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Special Column - Article

Urbanization does not affect red foxes' interest in anthropogenic food, but increases their initial cautiousness

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Abstract

Human presence and activities have profoundly altered animals' habitats, exposing them to greater risks but also providing new opportunities and resources. The animals' capacity to effectively navigate and strike a balance between risks and benefits is crucial for their survival in the Anthropocene era. Red foxes (*Vulpes vulpes*), adept urban dwellers, exhibit behavioral plasticity in human-altered environments. We investigated variations in detection frequency on trail cameras and the behavioral responses (explorative, bold, and fearful) of wild red foxes living along an urbanization gradient when exposed to a metal bin initially presented clean and then filled with anthropogenic food. All fox populations displayed an increased interest and similar explorative behavioral responses toward the anthropogenic food source, irrespective of the urbanization gradient. Despite no impact on explorative behaviors, foxes in more urbanized areas initially showed heightened fear toward the empty bin, indicating increased apprehension toward novel objects. However, this fear diminished over time, and in the presence of food, urban foxes displayed slightly reduced fear compared with their less urban counterparts. Our results highlight foxes' potential for adaptability to human landscapes, additionally underscoring the nuanced interplay of fear and explorative behavioral response of populations living along the urbanization gradient.

Key words: anthropization, bold, explorative, fearful, human footprint, *Vulpes vulpes*.

Human presence and activities are rapidly expanding, substantially transforming animals' natural habitats, and forcing them to encounter the considerable risks of human vicinity (Gaynor et al. 2019; Suraci et al. 2019). However, urban areas can also provide animals with novel and favorable opportunities, mainly represented by access to a stable food source (Prange et al., 2004; Oro et al. 2013), but also favorable climatic conditions (Williams and Newbold 2020), protection from predators (Ryder et al. 2010), and shelter (Lowry et al. 2013). The ability to make use of such resources, and navigating the intricate and dynamic peri-urban and urban environments, represents a crucial aspect of species' survival in the Anthropocene era (Sol et al. 2013).

Indeed, animal populations living in human-dominated environments have shown considerable behavioral variability. For example, they can flexibly adjust their diel and seasonal activity patterns (Murray and St. Clair 2015; Gaynor et al. 2018; Gallo et al. 2022), vary their spatial behavior (Lowry et al. 2013; Newsome et al. 2015; Ritzel and Gallo 2020; Brogi et al. 2023), and change their social organization (Macdonald et al. 2015; Łopucki et al. 2021; Gall et al. 2022) in response to resource distribution and the extent of human disturbance.

Behavioral plasticity (i.e., the change in the expressed phenotype of a genotype as a function of the environment; Scheiner 1993) may allow animals to exploit such novel and variable environments long before the onset of changes brought about by selective pressures. Two main behavioral responses have been considered particularly relevant for species living in more heavily anthropogenic environments: "explorative behavior" defined as the investigation of a novel environment or novel stimuli (Réale et al. 2007), and "boldness" defined as the propensity to take risks in a non-novel situation (Réale et al. 2007). Importantly, although both these behavioral responses can be temperament traits with an underlying genetic basis (Réale et al. 2007), they need not be because they can also be the result of an individual's capacity to flexibly alter their response in relation to the specific environmental conditions (Price et al. 2003). Thus the "population norm" along the bold-shy, explorative-avoidant gradient between two populations may differ as a result of the species' behavioral plasticity, without requiring an adaptive/selective change in the animals' genetically -determined personality trait.

On the one hand, enhanced explorative tendencies might favor urban colonizers or urban dwellers allowing animals to interact with a variety of novel and potentially advantageous environmental stimuli (Sol et al. 2013). Additionally, increased boldness, which has often been observed among urbanized animals (Lowry et al. 2013; Ritzel and Gallo 2020), might lead to an overall increased tolerance to disturbance and human proximity and a higher propensity to engage in risky but potentially

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rewarding situations (Breck et al. 2019; Gil-Fernandez et al. 2020). On the other hand, increased avoidance of novelty and shyness might protect animals in specific human-altered environments or situations (Greenberg and Mettke-Hofmann 2001; Miranda et al. 2013). Hence, a context-dependent balance between exploration-avoidance as well as shyness-boldness might allow subjects to carefully weigh the dangers and benefits of facing a potentially novel and/or risky situation and should be particularly relevant for animals living in extremely variable anthropogenic environments.

Overall, the behavioral changes required to adjust and thrive in human-altered habitats might vary between different species (Santini et al. 2019), between research methodologies (Greggor et al. 2015), and also between populations facing different environmental pressures (Griffin et al. 2016, 2017; Ellington and Gehrt 2019), as well as in relation to the stage of the "urban invasion" (Griffin et al. 2017). Thus, studies investigating such changes in urbanized animals have often found inconsistent results (Griffin et al. 2017). This inconsistency might additionally arise from significant differences in the categorization of "urban" and "non-urban" sites across different studies (e.g., threshold-based grouping, Gil-Fernandez et al. 2020, vs. stratified sampling based on pre-existing information, Johnson-Ulrich et al. 2021). Additionally, comparing discrete categories may entail a substantial information loss. Taking into account the urbanization gradient may reflect the nuances of animal behavior in relation to the different environmental challenges (Batáry et al. 2018).

Among mammals, red foxes (*Vulpes vulpes*) (hereafter "fox") are one of the most successful urban dwellers (Gloor 2002; Contesse et al. 2004; Scott et al. 2014; Handler et al. 2020). Studies have shown foxes' ability to exploit such environments highlighting changes in their diet (Contesse et al. 2004), movement patterns (Harris and Trewhella 1988; Walton et al. 2017; Lovell et al. 2022) and social structure (Macdonald et al. 2015) in urbanized areas. Foxes' behavioral plasticity together with their high diet diversity (Contesse et al. 2004; Hartová-Nentvichová et al. 2010; Balestrieri et al. 2011; Bassi et al. 2012; Castañeda et al. 2022), are likely important factors in their success in the human-altered environment.

Despite red foxes representing an interesting study subject to investigate the behavioral changes occurring in human-altered habitats, there are only 2 studies investigating the effect of urbanization on the foxes' behavior in relation to novel objects/resources (Gil-Fernandez et al. 2020; Morton et al. 2023). In line with previous findings on other carnivores (i.e., coyote, *Canis Latrans*: Breck et al. 2019; Brooks et al. 2020; and hyenas: Greenberg and Holekamp, 2017), the studies provide evidence that red foxes living in more urbanized environments tend to be bolder than their rural counterparts. In fact, foxes living in urban areas (defined as >900 habitations/km^2) were more likely than foxes living in peri-urban areas (900 habitations/km^2) to show bold behavior when approaching a lure attached to a canid pest ejector (i.e., interacting with a lure or marking around the area) (Gil-Fernandez et al. 2020). Interestingly, such a difference has not only been found when comparing 2 groups of foxes living in urban and peri-urban environments but has also been observed along an urbanization gradient, with foxes living in more human-altered environments being more likely to touch baited human-made objects (Morton et al., 2023).

To better understand the effect of human-driven environmental alteration on red foxes' explorative and bold behavioral responses, we assessed the patterns of detection frequency on trail cameras and the behavioral reactions to a metal bin along an urbanization gradient. The urbanization level was measured using the global Human Footprint (HF) index, encompassing various human activities (Mu et al. 2022). We assessed fox behavior in wooded areas spanning a range of HF values (from ~14 to ~43, on a scale from 0 to 50), including both wild and human-altered environments, but excluding strictly city-dwelling animals (Padovani et al. 2021).

Two test conditions were designed: an "empty bin" condition to examine explorative-avoidant behavioral response (sensu Réale et al. 2007; i.e., including that the behavioral response occurs in a "novel" situation) and a "full bin" condition to assess bold-shy behavioral response after habituation (sensu Réale et al. 2007; i.e., when the object was no longer novel, but now contained an anthropogenic food source, potentially enticing the animals into taking the risks of approaching the human artifact).

Foxes show opportunistic feeding habits that should make them strongly attracted to human waste (Reshamwala et al. 2018). Thus, we expected an overall increase in red foxes' detection frequency on cameras in the full bin condition compared with the empty bin condition as well as an increase in the likelihood of occurrence of behaviors that possibly denote interest in the resource, such as sniffing the air and looking at the bin. However, we expected a more marked increase in foxes' detection frequency and in the likelihood of sniffing and looking, the higher the HF. In fact, previous studies have shown that red foxes' use of anthropogenic food sources increases in more anthropogenic environments (Handler et al. 2020).

We predicted foxes' behavioral response to being more explorative and bolder (i.e., higher likelihood of approach, touch, and mark, Gil-Fernandez et al. 2020) in the full bin condition than in the empty bin condition due to the combined effect of longer exposure to the object and the additional interest elicited by the presence of the food. We additionally predicted both an overall more explorative and bolder behavioral response the higher the urbanization gradient, and a stronger increase of such behavior in the full bin compared with the empty bin condition with an increase of the urbanization gradient.

We predicted foxes' behavioral response to being overall less fearful (i.e., lower likelihood of run/startle/wince and wary stance) (Gil-Fernandez et al. 2020) in the full bin condition than in the empty bin condition due to the longer exposure to the object, and less fearful the higher the urbanization gradient. We additionally expected a stronger decrease in fearful behavior toward the full bin compared with the empty bin with an increase in the urbanization gradient.

Finally, because the length of exposure to the full versus empty bin may differently affect the foxes' behavior (e.g., a loss of interest in the empty bin, but an increase of interest in the increasingly smelly full bin), we investigated the potential effect of exposure time on foxes' detection frequency and on the likelihood of the occurrence of both explorative and fearful behavior.

Materials and Methods

Study area

Data were collected in the Tuscany region of Central Italy, between April and August 2021, 2022, and 2023 (see

Supplementary Table S1). With a total population of 3.65 million people over an area of around 23,000 km^2, Tuscany has a medium-high population density of around 160 people per km^2. We selected 28 sites across the provinces of Arezzo, Florence, Pisa, Pistoia, and Prato with a wide variability in landscape urbanization (Mu et al. 2022) (Figure 1, Table 1). We selected sites at least 3.70 km apart from each other. With fox's home range sizes averaging 1.24 km^2 in Central Italy (Cavallini and Lovari 1994), this choice substantially reduced the likelihood of testing the same individuals in different sites.

Sampling design

Test setting

All 28 sites were on paths frequented by humans in wooded areas, typically on junctions between trails that foxes often use to travel and where they typically scent marks (MacDonald 1980). We placed 2 no-glow video trail cameras (Browning Spec Ops Advantage BTC-8A) at each testing site to reduce the risk of data loss due to camera malfunctions and to achieve a more detailed view of the foxes' behavior (Jacobs and Ausband 2018). To obtain a complete view of the testing site, the cameras were positioned to face opposite directions, and both had the test apparatus in the frame (Figure 2; Video 1; https://figshare.com/s/7c879c2a539a5f0df276). We initially set both cameras to a 24-h working time. However, to avoid data loss due to memory card saturation, we checked each testing site after approximately 2 weeks and, in case of intense sunlight repeatedly triggered the cameras, we left one camera with a 24-h working time (camera A) and set the other camera to a reduced working time (camera B). Such setting for camera B excluded 2–6 h of time with intense sunlight, on the basis of local canopy cover and exposure (e.g., from 10:00 AM to 12:00 PM or from 10:00 AM to 04:00 PM). On account of the mainly nocturnal habits of the species (Díaz-Ruiz et al., 2016), camera B's schedule curtailed the possible loss of fox detections during the day, when anyhow camera A was active. Nonetheless, to ensure a reliable and rigorous count of fox visits across sites and testing conditions, we used only the data collected with camera A for the detection frequency analysis. The cameras were attached to trees, using cables and padlocks, and depending on the characteristics of the test site and setting, they were located between 1 and 3 m above the ground and 4–10 m distant from the testing apparatus. Trail cameras were equipped with 128 GB SD cards and an external battery (12V, 5Ah), which were changed every 2 weeks. Cameras were set to film for 1 min after the triggering of the PIR sensor. During the day, cameras continuously recorded if the subject was in sight and moving (function "smart video"), whereas during the night the cameras were set to record with their minimum recovery time of 0.6 s. At each testing site, we placed a metal bin of 20 × 20 × 24 cm. The bin was constructed with a metal grid reinforced with 2 metal plates on 2 sides and with a metal lid fixed on the top by 4 metal clamps to make its content

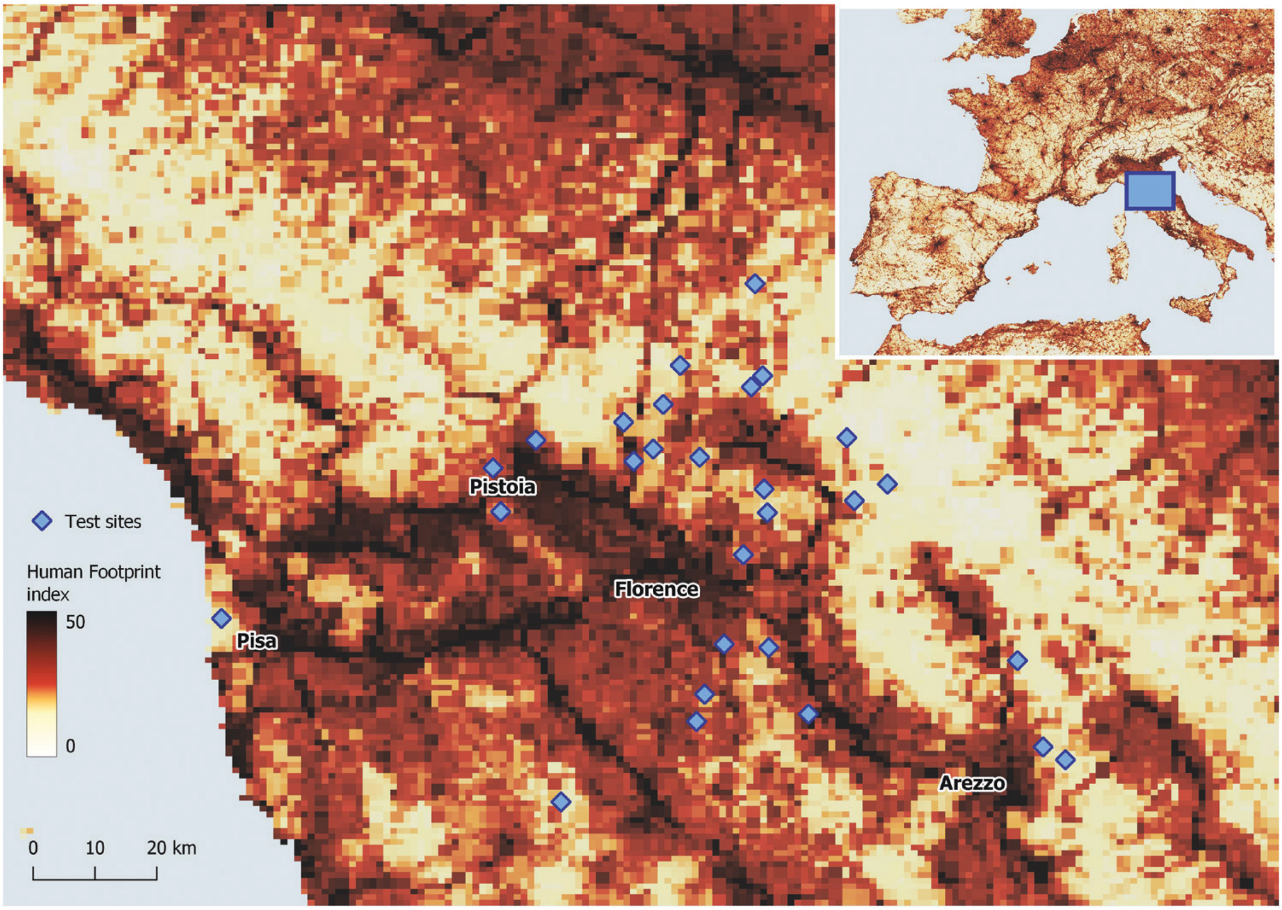

Figure 1. Study sites (blue dots) overlayed on a map showing the Human Footprint (HF) provided by Mu et al. (2022) (yellow: low HF, brown: high HF). The top-right panel shows the position of the study area (blue box) in Southern Europe.

Table 1. Landscape urbanization values and year of data collection for the 28 testing sites. Values of HF, which range from 0 to 50 (0 low; 50 high), have been averaged over a circular area covering half of the expected red fox home range (0.62 km^2) surrounding each test site

Site code	HF	Test year
FMC	14.44	2022
SGMS	14.45	2023
VEC1	14.6	2022
FFB	14.72	2022
CNT16	14.92	2021
PCBA	15.15	2021
SGVCA	15.2	2023
SRIM	15.32	2021
FCC	15.82	2023
SGCB	16.06	2023
BSCTB	16.84	2023
PNOMO	17.35	2021
BMCM	17.55	2023
POM1	17.64	2022
BMF	18.19	2023
POCC	18.75	2022
FPT2	19.62	2022
CEMP	20.09	2023
BSSCC	20.72	2023
FMA	22.4	2022
COTT	23.14	2022
PIPP	24.16	2022
PISVC	25.64	2022
COTC	26.95	2022
COAE	27.05	2022
PIGB	27.77	2022
CEGE	34.15	2022
POVT	42.84	2022

inaccessible to the animals. To ensure the rubbish bin would be a novel object for all foxes, the bin was home-built with materials bought from a hardware store. The bin was screwed to a tree whenever possible or fixed on the ground using metal pegs (Figure 3).

Test procedure

The test procedure consisted of 2 conditions, an empty bin condition followed by a full bin condition, both lasting 4 weeks. We chose each condition to last one month to allow animals to habituate to the empty bin by repeatedly passing by the bin location. During the first condition (empty bin) the bin was empty, whereas during the second condition (full bin) a bag of rubbish was placed inside it. The rubbish consisted of the typical content of a household (leftover vegetables and fruits, cheese, bread, cooked food such as pasta and rice) with a standardized addition of a 250 g mixture of cooked and raw meat. The rubbish bag was replaced after the first 2 weeks of the full bin condition. The smell of the human leftover food likely varied over time and between testing sites due to differences in humidity, temperature, and the composition of leftovers in each bin. This allowed us to test foxes' reaction toward human leftover food in general and not to some specific food item. Furthermore, no attempts were made to avoid leaving human-related smells when setting up or re-loading the apparatus, thereby creating a mix of odors that included the food items but likely also the humans manipulating the objects/rubbish.

Urbanization gradient assessment

To calculate the magnitude of landscape urbanization experienced by the tested foxes, we used the 1 × 1 km resolution Human Footprint index provided by Mu et al. (2022). We used the latest released version (2018) to ensure the representativeness of the real urbanization gradient experienced by the foxes during the study period. This index is expressed within the relative scale from 0 to 50 (0 low; 50 high) and considers the buildings in the environment, the human population density, nighttime lights, the prevalence of agriculture-modified environments, and the road and railway networks. To obtain a representation of the average HF of the area that was most likely used by the tested individuals, we averaged the HF index over circular buffers centered on each testing site and covering half of the expected home ranges of foxes in Central Italy (i.e., 0.62 km^2 (Cavallini and Lovari, 1994). Because mammals do not homogeneously use their home range, but rather concentrate movements within inner core areas (Samuel et al., 1985) and because we had no information on the real spatial distribution of the tested individuals' home range, using buffers half of the expected home range size allowed us to conservatively estimate the HF most likely experienced by the tested foxes.

Video analyses

Analysis of foxes' detection frequency

We performed the detection frequency analysis using only the data collected with camera A (1697 videos). Rather than using an arbitrary time threshold to identify independent detections (Suraci et al. 2019; Gallo et al. 2022), we estimated the temporal autocorrelation decay to rigorously establish objective time thresholds after which events may be considered as independent. For each site, we created a table with a row per minute and counted the events observed within that minute interval, by means of the software R. This resulted in a table representing the frequency of events for each minute. Then, we measured the correlation between observations at different time lags using the acf() R function to calculate the autocorrelation function (ACF) on the event frequency. Finally, we determined the lowest lag at which the absolute autocorrelation fell below 0.05, thus representing the threshold at which the likelihood of observing the species at that location became independent of previous events. We repeated the whole process separately for each site. One testing site was excluded from this analysis because we recorded only 3 events on different days, for 2 sites we merged events occurring within a 2-min interval, for 20 sites within a 3-min interval, and for 5 sites within a 4-min interval (see Supplementary Table S1). We identified a total of 1,478 independent fox detections (649 and 829 in the baseline and test conditions, respectively) and used their time of recording to assess the daily detection frequency. To account for the mainly nocturnal habits of the species (Dìaz-Ruiz et al. 2016) and hence use biologically meaningful daily timespans, we considered the continuity of events occurring before and after midnight by assigning detections recorded between 00:00 AM and 12:00 PM to the previous date. In other words, our "fox date" started at midday and ended at midday 24 h later. We then determined for each test site and

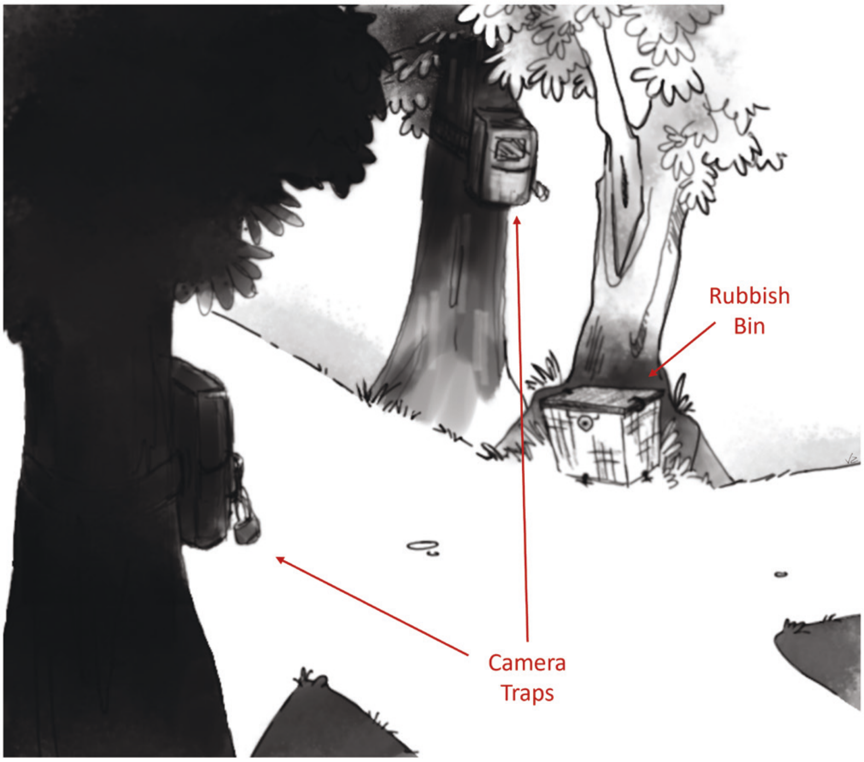

Figure 2. Example of the test setting. Two trail cameras are mounted on trees facing different directions of the paths and both have the bin in the frame.

Figure 3. Metal bins screwed to a tree used to assess foxes' explorative and fearful behavior along the urbanization gradient. The test consisted of 2 conditions, an empty bin condition and a full bin condition (shown in the picture). Photo by Andrea Boromello.

condition, the actual working days measured from the first to the last recorded video (regardless of whether it was empty or containing any species). We then counted the total number of independent fox detections per day during each "fox date" within each test site, assigning zero to the date/locations with no detections. This dataset comprised 1,634 dates/sites (804 and 830 in baseline and test conditions, respectively). We excluded from these analyses one site (POVT) in which only 3 independent detections were recorded. Finally, for each date/site, we calculated the number of days because our last visit to the test site, which occurred twice for each test condition (at the beginning and after approximately two weeks). This variable (hereafter "test day") ranged from 0 to 17 and was used in the subsequent models as a proxy to account for possible habituation and/or to account for the effect of variation in the bin odor over time.

Analyses of foxes' behavior

For all the videos collected by the trail cameras, in an Excel file, we noted the test site, the camera name, the date and time, the test condition, and the species observed using the independent software application "Wolf Tracker" (developed for this project by Dr Tiago Roldao). For the analyses of the foxes' behavior, we used the videos recorded by cameras A and B at each test site. We recorded a total of 2,226 fox visits from both trail cameras. Individual recognition of foxes was not possible thus we followed the same protocol described above to identify independent events. In the process of merging the videos occurring in the identified time intervals with the above-described method, we also merged the videos of the 2 cameras A and B, when simultaneously filming the same subject. This allowed us to avoid double coding of the same behavior filmed by both cameras. After merging the videos, we identified a total of 1,848 events over the 4 weeks of exposure for each condition (845 and 1,003 in the baseline and in test conditions, respectively). The occurrence of each behavior type (Table 2) (Video 2; https://figshare.com/s/66fe03e13a73e4b724d2) was recorded a maximum of once per event, independently from its frequency of occurrence. When more than one individual was simultaneously present on camera (21 videos), if at least one subject performed a specific behavior, that behavior was considered as having occurred in that event. Behavior data was recorded directly in the software Excel. Finally, analogously to the detection frequency dataset, we calculated the "test day" of each video as the number of days because our last visit to the test site (0–17 days).

Inter-observer reliability was carried out between 2 experimenters (ML, VN), each coding the same 20% of videos (intra-class correlation coefficient, 2-way model using the irr package: Look ICC = 0.928; Sniffing in the air ICC = 0.934; Approach ICC = 0.934; Touch ICC = 1; Fear response ICC = 0.771; Wary stance ICC = 0.887; Marking = 0.881).

Statistical analyses

We tested whether red foxes' detection frequency differed between test conditions (empty bin vs. full bin) across sites as a function of the varying urbanization gradient and time elapsed (increase in test days). To this end, we used a general linear mixed model (GLMM) with a negative binomial error structure and log link function (McCullagh and Nelder 1989). We included the number of detections per day of red foxes at each test site as the response variable. The test condition (empty bin, full bin), the average HF of each test site, and the test days were included as predictors. Additionally, we included the interaction between test condition and HF, and test condition and test day. The test site was included as a random intercept effect.

To test whether the likelihood of red foxes exhibiting specific behaviors differed between test conditions (empty bin vs. full bin) and across sites as a function of the varying anthropogenic landscape and the time elapsed, we carried out 7 different GLMM models with a binomial distribution, one for each response variable ("Look," "Sniffing air," "Approach," "Touch," "Fear response," "Wary stance," "Marking"). We included the likelihood of the occurrence of the behavior of interest (i.e., whether subjects performed such behavior or not) as the response variable, the test condition (empty vs. full bin), the average HF of each test site, and the test days as predictors. We additionally included the interaction between test condition and HF, and test condition and test day. The test site was included as a random intercept effect.

We fitted the models in R (version 4.1.1; R Core Team, 2021) using the functions glmer.nb and glmer of the package lme4 (Bates et al., 2015). Prior to fitting the models, we *z*-transformed HF and test days to achieve an easier interpretable model (Schielzeth, 2010) and ease model convergence. Additionally, to keep the type I error rate at the nominal level of 5% (Schielzeth and Forstmeier, 2009; Barr et al., 2013), we included condition and test days within the testing site as the random slope (condition was latter manually dummy coded and then centered) for all models. For the binomial models on foxes' behavior, we also included the random slope of the interaction of condition and test day within the testing site. Additionally, for these models, we did not include the correlations among random intercepts and slopes because they were not identifiable. We used the function vif of the R package car (Fox and Weisberg 2011) for screening the predictors for collinearity and multi-collinearity, but no issues arose (Quinn and Keough 2002). After fitting the binomial models on foxes' behavior, we inspected the distribution of the individual specific deviations from the common intercept and slopes (BLUPs). After fitting the model on foxes' detection frequency, we checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visual inspection of a QQ-plot of residuals and residuals plotted against fitted values (Quinn and Keough 2002). These indicated no deviations from these assumptions. With a dispersion parameter of 0.944 the response of the model on foxes' detection frequency was not overdispersed. We determined model stability by dropping levels of the random effects one at a time and comparing the estimates derived from models fitted on the respective subsets with those obtained for the full data set. The fitted models appeared to be of moderate to good stability, except for the estimate for the effect of HF and the interaction of HF with a condition for the model on foxes' detection frequency, and the whole model "Touch" (Supplementary Tables S2–S9). To obtain confidence intervals of the model estimates we used a parametric bootstrap (function bootMer of the package lme4; *N* = 1,000 bootstraps) (Supplementary Table S2a–S9b). As an overall test of the effect of the fixed effects and to avoid "cryptic multiple testing" (Forstmeier and Schielzeth, 2011) each full model was compared with a null model lacking condition, HF, test day, and their interactions but being otherwise identical to the full model. Because we hypothesized an effect of the HF as a fixed term on the red foxes' likelihood of exhibiting specific behaviors but not on their detection frequency, solely for the detection frequency analysis we included the HF

Table 2. Definitions of the coded behaviors

Behavior	Description
Look	The subject's head is oriented towards the bin.
Sniffing air	Although facing the bin, the subject lifts its nose in the air, wiggling the nose up and down in the direction of the bin.
Approach	The subject approaches the bin reaching a minimum distance between its front paws and the object of ≤ 1 body length.
Touch	The subject touches the bin with any part of its body.
Fear response	Run: after looking at the bin, the subject runs away. Startle: the subject exhibits a sudden, quick, and exaggerated movement directed away from the bin. Wince: the subject exhibits a brief, rapid, and slight recoil or flinching movement of the body although facing the bin.
Wary stance	Subjects' weight is shifted forward, with the muzzle/nose reaching towards the object and the back legs extended backward. The subject reaches toward the object but is ready to jump back in case of danger (Gil-Fernandez et al., 2020).
Marking	The subject urinates or/and defecates.

in the null model as well. In so doing, the significance of the full-null model comparison will reveal an effect of the condition as a fixed term and/or of its interaction with the HF, but not of HF per se, on red fox detection frequency. For the full-null model comparisons, we utilized a likelihood ratio test (R function "ANOVA") (Dobson and Barnett 2018). Whether the full-null model comparison resulted in significance we tested the significance of the interactions using the function drop1 with the argument "test" set to "Chisq." When these interactions did not result in significance we removed them from the model to inspect the main effect of the predictors.

Results

Fox detection frequency

We detected an average of 0.81 and 1.00 daily fox visits during the empty and the full bin conditions, respectively. However, the difference was not significant (i.e., no significant difference between the full compared with the null model; $\chi2 = 7.141$, $P = 0.129$) (Supplementary Table S2, Figure 4).

Behavior models

The Full–Null model comparison showed significance for all the models except for the model Touch (Table 3). We found that foxes were more likely to look at the bin, sniff the air, perform a wary stance, and mark in the full bin condition than in the empty bin condition, irrespective of the HF of the testing site and irrespective of the testing day (the interactions between condition and HF and between condition and test days were not significant for these models). Overall, the likelihood of approaching the full bin was 7 times higher than the likelihood of approaching the empty bin, however, this increase varied for the 2 conditions across the test day. In fact, we found a significant interaction between condition and test days in the approach model. In the full bin condition, the foxes demonstrated a higher likelihood to approach the bin during the initial testing days whereas in the empty bin, the behavior exhibited an opposite trend, with a higher likelihood of approaching the more time elapsed. Regardless of the condition, we found an overall decrease in the likelihood of looking, sniffing in the air, and performing fearful behavior with the increase in days elapsed. Furthermore, we found a significant interaction between condition and HF for the model Fearful. In fact, in sites with low values of HF, foxes showed an overall a low likelihood of fearful behaviors occurring which appeared similar in both test conditions. However, the higher the HF of the site, the more the foxes' behavior differed between conditions. In fact, in more urbanized sites, foxes showed a higher likelihood of fearful behaviors occurring in the empty bin condition compared with the full bin condition. Moreover, the higher the HF of the site, the lower the likelihood of foxes showing fearful behavior in the full bin condition (Table 3, Supplementary Table S3–TableS9, Figure 4).

Discussion

With the current study, we aimed to investigate the variation across the urbanization gradient in red foxes' explorative and bold behavioral response toward a human artifact and an anthropogenic food source (i.e., leftover household food). We presented an initially novel empty bin for one month (empty bin condition), which we subsequently baited with the food source for another month (full bin condition). Our results showed that overall, all fox populations were equally interested in the food source and did not differ in their explorative and bold behavioral responses (approaching and interacting) across the urbanization gradient. Despite all fox populations showing the same interest in human-related food sources, they did differ in the expression of their fearful behavioral response. In fact, in sites with a higher urbanization gradient, foxes appeared more likely to show a fearful reaction towards the empty bin. However, such reaction decreased in the full bin condition, where more urbanized foxes showed a reduced likelihood of showing a fear response compared with the less urbanized ones.

Previous studies showed an increase in detection frequency of red foxes and other carnivores due to the presence of scent lures and/or baits (Buyaskas et al. 2020; Avrin et al. 2021; Cozzi et al. 2022). In our study, we did not find an increase in foxes' detection frequency when adding anthropogenic food to the bin. However, the presence of the empty bin may have disrupted the foxes' behavior in the first place, thus without baseline information on the foxes' rate of passage without a stimulus being present, we cannot compare our results to previous studies. Indeed, future studies should include a baseline condition to additionally assess foxes' detection frequency in the absence of any stimuli.

Despite the presence of the leftover food not increasing the frequency of foxes' passages, the analyses of foxes' behaviors revealed that they were interested in the food source. In fact, behaviors such as looking at the bin and sniffing in the air toward the bin were more likely to occur in the full vs. empty bin condition. Interestingly, the likelihood of occurrence of these behaviors decreased over time for both test conditions, suggesting that the animals habituated to the presence of the novel object, and then also to the appearance of the food, or possibly did not express interest towards it anymore.

Contrary to what we predicted, we did not observe a higher increase in fox interest towards the full bin in sites with a higher urbanization gradient. Instead, the results suggest that all foxes were similarly attracted to the food source independently from their potentially different experience in exploiting such a resource. Thus, living in more anthropized areas where human-related food sources are more likely available and used by foxes (Handler et al. 2020) might not necessarily cause an increased attraction to such resources. This would be in line with studies showing red foxes' opportunistic foraging behavior (Contesse et al. 2004; Hartová-Nentvichová et al. 2010; Balestrieri et al. 2011; Bassi et al. 2012; Castañeda et al. 2022), highlighting the strong appeal that human leftover can elicit in foxes regardless of their previous experience.

We found that foxes were more likely to approach, but not touch the bin in the full bin condition than in the empty bin condition. However, the absence of difference in touch behavior was likely due to the low number of occurrences with only 41 touches out of 1,848 events. However, we observed that touching occurred just once in the empty bin condition and 40 times in the full bin condition. Thus, our findings suggest that overall exploratory and bold behavioral responses (i.e., approaching and touching the bin) increased in the full compared with the empty bin condition. We could speculate this to be the result of the conjoint effect of foxes' habituation to the empty bin and their heightened interest in the full bin on the introduction of the food. Foxes might have habituated to

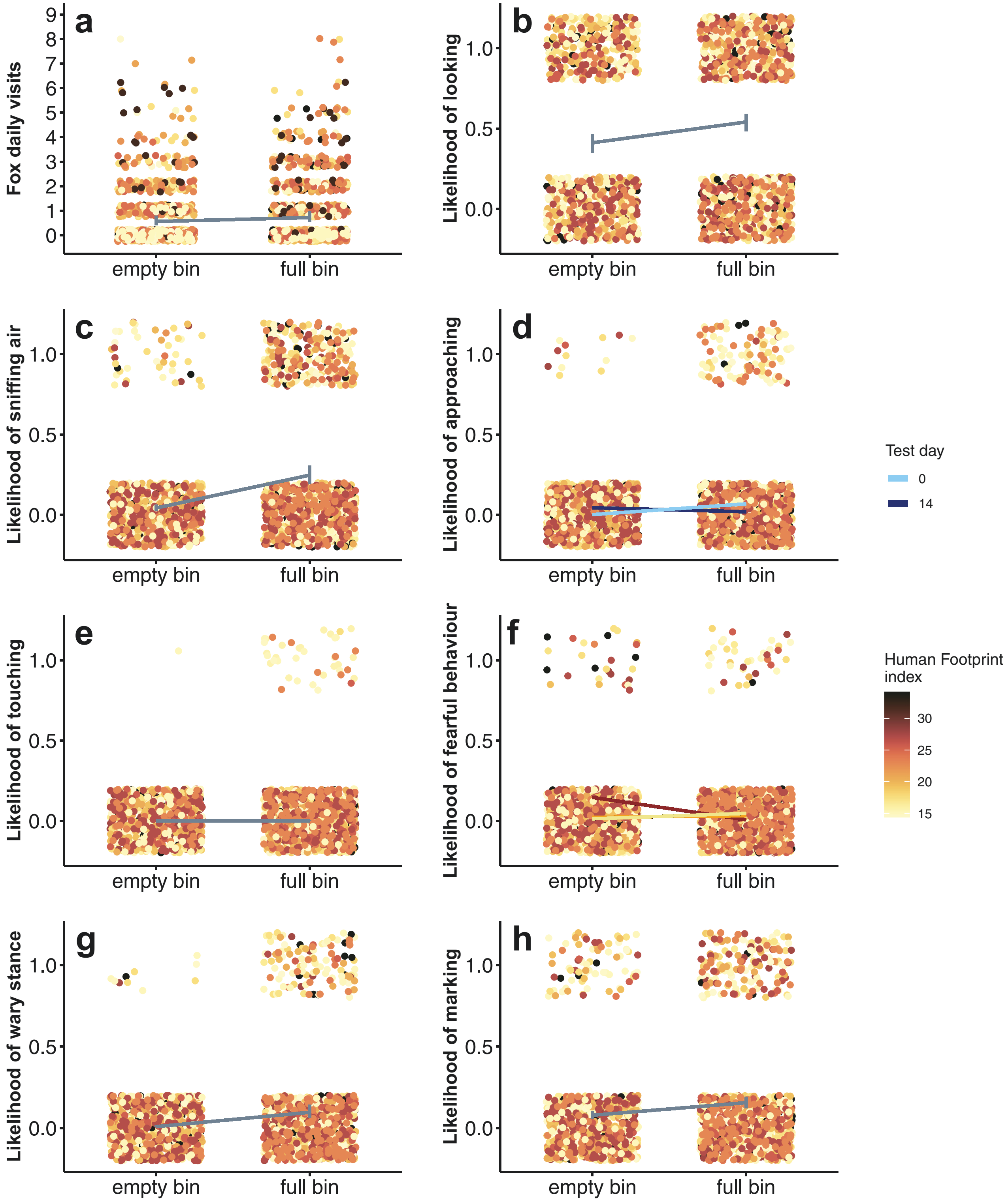

Figure 4. Foxes' detections per day (a) and the likelihood of occurrence of the behaviors of interest (b: looking; c: sniffing air; d: approaching; e: touching; f: fearful; g: wary stance; h: marking) in the two conditions along the urbanization gradient. The dots represent observed values, with the orange scale showing the level of urbanization of the test sites and both horizontal and vertical random noise added to ease the visualization by limiting dot overlapping. The grey line indicates the effect of the condition as estimated by the fitted model, with its 95% confidence intervals (vertical segments) for HF and test days being at their average. In d the colored lines show the effect of the experimental condition on the likelihood of approaching predicted for 0 and 14 days after the last manipulation of the test apparatus by the experimenter (light blue and dark blue, respectively). For each condition such manipulation occurred at the beginning and after two weeks. In f the colored lines show the effect of the experimental condition on the likelihood of showing fearful behavior predicted for the minimum, medium, and maximum HF (yellow, orange, and brown, respectively).

Table 3. Summary of the results for the behavior models. In the table are reported for each condition the percentages of the events where the behavior of interest occurred, the result of the Full–Null model comparison, and the effect of condition, HF, and test days once the interactions were excluded from the model. [a] Condition empty bin is the reference category; [b] z-transformed to mean = 0 and SD = 1; [c] not indicated because having a limited interpretation.

	Empty bin (845 events)	Full bin (1003 events)	Full vs.null	Interaction (HF and condition)	Interaction (test day and condition)	Effect of condition[a]	Effect of HF[b]	Effect of test days[b]
Look	40.42%	51.74%	$\chi^2 = 26.814$ df = 5 **$P < 0.001^{***}$**	$\chi^2 = 1.611$ $P = 0.204$	$\chi2 = 3.103$ $P = 0.078$	Est = 0.521 ± 0.147 $z = 3.540$ **$P < 0.001^{***}$**	Est = -0.147 ± 0.096 $z = -1.523$ $P = 0.128$	Est = -0.187 ± 0.064 $z = -2.895$ **$P = 0.004^{**}$**
Sniffing in the air	5.21%	25.52%	$\chi2 = 47.15$ df = 5 **$P < 0.001^{***}$**	$\chi_2 = 0.039$ $P = 0.843$	$\chi^2 = 0.540$ $P = 0.462$	Est = 1.997 ± 0.214 $z = 9.317$ **$P < 0.001^{***}$**	Est = −0.190 ± 0.161 $z = -1.178$ $P = 0.239$	Est = −0.204 ± 0.074 $z = -2.745$ **$P = 0.006^{**}$**
Approach	1.42%	9.97%	$\chi2 = 21.794$ df = 5 **$P < 0.001^{***}$**	$\chi2 = 0.039$ $P = 0.843$	$\chi2 = 5.423$ **$P = 0.019^{*}$**	Est = 2.300 ± 0.579 $z = 3.972$ P = NI[c]	Est = −0.317 ± 0.283 $z = -1.122$ $P = 0.262$	Est = 0.732 ± 0.358 $z = 2.046$ P = NI[c]
Touch	0.12%	3.99%	$\chi2 = 6.195$ df = 5 $P = 0.287$	\	\	\	\	\
Fear response	3.19%	3.89%	$\chi2 = 12.985$ df = 5 **$P = 0.023$**	$\chi2 = 5.473$ **$P = 0.019^{*}$**	$\chi^2 = 0.065$ $P = 0.798$	Est = 0.305 ± 0.362 $z = 0.844$ P = NI[c]	Est = 0.508 ± 0.246 $z = 2.063$ P = NI[c]	Est = -0.341 ± 0.139 $z = -2.463$ **$P = 0.014^{*}$**
Wary stance	1.18%	11.66%	$\chi2 = 37.227$ df = 5 **$P < 0.001^{***}$**	$\chi2 = 0.013$ $P = 0.910$	$\chi2 = 0.749$ $P = 0.387$	Est = 2.500 ± 0.365 $z = 6.849$ **$P < 0.001^{***}$**	Est = -0.301 ± 0.225 $z = -1.341$ $P = 0.180$	Est = −0.181 ± 0.101 $z = -1.792$ $P = 0.0732$
Marking	9.23%	17.05%	$\chi2 = 16.45$ df = 5 **$P < 0.01^{**}$**	$\chi2 = 0.052$ $P = 0.819$	$\chi2 = 0.008$ $P = 0.928$	Est = 0.771± 0.187 $z = 4.124$ **$P < 0.001^{***}$**	Est = -0.240 ± 0.130 $z = -1.843$ $P = 0.065$	Est = −0.048 ± 0.071 $z = -0.680$ $P = 0.496$

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

the presence of the empty bin, as evidenced by their increased likelihood of approaching as time passed, indicating a decline in their neophobic response to the initially novel object. On the contrary, in the full bin condition, the likelihood of approaching the full bin decreased over time, suggesting diminished interest in the food source, likely because it was unobtainable or because it degraded as time elapsed (Avrin et al. 2021).

Contrary to our initial expectation, we did not observe an increase in the likelihood of explorative and bold behavioral responses (i.e., approach and interaction with the stimulus) towards the bin along the urbanization gradient. In fact, approaching the full bin and/or touching it, other than marking (a behavior previously defined as "confident"; Gil-Fernandez et al., 2020), was not affected by the HF. Thus, the likelihood of foxes exploiting anthropogenic food might be independent of their experience along differently human-disturbed habitats but be rather driven by their motivation. The evidence that foxes' attraction to diverse food items was similar regardless of prior experience, may suggest that foxes' generalist diet and hence their curiosity towards any food source may play a major role in making red foxes one of the most successful mammals in the human-altered environments (Gloor, 2002; Contesse et al., 2004; Scott et al., 2014; Handler et al., 2020). However, it is also interesting to note that in just a few cases foxes touch the full bin (~4% of the total events, ~20% of testing sites). In a previous study on foxes tested along an urbanization gradient, the percent of cases in which a food puzzle box was touched was a bit higher (32% of testing locations) and in the latter study, this was the case without prior habituation to the object. However, when the food was left available on the ground without the presence of the object, it was always consumed by the foxes (Morton et al., 2023). Thus, although the anthropogenic food might have a similar appeal for all foxes, the subjects' motivation in obtaining it and hence facing the risk or/and effort in interacting with the object might play a major role in determining whether subjects do engage with human-made items. Future studies exploring the potential for foxes to exploit human resources should consider factors such as resource accessibility, the availability of alternative food sources, and the resource abundance within the environment.

The distinction between behaviors in a novel vs. known situation suggested by Réale et al, has not always been applied to the concept of personality (Réale et al., 2007). However, in studies of urbanization, this construct may be particularly useful because animals may require both greater caution when encountering novelty, and greater boldness once the risk of novelty has been overcome. Indeed, in the current study, the findings on variation in fearful behavior between conditions across the urbanization gradient lend support for this. In fact, although differently urbanized foxes did not differ in their explorative response towards the bin (approaching and touching it), their fearful behavior when encountering it did vary. Across the site and in both conditions, with the passing of time, there was a decrease in the likelihood of foxes exhibiting a fearful behavior, likely due to habituation to the novelty of the bin in the empty bin condition, and the novelty of the presence of food in the full bin condition. Moreover, in sites with lower urbanization gradients foxes showed a lower likelihood of exhibiting fearful behavior in both conditions compared with sites with a higher urbanization gradient. In contrast, in sites with a higher urbanization gradient, foxes exhibited more fearful behavior in the empty compared with the full bin condition. The fearful behaviors that we analyzed consisted mainly of winces when encountering the bin (see Video 2, https://figshare.com/s/66fe03e13a73e4b724d2), which might represent an expression of apprehension/surprise more than a strong fear reaction. The heightened likelihood of these behaviors among foxes living in more urbanized areas on encountering the empty bin might suggest an overall increased apprehension toward novel objects within those populations residing in more human-altered habitats. It is possible that foxes living in these areas experience a wider variety of human-related dangers due to human activities (for example, vehicle collision; Baker et al., 2007; Valerio et al., 2021) and might benefit from being more weary in novel situations and when encountering novel artificial objects (Greenberg and Mettke-Hofmann, 2001). However, once habituated to the bin, their fear responses continuously diminished and were lower than those of less urbanized foxes. Thus, it is possible that more urbanized foxes might be more attentive towards human-related dangers, such as novel artificial objects, but also habituate more quickly to their presence.

Nevertheless, it is important to note that variations in fearful behavioral responses between populations did not differently impact their interest and explorative responses (i.e., sniffing, approaching, etc.) as reported above. In a previous study, urban and rural foxes did not seem to differ in their interest toward a lure but did differ in their apprehensiveness when interacting with it, which drove urban foxes to interact more with the lure (62% probability of "confident" behavior, which included actively interacting with the lure) (Gil-Fernandez et al., 2020). In another study on red foxes, foxes residing in more anthropized areas, including strictly urban environments, were more likely to interact with lures or novel objects baited with food, often biting or touching them (32% of locations) (Morton et al., 2023). In our study, foxes approached (~10%) or touched (~4% of events, 20% of testing sites) the full bin very rarely despite being habituated to its presence. As previously discussed, no differences in foxes' likelihood to approach the bin across differently urbanized populations were observed despite the evidence for more urbanized foxes being less fearful than more rural foxes in the full bin condition. However, in contrast to previous studies, our study focused on populations inhabiting areas along an urbanization gradient but excluding strictly urban/city foxes. Comparability between studies is difficult due to the different procedural setups, measures of urbanization and behavioral coding methods. Nevertheless, together results may provide some indication that foxes' bold behavioral response may vary along the anthropogenic continuum. Differences in their behavioral response might primarily manifest as variations in fearfulness in the early stages of the urbanization (i.e., in areas with increased anthropogenic disturbance but not yet urban) and secondly, in more heavily urban areas, as variation in bold behavioral response (expressed as a willingness to interact with artificial objects). This highlights the need to consider populations along a wide urbanization gradient.

By focusing on populations residing in less disturbed areas our findings provide new insights into the behavioral response towards artificial novel objects and human-related food sources for foxes shifting from wilder to gradually more anthropogenic landscapes. Although in general animals showed little fear of the human artifact appearing in their environment, foxes living in more urbanized areas were more apprehensive toward the novel artificial object but habituated quickly to its presence, showing a reduced fearful response compared with rural foxes once habituated to it and in the presence of a possible human-related food. Nevertheless, all populations showed similar interest in the food source and similarly approached it, highlighting this species' capacity to adapt to the human landscape. Further research including a wider range of populations along the urbanization gradient and including repeated measures on identifiable subjects is warranted to explore this phenomenon in greater depth and to better understand the factors influencing the behavioral traits of foxes across urbanization stages. Indeed, a better understanding of the adaptive behavioral responses of urban wildlife becomes crucial for predicting the long-term viability of certain species within urban environments, particularly as human activities continue to alter habitats and available resources (Soulsbury and White 2015; Ritzel and Gallo 2020).

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Conflict of Interest statement

The authors declare they have no competing interests.

Ethics Statement

No animals were physically captured and manipulated during this study. All the data were collected using non-invasive methods in compliance with the ASAB/ABS Guidelines for the Use of Animals in Research (Guidelines for the treatment of animals in behavioral research and teaching, 2020) and all national and regional laws in Italy. No permission is needed to conduct such studies in Italy. Camera traps were placed on public land and all privacy rules were adhered to by advertising their use and erasing all the videos containing humans.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

References

Avrin AC, Pekins, CE, Sperry JH, Allen ML, 2021. Evaluating the efficacy and decay of lures for improving carnivore detections with camera traps. *Ecosphere* **12**:e03710.

Baker PJ, Dowding CV, Molony SE, White PC, Harris S, 2007. Activity patterns of urban red foxes (*Vulpes vulpes*) reduce the risk of traffic-induced mortality. *Behav Ecol* **18**:716–724.

Balestrieri A, Remonti L, Prigioni C, 2011. Assessing carnivore diet by faecal samples and stomach contents: a case study with Alpine red foxes. *Open Life Sci* **6**:283–292.

Barr DJ, Levy R, Scheepers C, Tily HJ, 2013. Random effects structure for confirmatory hypothesis testing: keep it maximal. *J Mem Lang* **68**:255–278.

Bassi E, Donaggio E, Marcon A, Scandura M, Apollonio M, 2012. Trophic niche overlap and wild ungulate consumption by red fox and wolf in a mountain area in Italy. *Mamm Biol* **77**:369–376.

Batáry P, Kurucz K, Suarez-Rubio M, Chamberlain DE, 2018. Non-linearities in bird responses across urbanization gradients: a meta-analysis. *Glob Change Biol* **24**:1046–1054.

Bates D, Mächler M, Bolker M, Walker S, 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* **67**:1–48.

Breck SW, Poessel SA, Mahoney P, Young JK, 2019. The intrepid urban coyote: a comparison of bold and exploratory behavior in coyotes from urban and rural environments. *Sci Rep* **9**:2104.

Brogi R, Apollonio M, Grignolio S, Cossu A, Luccarini S et al., 2023. Behavioural responses to temporal variations of human presence: Insights from an urban adapter. *J Zool* **321**(3):215–224.

Brooks J, Kays R, Hare B, 2020. Coyotes living near cities are bolder: implications for dog evolution and human-wildlife conflict. *Behaviour* **157**:289–313.

Buyaskas M, Evans BE, Mortelliti A, 2020. Assessing the effectiveness of attractants to increase camera trap detections of North American mammals. *Mamm Biol* **100**:91–100.

Castañeda I, Doherty TS, Fleming PA, Stobo-Wilson AM, Woinarski JC et al., 2022. Variation in red fox *Vulpes vulpes* diet in five continents. *Mammal Rev* **52**:328–342.

Cavallini P, Lovari S, 1994. Home range, habitat selection and activity of the red fox in a Mediterranean coastal ecotone. *Acta Theriol* **39**:279–287.

Contesse P, Hegglin D, Gloor S, Bontadina F, Deplazes P, 2004. The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. *Mamm Biol* **69**:81–95.

Cozzi F, Iacona E, Ferretti F, Corlatti L, 2022. Effectiveness of a commercial lure to attract red fox. *Mamm Res* **67**:511–517.

Díaz-Ruiz F, Caro J, Delibes-Mateos M, Arroyo B, Ferreras P, 2016. Drivers of red fox (*Vulpes vulpes*) daily activity: Prey availability, human disturbance or habitat structure? *J Zool* **298**:128–138.

Dobson AJ, Barnett AG, 2018. *An Introduction to Generalized Linear Models*. New York: CRC press.

Ellington EH, Gehrt SD, 2019. Behavioral responses by an apex predator to urbanization. *Behav Ecol* **30**:821–829.

Forstmeier W, Schielzeth H, 2011. Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behav Ecol Sociobiol* **65**:47–55.

Fox J, Weisberg S, 2011. *An R Companion to Applied Regression*. Thousand Oaks (CA): Sage publications.

Gall GE, Evans JC, Silk MJ, Ortiz-Jimenez CA, Smith JE, 2022. Short-term social dynamics following anthropogenic and natural disturbances in a free-living mammal. *Behav Ecol* **33**:705–720.

Gallo T, Fidino M, Gerber B, Ahlers AA, Angstmann JL et al., 2022. Mammals adjust diel activity across gradients of urbanization. *Elife* **11**:e74756.

Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS, 2019. Landscapes of fear: Spatial patterns of risk perception and response. *Trends Ecol Evol* **34**:355–368.

Gaynor KM, Hojnowski CE, Carter NH, Brashares JS, 2018. The influence of human disturbance on wildlife nocturnality. *Science* **360**:1232–1235.

Gil-Fernandez M, Harcourt R, Newsome T, Towerton A, Carthey A, 2020. Adaptations of the red fox (*Vulpes vulpes*) to urban environments in Sydney, Australia. *J Urban Ecol* **6**:juaa009.

Gloor S, 2002. *The Rise of Urban Foxes (Vulpes vulpes) in Switzerland and Ecological and Parasitological Aspects of a Fox Population in the Recently Colonised City of Zurich*. PhD Thesis. Universität Zürich.

Greenberg JR, Holekamp KE, 2017. Human disturbance affects personality development in a wild carnivore. *Anim Behav* **132**:303–312.

Greenberg R, Mettke-Hofmann C, 2001. Ecological aspects of neophobia and neophilia in birds. *Curr Ornithol* **16**:119–178.

Greggor AL, Thornton A, Clayton NS, 2015. Neophobia is not only avoidance: Improving neophobia tests by combining cognition and ecology. *Opin Behav Sci* **6**: 82– 89.

Griffin AS, Guez D, Federspiel I, Diquelou M, Lermite F, 2016. Invading new environments: A mechanistic framework linking motor diversity and cognition to establishment success. In: Weis JS, Sol D, editors. *Biological Invasions and Animal Behaviour*. Cambridge: Cambridge University Press, 26–46.

Griffin AS, Netto K, Peneaux C, 2017. Neophilia, innovation and learning in an urbanized world: A critical evaluation of mixed findings. *Curr Opin Behav Sci* **16**:15–22.

Handler A, Lonsdorf EV, Ardia DR, 2020. Evidence for red fox (*Vulpes vulpes*) exploitation of anthropogenic food sources along an urbanization gradient using stable isotope analysis. *Can J Zool* **98**:79–87.

Harris S, Trewhella W, 1988. An analysis of some of the factors affecting dispersal in an urban fox (*Vulpes vulpes*) population. *J Appl Ecol* **25**:409–422.

Hartová-Nentvichová M, Šálek M, Červený J, Koubek P, 2010. Variation in the diet of the red fox (*Vulpes vulpes*) in mountain habitats: Effects of altitude and season. *Mamm Biol* **75**:334–340.

Jacobs CE, Ausband DE, 2018. An evaluation of camera trap performance—What are we missing and does deployment height matter? *Remote Sens Ecol Cons* **4**:352–360.

Johnson-Ulrich L, Yirga G, Strong RL, Holekamp KE, 2021. The effect of urbanization on innovation in spotted hyenas. *Anim Cogn* **24**(5):1027–1038.

Łopucki R, Klich D, Kiersztyn A, 2021. Changes in the social behavior of urban animals: More aggression or tolerance? *Mamm Biol* **101**:1–10.

Lovell C, Li S, Turner J, Carbone C, 2022. The effect of habitat and human disturbance on the spatiotemporal activity of two urban carnivores: The results of an intensive camera trap study. *Ecol Evol* **12**:e8746.

Lowry H, Lill A, Wong BB, 2013. Behavioural responses of wildlife to urban environments. *Biol Rev Camb Philos Soc* **88**:537–549.

MacDonald DW, 1980. Patterns of scent marking with urine and faeces amongst carnivore communities. Presented at the Symposia of the Zoological Society of London, p. e139.

Macdonald DW, Doncaster P, Newdick M, Hofer H, Matthews F et al., 2015. Foxes in the Landscape. Ecology and Sociality. *Wildlife Conservation on Farmland*. Conflict in the Countryside; Oxford, UK: Oxf Univ Press, 20–27.

McCullagh P, Nelder JA, 1989. *Generalized Linear Models*. 2nd edn. Chapman and Hall: London, UK.

Miranda AC, Schielzeth H, Sonntag T, Partecke J, 2013. Urbanization and its effects on personality traits: A result of microevolution or phenotypic plasticity? *Global Change Biol* **19**:2634–2644.

Morton FB, Gartner M, Norrie E-M, Haddou Y, Soulsbury CD et al., 2023. Urban foxes are bolder but not more innovative than their rural conspecifics. *Anim Behav* **203**:101–113.

Mu H, Li X, Wen Y, Huang J, Du P et al., 2022. A global record of annual terrestrial human footprint dataset from 2000 to 2018. *Sci Data* **9**:176.

Murray MH, St Clair CC, 2015. Individual flexibility in nocturnal activity reduces risk of road mortality for an urban carnivore. *Behav Ecol* **26**:1520–1527.

Newsome SD, Garbe HM, Wilson EC, Gehrt SD, 2015. Individual variation in anthropogenic resource use in an urban carnivore. *Oecologia* **178**:115–128.

Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A, 2013. Ecological and evolutionary implications of food subsidies from humans. *Ecology Lett* **16**:1501–1514.

Padovani R, Shi Z, Harris S, 2021. Are British urban foxes (*Vulpes vulpes*)“bold?” The importance of understanding human–wildlife interactions in urban areas. *Ecol Evol* **11**:835–851.

Prange S, Gehrt SD, Wiggers EP, 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *J Mammal* **85**:483–490.

Price TD, Qvarnström A, Irwin DE, 2003. The role of phenotypic plasticity in driving genetic evolution. *Proc R Soc Lond Series B Biol Sci* **270**:1433–1440.

Quinn GP, Keough MJ, 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge: Cambridge University Press.

R Core Team, 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ, 2007. Integrating animal temperament within ecology and evolution. *Biol Rev Camb Philos Soc* **82**:291–318.

Reshamwala HS, Shrotriya S, Bora B, Lyngdoh S, Dirzo R et al., 2018. Anthropogenic food subsidies change the pattern of red fox diet and occurrence across Trans-Himalayas, India. *J Arid Environ* **150**:15–20.

Ritzel K, Gallo T, 2020. Behavior change in urban mammals: A systematic review. *Front Ecol Evol* **8**:576665.

Ryder TB, Reitsma R, Evans B, Marra PP, 2010. Quantifying avian nest survival along an urbanization gradient using citizen-and scientist-generated data. *Ecol Appl* **20**:419–426.

Samuel MD, Pierce D, Garton EO, 1985. Identifying areas of concentrated use within the home range. *J Anim Ecol* **54**:711–719.

Santini L, González-Suárez M, Russo D, Gonzalez-Voyer A, von Hardenberg A et al., 2019. One strategy does not fit all: Determinants of urban adaptation in mammals. *Ecol Lett* **22**:365–376.

Scheiner SM, 1993. Genetics and evolution of phenotypic plasticity. *Annu Rev Ecol Syst* **24**:35–68.

Schielzeth H, 2010. Simple means to improve the interpretability of regression coefficients. *Methods Ecol Evol* **1**:103–113.

Schielzeth H, Forstmeier W, 2009. Conclusions beyond support: Overconfident estimates in mixed models. *Behav Ecol* **20**:416–420.

Scott DM, Berg MJ, Tolhurst BA, Chauvenet AL, Smith GC et al., 2014. Changes in the distribution of red foxes (*Vulpes vulpes*) in urban areas in Great Britain: Findings and limitations of a media-driven nationwide survey. *PLoS One* **9**:e99059.

Sol D, Lapiedra O, González-Lagos C, 2013. Behavioural adjustments for a life in the city. *Anim Behav* **85**:1101–1112.

Soulsbury CD, White PC, 2015. Human–wildlife interactions in urban areas: A review of conflicts, benefits and opportunities. *Wildl Res* **42**:541–553.

Suraci JP, Clinchy M, Zanette LY, Wilmers CC, 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecol Lett* **22**:1578–1586.

Valerio F, Basile M, Balestrieri R, 2021. The identification of wildlife-vehicle collision hotspots: Citizen science reveals spatial and temporal patterns. *Ecol Process* **10**:1–13.

Walton Z, Samelius G, Odden M, Willebrand T, 2017. Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration. *PLoS One* **12**:e0175291.

Williams JJ, Newbold T, 2020. Local climatic changes affect biodiversity responses to land use: A review. *Diversity Distrib* **26**:76–92.