates the impact of urban characteristics on some cognitive processes that are related to novel problem solving. However, it can be more broadly seen in other contexts. For example, increased squirrel population size as well as direct and indirect human disturbance have decreased participation rate in the generalisation problem and a problem that the innovators are familiar with (i.e., the memory test) show that these urban characteristics have affected other cognitive processes (e.g., decision making or risk assessment) and non-cognitive traits (e.g., motivation) that are not directly measured in the food-extraction problems. An increase in these environmental characteristics broadly reflects increased risks and costs (e.g., increased exposures to humans or inta-conspecific competition) to approach, explore, and invest learning to solve novel problems. In more disturbed urban areas, such risks and costs may have outweighed benefits, leading some innovators not to engage in solving novel problems, an alternative adaptive strategy to minimise these risks and costs. For those innovators who have engaged in solving the problems, their enhanced learning and recall speed is likely a result of adaptive trade-off with the costs associated with these 'harsh' urban environmental characteristics (less green coverage, increased direct and indirect human disturbance).

Overall, we have demonstrated the far-reaching impacts of some urban environmental characteristics on two of the many problem-solving related cognitive processes. Our results not only allow us to identify relevant characteristics and their role in shaping cognitive performance, but also gain insights into the mechanisms that support wildlife species adapting to urban environments.

Methods

The field experimental protocol followed Chow and colleagues (1). Between May 2018 and January 2019, we followed 38 urban red squirrels in 11 sites (> 800 m between sites to avoid pseudo-replication) at Obihiro city, Hokkaido, Japan (site information in Table S6). These squirrels were innovators who had previously repeatedly solved a novel food-extraction problem (i.e., the original problem, Fig. 1C). All squirrels were identified by an established method (28) that required frame-by-frame analysis of their characteristics from video footage as well as mark-recaptured and mark-resight methods (see Note S2).

(a) Urban environmental characteristics

Four previously identified environmental characteristics and measurements were recorded (1) (detailed measurement in Note S3): 1) direct human disturbance (mean number of humans in a site per day that was the average of 4-5 times walking in a site either before or after checking/refilling the apparatus across all observation days); 2) indirect human disturbance (number of buildings includings houses and stores 50 m around a site); 3) total area covered by trees in a site (m^2) on Google satellite; and 4) squirrel population density (number of squirrels in each site divided by the site size (m^2) from regular field surveys, trapping records, and video footage).

(b) Food-extraction problems

The original problem had a cube-shaped top and a pyramid-shaped bottom (Fig. 1C). The top was secured by six steel legs, creating a 3.5 cm gap between the top and the bottom for the squirrels to receive a reward (hazelnut) upon successfully solving the problem. Each side of the top had ten horizontally, but not vertically, aligned holes. These holes were roughly aligned to the holes on the opposite side. We inserted ten (white) levers horizontally across the box through the holes, leaving 2.5 cm of both lever-ends outside the holes so that squirrels can manipulate the lever ends. Each lever had a nut container 2.5 cm away from one of its ends, which can be positioned inside the box. To solve this problem, a squirrel either had to push a lever end if it was close to a nut container, or pull the lever end if it was far from the nut container (video S1).

On the day after the innovators had completed the original problem, we assessed their generalisation performance using a similar but novel established apparatus (hereafter, the generalisation problem) (24) (Fig. 1B). The main feature of this problem was that it had the same successful solutions as the original problem (i.e., using levers to facilitate the application of learned successful solutions), but the apparatus had a different shape and colour (triangle front: 35 x 19 x 18 cm; length x width x height, rectangular side: 25 x 20 cm) to maximise the difference between this problem and the original problem. This apparatus had a transparent top and a rectangular plexiglas base. The top was secured by four steel legs, creating a 3 cm gap for the squirrels to retrieve a nut on successfully solving the problem. The front and the back of the top had five holes horizontally, but not vertically, aligned with each other. Five levers could be inserted into the apparatus across the holes. Each lever had a nut container located 1.5 cm away from one lever-end and positioned inside the box.

21 days after the generalisation problem, we examined innovators' memory for the successful solutions of the original problem using the original problem (Fig. 1C). The apparatus was presented to the innovators for one field day. Before the memory test, we kept the innovators visiting the location by carrying out other behavioural assays that did not involve any similar solutions for solving the generalisation problem or the memory test.

General procedure

The procedure of data collection followed (1) (detailed in Note S4). The key protocol included attracting squirrels to a location that was distant from major roads and close to trees. We then presented the food-extraction problems to the squirrels daily, during their most active period (from dawn to noon). During the experiment, we set the apparatus at where the original problem was, and checked (i.e., refilled) it 3-4 times per day (45 mins-1.5 hours between checks). In each check, we randomised the facing direction of the nut containers and the apparatus. For the generalisation problem, the coloured levers were randomly presented. For the memory test, we randomly chose which levers had a nut.

(c) Behavioural measurements

During a visit, the innovators may manipulate a lever more than once using any of its body parts. For each manipulation, we recorded the solving outcome (success or failure in causing a lever/nut drop), and solving latency (duration in seconds from a squirrel manipulating a level until it stopped doing so).

By using these records, we classified each innovator as a ‘repeated innovator’ (when an innovator solved a problem again and repeatedly) or a ‘non-repeated innovator’ (when an innovator only solved a problem once, or could not solve the problem throughout the task presentation). We calculated the proportion of success at site level (the number of repeated innovators divided by the total number of innovators that had participated in the problem). We also calculated the total solving latency of each repeated innovator by summing the latencies of all unsuccessful manipulations until a success occurred. To minimise confusion, we referred the total latency in the original problem to ‘innovation latency’, ‘generalisation latency’ for the generalisation problem and ‘memory latency’ for the memory test.

(d) Data analysis

We analysed data using R (version 3.5.2) (30) and SPSS (version 25). We report the original values of mean (M) ± standard errors (S.E). A two-tailed test with $\alpha \leq 0.05$ is considered as significant. Before model analyses, we used Pearson correlations (r) to examine the relationships between characteristics, and avoid multicollinearity by selecting variables that were moderately or highly correlated ($r \geq 0.5$) (Table S7-S10). Following (1), we retained squirrel population size for model analyses because an alternative variable, population density, was moderately to highly correlated with one or more variables of interest but positively correlated with population size (r = 0.56 - 0.71). We further used VIF in package ‘car’ (31) to detect multicollinearity in each model. All models included four standardised, and thus comparable on the same scale, environmental characteristics (fixed factors: direct human disturbance, indirect human disturbance, green coverage (m^2), and squirrel population size) for us to calculate the total effect of each characteristic. We checked the randomness of error-distribution in each model.

Beta regression in the package 'betareg' (32) was used to examine participation rate (the number of innovators that had participated in the original task returned to the generalisation/memory test) and the proportion of success at site level. Generalized Linear Mixed Model (GLMM) with gamma log link distribution alongside individual identity as the random variable were used to accommodate positively skewed continuous response variables. We compared 1) the repeated innovators' first generalisation latency with their first and last innovation latency to assess whether they quickly applied the learned solutions in the generalisation problem; 2) each generalisation latency successes (e.g., 1st vs. 3rd) with the last innovation latency to assess their performance within the problem; 3) their first memory latency with their first and last innovation latency to assess their memory of the successful solutions of the original problem; 4) recall latency across successes (1st-5th success), 5) environmental characteristic predictors for the first generalisation latency, 6) early learning (1st-5th success), 7) late learning (6-10th success), 8) first memory latency; and 9) memory latency across successes.

We ran path analyses using the 'glmmTMB' package (33) to examine the proposed model (Fig. 2A). In each analysis, one of the four environmental characteristics was set as a dependent variable, and the other three characteristics as the independent variables. We modelled direct human disturbance and green coverage using Gamma log link distribution whereas indirect human disturbance and squirrels population size using Poisson log link distribution. As changes of the total effect size become minimal (<0.001) when including the second mediators, we considered all possible direct and indirect paths up to two mediators.

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Competing Interest Statement: We declare there is no competing interest.
Ethics. This study was approved by Hokkaido University (ethics number: 606) and Obihiro University.
Open data access. All raw data can be downloaded from OSF (here).
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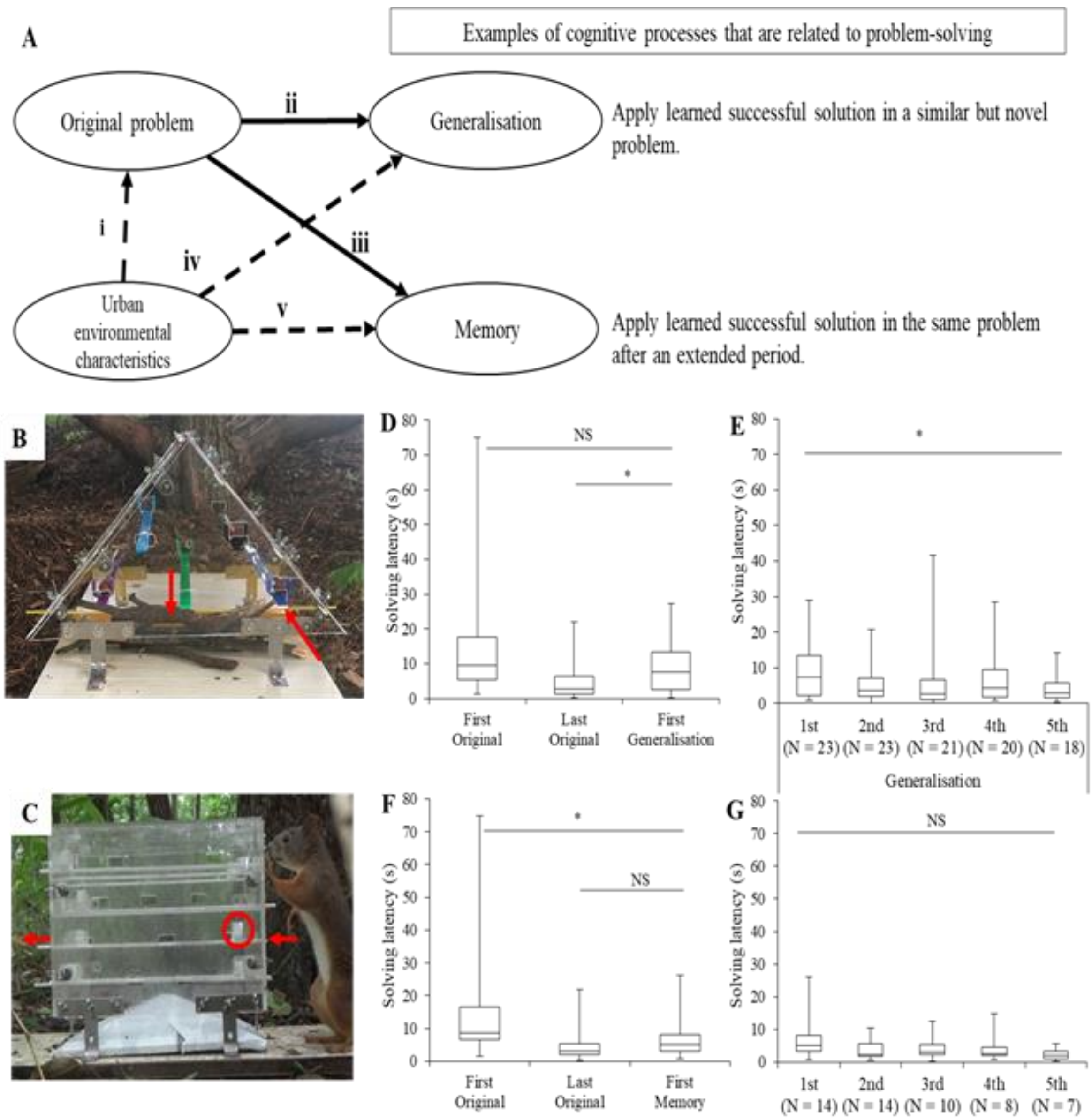

Figure 1. The ripple effect hypothesis: urban environmental characteristics affect the performance in solving a novel problem (i)**(A)**. Affected performance carries onto other related cognitive processes such as generalisation (ii) or memory (iii)**(A)**. These cognitive processes are simultaneously affected by the urban environmental characteristics (iv and v)**(A)**. The generalisation problem that was used to assess the ability to apply learned successful solutions to solve a similar but novel problem **(B)**. The original problem that was used in the recall test for assessing retention of the successful solutions **(C)**. Innovation latency (seconds) of the first and the last success of the original problem as well as the first generalisation latency (N = 23) **(D)**. Generalisation latency across 5 successes **(E)**. Innovation latency (seconds) of the first and the last success of the original problem as well as the first memory latency (N = 14) **(F)**. Memory latency across 5 successes **(G)**. *P < 0.05; NS = Non-significant.

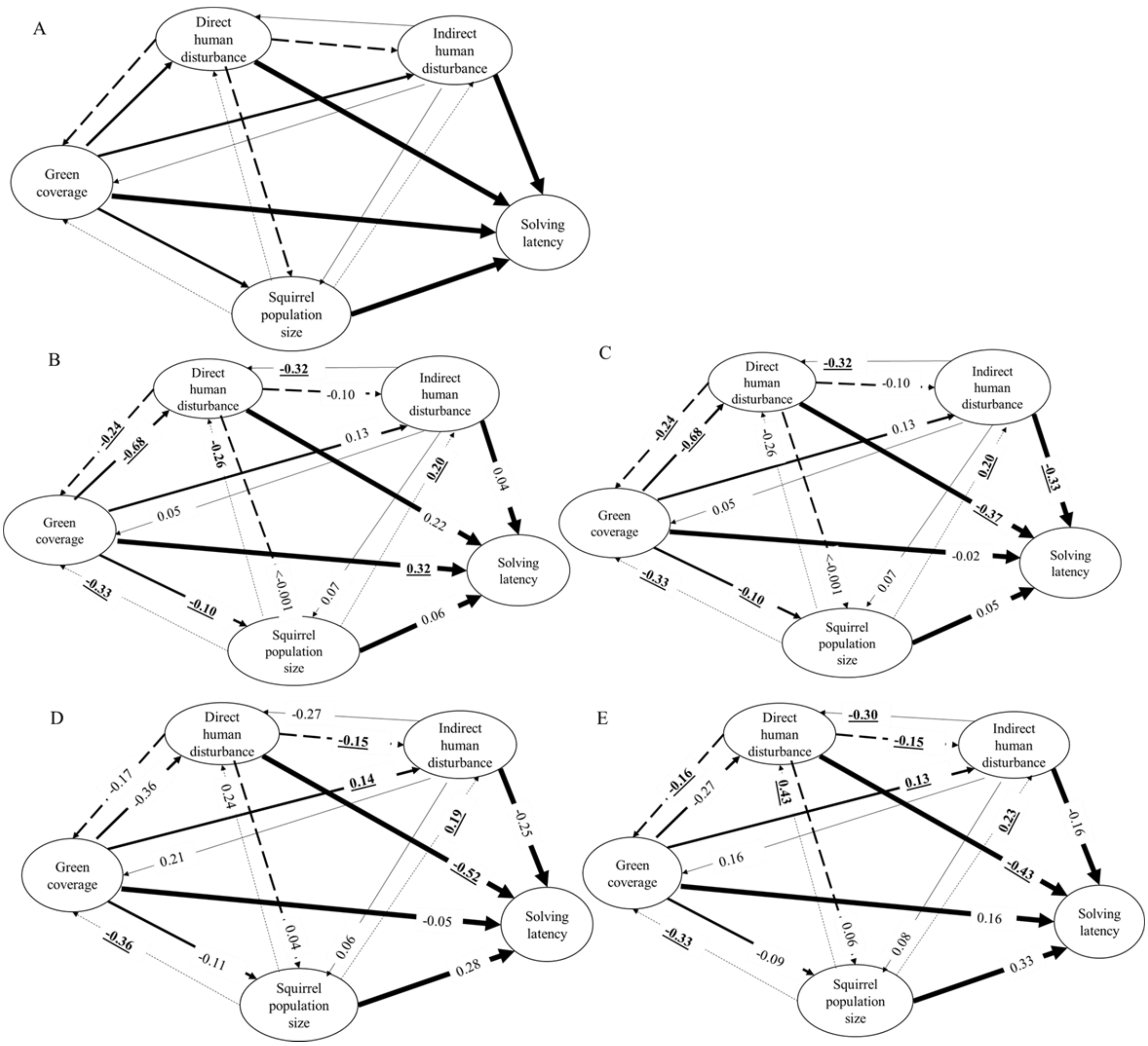

Figure 2. Path analysis to examine direct and indirect effects of urban environmental characteristics on problem-solving performance. Environmental characteristics include direct human disturbance, indirect human disturbance, green coverage, and squirrel population size. Proposed model including all direct and indirect paths between environmental characteristics and solving latency **(A)**. Path analysis results for the generalisation latency in early learning (1^{st}-5^{th} successes) **(B)**, late learning (6-10^{th} successes) **(C)**, first memory latency **(D)**, and memory latency across successes **(E)**. Underlied values indicate significant P < 0.05.

Table 1. Predictors of urban environmental characteristics (direct human disturbance, indirect human disturbance, green coverage and population size) for performances in the generalisation problem (A) and the memory test (B). Performances include proportion of success at the site level (i), individual solving latency on the first success (ii), and across successes in early learning (iii) and late learning (iv). This table contains estimates (est), standard errors (S.E), *Z* and P values. Bold values indicate significant P < 0.05.

			A. Generalisation problem					B. Memory test				
	Response variable	Environmental characteristics	Est	S.E	Z	P	Total effect	Est	S.E	Z	P	Total effect
a	Proportion of success	Direct human disturbance	0.02	0.43	0.05	0.957		0.11	0.56	0.19	0.848	
		Indirect human disturbance	-0.45	0.43	-1.05	0.295		-0.48	0.52	-0.92	0.359	
		Green coverage	0.14	0.42	0.34	0.737		0.25	0.44	0.56	0.574	
		Population size	0.44	0.40	1.12	0.263		0.68	0.60	1.15	0.251	
b	Solving latency (1st success)	Direct human disturbance	0.29	0.23	1.30	0.193		-0.52	0.23	-2.29	**0.022**	**-0.45**
		Indirect human disturbance	0.03	0.27	0.10	0.917		-0.25	0.26	-0.98	0.329	-0.08
		Green coverage	0.20	0.29	0.69	0.493		-0.05	0.27	-0.19	0.850	0.10
		Population size	0.27	0.26	1.03	0.303		0.28	0.24	1.16	0.247	0.10
c	Latency across successes - early learning (1st-5th successes)	Direct human disturbance	0.22	0.14	1.56	0.118	0.14	-0.43	0.13	-3.20	**0.001**	**-0.42**
		Indirect human disturbance	0.04	0.14	0.29	0.775	<-0.01	-0.16	0.14	-1.15	0.250	0.02
		Green coverage	0.32	0.16	2.08	**0.038**	**0.17**	0.16	0.14	1.16	0.248	0.25
		Population size	0.06	0.15	0.43	0.664	-0.06	0.33	0.14	2.34	**0.019**	0.06
d	Latency across successes - late learning (6-10th successes)	Direct human disturbance	-0.37	0.18	-2.06	**0.039**	**-0.32**					
		Indirect human disturbance	-0.33	0.17	-1.96	**0.050**	-0.19					
		Green coverage	-0.02	0.18	-0.11	0.912	0.17					
		Population size	0.05	0.16	0.29	0.773	0.03					

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