Time in the city: Exploration and problem-solving behaviours reveal long-term urban adaptation in wild red foxes (*Vulpes vulpes*)

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Abstract

Urbanisation is one of the most important forms of human-driven landscape change, creating novel situations in which some species thrive. Animals' willingness to touch, explore, and solve novel challenges, such as exploiting unfamiliar resources, are thought to be key behavioural characteristics for urban adaptation. Little is known about the impact of spatiotemporal patterns of urbanisation, particularly historical patterns of change, on these behaviours. We tested this in the world's most urbanised carnivore, the red fox, using novel tasks deployed across 284 sites in the United Kingdom. We compared tactile and problem-solving behaviours in rural populations, recently colonised urban populations, and long-established urban populations (>40 years). Similar to previous work, urban foxes were more likely to touch the tasks compared to rural populations; however, in our new extended dataset, we show for the first time that older urban populations – particularly from London – display greater exploratory diversity and higher problem-solving success, despite more recent urban populations being equally likely to touch them. Our findings suggest that certain population characteristics, such as the likelihood of touching/engaging with novelty, emerge early in urbanisation while other characteristics, such as exploratory diversity and behavioural innovation, may emerge after long-term urban exposure across many decades.

Key words: rapid environmental changes, behavioural innovation, boldness, biodiversity crisis, urbanisation, problem-solving ability

Introduction

Earth is presently facing a catastrophic decline in biodiversity, often termed the sixth mass extinction or biodiversity crisis (1, 2). This decline is largely the result of human-driven environmental changes (hereafter “environmental changes”) (3). One of the most important forms of environmental change on the planet is urbanisation (4), defined as a dynamic process characterised by expanding human settlements, such as increased infrastructure (e.g., housing and building densities), human population growth, and reduced habitat heterogeneity (5, 6). By 2050, over 68% of the world human population is expected to live within cities, compared to only 30% in 1950 (4). Such rapid changes expose wildlife to a wide variety of novel situations, such as new or modified habitats (7), anthropogenic resources (8), competitive interactions (9), and potential predators and diseases (10, 11). Most species are experiencing these changes for the first time in their evolutionary history; meaning, evolution has not necessarily equipped them to withstand such unprecedented conditions (12-14). While many species are at risk of decline or extinction due to slow adaptation, others are unexpectedly thriving for reasons that are still unclear (12, 15). Thus, there is a pressing need to better understand what factors help wildlife respond and adapt to environmental changes, particularly those related to urbanisation.

Animals’ initial responses to environmental changes are often the result of behavioural plasticity, not rapid genetic evolution (16). Several behavioural phenotypes have been proposed as being important for coping with novel situations arising from environmental changes. One is bold behaviour, broadly defined as an animal’s willingness to engage with novelty (17, 18). Another behaviour is exploration, which reflects an animal’s tendency to actively investigate situations within its environments (19). Unlike boldness, exploration does not always necessarily involve risk-taking and, instead, can be driven by other factors, such as curiosity or persistence (20, 21). Finally, a third behaviour is innovation, defined as using a new or modified behaviour to solve a new or familiar task (22, 23). Bolder animals are more likely to touch and engage with unfamiliar, and therefore potentially risky, resources compared to other organisms (24-26). Animals with greater exploratory and innovative tendencies are

better equipped to gain information and discover solutions to novel challenges (19, 21, 23, 27). Thus, greater environmental changes are often hypothesised to favour bolder, more exploratory and innovative behaviours (14, 28), potentially shaping the likelihood of these behaviours being observed within a population (29). However, the likelihood of animals displaying such behaviours is not always related to the magnitude of environmental change (14, 26, 28, 29). In terms of urban-rural gradients, for example, many studies find that urban populations are more likely to display bolder and more innovative behaviour than rural populations, while other studies show that rural populations can be more, or equally, as bold and innovative as their urban counterparts (18, 26, 28-30). Thus, the relationship between environmental changes and how animals respond to novelty is complex and warrants further research.

One underexplored factor is the long-term historical patterning of environmental changes, such as the rate at which such changes occur over decades. Most studies examining the impact of environmental changes on animals' behavioural responses to novelty are based on static, cross-sectional ecological gradients from the present day (14, 26, 28, 29). While such analyses are important for understanding how different degrees or "magnitudes" of change might impact animal populations (e.g., a steeper gradient suggests greater impact), behavioural characteristics of present-day populations are often a reflection of their ecological past, and so cross-sectional analyses cannot account for historical patterning. If urbanisation, for example, follows a gradual and contiguous pattern, populations may have longer to adapt to human pressures, leading to incremental behavioural changes across many generations. By contrast, if urbanisation is abrupt and rapid, such as sudden expansion or land-use changes, it may trigger an abrupt shift in population-level behaviour, favouring animals that quickly learn or already possess these behavioural characteristics (12, 26, 31). Thus, to better understand how wildlife might adapt to environmental changes, there is a pressing need to understand whether (and how) historical patterns of environmental change predict the likelihood of populations displaying bold, exploratory, and innovative behaviours.

Red foxes, *Vulpes vulpes*, offer a powerful model for understanding how historical patterns of urbanisation influence present-day behavioural adaptation. As the most globally widespread terrestrial carnivore on the planet (32), foxes were among the first mammals on record to have expanded their ecological niche to urban areas (33). Reports of urban foxes have existed in British cities at least since the 1930s (33). In more recent decades, foxes have established themselves in other cities throughout Europe, Asia, Australia, and North America (8, 34-36). Although urbanisation is a relatively recent phenomenon in this species' evolutionary history, notable behavioural and morphological differences are already being documented in urban fox populations compared to the countryside. Compared to their rural counterparts (29, 36), for instance, urban foxes often have smaller dietary repertoires (37), consume anthropogenic food more frequently (8, 37, 38), occupy smaller home ranges (39, 40) and display bolder behaviours. There is also some evidence that urban foxes are evolving to have smaller skulls (41) which, taken together, suggests that urbanisation may lead to microevolution of behaviours and other phenotypes, including morphology. The colonization of urban areas by foxes, however, has been an uneven process (42). If microevolution or other long-term processes are occurring, we should expect there to be localized variation in the speed and timing of behavioural changes within the species – a possibility that has not yet been formally tested.

In the current study, we investigated whether long-term historical patterns of urbanisation predict population differences in bold, exploratory, and innovative behaviours in present-day foxes from the United Kingdom (UK). Specifically, we tested whether present-day urban fox populations differ from rural populations in these behaviours, and whether such differences are predicted by historical spatio-temporal patterns of urbanisation over the last several decades. We also tested whether populations from relatively older, more established urban areas (before 1986) are more likely to display bolder, more exploratory and innovative behaviours compared to more recently urbanized areas. By integrating behavioural data with historical patterns of urban development, we aim to clarify how past environmental changes

potentially shape present-day behavioural strategies, offering new insights into the adaptive potential of wildlife's exposure to urbanisation.

Methods

Study Sites and Subjects

We studied 284 locations throughout Great Britain (Figure 1a), including areas within and around many towns and cities (e.g. London, Glasgow, Edinburgh, Bristol, Southampton, and York). Landscapes for these locations were diverse, including public parks, residential gardens, monostand pine/spruce plantations, open fields (including farms), mixed woodland, and coastal and mountainous scrubland. Foxes were not tagged and their participation in our behavioural tests was entirely voluntary. We acquired permission to visit 242 of these locations by contacting city councils and other organizations that owned the land. The remaining 42 locations were accessed by advertising the study through social media and regional wildlife groups; these locations were primarily comprised of golf courses and residential gardens. All locations were spaced at least 3.5 km away from any of our other study locations, which reduced the likelihood of acquiring data on the same foxes visiting multiple locations since $\geq$ 3.5 km is larger than the typical dispersal distance and home range diameter of foxes within the UK (43, 44).

Measuring population-level differences in bold, exploratory, and innovative behaviours in foxes

We used methods already developed and validated to assess population-level differences in foxes' behavioural responses to novel tasks, the details of which can be found in Morton et al. (29). Data from 200 of our locations come from our original Morton et al. (29) study, collected between August 2021 and November 2022. Data from an additional 84 locations were collected specifically for the current analysis, between March 2023 and May 2024.

157 Briefly, a single novel food-related task was selected from a battery of eight designs
158 (Figure S1) and deployed at a given location for 15.6 ± 1.8 days before it was retrieved by
159 researchers. Each object varied in terms of design and was made from basic household
160 materials (e.g., PVC piping, metal screws and wooden rods). Tasks were counterbalanced
161 across locations to ensure that our findings were not unique to any particular type of task and,
162 instead, were more generalisable. Our previous work found that, for these specific task
163 designs, population differences in fox behaviour were not significantly influenced by the type
164 of design deployed at a location (29). Some tasks were sprayed with scent deodorizer to
165 understand whether the scent of objects (e.g. human odour) influenced fox behaviour which,
166 in our previous study (29), was also shown to have no significant effect.

167 All tasks had bait scattered around them to attract foxes to those locations. The objects
168 also contained a food reward inside them, which could be obtained by foxes performing natural
169 behaviours (e.g., lifting, biting, pushing, or pulling materials). Examples of these behaviours
170 can be found here: https://youtu.be/SYHyjXPdcZs (29). The tasks were designed to
171 understand animals' *willingness* to engage with novelty, and so in this context, solving a task
172 meant that animals needed to be bold (and otherwise motivated) enough to physically touch
173 and explore it during the two-week period in which it was available. Stemming from this, many
174 factors can potentially underpin animals' willingness to display bold, exploratory, and
175 innovative behaviours (23, 45-47). For example, animals that are too afraid, not hungry, or not
176 persistent may be less likely to exploit novel food-related objects. Importantly, however, the
177 purpose of our study was to determine *whether*, not why, our study species would display
178 bold, exploratory, and innovative behaviours, and so the only way they could do this was by
179 physically engaging with the tasks and displaying those behaviours.

180 Fox visitations occurred when researchers were not present, and 'no glow' (940 nm)
181 infrared motion-sensor cameras (Apeman H45) were used to record fox behaviours. Across
182 all locations, we measured whether a fox was detected on camera (1=yes, 0=no) as well as
183 the total number of visits made by foxes during the period in which a task was deployed at that
184 location. To reduce temporal autocorrelation between successful visits, we considered a "visit"

185 to have ended if a fox was absent from the camera's field of view for ≥10 minutes. The use of
186 this time interval to measure independent red fox detections has been validated in a previous
187 trail camera study (48). Because foxes were free ranging and their participation was entirely
188 voluntary, we based our analysis on foxes that were at least able and willing to visit the
189 locations, which still enabled us to assess urban-rural differences in foxes' behavioural
190 responses to the novel tasks (29).

191 We only coded behaviours from locations where foxes clearly acknowledged the task
192 during their visit, which we defined in terms of the fox turning its head to look/smell in the
193 object's direction. As in our previous study (29), we measured the likelihood of behavioural
194 innovation occurring within fox populations in terms of the number of locations in which we
195 saw (1=yes, 0=no) a fox displaying a behaviour at any point that led it to operate and
196 successfully gain access to the food inside the novel task within the timeframe in which the
197 task was available at that location. Also, we were not interested in trait boldness in the current
198 study, which describes stable individual differences in behaviour across a wide variety of
199 contexts (17). Instead, as with Morton et al. (29) and other studies of free-ranging animals (18,
200 20, 47), we were interested in the likelihood of fox populations displaying outwardly bold
201 behaviour, which we defined in terms of a fox physically touching (yes or no) the object at any
202 point within the timeframe in which the task was available at that location (e.g., pushing,
203 pulling, licking, or biting it).

204 Of the foxes that were bold enough to make physical contact with the novel tasks, we
205 also quantified four additional behavioural measures. First, latency to first touch was defined
206 as the time from the first acknowledgement of a task by any fox at a location until the first
207 instance of physical contact by a fox from that location. Second, we measured the total time
208 foxes spent engaged in tactile exploration of the task at a location, which captured foxes'
209 sustained interactions with the task within a given area. Third, we recorded exploration
210 diversity (21), defined here as the total number of distinct exploratory behaviours directed at
211 the task at any point by foxes during the period in which it was deployed at a location (Table
212 1). Finally, we measured latency to solve, which we defined in terms of the amount of time

elapsed between the first time a fox touched the object until the time when a fox ultimately solved it by gaining access to the food inside.

Table 1. Ethogram of behaviours used by foxes to physically explore novel food-related tasks.

Behaviour	Definition
Nip	Quick contact with object using teeth, with a fast recoil. Quickly moving body or head away from object after making contact.
Bite	Longer contact with teeth compared to a 'nip'. Not moving position of the mouth, staying stationary. Each close of the jaw counts as a new bite.
Teeth pull	Grabbing the object with teeth and trying to pull it towards their body. Each close of the jaw counts as new pull.
Rostrum touch	Contact with the front of face/nose, which does not include teeth, such as pushing snout into or towards the object, or licking it.
Left paw contact	Using left paw to make contact with the object other than standing on the object.
Right paw contact	Using right paw to make contact with the object other than standing on the object.
Combined paw scratch	Quick contact with the object using both paws at the same time. One paw may make contact first, but both must be touching at some point during the behaviour for combined contact.

Measuring rates of environmental change due to urbanisation

We obtained spatial data on landscape changes typically associated with urbanisation at each of our study locations from 1994 to 2020, which was the maximum consistent timeframe available. These landscape changes were based on predefined categories from ESA Land Cover Time Series with a resolution of 300 metres (49). Buffers of 3,500 metres

were created around each location to analyse the proportion of urban land cover present; this buffer distance corresponded to the typical annual home range of male and female foxes in the UK (43, 44). For each buffer, we calculated the proportion of urban habitat, allowing us to quantify urbanisation in 1994, 2020, and the amount of change between these two time points. Raster data processing was performed with ArcGIS Pro (ESRI), and landscape cover and change analysis were performed with R version 4.4.2 (50).

Measuring length of exposure to urbanisation

The exact timing of urban foxes colonising different cities is uncertain. We do, however, have a snapshot from a national survey of 378 local UK authorities from 1986 which documented urban fox population status as being either present, absent, or uncertain (51). We therefore cross-referenced data on fox presence/absence from our current study with records from 1986; two locations from 1986 were uncertain, both in Hamilton, Scotland, and were excluded, resulting in 84 locations for our analysis. Locations where urban foxes were already present in 1986 were defined as relatively “older” urban populations, whereas locations where foxes were absent in 1986 (but present in the current study) were defined as relatively “newer” urban populations.

Statistical Analyses

We used Cohen’s kappa tests and intra-class correlation coefficients (ICC 3,1) to evaluate interobserver agreement for all fox behaviours coded from videos. There was excellent agreement across all coders (Tables S1-S8).

We first identified clusters of high or low values and spatial outliers of foxes touching and then solving the novel tasks using the Local Moran's I statistic, i.e., a local indicator of spatial association (LISA), using the R package *spdep* (52). To ensure coverage of the UK, we created a neighbour list using a distance threshold of 35 km to identify spatial relationships between points. The results were visualized using Moran's scatterplots and maps, highlighting areas of significant spatial autocorrelation, with permutation tests providing p-values to assess

251 the statistical significance of the observed spatial patterns either as areas of high-high (hot
252 spots) or low-low (cold spots) of behaviours.

253 We then tested whether foxes were more likely to display our target behaviours
254 depending on the length of time in which the trail camera was operational (29); however, we
255 found no significant effect (Table S9), and so we excluded camera operation time as a variable
256 in our main analysis to avoid model oversaturation. We then tested whether (a) touching
257 (yes/no) or (b) solving the task (yes/no) was associated with current (2020) urbanisation data
258 using binomial general linear models (GLMs). We also used poisson GLMs to examine the
259 effects of urbanisation on the number of visits and exploratory diversity of foxes at each
260 location, followed by GLMs to assess how urbanisation predicted the time taken to touch or
261 solve the task.

262 We tested whether change in the environment was a key driver of behaviour using
263 binomial GLMs, comparing the (a) probability of touching and (b) solving the tasks in relation
264 to the increase in urbanisation between 1990 (earliest available data) and 2020. Finally, we
265 compared the likelihood of older versus newer urban fox populations (a) touching and (b)
266 solving the tasks using binomial GLMs, as well as their (c) latency to solve the tasks using
267 GLMs and (d) number of exploratory behaviours using poisson GLMs.

268

269 **Results**

270 *Spatial patterns of fox behaviour*

271 Foxes touched the novel tasks at 27.4% of locations (34/124; Figure 1b) and solved
272 them at 12.4% of locations (14/122; Figure 1c). Foxes mainly solved tasks in urban areas,
273 including Leeds, Edinburgh, Sheffield and London (Figure 1c). The local indicators of spatial
274 association (LISA) identified multiple hotspots for foxes acknowledging the tasks (Figure S2),
275 but only indicated a cluster of 13 significant hot spots for both touching and solving them – all
276 in and around London (Figure 1d). Similar to our previous work, the likelihood of touching a
277 task was positively associated with urbanisation (Likelihood Ratio (LR) χ^2=11.05, p<0.001;

Figure 2a). However, in our extended dataset, there was also a significant positive association between urbanisation and the likelihood of foxes solving the task (LR χ^2=15.6-, p<0.001; Figure 2b).

Behavioural differences between urban and rural fox populations

Number of fox visits to tasks was positively related to urbanisation (LR χ^2=1205.5, p<0.001; Fig S3). For locations where foxes touched a task, there was no effect of urbanisation on the latency to touch (LR χ^2=2.03, p=0.153) or solve (LR χ^2=0.47, p=0.491) the tasks. Urban foxes did not display more exploratory behaviours when interacting with the tasks (LR χ^2=0.03, p=0.866), nor did they spend any longer exploring the tasks (LR χ^2=0.12, p=0.732), compared to rural populations.

Temporal drivers of fox behaviour

The majority of locations (80.2%, 228/284) showed some increase in urbanisation between 1994 and 2020. However, most of these locations had relatively small changes in the amount of urbanisation across this timeframe (mean$\pm$SE=0.008$\pm$0.004), with only 12 locations showing an increase in urbanisation by >2%. Areas with the greatest increases in urbanisation between 1994 to 2020 did not have a higher likelihood of a fox touching (LR χ^2=2.82, p=0.093) or solving (LR χ^2=0.01, p=0.976) the tasks.

When comparing relatively older versus newer urban fox populations, there was no difference in the likelihood of foxes touching the tasks (LR χ^2=0.90, p=0.341), but older population were significantly more likely to solve them (LR χ^2=8.11, p=0.004). In total, 26.1% (12/46) of foxes from older urban populations solved the tasks compared with 0% (0/16) of foxes from newer populations. Older urban populations also displayed significantly more exploratory behaviours when interacting with tasks (LR χ^2=9.08, p=0.002; Figure 3). There was only a tendency for older urban populations to touch the tasks faster (LR χ^2=2.06, p=0.154) and spend longer exploring them (LR χ^2=3.03, p=0.081). Removing locations in

London (identified as a major hotspot) yielded similar results across all analyses (touch: LR χ^2=0.27, p=0.605; solve: LR χ^2=4.22, p=0.039), indicating that behavioural differences between old versus new urban populations are not solely driven by factors unique to London and, instead, more likely reflect broader patterns of urbanisation among our study sites.

Discussion

Consistent with our previous findings (29), the current study found that urban foxes were more likely to touch novel food-related tasks. We also extend this work by showing, for the first time, that certain urban fox populations are more likely to solve novel tasks using innovative behaviour, and that older, more established urban populations display greater exploratory diversity and problem-solving success compared to more recent urban populations. Collectively, these new findings suggest that historical patterns of urbanisation – specifically, where and how long a city has been inhabited by foxes – may contribute to population differences in bold, exploratory, and innovative behaviours.

Although behavioural innovation was observed in multiple urban locations, London emerged as a particular hotspot, likely reflecting its status as the oldest urban fox population in the UK (34). This population has previously shown distinct phenotypic changes in skull morphology (41), suggesting that behavioural and morphological phenotypes may be influenced by long-term exposure to urban environments. By contrast, foxes from Bristol, which are another relatively old urban population, did not display bold, exploratory, or innovative behaviours. Historical declines from sarcoptic mange in Bristol during the 1990's (53), followed by recolonisation from surrounding rural areas, may have introduced a genetic pool that is less-shaped by urban selective pressures, reducing the likelihood of such behaviours (54). If so, then local population history could play a potential role in shaping urban adaptation, including the age of colonisation, demographic events, and recolonisation dynamics. Such ecological factors might also help explain why urban-rural differences in behaviour are not always consistent between studies (26, 28).

Urban foxes were first reported in UK cities in the 1930s (34), with 33.1% (125/378) of surveyed urban areas hosting populations by the mid-1980s (51). Colonisation has continued, meaning that some of our study populations are older than others (51, 55). A key finding from our study is that the rate of urbanisation between 1994 and 2020 did not appear to influence urban-rural differences in our target behaviours, which may reflect the modest changes to urban areas in the UK during this period. Alternatively, this result could reflect the spatial resolution of available landscape datasets, which may not have detected more subtle environmental changes, such as fine-scale shifts in human activity. Regardless, exploratory diversity and problem-solving success were more common in older, more established urban fox populations, even though newer populations (established after 1986 or <40 years ago) were equally likely to touch the tasks. Since foxes first colonised UK cities ~90 years ago (34), these findings suggest that certain behaviours, such as the likelihood of touching/engaging with novelty, may emerge relatively early (<40 years), whereas other behaviours, including exploratory diversity and innovative behaviour, may require 40-90 years of urban exposure. In other words, the behavioural characteristics of older urban fox populations suggest a more gradual pattern of adaptation rather than more recent rates of urbanisation, potentially via individual learning, cultural transmission, dispersal patterns, or a combination of these and other mechanisms across many generations. Newer urban populations may not yet exhibit these behaviours to the same extent, being in earlier stages of adjustment or colonisation.

Adaptation to urban environments, including the micro-evolutionary or other long-term processes that drive it, may take time to emerge in at least some, but not necessarily all, contexts. Indeed, evidence from our study supports this notion. In other species, older urban coot populations (*Fulica atra*) are bolder (56) while older commensal house mice populations are better problem-solvers (57) compared to younger urban populations. By contrast, Johnson-Ulrich et al. (58) found that rural hyenas (*Crocuta Crocuta*) were more innovative than relatively newer and older urban populations. Whether such differences are explained by genetic or non-genetic factors is not clear (59), highlighting the need for longitudinal research to better understand urban-rural divergence in behaviour.

Building on our proposed temporal framework for behavioural adaptation in foxes, studies in other species show that bold and innovative behaviours sometimes co-occur within the same population, with novelty avoidance potentially limiting innovation (19, 60). In our study, innovation required foxes to display sufficient boldness to interact with the tasks, but not all bold fox populations displayed innovative behaviour (e.g., 59% of tasks that were touched were not solved). Although further research is needed, such patterns could be explained by the notion of a temporal sequence, where innovation emerges over time after urban fox populations are sufficiently bold to engage with novelty (61). Because our study focused on population-level behavioural patterns, future research should test whether bold and innovative behaviours co-occur within the same individuals, as suggested in some other species (60).

Urban areas typically have higher fox densities than rural settings (34), and in the current study, urban foxes were also more likely to visit the tasks. This raises the possibility that differences in density or visitation could influence the likelihood of observing our target behaviours. However, several lines of evidence suggest that these factors alone cannot account for our results. First, among locations where foxes interacted with tasks, urban and rural populations did not differ in their latency to touch or solve the tasks, nor did they differ in terms of the number of exploratory behaviours or the time spent engaging with tasks. Second, spatial hotspots for touching and solving were concentrated in specific areas (e.g., London), rather than being more uniform across all high-density urban fox sites (e.g., Glasgow). Third, the overall likelihood of problem-solving was relatively low across all urban and rural fox populations (12.4% of locations), suggesting that sheer fox numbers or visits cannot fully explain the observed behavioural differences. This suggests that other factors associated with long-term urban exposure may provide a more parsimonious explanation for these findings. For instance, urban environments, particularly older cities, likely expose foxes to greater diversity of human-made objects, such as discarded litter (62), providing repeated opportunities to discover, explore, and learn how to exploit novel resources (63). Alternatively, novel food-related objects, including those used in our study, may represent relatively easy-

to-access resources in urban habitats, where high fox densities and smaller home ranges intensify competition and increase the attractiveness of such resources. Further research is needed to explore these and other possibilities.

Conclusions

Overall, our study demonstrates that historical patterns of urbanisation, particularly the length of time populations have been established in urban environments, are an important predictor of population differences in bold, exploratory, and innovative behaviours in wild red foxes. While initial engagement with novel food-related opportunities, such as our novel tasks, may emerge relatively quickly in newly established urban populations, more complex behaviours – such as diverse exploration and problem-solving – were predominantly observed in older urban populations (particularly London), highlighting the potential role of local variation and long-term exposure to urbanisation in shaping population behaviour. By linking long-term urbanisation history to present-day behavioural traits, our findings provide new insights into the temporal and spatial processes underlying wildlife adaptation to human-altered environments.

Ethical Note

This research was granted ethical approval by the Animal Welfare Ethics Board of the University of Hull (FHS356) and followed all ASAB/ABS guidelines. Foxes were not handled, trail cameras were placed away from footpaths to reduce public disturbance, and all food items used to attract foxes were safe for ingestion by other species.

Data Availability

All data are provided in data set S1 in the Supplementary material.

Declaration of Interest

The authors declare no conflict of interest.

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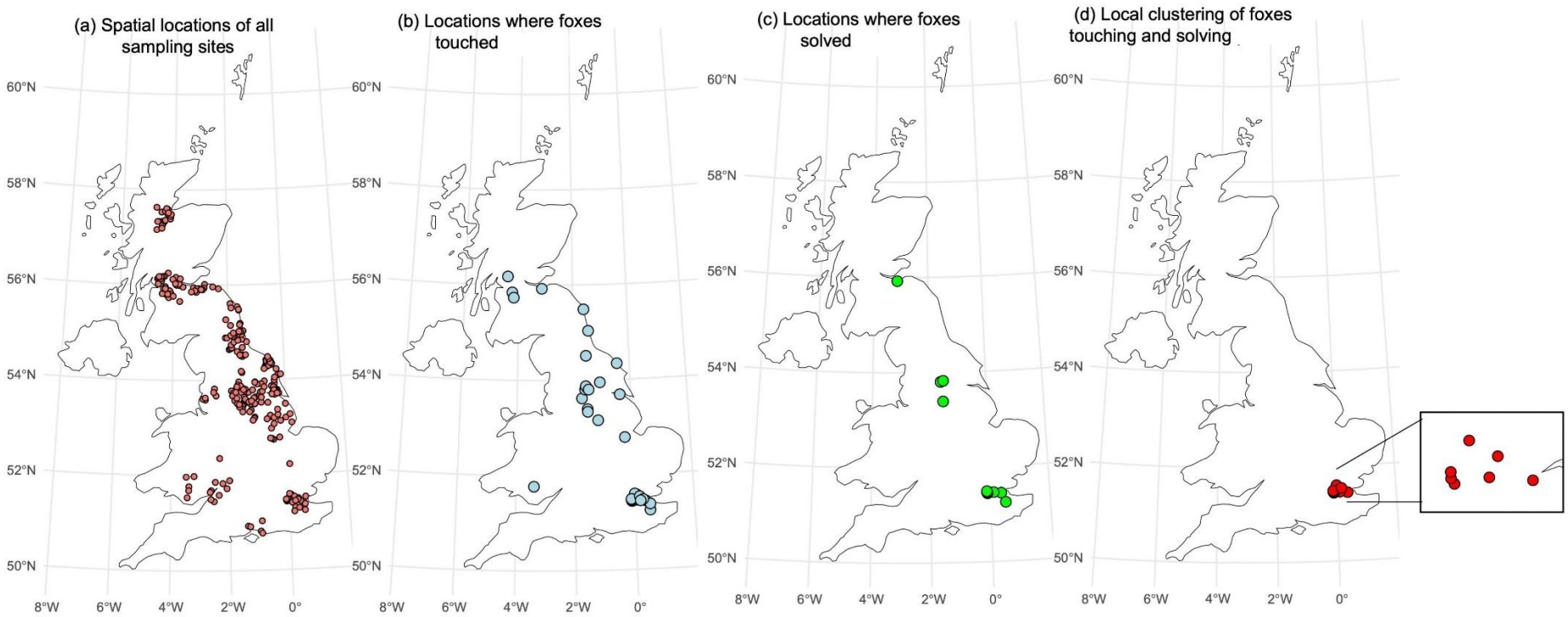

Figure 1. (a) The spatial locations of all sampling sites across the UK (dark red points), (b) the recorded locations where foxes touched the novel tasks (light blue points), (c) the recorded locations where foxes solved the tasks (light green points), and (d) significant ($p<0.05$) local clustering of locations where foxes touched then solved the tasks (red points).

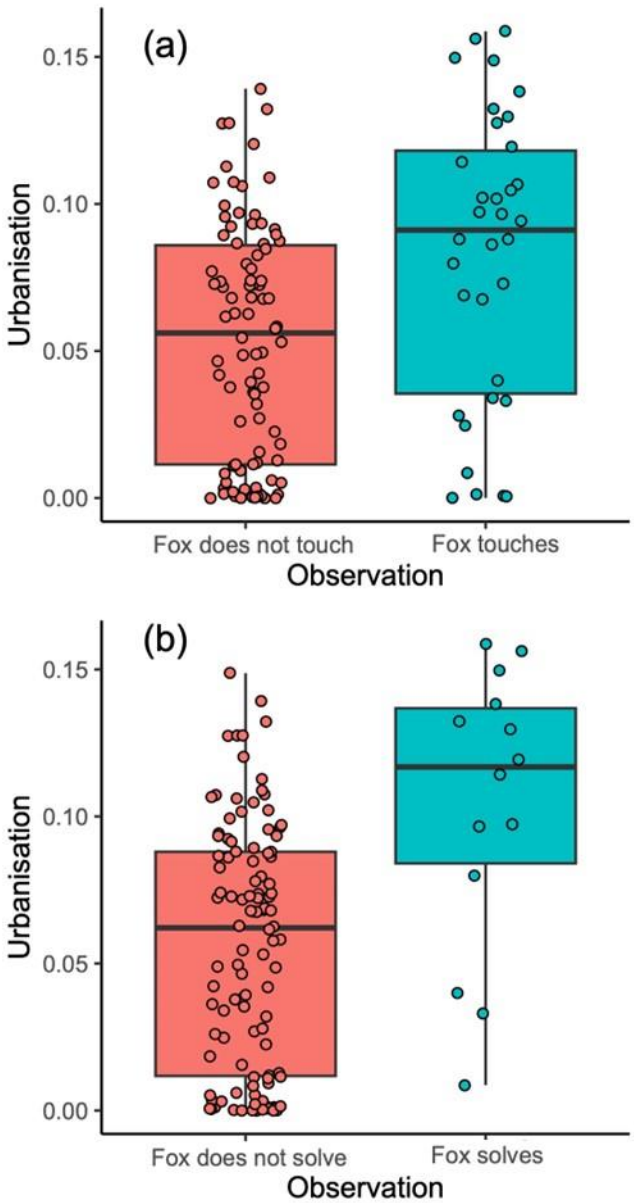

Figure 2. The relationship between urbanisation and whether a fox from a given location (a) does not touch (red) or touches (green) a task, and (b) does not solve (red) or solves (green) a task.

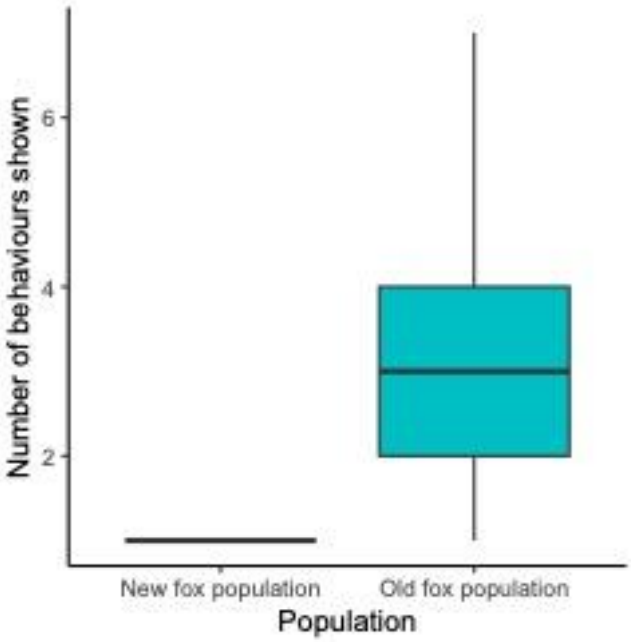

Figure 3. Exploratory diversity (based on the number of unique tactile behaviours from Table 1) displayed by foxes physically interacting with the novel tasks from relatively newer (post-1986) versus older (pre-1986) urban fox populations.