# No evidence that urbanisation encourages wild red foxes (*Vulpes vulpes*) to exploit unfamiliar food-related objects when first discovered

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## Abstract

Urbanisation is the fastest form of landscape transformation on the planet, but our understanding of how wildlife responds to such changes is still in its infancy. Red foxes (*Vulpes vulpes*) are renowned for thriving in urban settings where they have many opportunities to exploit food within or in close proximity to a wide variety of human-made objects (e.g., litter and contents of outdoor bins). The visibility of such behaviour has likely contributed to urban foxes being labelled as 'bolder', 'cunning', and a general nuisance to people. Studies in other animals show that frequent exposure to novel objects can sometimes lead them to overcome their aversion to unfamiliar objects in general (e.g., stimulus generalisation). However, it is unclear whether this applies to the willingness of urban fox populations to exploit food-related objects, particularly when they are first discovered and hence the most novel. To test whether urbanisation encourages wild foxes to exploit food-related objects, we administered eight types of novel objects containing food to 87 free-ranging foxes across a large urban-rural gradient (one object per location). One fox approached and exploited an object in the first instance, while the remaining 86 foxes avoided them. After two weeks, five foxes exploited the objects, while another 13 foxes touched the objects but quit before gaining access. Urban variables (e.g., road, greenspace, and human population density) did not predict whether foxes acknowledged or touched the objects, but their likelihood of touching them was predicted by the type of novel object encountered. When objects were absent, foxes willingly consumed the food. Thus, as with rural populations, urban foxes in the current study displayed an initial aversion to novel objects, suggesting that increased access to food-related objects through urbanisation does not necessarily encourage all foxes to exploit such resources when first discovered. Other factors are needed to overcome their initial aversion, which may have important implications for changing the general perception and management of this species.

**Key words:** innovation, boldness, neophobia, urban wildlife, human-wildlife conflict, behavioural adaptability, public attitudes, dangerous niche hypothesis

## Introduction

Urbanisation is currently the fastest form of landscape transformation on the planet (Angel et al., 2011). Many factors likely contribute to whether or how wildlife can adapt to such environments (e.g., dispersal, morphology, and dietary generalism) (Thompson et al., 2021). In terms of opportunistic behaviour, a growing number of studies show that particular behavioural characteristics (e.g., boldness, neophilia, exploration, persistence, and innovation) can increase urban animals' willingness to spontaneously or quickly exploit novel resources when first discovered (Dammhahn et al., 2020; Ducatez et al., 2017; Griffin et al., 2017; Mazza et al., 2021; Mazza & Guenther, 2021). Such findings suggest that being able and willing to rapidly exploit novel ecological opportunities, rather than avoid or ignore them, may help at least some species thrive within urban settings. To date, however, not all studies find differences in opportunistic behaviour between urban and rural animals for reasons that are still unclear (Griffin et al., 2017; Vincze & Kovacs, 2022), making it difficult to predict whether (or how) such behaviour is impacted by urbanisation within and across species. On the one hand, trying to exploit novel resources whenever they arise may help animals improve their fitness by allowing them to acquire additional resources before they are taken by competitors (Webster et al., 2009). On the other hand, the benefits of such behaviour must also be weighed against other factors, such as animals' opportunities and need for such behaviour (Lee, 1991; Lee & Moura, 2015), as well as the likelihood of their actions exposing them to risk, such as predators, traps, toxic food, and direct hostile encounters with people (Schell et al., 2021; Soulsbury & White, 2015).

In the current study, we investigated the relationship between urbanisation and the willingness of wild red foxes (*Vulpes vulpes*) to exploit novel objects containing food. Red foxes are one of the most widely distributed carnivorans in the world and are renowned for thriving within urban landscapes, particularly British cities within the last century (Collenette, 1937; Scott et al., 2014; Soulsbury et al., 2010; Teagle, 1967; Wilkinson & Smith, 2001). As a generalist carnivore, urban foxes willingly scavenge anthropogenic food within or in close proximity to a wide variety of human-made objects, such as discarded litter and the contents of household bins (Contesse et al., 2004; Doncaster et al., 1990). Since most people live within cities, urban foxes have greater opportunities to exploit these anthropogenic resources compared to rural populations. The visibility of such behaviour has likely contributed to urban foxes being labelled as ‘bold’, ‘cunning’, and a general nuisance to people (Brand & Baldwin, 2020; Bridge & Harris, 2020).

The dangerous niche hypothesis proposes that the primary benefit of having an aversion to novelty is protection from danger (Greenberg, 2003), which may be particularly relevant to foxes because they have a long history of conflict with people (e.g., hunting and pest control) (Soulsbury & White, 2015). Learning from past experiences can play a crucial role in the willingness of animals to overcome their aversion to novelty (Greenberg & Mettke-Hofmann, 2001). In terms of novel objects, studies on a range of animals, including birds, fish, and mammals, have found that frequent exposure to novel objects can sometimes lead to a reduction in their aversion to unfamiliar objects in general, which may arise through a combination of different psychological processes (e.g., habituation, associative learning, object recognition, and stimulus generalisation) (Anderson et al., 2013; Christensen et al., 2011; Gatto et al., 2022; Meehan & Mench, 2002). To date, it is unclear whether this applies to urban foxes’ willingness to exploit novel food-related objects. For example, urban foxes maintain natural diets and also exploit food readily found within peoples’

gardens (Contesse et al., 2004; Harris, 1981). Thus, resident urban foxes have access to resources that are likely more abundant, familiar, and easily accessible to them, which may obviate any need for exploiting unfamiliar human-made objects.

Previous studies have administered novel object tests to urban foxes (Padovani et al., 2021), but these objects did not contain food which makes it difficult to evaluate opportunistic behaviour within a foraging context, and data from rural populations are also needed for comparison. Studies have also found that urban foxes can behave more opportunistically than less urbanised populations in certain contexts (e.g., unfamiliar bait) (Gil-Fernandez et al., 2020), but responses to one form of novelty do not necessarily reflect how animals might react to other forms of novelty, including objects (Miller et al., 2022). Thus, in the current study, we administered novel food-related objects to urban and rural foxes to determine whether their degree of urbanisation predicted their willingness to exploit such resources when first discovered.

## Methods and materials

### Ethical statement

This study was ethically approved by the Animal Welfare Ethics Board of the University of Hull (FHS356), and was carried out in accordance with guidelines outlined by the Association for the Study of Animal Behaviour (ASAB, 2020). No foxes were handled.

### Study sites and subjects

We studied 181 locations throughout Scotland and England (Figure 1), including a wide variety of landscapes in and around different cities (e.g., Glasgow, Edinburgh, Stirling, Leeds, Hull, Lincoln, Sheffield, and York), including recreational parks, private gardens, tree plantations, meadows, mixed woodland, coastal and mountainous scrubland, and farmland. Foxes were unmarked and their participation in the study was entirely voluntary. We gained access to 152 of

these locations by contacting city councils and other organisations that owned land. The remaining 29 locations were private gardens, which we accessed by advertising the study through regional wildlife groups. Our criteria for including any location in the study were: 1) landowner permission, 2) accessibility to foxes (e.g., no barriers/fences), 3) ability to place our equipment out of public view to avoid theft or vandalism, and 4) the location could not be ≤3.5km from another study area. This latter criterion was used to reduce the chances of sampling the same fox across more than one location because ≥3.5km is larger than the typical dispersal distance and home range diameter of British foxes (Soulsbury et al., 2011b; Trewhella et al., 1988). We did not have prior knowledge of fox presence before contacting landowners, and we included locations in the study regardless of whether landowners said foxes lived on or near their land.

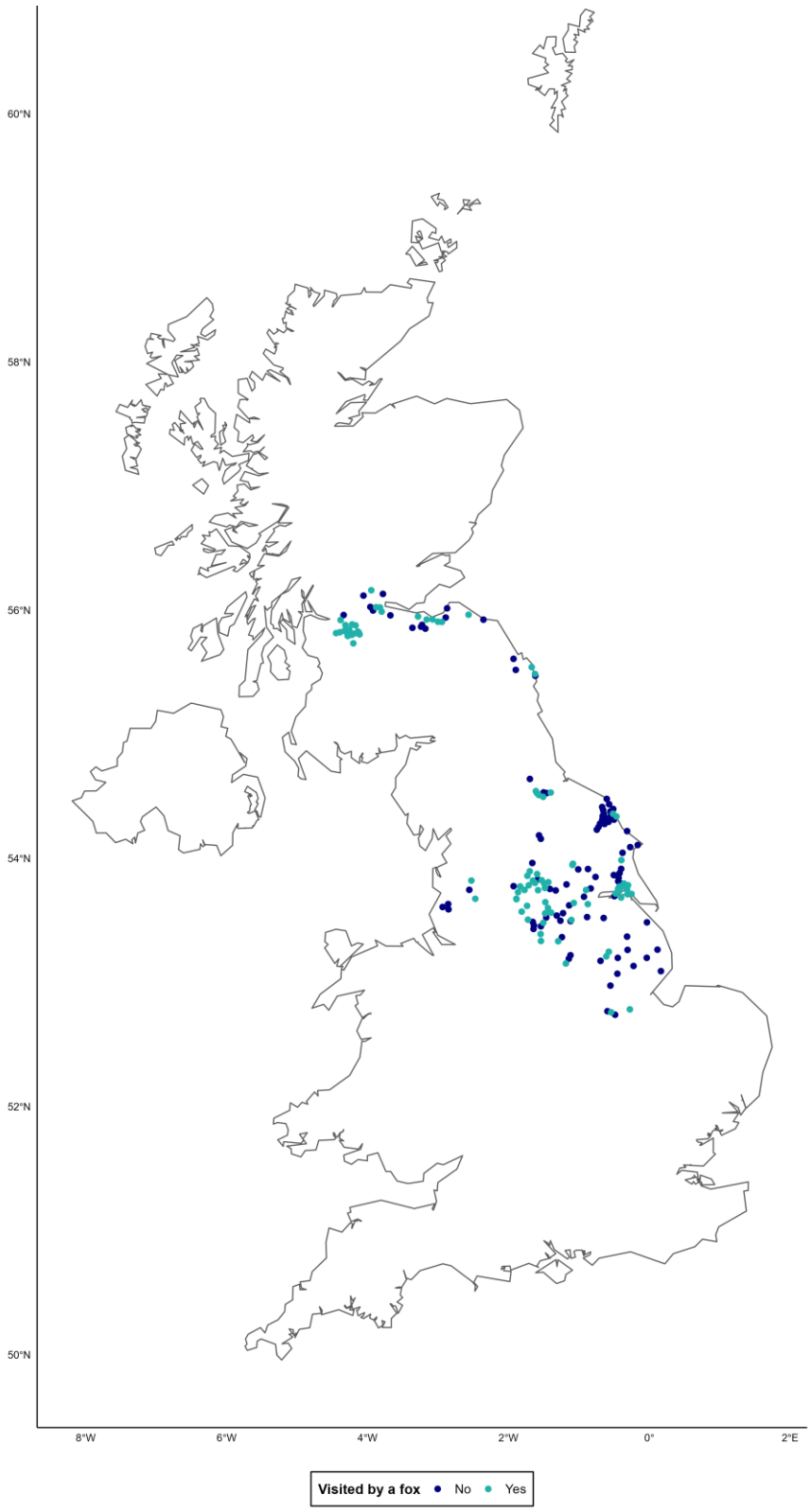


Figure 1. Distribution of zones in Scotland and England where novel objects were deployed.

**Novel object testing**

To determine whether urban foxes were more likely than rural populations to try to exploit novel food-related objects, we administered eight types of novel objects (Figure 2) over a 12-month period between August 2021 and 2022. Only a single object was administered per location. Each object contained desirable food items (e.g., dried dog food and chicken) (Table S1). Some of the designs were based on studies in other species (Morton, 2021; Rossler et al., 2020; Thornton & Samson, 2012; Visalberghi & Limongelli, 1994). Objects varied in terms of design and materials to test whether the type of novel object impacted foxes' behavioural responses. Foxes could gain access to the rewards inside objects using persistence and simple behaviours that they would likely need to exploit human-made objects in the real world (e.g., using their mouth, nose, and/or paws to bite, push, pull, or lift materials). Because we designed the objects ourselves, we could guarantee that the specific combination of materials used to build them would be novel to foxes.

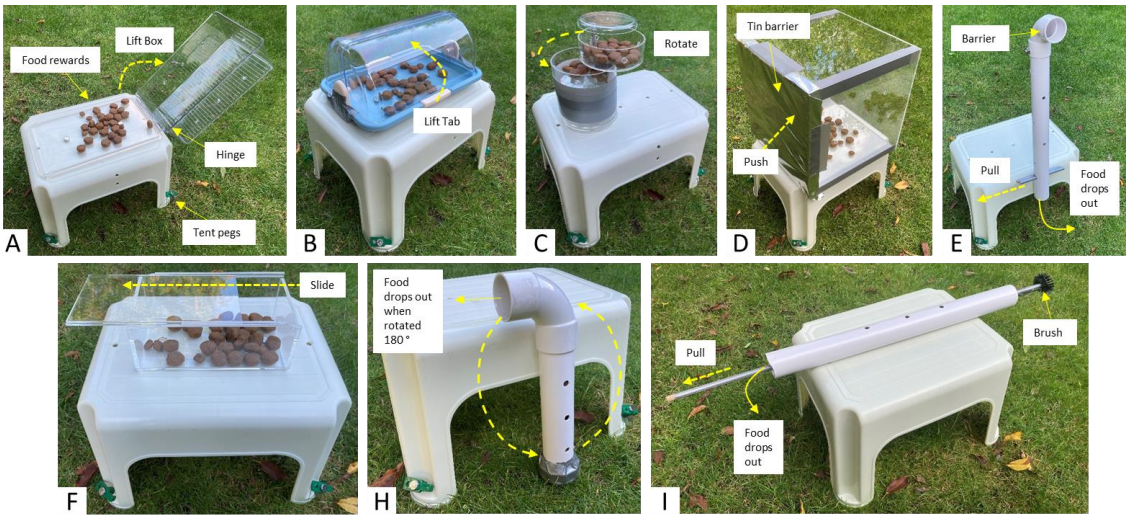


Figure 2. Novel objects administered to foxes. Yellow dashed arrows indicate the direction of each behaviour needed to retrieve the food rewards inside. Task G was never deployed in the field and hence not depicted in this figure.

The objects were made from basic household materials (e.g., PVC piping, metal screws, and wooden rods). To access the rewards in Object D, foxes simply had to push through the aluminium side of the box. Object C had two levels, each containing food. The lid of Object F was fixed in place and could only be solved by sliding it either to the left or right. Object H had a hidden axle to allow 360° rotation. Object I was administered with the stick already inside the pipe; animals merely had to remove the stick using their mouths, which would indirectly rake the food out. All objects were anchored to the plastic platform and had holes drilled into them to facilitate odour cues. Ten pegs were used to anchor the platforms to the ground. To further help foxes detect the objects, we scattered "free food" approximately ≤1m away. To test whether the free food and rewards inside objects had an impact on fox motivation, we varied the free food and rewards by quality and quantity across all locations (Table S1); each location contained a reward and 'free food' condition.

A single object was available at each location for 15.5 ± 1.7 days. Researchers were not present when foxes visited, and we did not touch or replenish the food to avoid unnecessary disturbance to the objects. Following APHA guidelines, we cleaned objects with antibacterial soap and 70% alcohol wipes after retrieving them to prevent possible pathogen transmission. We then washed and dried them prior to redeployment. Forty objects (28.4%) were sprayed with scent deodoriser to test whether the scent of objects (e.g., human odour) had a significant effect on fox behaviour.

Since foxes were free-ranging and their participation in the study was entirely voluntary, some foxes might have avoided our testing locations. Nevertheless, the goal of this study was to test foxes' willingness to *exploit* novel objects to access the food, which required them to

physically touch the objects (and hence be detected on camera). We therefore based our analysis on foxes that were at least able and willing to visit the locations.

**Recording fox activity**

At each location, we horizontally placed a 'no glow' (940 nm) infrared motion-sensor camera (Apeman H45) approximately 4 metres away on a tree trunk. Cameras had a 120 ° sensing angle and a triggering distance of 20 metres. Video lengths were set to record for 5 minutes, with a 5 second trigger delay and a 30 second interval in between each video. Camera lenses were sprayed with defogger and, where possible, minor amounts of understory vegetation were removed between the camera and object to ensure optimal visibility.

**Behavioural responses to novel objects when first discovered**

We recorded the initial behavioural responses of foxes to the objects using the very first video of a fox from each location, i.e., when objects were likely to be the most novel to them. All behaviours were measured before each fox turned away from the object and left the camera's frame of view for >15 seconds; this further ensured we captured foxes' initial responses and also reduced the likelihood of us counting multiple foxes as a single individual if, for example, more than one fox happened to be visiting a location at the same time. We recorded behavioural responses at any point during the two weeks in which objects were deployed, which captured a larger window of opportunity for foxes to engage with the objects if, for example, it took them more than one visit to realise the objects were there.

A myriad of factors can underpin animals' responses to novelty, which are not necessarily underpinned by any one variable (Lee & Moura, 2015; F. B. Morton et al., 2021; Reader & Laland, 2003). However, our goal was to determine *whether* (not why) subjects were successful at exploiting novel objects with food when discovered. Thus, during each video, we recorded whether

or not (1, 0) the fox acknowledged the novel object, which we defined in terms of the fox turning its head to look/smell in the object's direction. We also recorded whether or not (1, 0) the fox touched the object, for instance, by pushing, pulling, and/or biting it, and whether or not (1, 0) they ultimately gained access to the rewards inside. Finally, during their initial visits to objects, we coded whether or not (1, 0) the fox appeared interested but too hesitant to approach the object, which we defined in terms of the fox stopping short of the object, with legs anchored firmly to the ground while they stretched their body out to look/smell the object; these behaviours could be supplemented by the fox occasionally jumping/moving away from the object with their ears flattened and/or the fox scanning their surroundings while visually inspecting the object.

**Food tests**

Foxes are generalist carnivores and should be highly motivated to consume the food rewards in our study (Saunders & Harris, 2000). To confirm this, we revisited 30 of our locations 6 months later to leave up to three food conditions, one at a time, on the ground without a novel object:

- *Condition 1:* 30 chicken-flavoured dried dog food pellets
- *Condition 2:* 15 dried dog food pellets, 15 unsalted peanuts, 1 slice of deli chicken, and 5 sprays of 35mL fish oil mixed with 900mL water
- *Condition 3:* 15 dried dog food pellets, 15 unsalted peanuts, 15 mL honey, 15 mL strawberry jam

We then returned every 3 to 7 days for approximately two weeks to either replenish the same condition or replace it with one of the other three conditions until foxes at each location had an opportunity to discover at least one of the food conditions. Since our goal was to determine whether foxes were willing to consume the food items used for novel object testing, we recorded

the following for all fox visits: 1) whether the food was still visible when the fox arrived, 2) whether the fox acknowledged the presence of the food by directing its head and/or nose in the exact spot where we left the food, and 3) whether the fox consumed the food, including food remnants if some of the food was taken beforehand by another species.

## Factors affecting fox behavioural responses to novel objects

### *Methodological variables*

We examined the impact of novel object type because animals often respond differently to different objects. We examined the effect of seasonality as well as our free food and reward conditions because this might have impacted foxes' motivation to engage with the objects. We examined the effect of the deodoriser spray because the scent of the puzzles could have deterred foxes (e.g., human scent). Since animals' acknowledgement of objects plays a crucial role in whether animals will have the opportunity to exploit them, we also considered whether fox behaviour was impacted by the number of days from the time an object was first acknowledged by a fox until the time we retrieved the equipment. Finally, rewards were sometimes exploited by rodents and other organisms that were tiny enough to fit through the holes of objects; thus, whenever possible, we kept records of the presence/absence of rewards at the time of foxes' initial visits since this might have impacted their ability to detect and engage with the objects. This was done two ways: 1) by taking a photo of the object whenever researchers visited to switch out the camera's SD card, and 2) looking at the trail camera footage to see whether food was still present. Sometimes we could not determine whether food rewards were still present if, for example, the object was opaque, or we did not return to the location before a fox visited, or the camera footage was not clear enough for us to see inside the transparent objects.

*Landscape variables*

Most UK residents live within cities and produce many millions of tonnes of waste per year, which leads to significant problems with litter (DEFRA, 2022). Thus, as discussed, foxes exposed to relatively higher levels of urbanisation will have greater access to anthropogenic food-related objects. However, there is no single best way to classify an "urban" versus "rural" population of animals given that the characteristics of urbanisation are so multi-faceted. Hence, to allow us to more accurately evaluate the degree of urbanisation likely experienced by foxes across our study locations, we used a range of variables recommended by Mu et al. (2022), including human population density, road and greenspace density, land coverage (e.g., cropland), and species richness. We also included measures of rainfall, temperature, and elevation because, for example, they factor into cropland suitability.

Landscape data extraction was repeated for a series of circular buffers at 3.5km from the epicentre of each zone in Figure 1. A Digital Elevation Model raster was sourced from the AWS Open Data Terrain Tiles through the *elevatr* package at a 200m$^2$ pixel resolution (Hollister et al., 2021). Average daily mean air temperature over the calendar year (in degrees Celsius) and total precipitation over the calendar year (in millimetres) were obtained from the *HadUK-Grid* climate observation dataset for the year 2021, the most recent available data, at a spatial resolution of 1km$^2$ per pixel (Hollis et al., 2019). Human population size data were collected from the *UK gridded population census 2011* at a 1km$^2$ pixel resolution (Reis et al., 2017). Elevation, temperature, rainfall, and human population size were extracted as the mean raster pixel value within each buffer size. Road density (in m/m$^2$) within each buffer was computed by sourcing the highway/road class vector layer from OpenStreetMap (*Planet dump*, 2022). Urban greenspace density (in m$^2$/m$^2$) was obtained from the *Ordinance Survey Greenspace* vector layer (OPENGREESPACE, 2022).We

extracted percent coverage of five land cover classes by employing the UK Centre for Hydrology and Ecology Land Cover 2020 product at a $10m^2$ resolution (C. S. Morton et al., 2021). The raster is composed of uniquely classified pixels according to categories following the UK Biodiversity Action Plan, whom we aggregated into five main land cover categories: *urban* (class 20 and 21), *forest* (class 1 and 2), *grassland* (class 4, 5, 6, 7, 9 and 10), *cropland* (class 3), and *wetland* environments (class 8, 11, 12, 13, 14, 15, 16, 17, 18 and 19). Percent coverage was computed by counting how many pixels within each buffer corresponded to each classified land cover and dividing by the total number of pixels in each buffer. Landscape heterogeneity was also quantified as the effective number of distinct land covers present in each buffer and computed as the exponential of the Shannon-Wiener diversity index (Hill's numbers equivalent for q=1) (Chao et al., 2014; Hill, 1973), resulting in a measure that not only accounts for the absolute richness of diverse land cover categories but also weighs the relative abundance of each category.

**Statistical analyses**

Cohen's kappa coefficients were calculated between F.B.M. (who developed the behavioural definitions) and two independent observers (who coded 25% of videos) to ensure that the definitions were reliable (Table S2). Cohen's kappa coefficients were also calculated between K.A. (who coded all videos) and F.B.M. (who trained K.A.) using 25% of videos to ensure that K. A. was reliable prior to coding all of them (Table S3). Finally, Cohen's kappa coefficients were calculated between 25% of K.A.'s videos at two different time periods (separated by several months) to test for intra-observer consistency in K.A.'s codings (Table S4).

Landscape variables were calculated using the R programming language version *4.2.0* within the RStudio IDE version *"Prairie Trillium"* (Team, 2002; Team, 2022). Geospatial vectorial operations were processed utilizing the *sf* R package (Pebesma, 2018) while raster

extraction employed the *exactextractr* package (Baston, 2021). Data processing was conducted through the use of the *tidyverse* R packages family (Wickham et al., 2019).

To obtain a global measure of urbanisation from each study location, we entered our landscape variables into a Principal Components Analysis (PCA) with varimax rotation (Team, 2002). A scree test and parallel analysis were used to determine the number of components to extract (Horn, 1965; Morton & Altschul, 2019). Item loadings $\geq |.4|$ were defined as salient for the PCA; items with multiple salient loadings were assigned to the component with the highest loading.

We used Chi-square tests to determine whether foxes were more likely than not to acknowledge, touch, and exploit novel objects. We used multiple logistic regressions to test the effects of our independent variables (i.e., methods and landscape characteristics) on whether foxes acknowledged, physically touched, and ultimately exploited objects by gaining access to the rewards inside.

Chi-square tests, Cohen's kappa tests, the PCA, and multiple logistic regressions were conducted in IBM SPSS (Version 27). All datasets are provided in Datasets S1 and S2.

## Results

### The fate of novel objects

Foxes were recorded at 87 out of 181 locations (Figure 1). One fox successfully exploited an object in the first instance (Video S1). After two weeks, foxes from another four locations had gained accessed to the rewards (Video S2). Eleven objects (12.6%) were solved by other species, while 65 objects (74.7%) had not been solved when researchers returned to retrieve them. The fate of six objects (6.9%) could not be determined. Objects were more likely to remain unsolved by the

end of the two-week period compared to objects from all other locations, $\chi 2$ (1, N = 87) = 21.3, p < .001.

**Behavioural responses to novel objects**

Cohen's kappa coefficients were $k \geq .75$ for foxes' acknowledgement and apprehensiveness towards objects, indicating excellent inter-observer agreement (Tables S2-4). Out of the 87 locations where foxes were recorded, eight locations were omitted from the behavioural analysis due to poor visibility or camera malfunctions preventing us from observing their initial responses to the objects. Of the remaining 79 locations, all foxes were solitary during their initial visits. Sixty-four of these foxes (81%) acknowledged the novel objects by looking and sniffing in their direction. Foxes were significantly more likely to acknowledge than ignore the objects, $\chi^2$ (1, N = 79) = 30.4, p <.0001.

Of the foxes that acknowledged the objects, 27 foxes (42.2%) were too hesitant to approach in the first instance (Video S3), while 37 foxes (57.8%) avoided the objects without appearing apprehensive (Video S4). Collectively, foxes were equally likely to hesitate versus not hesitate when they first discovered the objects, $\chi^2$ (1, N = 64) = 1.56, p = .211.

In terms of their behavioural responses at any point during the two weeks in which objects were available, we could not determine whether foxes from 9 locations acknowledged them (e.g., poor visibility and camera malfunctions). At the remaining 78 locations, objects were acknowledged at least once by foxes approximately 11.2 ± 3.6 days before we retrieved the equipment. By the time we retrieved the equipment, foxes from at least 18 of these locations (23.1%) had physically touched the objects, including the 5 foxes that successfully exploited them and another 13 foxes that touched the objects but quit before gaining access (Video S5). Foxes that acknowledged the objects at any point during the two weeks were more likely to avoid the objects

without touching them, $\chi2$ (1, N = 78) = 22.62, $p < .001$. Foxes that touched the objects were equally likely to quit versus exploit them, $\chi2$ (1, N = 18) = 3.56, $p = .06$.

**Food tests**

Of the 30 locations where we deployed food without novel objects, foxes were detected at 23 locations, and 18 foxes discovered at least one of the food conditions before other animals exploited them. All of these foxes willingly approached and consumed the food (Table 1 and Video S6).

Table 1. Food conditions consumed by foxes.

| Location | Condition 1 | Condition 2 | Condition 3 |
|---|---|---|---|
| 1 | Yes | Yes | Yes |
| 2 | --- | Yes | Yes |
| 3 | --- | Yes | --- |
| 4 | --- | Yes | --- |
| 5 | Yes | Yes | Yes |
| 6 | Yes | Yes | Yes |
| 7 | Yes | Yes | Yes |
| 8 | --- | Yes | Yes |
| 9 | --- | --- | Yes |
| 10 | --- | Yes | Yes |
| 11 | Yes | Yes | Yes |
| 12 | Yes | Yes | Yes |
| 13 | --- | --- | Yes |
| 14 | --- | Yes | Yes |
| 15 | --- | --- | Yes |
| 16 | --- | Yes | --- |
| 17 | --- | Yes | --- |
| 18 | Yes | Yes | Yes |

*Note*. "---" = food condition was not administered.

**Principal components analysis of landscape characteristics**

Across all 181 of our study locations, a PCA of our ecological and urban measures revealed three components and explained 32.52, 28.71, and 11.98% of the variance, respectively (Table 2,

Figure S1, Table S5). Component 1 was labelled "Wilderness" because it was characterised by item loadings related to lower levels of cropland and higher levels of natural and remote spaces (e.g., forests, grasslands, and higher elevations). Component 2 was labelled "Urbanisation" because it was characterised by higher levels of human, road, and greenspace densities, but lower levels of cropland. Component 3 was labelled "Biodiversity" because it was characterised by high levels of landscape heterogeneity and wetlands (i.e., an important habitat for many terrestrial and aquatic species).

Table 2. Principal components analysis of ecological and urban variables (N = 181 locations).

| | Varimax-rotated components | | |
|---|---|---|---|
| Item | PC 1 | PC 2 | PC 3 |
| Elevation | **.892** | -.001 | .16 |
| Rainfall | **.813** | .212 | .125 |
| LCC: Grassland | **.775** | -.117 | .268 |
| LCC: Forest | **.622** | -.14 | -.105 |
| Landscape heterogeneity 1 | .376 | .034 | **.741** |
| Landscape heterogeneity 0 | .236 | -.059 | **.682** |
| Greenspace density | .054 | **.727** | .021 |
| Road density | -.064 | **.965** | -.084 |
| Human population size | -.158 | **.918** | -.103 |
| LCC: Urban | -.183 | **.953** | -.123 |
| LCC: Wetland | -.344 | -.131 | **.758** |
| LCC: Cropland | **-.561** | **-.653** | -.352 |
| Temperature | **-.856** | .185 | -.04 |

*Note.* Salient loadings are in boldface. LCC=Land cover category. PC = principal component.

**Factors affecting fox behavioural responses to novel objects**

At 56 locations, we were able to determine whether food rewards were still present at the time of foxes' initial visits, but since rewards were missing at only three of these locations, we omitted this variable from further analysis given the strong homogeneity of the data. When

considering the first fox video across locations (N = 79 foxes), none of the other methodological variables or landscape composite scores (derived from each principal component) had a significant effect on whether foxes acknowledged the novel objects (Table 3). Of the 64 locations where foxes acknowledged the objects, the methodological variables and landscape composite scores also did not significantly predict their hesitation to approach the objects when first discovered (Table 4). Of the locations where foxes acknowledged the objects at some point during the two weeks, type of novel object was the only predictor of foxes' likelihood of touching them (Table 5), with foxes being more likely to touch objects B, E, F, H, and I (Figure 2 and 3).

Table 3. Multiple logistic regression predicting whether foxes acknowledged novel objects when first discovered (N = 79 foxes).

| Variable | Exp (β) | p | 95% CI | |
|---|---|---|---|---|
| | | | Lower | Upper |
| Month | .947 | .605 | .772 | 1.162 |
| Object type | .816 | .095 | .643 | 1.036 |
| Food condition | .935 | .487 | .773 | 1.13 |
| Deodoriser | .792 | .757 | .181 | 3.473 |
| PC 1 (Wilderness) | .985 | .965 | .516 | 1.883 |
| PC 2 (Urbanisation) | 1.039 | .895 | .583 | 1.853 |
| PC 3 (Biodiversity) | 1.186 | .631 | .592 | 2.376 |

*Note*. PC = principal component.

Table 4. Multiple logistic regression predicting whether foxes behaved apprehensively towards novel objects when first discovered (N = 64 foxes).

| Variable | Exp (β) | p | 95% CI | |
|---|---|---|---|---|
| | | | Lower | Upper |
| Month | .942 | .521 | .784 | 1.131 |
| Object type | .933 | .548 | .743 | 1.171 |
| Food condition | 1.039 | .630 | .888 | 1.217 |
| Deodoriser | 1.71 | .399 | .491 | 5.954 |
| PC 1 (Wilderness) | .684 | .202 | .381 | 1.226 |
| PC 2 (Urbanisation) | 1.146 | .603 | .685 | 1.917 |
| PC 3 (Biodiversity) | .86 | .623 | .471 | 1.57 |

*Note*. Significant results in bold. PC = principal component.

Table 5. Multiple logistic regression predicting the likelihood of foxes touching a novel object at any point during the two weeks after they were discovered (N = 78 locations).

| Variable | Exp (β) | p | 95% CI | |
|---|---|---|---|---|
| | | | Lower | Upper |
| Month | .919 | .418 | .748 | 1.128 |
| Object type | **.712** | **.027** | **.527** | **.962** |
| Food condition | 1.01 | .917 | .84 | 1.215 |
| Deodoriser | .409 | .184 | .109 | 1.529 |
| Days since fox acknowledged object [a] | .915 | .418 | .738 | 1.135 |
| PC 1 (Wilderness) | 1.28 | .526 | .597 | 2.745 |
| PC 2 (Urbanisation) | .743 | .336 | .406 | 1.36 |
| PC 3 (Biodiversity) | 1.027 | .947 | .467 | 2.261 |

*Note*. Significant results in bold. [a] Number of days since first video of a fox acknowledging object (i.e., opportunity to touch/exploit). PC = principal component.

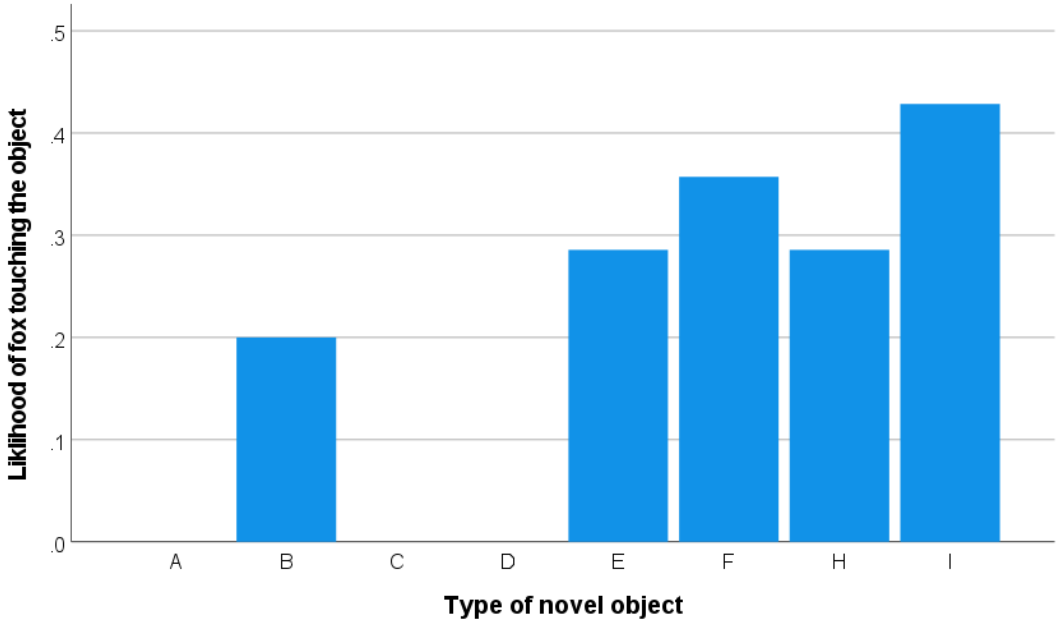


Figure 3. Proportion of objects touched by foxes (at any point during two weeks) divided by the number of objects (per type) deployed across 64 locations where foxes discovered them. Photos of each object are depicted in Figure 2.

## Discussion

We investigated the relationship between urbanisation and the likelihood of wild red foxes exploiting novel food-related objects when first discovered. Of the foxes that acknowledged the novel objects, most of them avoided the objects without gaining access. Given that we were able to determine the fate of all objects, this rules out the possibility that our cameras significantly missed footage of foxes visiting and exploiting their contents without us knowing it. Collectively, our findings do not support the hypothesis that urbanisation encourages fox populations to exploit novel food-related objects when first discovered; rather, as with rural populations, urban foxes within the current study still displayed an initial aversion to such novelty.

Urban foxes clearly differ from rural populations in significant ways, for instance, in terms of their diet and skeletal morphology (Parsons et al., 2020; Soulsbury et al., 2010), but our findings

are consistent with a growing number of studies in other species that show urbanisation is not always a significant predictor of urban-rural differences in opportunistic behaviour, including responses to novel objects (Griffin et al., 2017; Vincze & Kovacs, 2022). Although we are unable to comment on other fox populations, our data suggest that foxes within the current study are unlikely to thrive and maintain viable populations in urban settings by showing a greater willingness to quickly exploit these novel opportunities in *general* (i.e., all contexts). Indeed, if that was the case, then more urban foxes would have been willing to touch and exploit the objects used in the current study.

Foxes always consumed the food rewards when objects were absent despite the presence of a trail camera, ruling out the possibility that the cameras were a significant deterrent for them in the novel object condition. Since foxes were willing to consume the food rewards when novel objects were absent, it also rules out the possibility that food-related motivation explains why foxes avoided the objects. Finally, as reported in Padovani et al. (2021), we found in our larger multi-site sample no seasonal differences in foxes' responses to novel objects, which rules out seasonal differences in food abundance, and hence, variation in their motivation due to hunger.

Further studies are needed to understand how foxes might balance decisions to exploit versus avoid novel food-related objects, particularly in terms of the benefits, risks, and need for doing so. Object neophobia, for example, could explain why foxes initially avoided the food when objects were present, particularly foxes that showed clear signs of apprehension towards the objects (Greggor et al., 2015; Miller et al., 2022; Travaini et al., 2013). If so, then present ecological conditions within urban settings included in our study may not favour urban-rural differences in object neophobia among foxes (Griffin et al., 2017). Factors, such as speed of habituation, may be crucial for them to overcome their aversion to such novelty (Vincze et al.,

2016). Age, sex, dominance, associative learning, and/or personality are also some of the many other factors that might influence foxes' decision-making (Fawcett et al., 2017; Griffin et al., 2013; Padovani et al., 2021; Soulsbury et al., 2011a). As previously discussed, foxes may simply prefer to exploit easy-access resources wherever possible, similar to what has been proposed for challenging tasks in some populations of wild raccoons (*Procyon lotor*) (Morton, 2021). Finally, as with some other species (e.g., corvids), foxes' responses to novel objects may be very nuanced and depend on the particular context, such as the type of novel object encountered.

*Implications for red fox public perception and management*

Our findings have potentially important implications for changing the public perception and management of foxes. In terms of public perception, our data support a more nuanced view of urban fox behaviour by demonstrating that, in some respects, they can be shy and similar to rural populations. Although further studies are needed, some household surveys show that many residents label foxes as a 'nuisance' despite never actually experiencing a problem themselves (Baker et al., 2020; Harris, 1981), which may be explained in part by the patterns of fox behaviour observed in the current study.

In terms of fox management, many websites recommend chemicals (e.g., ammonia), ultrasonic noise makers, or more lethal means of controlling nuisance foxes (e.g., removal/shooting). Based on our findings, however, we suggest that an alternative and more humane approach may be to use novel objects as a deterrent. Indeed, foxes from our study were still unwilling to exploit objects even when the reward quantity was high (e.g., 90 dog food pellets). It is important to note that fox populations outside the current study may not necessarily respond to novel objects in the same way, and novel objects will only be effective until foxes overcome their aversion through habituation. Thus, to establish whether this management practice could be

effective for a given fox population, further research will need to understand, for example, what characteristics of novel objects are better at deterring those foxes (e.g., size, shape, and proximity to food), and how long the foxes will continue to avoid novel objects before they need to be replaced with new ones.

## Conclusions

Red foxes thrive within urban settings, but contrary to what has been found in some species, we found that wild urban foxes were no more likely than rural populations to exploit novel food-related objects when first discovered. These findings do not support the hypothesis that increased access to such resources through urbanisation encourages foxes, at least within the current study, to exploit them when first discovered; instead, other factors are likely needed for urban foxes to overcome their initial aversion.

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