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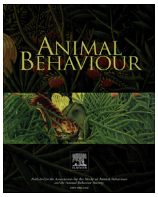

Urban foxes are bolder but not more innovative than their rural conspecifics

F. Blake Morton [a, *], Marieke Gartner [b], Ellie-Mae Norrie [a], Yacob Haddou [c], Carl D. Soulsbury [d], Kristy A. Adaway [a]

[a] *Department of Psychology, University of Hull, Hull, U.K.*
[b] *Atlanta Zoo, Atlanta, GA, U.S.A.*
[c] *Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, U.K.*
[d] *School of Life and Environmental Sciences, University of Lincoln, Lincoln, U.K.*

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Urbanization is the fastest form of landscape transformation on the planet, but researchers' understanding of the relationships between urbanization and animal behaviour is still in its infancy. In terms of foraging, bold and innovative behaviours are proposed to help urban animals access, utilize and exploit novel anthropogenic food sources. Red foxes, *Vulpes vulpes*, are one of the most widespread carnivores on the planet. However, despite frequent stories, images and videos portraying them as 'pests' in urban areas due to their exploitation of food-related objects (e.g. raiding the contents of outdoor bins), it is unknown whether they are bolder and more innovative in terms of their likelihood of exploiting these resources compared to rural populations. In the current study, we gave novel food-related objects to foxes from 104 locations (one object per location) across a large urban–rural gradient. To access the food, foxes had to use behaviours necessary for exploiting many food-related objects in the real world (e.g. biting, pushing, pulling or lifting human-made materials). Despite foxes from 96 locations acknowledging the objects, foxes from 31 locations touched them, while foxes from 12 locations gained access to the food inside. A principal component analysis of urban and other landscape variables (e.g. road, greenspace and human population density) revealed that urbanization was significantly and positively related to the likelihood of foxes touching, but not exploiting, the objects. Thus, while urban foxes may be bolder than rural populations in terms of their willingness to physically touch novel food-related objects, our findings are inconsistent with the notion that they are more innovative and pose a general nuisance to people by regularly exploiting these anthropogenic resources on a large geographical scale.

Urbanization is the fastest form of landscape transformation on the planet (Angel et al., 2011; Grimm et al., 2008), with 55% of the global human population now living within cities (United Nations, 2019). Urban environments present wildlife with a range of novel challenges that can include coping with habitat loss and fragmentation (Šálek et al., 2015), increased or novel human disturbances (Rodrigo-Comino et al., 2021), altered competitive interactions (Martin & Bonier, 2018) and new predators or parasites (Guiden et al., 2019; Pedroso-Santos & Costa-Campos, 2020). Species can be characterized based on a gradient of how well they adapt to urban environments, including (1) 'urban avoiders', which are restricted to nonurban or remnant natural habitats, (2) 'urban utilizers', which make occasional use of urban areas and (3) 'urban dwellers', which actively exploit and benefit from urban areas (Fischer et al., 2015). The ability of species to persist and thrive in urban environments is related to a suite of life history, morphological, physiological, behavioural and cognitive factors (Charmantier et al., 2017; Sol et al., 2014), but researchers' understanding of how animals adapt to urban environments is still in its infancy.

In terms of foraging, species dwelling in urban areas are likely to encounter novel anthropogenic food sources (Murray et al., 2015, 2018) and certain behaviours, particularly boldness (defined broadly as animals' responses to unfamiliar situations; Bergvall et al., 2011; Breck et al., 2019) and innovation (defined here as using new or modified behaviours to solve new or old tasks; Lee, 1991; Reader & Laland, 2003), are proposed to help urban

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* Corresponding author.
E-mail address: b.morton@hull.ac.uk (F. B. Morton).

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animals access, utilize and exploit these resources (Dammhahn et al., 2020; Ducatez et al., 2017; Griffin et al., 2017; Mazza et al., 2021; Mazza & Guenther, 2021). Having a greater tendency to innovate can provide urban wildlife with the behavioural flexibility needed to exploit a wide variety of resources (Reader & Laland, 2003). Being more likely to quickly display such behaviour can enable urban wildlife to exploit these opportunities before they are taken by other animals or removed by city cleaners (Webster et al., 2009). Not all studies, however, have found that urban dwellers are bolder and more innovative for reasons that remain unclear (Griffin et al., 2017; Vincze & Kovacs, 2022).

Red foxes, *Vulpes vulpes*, are one of the most widespread carnivores in the world (Marsh et al., 2022; Soulsbury et al., 2010). They are an opportunistic generalist, which enables them to exploit a diverse range of food items, including mammals, birds, invertebrates and plants. In urban areas, foxes will also scavenge a wide variety of anthropogenic food items from various sources, including bird feeders, compost heaps, bins and food provisioned by people (Contesse et al., 2004; Doncaster et al., 1990; Saunders et al., 1993). Such use of anthropogenic materials suggests that urban foxes are willing to exploit new feeding opportunities, but although urban foxes are often labelled as being generally bolder than their rural counterparts, it is unknown whether this is true in all contexts. It is also unknown whether they are more innovative.

Urban foxes often encounter food-related objects that are temporally, physically and spatially ‘novel’ to them, including (1) continuous changes to the combination of objects found on streets or in outdoor bins, (2) objects that look physically different to what animals are accustomed to seeing (e.g. new or modified containers) and (3) new or familiar objects found in unexpected locations (e.g. randomly discarded trash). Such dynamic changes, combined with frequent encounters, may favour bolder and more innovative behaviour in foxes by enabling them to use new or modified behaviours (i.e. ‘innovations’) to exploit these resources, particularly shortly after discovering them (e.g. overnight; Dammhahn et al., 2020; Ducatez et al., 2017; Griffin et al., 2017; Mazza et al., 2021; Mazza & Guenther, 2021). However, despite frequent stories, images and videos within popular culture portraying urban foxes as ‘pests’ due to their opportunistic foraging behaviour (Soulsbury & White, 2015), it is unclear whether or to what extent such attitudes are due, in part, to their exploitation of food-related objects, including discarded litter and items found in outdoor bins (Baker et al., 2020; Harris, 1981).

In the past, studies have given novel objects to urban foxes (Padovani et al., 2021), but the objects did not contain food and comparisons with rural populations were not made, making it impossible to evaluate the likelihood of urban foxes behaving more boldly and more innovatively within this context. Although urban foxes may be more likely than rural populations to consume novel bait (Gil-Fernandez et al., 2020), this does not necessarily reflect how animals react to other forms of novelty, including human-made objects (Miller et al., 2022, p. P74). Hence, the current study had two aims: first, to test whether urban foxes are bolder and more innovative than rural populations in terms of exploiting novel food-related objects, and second, to test to what extent urban foxes are a general nuisance to people because they exploit these anthropogenic resources.

METHODS

Ethical Note

This study was ethically approved by the Animal Welfare Ethics Board of the University of Hull (FHS356), and was carried out in accordance with the ASAB/ABS guidelines. No foxes were handled, all trail cameras were placed away from footpaths to minimize public disturbance and food items used to attract foxes were not harmful if ingested by other animals, including outdoor pets.

Study Sites and Subjects

We studied 200 locations throughout Scotland and England, including areas in and around different cities (e.g. London, Glasgow, Edinburgh, Stirling, Leeds, Hull, Lincoln, Sheffield and York). These locations covered a wide variety of landscapes, 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 162 of these locations by contacting city councils and other organizations that owned land. The remaining 38 locations were private gardens, which we accessed by advertising the study through Twitter and regional wildlife groups. Our criteria for including any location in the study included: (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 $\leq$ 3.5 km from another study area. Because foxes could not be individually identified, this latter criterion was used to reduce the chances of sampling the same fox across more than one location because $\geq$ 3.5 km is larger than the typical dispersal distance and home range diameter of British foxes (Soulsbury et al., 2011; Trewhella et al., 1988). We did not have prior knowledge of fox presence before contacting landowners, and we included locations in the study even if foxes were not known to visit them.

Designs and Deployment of Novel Food-Related Objects

We deployed eight types of food-related objects (Fig. 1) across our study locations between August 2021 and November 2023. Only a single object was placed per location, and they were available to foxes for 15.5 ± 1.64 days before we removed them. Although foxes might, of course, respond differently to food-related objects that are left for longer, 2 weeks is a very typical timeframe for many food-related objects available to British urban foxes (e.g. regular street cleaning and bin services every 1–2 weeks).

The objects were made from basic household materials (e.g. PVC piping, metal screws and wooden rods). Objects varied in terms of design and materials to ensure that our data on foxes' behavioural responses were more generalizable and not specific to just one type of object. Objects were ‘novel’ in terms of their location, which we verified by searching for similar objects within the surrounding areas. They were also novel in terms of their design, which we assembled ourselves using a unique combination of materials to create objects that are not widely commercially available, making it highly unlikely that foxes would have seen those specific combinations before. Each object had a single ‘free food’ and ‘reward’ condition (Table A1); the ‘free food’ was scattered approximately 1 m away from each object. We used different types, combinations and quantities of food to ensure that our data on foxes' behavioural responses were more generalizable and not specific to any particular food. All objects were anchored to the plastic platform and had holes drilled into them to facilitate dispersion of odour cues. Tent pegs were used to anchor the platforms to the ground.

Object A (Fig. 1) could be opened by simply lifting the box, which was on a hinge. Object B could be opened by lifting one (not both) of the white tabs on the cover. Object C had two levels, each containing food. To access the rewards in Object D, foxes simply had to push through the aluminium side of the box. Object E could be

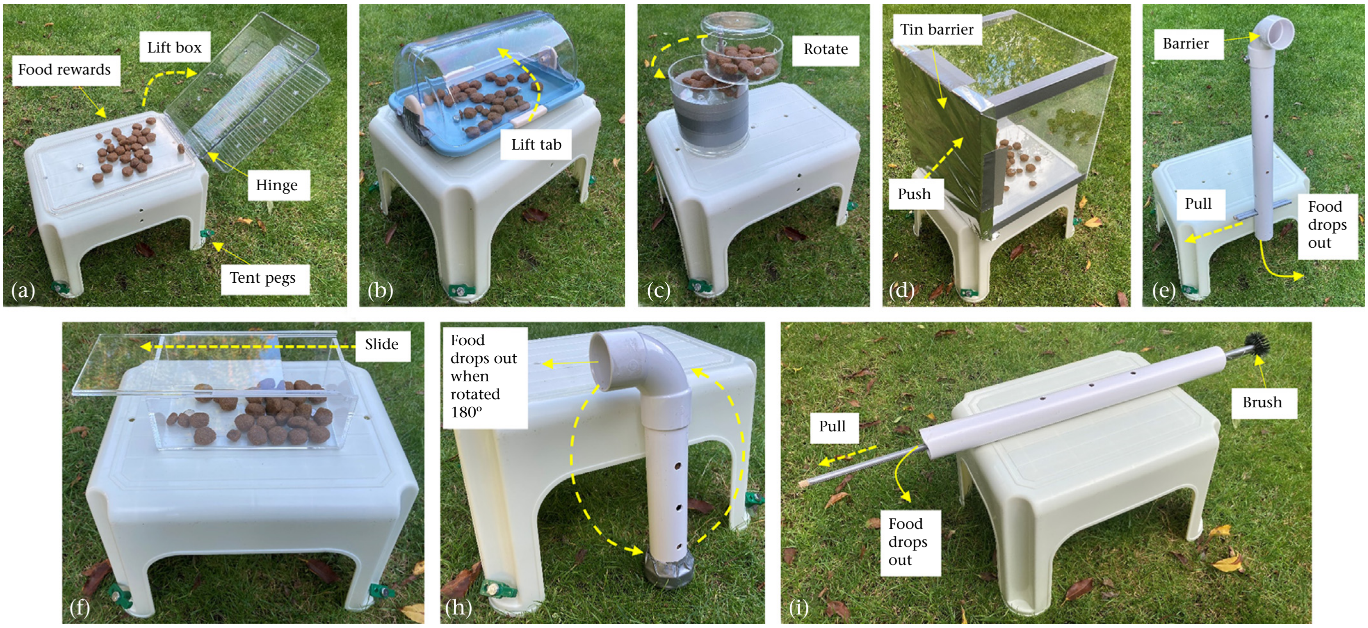

Figure 1. Food-related objects (objects A, B, C, D, E, F, H and I) presented to foxes. Yellow dashed arrows indicate the direction of each behaviour needed to retrieve the food rewards inside. Object G was never deployed in the field and hence is not depicted in this figure.

accessed by removing three small horizontal sticks that were blocking food from falling out of a vertical pipe. The lid of Object F was fixed in place and could only be opened by sliding it either to the left or right. Object H had a hidden axle to allow 360° rotation. Object I was placed with the stick already inside the pipe; animals merely had to remove the stick using their mouths, which would indirectly rake the food out.

Researchers were not present when foxes visited, and we did not touch or replenish the food to avoid unnecessary disturbance to the objects. Following U.K. Animal and Plant Health Agency guidelines (https://www.gov.uk/government/organisations/animal-and-plant-health-agency), 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-two objects (21%) were sprayed with scent deodorizer 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' likelihood of being bold and innovative enough to exploit the objects within a 2-week period, 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 Behaviour From Trail Cameras

At each location, we horizontally placed a ‘no glow’ (940 nm) infrared motion-sensor camera (Apeman H45) approximately 4 m away on a tree trunk. Cameras had a 120° sensing angle and a triggering distance of 20 m. Video lengths were set to record for 5 min, with a 5 s trigger delay and a 30 s 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.

Measuring Urban–Rural Differences in Bold and Innovative Behaviour

A myriad of factors can underpin bold and innovative behaviour, which are not necessarily due to any single variable (Griffin et al., 2014; Lee & Moura, 2015; Morton, Marston, et al., 2021, Morton, Buchanan-Smith et al., 2021; Reader & Laland, 2003). Animals, for example, may not use such behaviour to exploit novel objects if they are too afraid or not hungry. Crucially, however, our goal was to determine whether (not why) subjects would display bold and innovative behaviour to exploit food-related objects, and so the only way they could do this was by physically engaging with novel objects themselves.

Foxes were considered to have acknowledged a novel object if they turned their head to look/smell in the object's direction. As previously discussed, bold behaviour is often broadly defined in terms of animals' responses to unfamiliar situations, which can include responses to novel objects (Bergvall et al., 2011; Breck et al., 2019). In the current study, we were not interested in trait boldness, which describes stable individual differences in behaviour across a wide variety of contexts (Bergvall et al., 2011). Instead, we operationalized bold behaviour in foxes within our specific food-related context if they physically touched a novel object by pushing, pulling, licking and/or biting them, or making physical contact with their nose while smelling them. This is because our research question was related to whether foxes were bold enough to exploit unfamiliar food-related objects, which required them to physically touch the objects.

Foxes could gain access to the food rewards through persistence and by using simple behaviours used 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). Some of the designs were inspired from studies of behavioural innovation in other species (Morton, 2021; Rossler et al., 2020; Thornton & Samson, 2012; Visalberghi & Limongelli, 1994). As previously discussed, innovation is often broadly defined as using a new or modified behaviour to solve a new or old task, which includes animals gaining access to unfamiliar objects such as those used in the current study (Lee, 1991; Reader & Laland, 2003). Thus, as with studies in many other species, we classified foxes as ‘innovative’ if they displayed behaviours that allowed them to operate and successfully gain access to the food inside each object (Boogert et al., 2008; Huebner & Fichtel, 2015; Klump et al., 2022; Laland & Reader, 1999; Morton, Marston, et al., 2021, Morton, Buchanan-Smith et al., 2021; Reader & Laland, 2003; Rossler et al., 2020; Thornton & Samson, 2012).

To determine whether urban foxes were faster to display bold and innovative behaviours, we compared population differences in urban and rural foxes' likelihood of touching and exploiting (at any point) the objects. This was done by coding whether foxes from a given location displayed (1) or did not display (0) bold and innovative behaviour at any point during the period in which objects were available to them, i.e. one data point per location. While there might indeed be alternative ways of measuring how quickly foxes display bold behaviour, such as walking speed or the latency to approach the objects to within a certain body length, as mentioned before, our research question was related to whether foxes were bold enough to try to exploit the objects at any point during the period in which they were available, which required foxes to physically touch the objects regardless of how long (or how many individuals) it might have taken before such behaviour was observed. Similarly, while there may be alternative ways of measuring how quickly foxes innovate, such as the amount of time spent operating the task until a solution was found, this was not possible due to occasional camera malfunctions or some of the videos having poor visibility (e.g. fog or raindrops on the lens); thus, it was more practical, and equally fit for purpose, to analyse how likely urban and rural fox populations were to exploit the food rewards as a function of how many days since the objects were discovered.

Food Tests

Although foxes are generalist carnivores and therefore eat many food items, they still have dietary preferences (Saunders & Harris, 2000). Hence, foxes that avoided our novel objects may have done so because they did not like the food. We could not establish this based on foxes' responses to the ‘free food’ conditions around each object because, for example, they might have avoided the free food if they were too afraid to approach the objects that were next to them. Thus, administering our food conditions when the objects were completely absent allowed us to control for this latter possibility. To do 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 an object: (1) 30 chicken-flavoured dried dog food pellets; (2) 15 dried dog food pellets, 15 unsalted peanuts, one slice of deli chicken and five sprays of 35 ml fish oil mixed with 900 ml water; and (3) 15 dried dog food pellets, 15 unsalted peanuts, 15 ml honey and 15 ml strawberry jam.

All these locations were within the Yorkshire area. We returned every 3–7 days for approximately 2 weeks to either replenish the same condition or replace it with one of the other three conditions until foxes at each location had had an opportunity to discover at least one of the food conditions. Since our goal was to determine whether foxes would consume the food items placed within objects, 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 Detection and Responses to Objects

Methodological variables

We examined the impact of object type (Fig. 1) and each of our 12 food conditions (Table A1), because these may have impacted foxes' motivation to engage with the objects. We examined the effect of the deodorizer spray because the scent of the objects could have deterred foxes (e.g. human scent). Since cameras were not always fully operational (e.g. SD cards full or batteries died), we also examined the impact of the amount of time each camera operated (divided by total days deployment time) after objects were acknowledged by foxes.

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 in 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. At 78 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 five (6.5%) of these locations, we omitted this variable from further analysis given the strong homogeneity of the data.

Landscape variables

Most U.K. 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 urbanization 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 urbanization are so multifaceted. Hence, to allow us to more accurately evaluate the degree of urbanization likely experienced by foxes across our study locations, we used a range of variables recommended by Mu et al. (2022, p. 176), 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 3.5 km from the epicentre of each location. A digital elevation model raster was sourced from the AWS Open Data Terrain Tiles through the elevatr package at a 200 m^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 data set for 2021, the most recent available data, at a spatial resolution of 1 km^2 per pixel (Hollis et al., 2019). Human population size data were collected from the U.K. gridded population census 2011 at a 1 km^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 (OpenStreet Map contributors, 2015). Urban greenspace density (in m^2/m^2) was obtained from the Ordinance

Survey Greenspace vector layer (Ordnance Survey, 2022). We extracted percentage coverage of five land cover classes by employing the U.K. Centre for Hydrology and Ecology Land Cover 2020 product at a 10 m^2 resolution (Morton, Marston, et al., 2021, Morton, Buchanan-Smith et al., 2021). The raster is composed of uniquely classified pixels according to categories following the U.K. Biodiversity Action Plan, which 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). Percentage 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).

Landscape variables were calculated using R version 4.2.0 within the RStudio IDE version ‘Prairie Trillium’ (R Core 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).

Statistical Analyses

We used Cohen's kappa tests to determine interobserver agreement for all behaviours. There was excellent agreement ($k > 0.75$) between K.A. (who coded all videos), F.B.M. (who developed the definitions and trained K.A.) and several independent coders (Tables A2–A5).

To obtain a global measure of urbanization from each study location, we entered our landscape variables into a principal component analysis (PCA) with varimax rotation (Morton & Altschul, 2019). A scree test and parallel analysis were used to determine the number of components to extract (Horn, 1965; Morton & Altschul, 2019). Item loadings ≥ $|0.4|$ were defined as salient for the PCA; items with multiple salient loadings were assigned to the component with the highest loading.

We first tested whether our methodological variables (object type, deodorizer, camera operation time and food conditions) impacted the likelihood of (1) a fox being detected or (2) a fox touching the object, using binary logistic regression. We then carried out binary generalized linear mixed-effects models (GLMMs) to test the effect of urbanization on fox behaviour. In our first model, we tested whether detecting a fox was related to habitat (PCA1, PCA2, PCA3), with food type included as a random factor. In our second model, we tested whether the fox touching the object was related to habitat (PCA1, PCA2, PCA3). We also included ‘camera’ (i.e. the proportion of time the camera operated after objects were acknowledged by foxes) as an additional covariate and food as a random effect. Finally, for foxes that touched the objects, we tested whether their ability to access the food inside them was related to habitat (PCA1, PCA2, PCA3). Again, we included the variable ‘camera’ as an additional covariate and food as a random effect. All GLMMs were run using the lme4 package (Bates et al., 2015), with the significance of fixed effects in binomial GLMMS tested using Wald chi-square tests implemented in the ANOVA function of the car package (Fox & Weisberg, 2019).

Chi-square tests, Cohen's kappa tests and the PCA were conducted in IBM SPSS (version 27, IBM, Armonk, NY, U.S.A.). All other analyses were conducted in R version 4.1.1 (R Core Team, 2021).

RESULTS

Food Tests

Of the 30 locations where we conducted food tests, foxes were detected at 23 locations, and 17 foxes discovered at least one of the food conditions before other animals exploited them. All these foxes approached and consumed the food (Table A6 and see video at https://youtu.be/PjJEvKzXMoA).

Likelihood of Foxes Touching and Exploiting Objects

During the period in which objects were deployed, foxes were recorded at 104 (52%) locations (Fig. 2a). Of the 104 locations where foxes were recorded, it was not possible to tell whether foxes acknowledged objects at eight (7.7%) locations due to poor visibility or camera malfunctions. In all the remaining 96 locations across all habitats, foxes acknowledged the objects. Foxes went on to touch the objects at 31 locations (32%), and of these, 12 (40%, one location could not be determined) exploited the food inside objects (Fig. 2b and see video at https://youtu.be/SYHyjXPdcZs). Information about the objects that were solved can be found in Table A7.

Principal Component Analysis of Landscape Characteristics

Across our 200 study locations, a PCA of our ecological and urban measures revealed three components and explained 29.23, 29.05 and 14.47% of the variance, respectively (Table 1, Fig. A1, Table A8). Component 1 was labelled ‘Wilderness’ because it was characterized 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 ‘Urbanization’ because it was characterized by higher levels of human, road and greenspace densities, but lower levels of cropland. Component 3 was labelled ‘Biodiversity’ because it was characterized by high levels of landscape heterogeneity and wetlands (i.e. an important habitat for many terrestrial and aquatic species).

Effect of Methodological Variables

Fox detection on camera was not significantly affected by object type, food condition or deodorizer spray (Table 2). Similarly, the likelihood of foxes touching an object was not related to the object used, deodorizer spray or the proportion of time the camera was operational (Table 2). There was no significant effect of food condition on the likelihood of foxes touching objects (Table 2).

Effect of Landscape Characteristics

The probability of detecting a fox on camera was significantly lower in areas with higher wilderness scores (PCA1, Fig. 3a) and greater in more urbanized (PCA2) areas (Table 3, Fig. 3b). PCA2 (Urbanization) was significantly positively associated with foxes touching an object (Table 3, Fig. 4, Fig. A2), but there was no effect of PCA1 (Wilderness) or PCA3 (Biodiversity) (Table 3). Finally, of those foxes that touched the objects, there was no effect of habitat (PCA1, PCA2, PCA3) on the likelihood of the objects being exploited (Table 3).

DISCUSSION

We investigated whether urban foxes are bolder and more innovative than rural populations in terms of exploiting novel food-related objects, and whether such behaviour is consistent with the

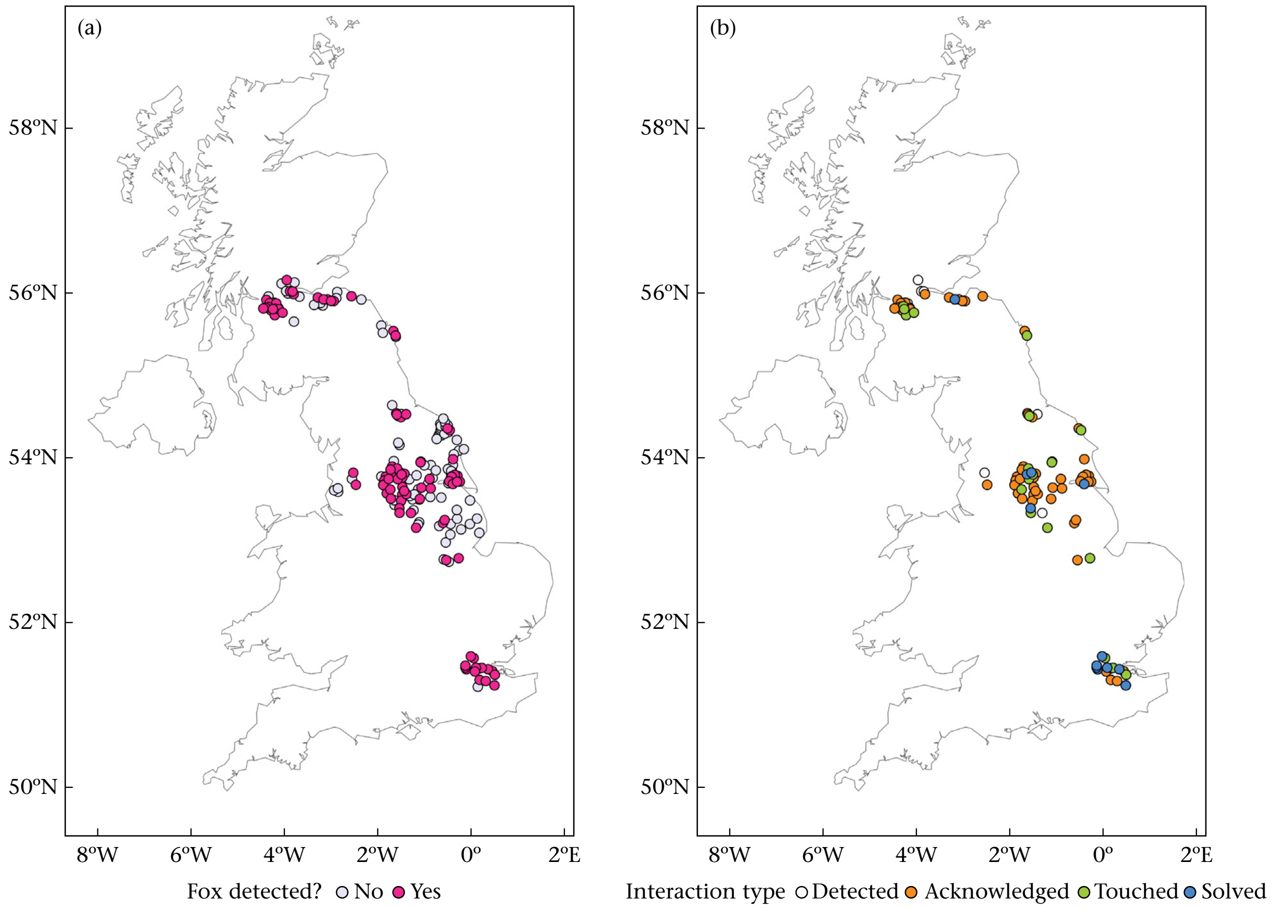

Figure 2. Distribution of locations where objects were deployed across Scotland and England, with (a) foxes detected (yes or no) and (b) whether foxes acknowledged, touched or exploited ('solved') the food-related objects. Foxes were detected at 104 locations, acknowledged objects at 96 locations, touched objects at 31 locations and exploited them at 12 locations.

popular notion that urban foxes are a 'pest' because they exploit these anthropogenic resources. Although foxes acknowledged the objects deployed in the current study, urbanization was significantly and positively related to the likelihood of foxes touching, but not exploiting, them. Thus, while urban foxes may be bolder than rural populations in terms of their willingness to physically touch novel food-related objects, our findings are inconsistent with the notion that urban foxes are also comparatively more innovative and pose a general nuisance to people by being more likely to exploit them.

Table 1
Principal component analysis of ecological and urban variables

Item	Varimax-rotated components		
	PC 1	PC 2	PC 3
Temperature	**−0.811**	0.349	−0.009
Rainfall	**0.827**	0.179	0.11
Elevation	**0.883**	−0.008	0.167
Human population size	−0.238	**0.875**	−0.091
Greenspace density	0.066	**0.71**	−0.031
Road density	−0.143	**0.959**	−0.068
LCC: Urban	−0.227	**0.939**	−0.103
LCC: Forest	**0.629**	−0.148	−0.094
LCC: Grassland	**0.773**	−0.131	0.267
LCC: Cropland	**−0.507**	**−0.702**	−0.348
LCC: Wetland	−0.346	−0.133	**0.744**
Landscape heterogeneity 0	0.203	0	**0.716**
Landscape heterogeneity 1	0.365	−0.031	**0.742**

$N = 200$ locations. Salient loadings are in bold. LCC = land cover category. PC = principal component.

Given that we were able to determine the fate of most objects, this rules out the possibility that our cameras significantly missed footage of foxes visiting and exploiting their contents without us knowing it. Foxes always consumed the food rewards when objects were absent despite the presence of a trail camera, ruling out the possibility that the cameras, rather than the food-related objects, were a significant deterrent for them. Since foxes consumed the food rewards when objects were absent, it also rules out the possibility that food-related motivation explains why foxes avoided the objects.

Table 2
Fixed effects from binary logistic regression models tested using likelihood ratio χ^2

Model	Parameter	Likelihood ratio χ^2	*df*	*P*
Fox detection	Object	7.03	7	0.426
	Food	10.91	11	0.451
	Deodorizer	0.12	1	0.731
Fox touches object	Object	3.45	7	0.578
	Food	18.01	11	0.081
	Deodorizer	0.91	1	0.341
	Camera	0.93	1	0.335

In each model, we tested methodological variables and their likely impact on fox detection and foxes' physical engagement with objects. 'Camera' is the proportion of time the camera operated after objects were acknowledged by foxes.

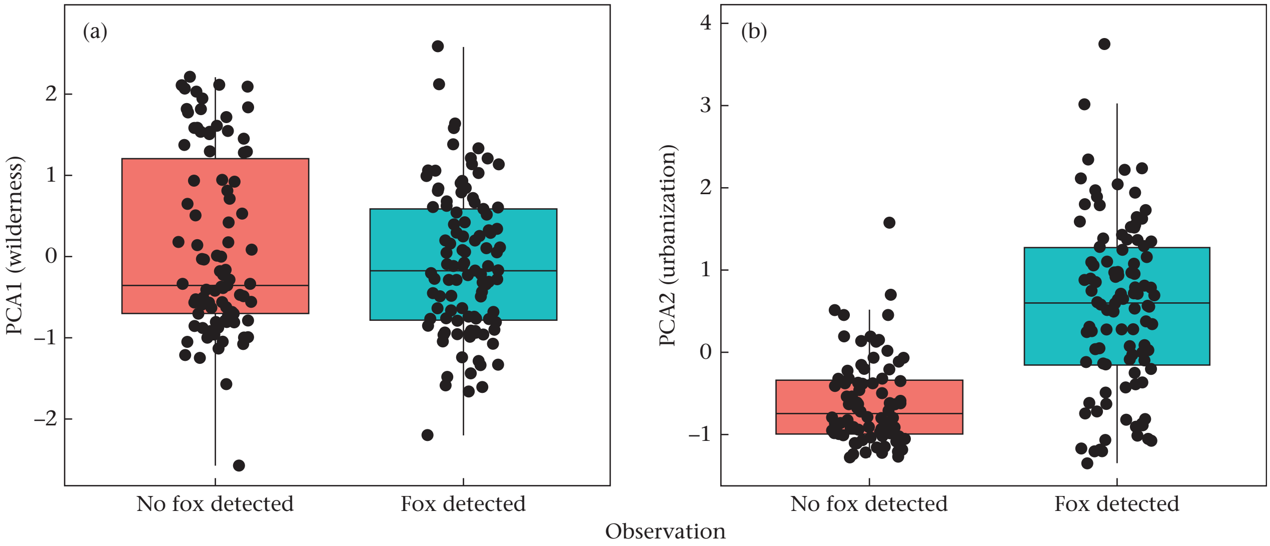

Figure 3. The relationship between (a) foxes being detected by camera in relation to the degree of wilderness (PCA1) and (b) foxes being detected by camera in relation to the degree of urbanization (PCA2). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are data points.

As previously discussed, studies in other species show urban-dwelling animals are more likely than rural populations to physically touch and gain access to novel food-related opportunities (Dammhahn et al., 2020; Ducatez et al., 2017; Griffin et al., 2017; Mazza et al., 2021; Mazza & Guenther, 2021). However, our findings, along with others, illustrate that the relationship between bold and innovative behaviour, particularly with regard to urbanization, is complex and difficult to generalize across all situations and species (Griffin et al., 2017; Vincze & Kovacs, 2022). Indeed, many other factors are likely to contribute to whether or how wildlife can adapt to such environments (e.g. dispersal, morphology and dietary generalism; Thompson et al., 2021). These studies show, for example, that animals are more innovative in urban environments (field mice, *Apodemus agrarius*; Mazza & Guenther, 2021), more innovative in rural environments (spotted hyaena, *Crocuta crocuta*; Johnson-Ulrich et al., 2021) or equally innovative in both (this study; house sparrows, *Passer domesticus*; Papp et al., 2014). This latter point is a particularly important reminder that many studies are likely to be needed for comparison to get a good enough sense of what is really going on within a given population or species before any solid conclusions can be drawn. Thus, for now, although our study suggests that urbanization may somehow favour (for whatever reason) bolder behaviour in foxes, such behaviour does not necessarily favour them using innovation to exploit food-related opportunities in all contexts (Greggor et al., 2016; Griffin et al., 2017).

Table 3
Fixed effects for three binomial GLMM models tested using Wald χ^2 tests

Model	Parameter	Wald χ^2	*df*	*P*
Fox detection	**PCA 1 (Wilderness)**	**6.07**	**1**	**0.014**
	PCA 2 (Urbanization)	**46.33**	**1**	**<0.001**
	PCA 3 (Biodiversity)	0.29	1	0.589
Fox touches object	PCA 1 (Wilderness)	1.47	1	0.225
	PCA 2 (Urbanization)	**9.99**	**1**	**0.002**
	PCA 3 (Biodiversity)	1.48	1	0.224
	Camera	0.04	1	0.844
Fox exploits object	PCA 1 (Wilderness)	2.04	1	0.153
	PCA 2 (Urbanization)	1.71	1	0.191
	PCA 3 (Biodiversity)	0.63	1	0.426
	Camera	0.15	1	0.697

In each model, we tested the impact of landscape characteristics on the likelihood of fox detection and foxes touching and exploiting objects. Significant values are in bold. ‘Camera’ is the proportion of time the camera operated after objects were acknowledged by foxes.

Multiple key factors may separate bold and innovative behaviour. Evidence from birds, at least, suggests that species that are habitat generalists are better at incorporating novel food into their diet, while dietary generalists are more innovative in terms of how they physically acquire food (Ducatez et al., 2015). Red foxes are both habitat and dietary generalists, so it is unclear whether we would predict greater boldness, greater innovation, or indeed both. Our data suggest that boldness is the key behavioural trait; foxes, regardless of location, always consumed food rewards when objects were absent, but not when objects were present. Object neophobia might explain why some foxes avoided the food-related objects (Greggor et al., 2015; Miller et al., 2022, p. P74; Travaini et al., 2013). Alternatively, given that food resources in urban environments are also very abundant (Ansell, 2005; Contesse et al., 2004; Harris, 1981), this could explain why urban foxes were motivated to touch, but not necessarily persist and exploit, the unfamiliar food-related objects used in our study. Finally, individual characteristics such as age, sex, dominance, learning speed and personality might have contributed to fox decision making and are therefore worth investigating in the future (Fawcett et al., 2017; Griffin et al., 2013; Morton, Marston, et al., 2021, Morton, Buchanan-Smith et al., 2021; Padovani et al., 2021; Soulsbury et al., 2011).

Despite being labelled as a pest, foxes remain a beloved part of urban fauna (Baker et al., 2020; Baker & Harris, 2007; Brand & Baldwin, 2020; Konig, 2008; Nardi et al., 2020), and so future management needs to balance the co-occurrence of both positive and negative human–wildlife interactions within cities (Soulsbury & White, 2015). As previously discussed, a common belief about urban foxes is that they exploit the contents of outdoor bins. However, while some urban foxes do indeed engage in such behaviour, most household surveys (Baker et al., 2004; Harris, 1981), dietary studies (Contesse et al., 2004) and direct observations (Plumer et al., 2014) show that the image of foxes foraging from bins is uncommon, rather than the norm. Even in our study, most foxes were unlikely to exploit objects when the rewards were

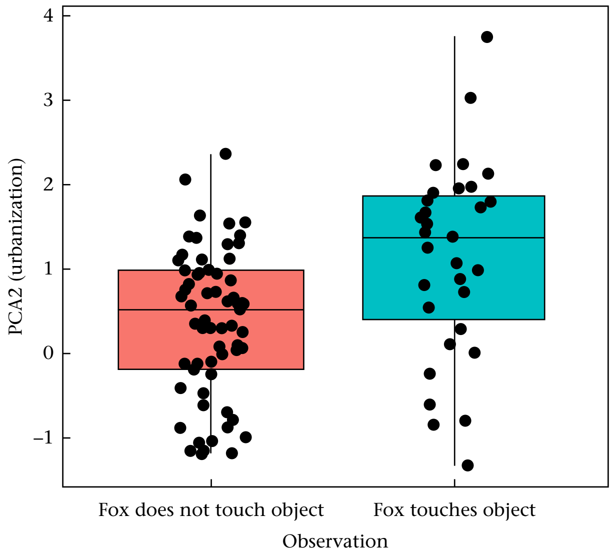

Figure 4. The likelihood of a fox touching a food-related object in relation to the degree of urbanization (PCA2). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are data points.

relatively large (e.g. 90 dog biscuits). By contrast, our findings from the 'free food' condition as well as other studies (Gil-Fernandez et al., 2020) show that when anthropogenic resources are more easily accessible (e.g. no physical barriers), urban foxes may be more likely to exploit such opportunities, which could be due to minimal effort, risk or both. Although it is possible that the novel objects used in the current study may not necessarily be a representative gauge of how likely urban foxes are to exploit opportunities that are more consistently present in the environment, such as outdoor bins, it is worth noting that even outdoor bins are constantly changing and will therefore fluctuate in their degree of familiarity to foxes (e.g. daily or weekly differences in the combinations, types and quantities of odours and objects that are thrown away). Thus, while further work is of course needed, we suggest that public beliefs about fox exploitation of outdoor bins may stem from specific, highly publicized individuals and provocative imagery rather than being typical of all urban foxes in general.

Conclusions

Red foxes thrive within urban settings, but contrary to what has been observed in some species, we found that wild urban foxes are, for the most part, no more likely than rural populations to take advantage of novel food-related objects. Thus, while urban foxes may be bolder than rural populations in terms of their willingness to physically touch novel food-related objects, they do not always use innovation to exploit them. The low exploitation rate of food-related objects found in the current study is also contrary to the notion that urban foxes pose a general nuisance to people by regularly exploiting these anthropogenic resources, and therefore calls for a more nuanced view of urban fox behaviour, particularly when it comes to opportunistic foraging.

Author Contributions

F. Blake Morton: Conceptualization, Data collection, Data analysis, Writing–Reviewing and editing; **Marieke Gartner:** Data analysis, Writing–Reviewing and editing; **Ellie-Mae Norrie:** Data collection; **Yacob Haddou:** Data analysis, Writing–Reviewing and editing; **Carl D. Soulsbury:** Data analysis, Writing–Reviewing and editing; **Kristy Adaway:** Data collection, Data analysis.

Data Availability

All data are provided in data sets S1 and S2 in the Supplementary material.

Declaration of Interest

The authors declare no conflict of interest.

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Supplementary Material

Supplementary material associated with this article is available in the online version at https://doi.org/10.1016/j.anbehav.2023.07.003.

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Table A2

Interobserver reliability tests for foxes' acknowledgement of objects

Fox video	Acknowledged object?		
	F.B.M.	Coder 2	Coder 3
1	1	1	1
2	0	1	0
3	0	1	1
4	1	1	1
5	1	1	1
6	1	1	1
7	1	1	1
8	1	1	1
9	1	1	1
10	0	0	0
11	1	1	1
12	1	1	1
13	0	0	0
14	1	1	1
15	1	1	1
16	1	1	1
17	1	1	1
18	1	1	1
19	1	1	1
20	1	1	1
21	1	1	1
22	1	1	1
23	0	0	0
24	0	0	0

1 = behaviour observed, 0 = behaviour not observed. Interobserver reliabilities between F.B.M. and the two independent coders were $k = 0.75$ and $k = 0.88$, respectively.

Appendix

Table A1

Food conditions placed 1 m around and inside each novel object

Food condition	Free food (1 m around objects)	Food rewards (inside objects)
1	15 dried dog food pellets	30 dried dog food pellets
2	30 dried dog food pellets	15 dried dog food pellets
3	15 dried dog food pellets	90 dried dog food pellets
4	90 dried dog food pellets	15 dried dog food pellets
5	15 dried dog food pellets	15 dried dog food pellets, plus 15 unsalted peanuts (no shells), plus 1 slice of thinly pressed deli chicken, plus five sprays of 35 ml fish oil mixed with 900 ml water
6	15 dried dog food pellets, plus 15 unsalted peanuts (no shells), plus 1 slice of thinly pressed deli chicken, plus five sprays of 35 ml fish oil mixed with 900 ml water	15 dried dog food pellets
7	15 dried dog food pellets	45 dog food pellets, 45 peanuts, 3 slices of chicken, plus five sprays of 105 ml fish oil mixed with 900 ml water
8	45 dog food pellets, 45 peanuts, 3 slices of chicken, plus five sprays of 105 ml fish oil mixed with 900 ml water	15 dried dog food pellets
9	15 dried dog food pellets	15 dried dog food pellets plus 15 unsalted peanuts (no shells) mixed with 15 ml honey and 15 ml fruit jam
10	15 dried dog food pellets plus 15 unsalted peanuts (no shells) mixed with 15 ml honey and 15 ml fruit jam	15 dried dog food pellets
11	45 dried dog food pellets, 45 unsalted peanuts, 45 mL of honey and 45 mL of fruit jam	15 dried dog food pellets
12	15 dried dog food pellets	45 dried dog food pellets, 45 unsalted peanuts, 45 ml honey and 45 ml fruit jam

Table A3
Reliability test between K.A. and F.B.M. for foxes' acknowledgment of objects

Fox video	Acknowledged object?	
	Coder 1	Coder 2
1	1	1
2	0	0
3	0	0
4	1	1
5	1	1
6	1	1
7	1	1
8	1	1
9	1	1
10	0	0
11	1	1
12	1	1
13	1	0
14	1	1
15	1	1
16	1	1
17	1	1
18	1	1
19	1	1
20	1	1
21	1	1
22	1	1
23	0	0
24	0	0

1 = behaviour observed, 0 = behaviour not observed. Interobserver reliability between both coders was $k = 0.88$.

Table A4
Test–retest consistency for foxes' acknowledgment of objects

Fox video	Acknowledged object?	
	Time 0	Time 1
1	1	1
2	0	0
3	1	1
4	1	1
5	1	1
6	1	1
7	1	1
8	1	1
9	1	1
10	1	1
11	1	1
12	1	1
13	1	0
14	1	1
15	0	0
16	1	1
17	1	1
18	1	1
19	0	0
20	1	1
21	1	1
22	0	0

1 = behaviour observed, 0 = behaviour not observed. Agreement between K.A.'s scores at Time 0 and 1 was $k = 0.86$. Data were coded by K.A. at two time periods separated by several months to test for intraobserver consistency.

Table A5
Reliability tests for coding foxes touching and exploiting food-related objects

Video	Fox detected?		Did a fox touch object within 2 weeks?		Did a fox exploit object within 2 weeks?	
	K.A.	Coder 2	K.A.	Coder 2	K.A.	Coder 2
1	1	1	0	0	0	0
2	1	1	0	0	0	0
3	1	1	1	1	1	1
4	1	1	1	1	1	1
5	1	1	0	0	0	0
6	0	0	–	–	–	–
7	1	1	1	1	0	0
8	1	1	1	1	0	0
9	1	1	1	1	0	0
10	1	1	1	1	1	1
11	1	1	1	1	1	1
12	1	1	1	1	0	0
13	1	1	1	1	1	1
14	1	1	1	1	1	1
15	1	1	0	0	0	0
16	1	1	1	1	1	1

1 = behaviour observed, 0 = behaviour not observed. Interobserver reliabilities between observers were $k = 1$ for all behaviours. '–' indicates fox was not detected at location. Data were coded by K.A. (who coded all the videos) and an independent observer.

Table A6
Food conditions consumed by foxes

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

'–' indicates food condition was not deployed.

Table A7
Information about objects that were solved

Object type	No. of locations where foxes solved object	No. of locations where foxes acknowledged object	% Solved
A	0	13	0
B	0	11	0
C	1	7	14.3
D	1	5	20
E	1	9	11.1
F	4	18	22.2
H	4	24	16.7
I	1	9	11.1

'% Solved' is based on objects solved by foxes (at any point during 2 weeks) divided by the number of objects (per type) deployed across locations where foxes discovered them.

Table A8
Random data eigenvalues from parallel analysis

Component	Mean eigenvalue	Percentile eigenvalue
1	1.440556	1.532997
2	1.325796	1.404585
3	1.243438	1.305825
4	1.169502	1.219462
5	1.101734	1.147657
6	1.043224	1.088601
7	0.982809	1.034463
8	0.928814	0.974348
9	0.871461	0.908924
10	0.813521	0.853746
11	0.756786	0.806806
12	0.698160	0.754805
13	0.624200	0.677534

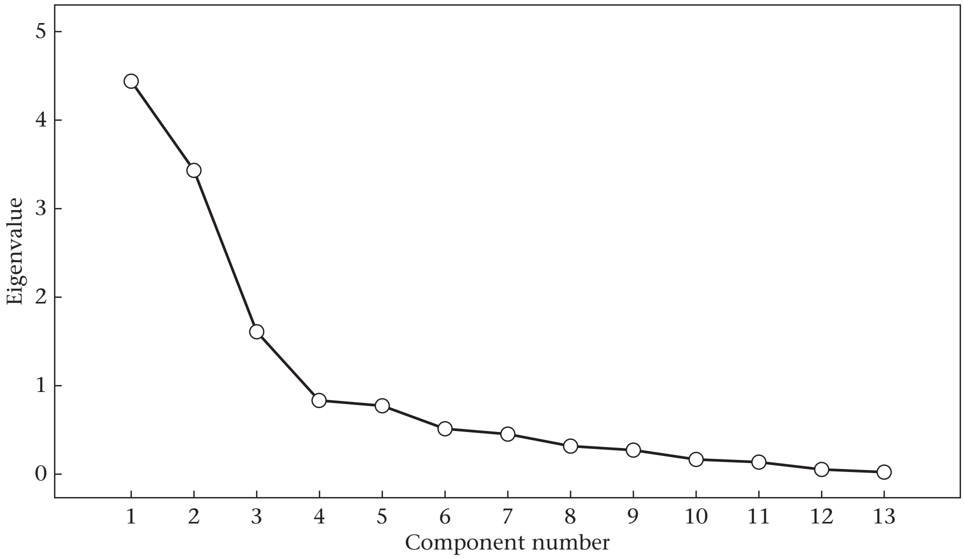

Figure A1. Scree plot for the PCA of ecological and urban variables ($N = 200$ locations).

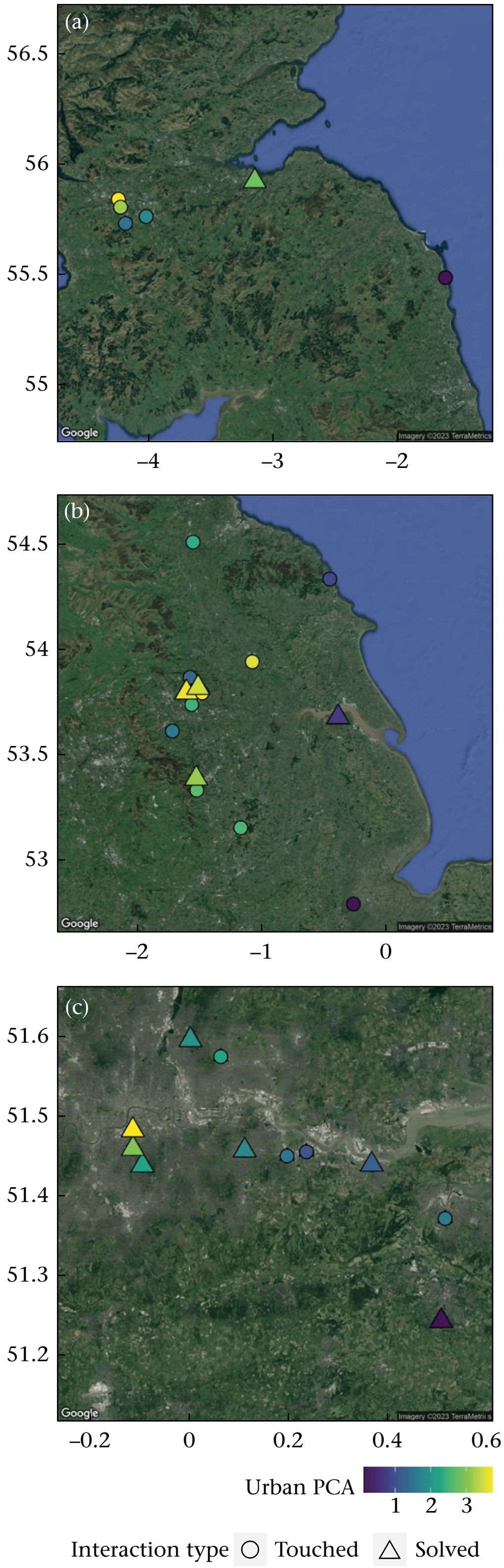

Figure A2. Locations where foxes touched versus exploited ('solved') food-related objects in relation to the degree of urbanization (🟪 = least urban, 🟨 = most urban), including (a) locations from Scotland and Northumberland, (b) Yorkshire, Lincolnshire and Nottinghamshire, and (c) London and Kent.