Winter Dietary Shift of the Red Fox Under Urbanisation Pressure

An Increased Reliance on Vertebrate Prey After Snowfall

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Abstract

Although urbanisation is reshaping the ecology of many free-ranging mammals, the dietary responses of omnivorous carnivore species to human-altered environments remain under-explored. This study investigated how snowfall and the degree of urbanization affect the feeding habits of red foxes (*Vulpes vulpes*) in Umeå, northern Sweden. Scat samples were collected in urban and semi-urban areas both pre- and post-snowfall, and analysed to determine food composition, including anthropogenic items. Non-parametric permutation tests were then used to compare dietary patterns across periods and environments. Similar significant seasonal shifts were revealed in both study sites: natural prey dominated in winter, whereas anthropogenic resources, including food waste and plastic, remained negligible in both periods . These findings highlight the flexibility of red foxes in exploiting resources in a highly human-reshaped environment and underline the potential impacts of urbanism on their foraging ecology. Understanding these patterns is crucial for urban wildlife management and mitigating human–wildlife conflicts.

Keywords: Vulpes vulpes | urban ecology | diet | anthropogenic influence | seasonal variation | faecal analysis

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1. Introduction

1.1 Red Fox: Taxonomy, Habitat, and Geographic Range

The red fox (*Vulpes vulpes*) is an opportunistic mesocarnivore (Ferreras & Fernandez-de-Simon, 2019) and the most widely distributed terrestrial member of the order Carnivora (IUCN, 2022). Typically measuring 62–72 cm in length and weighing an average of 6 kg, red foxes are the largest species in the *Vulpes* genus (The Wildlife Trusts, 2018). With a lifespan of 2 to 3 years, they can inhabit a wide range of habitats, including tundra, deserts, forests, and even artificial landscapes (The Wildlife Trusts, 2018). They live alone or in groups within burrow systems, with several individuals from the same family sharing the same territory (Harris et al., 2008). They mark this territory with urine and faeces (The Wildlife Trusts, 2018). The size of a red fox's territory depends on food availability and habitat type, ranging from 4 to 7 km² (Needham et al., 2014). Consequently, the species can be found throughout its native range in Europe and Asia, where populations are still expanding, as well as in North America and Australia, where it has been introduced for hunting and has become established (Figure 1). Red foxes inhabit altitudes ranging from sea level to 4,500 metres (IUCN, 2022; IUCN GISD, 2021; The Wildlife Trusts, 2018). They thrive particularly well in urban areas such as Paris and Stockholm, most commonly in residential suburbs (The Wildlife Trusts, 2018).

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Figure 1. Global distribution of the red fox. (Britannica (Last updated: 2025-07-16). Range of the red fox (Vulpes vulpes). [map].range of the red fox (Vulpes vulpes)[2025-08-16])

1.2 Diet and Effects on Other Species

The fox's diet is varied but mostly consists of meat, with a dominant prey species that often belongs to the Microtine rodent family (Helldin & Danielsson, 2007). In Scandinavia, foxes ecology, and even their reproductive patterns, depend strongly on voles. According to rodent population peaks that occur every 3–4 years, the consumption of this small prey follows an oscillatory predator–prey model (Carricondo-Sanchez et al., 2016; Kleiven, 2022). Consequently, when the population of its primary prey declines, the fox can shift to an alternative dominant prey species (Carricondo-Sanchez et al., 2016; Kidawa & Kowalczyk, 2011; Needham et al., 2014).

Throughout the year, the red fox supplements its diet with various other food sources, such as plant material, insects and reptiles (Needham et al., 2014). (Needham et al., 2014). If the fox's habitat is near populated areas where livestock farming occurs, it may opportunistically attack domestic animals such as sheep as well as scavenge on other predators' prey (Helldin & Danielsson, 2007; Rafaqat et al., 2024). It may also, albeit rarely, attack juvenile or sick adult deer (SLU Artdatabanken, 2024). Other synanthropic species, such as house mice or rats, may also be part of its diet. Its diet varies seasonally, shifting towards a more prey-based diet in winter, especially in locations experiencing severe winter conditions (Helldin & Danielsson, 2007; Kidawa & Kowalczyk, 2011; Needham et al., 2014).

The fox plays a central role in the ecosystems it inhabits due to the diversity of its diet. It is also considered one of the world's 100 worst invasive species due to its impact on native species (IUCN GISD, 2021). As both a predator and a scavenger, the red fox plays a key role in regulating rodent populations and influencing the population dynamics of their prey (Ferreras & Fernandez-de-Simon, 2019; Kidawa & Kowalczyk, 2011). This takes an important place in disease regulation since rodents are often vectors of zoonoses and can cause significant crop damage (Kleiven, 2022). Furthermore, the consumption of plant material by red foxes, e.g., berries (Ferreras & Fernandez-de-Simon, 2019), suggests that they play a crucial role in seed dispersal, particularly during the warmer months (Rafaqat et al., 2024). They also contribute to nutrient cycling by consuming the carcasses of large herbivores in winter (Carricondo-Sanchez et al., 2016) and scavenging remains often left behind by apex predators. In Europe, these mainly include lynx (*Lynx lynx*) and wolves (*Canis lupus*) (Helldin & Danielsson, 2007). The red fox also influences the distribution of other species. For example, in Scandinavia, its expansion has displaced Arctic foxes (*Vulpes lagopus*) from lower elevations into northern and alpine regions due to competition for resources (Frafjord et al., 1989).

Thus, the diet and distribution of the red fox are shaped by various environmental factors, including prey availability, habitat type, the presence of large predators, and human activity. This makes the red fox a valuable indicator of ecosystem health (Angerbjörn et al., 1994). However, the multifaceted impact of the fox's lifestyle can also have negative consequences, resulting in it being feared and closely monitored by humans. Consequently, red fox populations are managed as vectors of disease and as predators of livestock, game, and endangered species (Ferreras & Fernandez-de-Simon, 2019). Although red foxes generally do not pose a direct threat to humans in urban areas, the occasional predation of poultry or domestic animals can lead to conflict (Peterson et al., 2021).

1.3 Fox and Humans

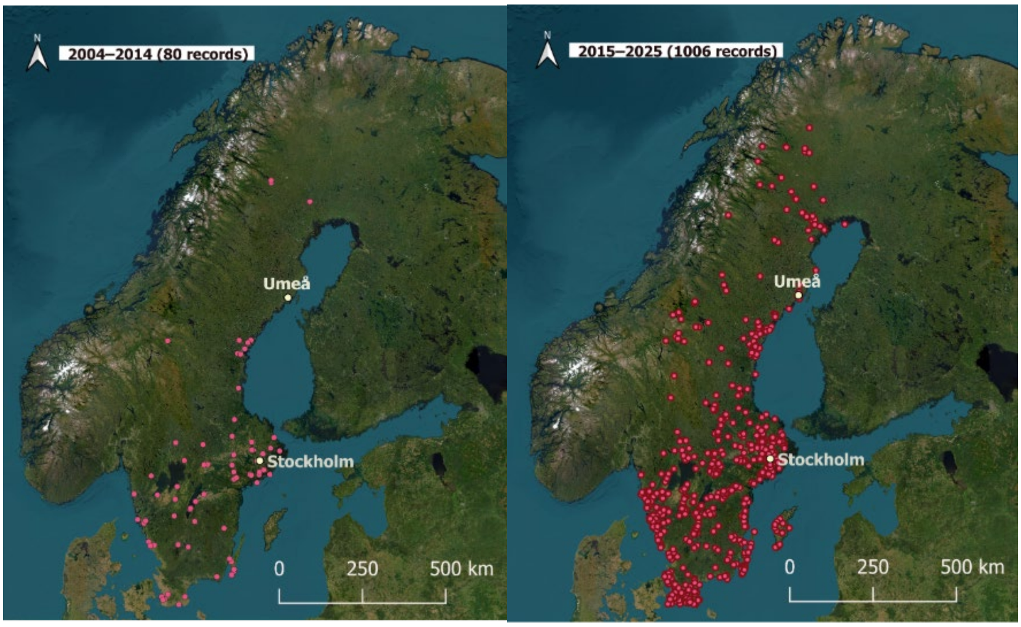
Human activity strongly impacts the ecology of red foxes (Carricondo-Sanchez, 2016; Rafaqat et al., 2024). In recent decades, the increased availability of easily accessible food for foxes in urban areas has driven changes in their spatial and feeding behaviour. Their reliance on these anthropogenic sources has increased, thereby altering their ecological role (Carricondo-Sanchez et al., 2016; Rafaqat et al., 2024). Therefore, depending to their proximity to urbanised areas, foxes' diets can be human-driven to a greater or lesser extent.

This can happen indirectly through ungulate herding, which increases the amount of carrion available. It can also happen as a consequence of clear-cutting, which reduce the population of forest-specialist rodents, as they prefer non-fragmented habitats (Carricondo-Sanchez et al., 2016). The fox’s diet can also be directly affected by waste production, which provides an additional food source (e.g., scavenging in bins) (Carricondo-Sanchez et al., 2016). In urban areas of the United Kingdom, it has been estimated that food provided by humans, either directly or indirectly, constitutes around 35% of the diet of urban red foxes, compared to just 6% in rural areas (Fletcher et al., 2025). The long-term consumption of such ultra-processed foods (high in sugar and saturated fats, and low in nutrients) can be harmful, as they are linked to pathologies such as obesity, insulin resistance, and oxidative stress (Fletcher et al., 2025; Wilson & Thomas, 2022).

On a global scale, the red fox is primarily threatened by human-related disturbances such as habitat loss and fragmentation, as well as persecution (IUCN, 2022). According to Murphy & Romanuk (2014), such changes have caused a 33.2% decline in endotherm species richness and a 22.4% decline in terrestrial biomes, both of which influence the red fox. However, its varied diet has ensured its persistence despite these changes, although it does suggest a significant dietary shift (IUCN, 2022).

1.4 Red Fox in Sweden

Sweden's ecosystems are shaped by pronounced seasonal variations, with harsh winters and resource-abundant summers (Carricondo-Sanchez et al., 2016). The country encompasses a diverse range of landscapes, including vast taiga forests which cover most of the territory (Angerbjörn et al., 1994; Helldin & Danielsson, 2007). This has facilitated the expansion of the red fox population, which grew rapidly in Scandinavia between the 1940s and 1970s (Kidawa & Kowalczyk, 2011). The species' high ecological plasticity, coupled with successful oral vaccination campaigns against rabies and declining hunting pressure, has contributed to a significant population increase across all of Europe since the 1980s (Kidawa & Kowalczyk, 2011). Today, the species inhabits the entire Northern Hemisphere and is present throughout Sweden (Figure 2) (Angerbjörn et al., 1994; Artdatabanken, 2024).



Base map © OpenStreetMap contributors. Dataset from Artfakta, SLU Artdatabanken.

Figure 2. Distribution of the red fox in Sweden. The map shows the number of reported observations but does not reflect their exact distribution. Each red point represents a verified observation of an individual. (SLU Ardatabanken (Last updated: 2025). fyndkartor[2025-08-16]).

A study by Helldin & Danielsson (2007) in central Sweden revealed that the fox's summer diet mainly consisted of *Microtine* rodents, plant material, and invertebrates, with occasional occurrences of fish and reptiles (Needham et al., 2014). However, in winter, these food sources decline sharply or disappear altogether, while rodents, although still present, become less accessible due to snow cover. This prompts the fox to shift towards a predominantly meat-based diet during this season (Needham et al., 2014). In areas where other predators, such as wolves, are present, red foxes scavenge on ungulate carcasses throughout the year. These carcasses make up a significant proportion of the red foxes' diet compared to other food sources (Angerbjörn et al., 1994; Carricondo-Sanchez et al., 2016; Helldin & Danielsson, 2007). Helldin and Danielsson (2007) found that approximately half of the red fox's winter diet and 38% of its summer diet consisted of roe deer in Grimsö, southern Sweden. Similar findings were reported by Needham et al. (2014) in Hedmark, in south-eastern Norway.

In central Sweden, foxes are more susceptible to resource scarcity, particularly in winter when snow depth negatively affects their consumption of small prey (Carricondo-Sanchez et al., 2016; Kleiven, 2022). This results in larger fox territories in the north of the country (Needham et al., 2014). Rodent populations, such as the grey-sided vole (*Myodes rufocanus*), thrive in continuous forests like those in Västerbotten, providing an important food source for foxes (Magnusson et al., 2013). However, recent urban expansion tends to displace these populations (Carricondo-Sanchez et al., 2016). This could potentially impact foxes (Carricondo-Sanchez et al., 2016) as rodent population dynamics are crucial for the survival, breeding density, and reproductive success of many northern mammals, including red foxes (Kleiven, 2022).

The human population of Sweden, and specifically in Västerbotten County, has grown continuously every year since 2000 (Statistics Sweden (SCB), 2025). Between 2024 and 2025, the population increased by 0.7%, which is three times higher than the 0.2% increase recorded over a five-year period two decades ago (Statistics Sweden (SCB), 2025). Umeå, the largest municipality in the region, is 67% covered by natural forest (Global Forest Watch, 2024), and is planning expansion. In response to the population decline in the wider Norrland region, which endangers the sustainability of public services, the municipality intends to attract an additional 70,000 residents by 2050 (Umeå Kommun, 2025). Ongoing demographic growth in Västerbotten, combined with environmental changes, could lead to a decline in species richness and a shift in prey availability near urbanised areas. This could result in changes to the red fox's diet in the coming years (Carricondo-Sanchez et al., 2016; Murphy & Romanuk, 2014).

This raises the question of how the red fox will react to these changes. Changes in snow conditions and an increase in the frequency of extreme weather events during winter could have a detrimental impact on small mammal populations (Kleiven, 2022; Mölle et al., 2021). Consequently, there has been an increase in the availability of prey for red foxes, enabling them to expand to higher altitudes where the climate is becoming more favourable, as has been observed in the Arctic (Carricondo-Sanchez et al., 2016). However, human population growth reduces the availability of fox habitat, which could offset this potential territorial expansion and lead to foxes consuming more rubbish in areas close to urban settlements (Fletcher et al., 2025). This could affect their diet composition and health (Fletcher et al., 2025; Murphy & Romanuk, 2014).

2. Aims and Goals

Previous studies have provided a clear picture of the red fox's diet. As a generalist species, it can adapt very easily, which explains why it is found all over the world. However, given the significant urban expansion in Central Sweden, the potential consequences for the red fox are reasonable grounds for concern. This study, conducted in Umeå, Västerbotten County, aims to determine the impact of human presence on the species' diet by comparing two levels of urbanisation: urban and semi-urban. Additionally, in order to determine whether the species can rely on humans for survival during snowy months, a comparison has been made between the diet before and after snowfall.

The objectives of this study are as follows:

- Investigate whether the level of urbanisation influences the composition of the red fox's diet.

- Investigate whether the red fox's diet varies between pre- and post-snowfall periods, and whether this seasonal variation differs at different levels of urbanisation.

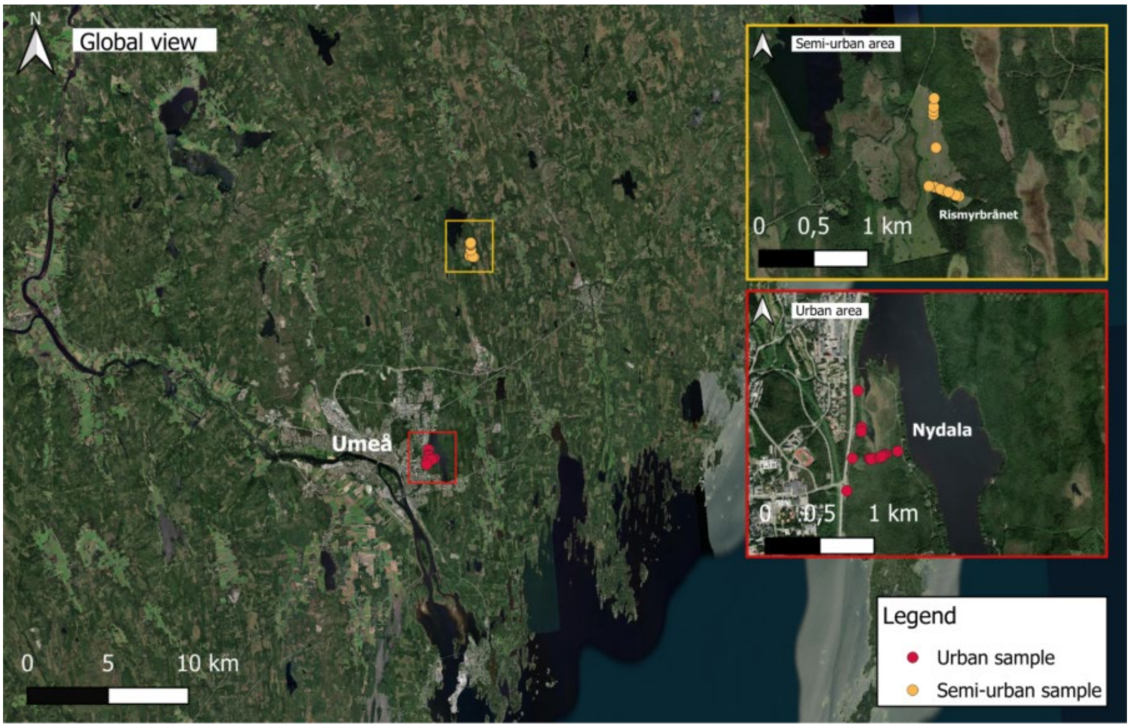
It is hypothesised that following snowfall, the red fox's diet will change, with a decrease in the consumption of berries and invertebrates, and an increase in vertebrate prey. In urban areas, this shift may be partially offset by an increased consumption of human-derived waste.

It is expected that human activity will have a greater impact in urban areas than in semi-urban ones. The proportion of anthropogenic waste in the foxes' diet is expected to be higher in urban areas. Human presence (e.g., berry picking or noise disturbance) may also reduce the availability of natural resources. Consequently, dietary variation is predicted to be greater in urban foxes due to the more heterogeneous and unpredictable availability of human-related food sources.

3. Materials and Methods

3.1 Study Area

The study was conducted in the municipality of Umeå in central Sweden's Västerbotten County. Two sample collection sites were selected, one classified as "urban" and the other as "semi-urban", to determine and compare the diets of red foxes according to urbanisation levels, through the collection and analysis of faecal samples. Figure 3 shows a map of the two sites and their sampling points, including major human infrastructure.



Base map © OpenStreetMap contributors.

Figure 3. Spatial distribution of faecal samples over both pre- and post-snowfall periods in the municipality of Umeå, Sweden.

The "urban" site is located near Lake Nydala, within the city of Umeå, which had more than 37,000 inhabitants in 2024 (SCB). Nydala is a 9 km-long lake situated inside the city, approximately 4 km from the city centre (Visit Umeå!, 2022). The area is wooded but interspersed with numerous recreational infrastructures, such as adventure trails and playgrounds. Although the sampling site is not directly in the city centre, it is surrounded by residential areas less than 300 m away on the west and 800 m on the south side, as well as roads nearby, making it a heavily frequented area (Visit Umeå!, 2022). The sampling site itself lies about 200 m from a major road, so the human impact is not only physical but also acoustic, due to constant car traffic.

The “semi-urban” site is located within the Rismyrbrånet nature reserve, classified as a Natura 2000 area (Länsstyrelsen Västerbotten, 2018). It lies in the municipality of Umeå, approximately 20 km from the urban site. Covering an area of 18 hectares, the reserve is sufficiently distant from the city to avoid road traffic disturbance and continuous human presence (Länsstyrelsen Västerbotten, 2018). The site is fairly isolated, with no major roads nearby; the closest houses are situated about 3 km away and are very dispersed. The only notable activity in the vicinity is hunting, although it does not occur within the reserve itself. However, the reserve remains open to the public year-round, and there are a few dwellings scattered in the surrounding countryside. As a result, the trails around the reserve are regularly used, even during winter.

The two habitats are quite similar in terms of vegetation cover. Both are mixed boreal forests, mainly consisting of Norway spruce (Picea abies) and Scots pine (Pinus sylvestris), as well as some deciduous trees, particularly birch (Betula sp.). Both sites have a field layer covered with lingonberries and blueberries.

In this region, the ground is generally snow-covered from December to March (Helldin & Danielsson, 2007). In the municipality of Umeå specifically, the average autumn temperature is 6°C, compared to an average winter temperature of –4°C (SMHI, 2025). Winter usually begins around 10 November and lasts for approximately 140 days, while spring begins on 10 April and lasts around 60 days, with an average temperature of 3 °C (SMHI, 2025). The average annual snow depth is 75 cm, typically reaching its maximum in January (SMHI, 2025).

3.2 Study Design

3.2.1 Faecal Sample Collection

Red fox faeces were collected within a 2 km^2 perimeter along existing paths at both sites, during two defined periods: “before snowfall” and “after snowfall”, as shown in Figure 4. The first period, before snowfall, extended from October 22 to November 12, 2024. The second period, which followed the beginning of snowmelt, took place between March 24 and April 4, 2025.

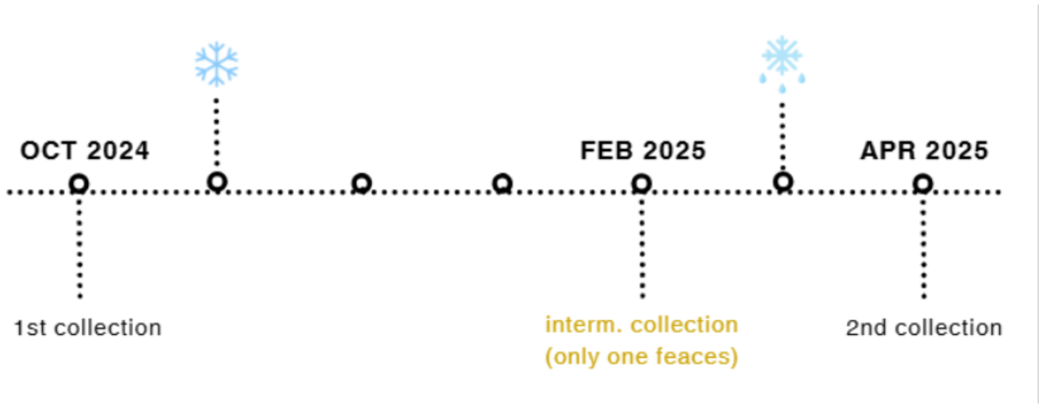


Figure 4. Timeline of sampling periods and snow cover conditions. The snowflake symbolises the first snowfall, while the leaking snowflake symbolises the beginning of the snow cover melting.

The second sampling was initially scheduled for midwinter in February, several weeks after the first snowfall. The aim was to observe the impact of prolonged, heavy snowfall on the animals' diet. However, unseasonably warm weather made observation difficult this year, as there was no prolonged snowfall. Consequently, only one sampling attempt took place between 14 and 28 February, during which there was abundant snow (see Figure 4, labelled “FEB 2025”). At that time of year, thick snow cover is usually the result of earlier snowfall that is maintained by low temperatures. However, the intermittent snow cover and the unexpectedly thick ice layer during this period made locating samples at the sites more difficult, as tracking was prevented. Consequently, only one faecal sample was found at the semi-urban Rismyrbrånet site on 14 February 2025. Therefore, the “snow period” of this study is represented by a subsequent collection attempt, which took place when the snow began to melt in late winter (see Figure 4, labelled “APR 2025”).

Although the second sampling took place at the beginning of spring, the food resources were not drastically different to those in typical winter conditions, which involved substantial snow cover. There was still around 40 cm of snow on the ground in Rismyrbrånet and around 15 cm in Nydala, where rodents take shelter. There were also no insects or fresh berries yet. The only notable difference is that some berries from the previous season, which had been preserved under the snow, were more easily accessible to foxes during the post-snowfall period than they would have been if the sampling had occurred during a prolonged period of snow cover, as had initially been planned. Therefore, the results may show a higher berry count during the post-snowfall period than initially expected.

A total of 39 samples were identified as red fox faeces based on the morphological characteristics described in Baffault (2021)'s tracking guide. These samples were distributed across the two sites and the two collection periods, as shown in Table 1. Specifically, 11 faeces were collected at the urban site before snowfall and five after. At the semi-urban site, 17 faeces were collected before snowfall and six after.

Table 1. Number of red fox faeces samples collected per site and period.

	Urban	Semi-urban	**Total**
Before snowfall	11	17	28
After snowfall	5	6	11
Total	16	23	39

3.2.2 Food Category Quantification

The samples were analysed using a combination of the methods described by Needham et al. (2014) and Wikar (2019). As shown in Figure 5, the following steps were performed:

1. **Initial drying**. Faecal samples were oven-dried at 80 °C to eliminate all bacteria and moisture (Needham et al., 2014).
2. **First weighing**. The dry mass of each faecal sample was recorded.
3. **Rehydration and sieving**. Samples were placed in water for 48 hours to allow rehydration and facilitate subsequent filtering through a 0.5 mm sieve. This step enabled the recovery of undigested dietary remains and the removal of faecal matter.
4. **Second drying**. The recovered food remains were oven-dried again at 50 °C for 24 hours.
5. **Second weighing**. A second weighing was performed to determine the proportion of the initial total dry mass of the faeces that consisted of undigested remains.
6. **Sorting and identification**. The dried remains were manually sorted into dietary categories after visual inspection. A binocular optical microscope with incident illumination (×10 magnification) was used to assist identification. The following categories were defined:
    - **Vertebrate**: hair, feathers, skin, beaks, claws, bones or other identifiable parts of vertebrates (Figure 4).
    - **Fruit**: all berry remains and, occasionally, other fruit remains (peels and seeds).

- **Invertebrate**: insect remains (e.g., exoskeletons, legs, antennae and ommatidia) and mites.
- **Other protein**: eggshells only.
- **Trash**: any human-origin waste (e.g., packaging).
- **Other**: unidentifiable material or items not fitting into the above categories, mostly consisting of accidentally ingested matter such as stones, non-nutritive vegetation (e.g., pine needles, herbaceous material), and woody fragments (e.g., bark, twigs).

7. **Category weighing**. Each dietary category was then weighed to determine its proportion within the undigested remains.

The mean masses of faeces and total food remains, as well as the minimum and maximum masses recorded for each food category, are available in Appendix B.

Figure 5. Workflow for the extraction and sorting of food remains from faecal samples.

A final verification step was carried out to confirm the fox origin of each scat in cases of doubt, particularly for a few highly degraded or snow-covered samples. Several visual indicators were considered in these cases, such as the absence of bones and/or minimal amounts of hair or feathers, the absence of fruit, a composition consisting mainly of faecal matter with few undigested remains, the presence of chewed wooden sticks and anthropogenic debris typically associated with domestic dogs (e.g. stuffing from plush toys).

While most faecal samples were reliably identified in the field during collection, seven were excluded based on the following indicators: three from the urban site and four from the semi-urban site. These samples contained material more typical of domestic dogs, such as faecal matter, chewed sticks, balloon fragments, gloves, and plush stuffing.

3.2.3 Statistical Analysis of Dietary Shifts

Faecal samples were analysed using two complementary approaches. First, the composition of the diet was described in terms of occurrence, which is defined as the presence or absence of each food category in a sample, regardless of quantity. Occurrence was calculated by converting non-zero mass values into presence data, which was then expressed as the number and percentage of faecal samples containing each category across the site and sampling period. While this provides a general overview, it tends to overestimate the importance of small prey items (Klare et al., 2011). Secondly, the mean mass proportion of each food category was calculated relative to the total dry mass of the dietary remains in each sample. This approach reflects the actual dietary contribution of each item and avoids overestimation of small prey (Klare et al., 2011; Peterson et al., 2021). Using both methods together provides a fuller understanding: frequently occurring items may represent a small proportion of the diet, while less frequent items may contribute substantially (Forman, 2005; Peterson et al., 2021).

Comparisons were made across two factors: site (urban vs semi-urban) and snowfall (before vs after onset). Statistical analyses of mean proportions were performed using unpaired two-sample permutation tests (10,000 iterations) to assess spatial and seasonal variation. Unpaired tests were used due to unequal sample sizes, the lack of individual matching and the presence of very small or zero values, as well as low post-snowfall sample sizes (Table 1). Permutation tests are robust to unbalanced data and non-normal distributions, making them suitable for this study. All statistical analyses and bar plots of mean proportions were produced in R (v4.4.0; R Core Team, 2024) using the tibble and tidyverse packages. Maps were generated using QGIS Desktop 3.40.9.

4. Results

Although the “Other” category is included in the figures for transparency purposes, it will not be described in detail as it does not represent actual food resources (e.g., wood fragments, stones, herbs, non-edible vegetation, and unidentified remains). The content and quantity also depend on the weather conditions (the state of the scats was altered by rain and ice), so it is highly variable between samples.

4.1 Faecal Content Analyses

4.1.1 Urban Site

Occurrences

Across all urban samples (before and after snowfall), vertebrate remains were present in almost all scat samples, with only one absence recorded before snowfall (Figure 6). The remains were mostly of small prey, likely to be rodents, with only two occurrences of birds before snowfall and one after. One occurrence of larger prey (hare) was recorded during the post-snowfall period.

Fruit was the second most common food type, found in 63.6% of samples before snowfall and slightly less frequently afterwards (60%, Figure 6). The fruit was mainly lingonberry (*Vaccinium vitis-idaea*) remains, with two plum seeds and two unidentified seeds found before snowfall being the only other types found across all samples.

Invertebrate remains were present in 36.4% of samples before snowfall, dropping to 20% afterwards (Figure 6). Notably, this 20% represents a single post-snowfall scat that contained the remains of a hare and an embedded tick, likely resulting from secondary ingestion.

Anthropogenic waste was present in 27.3% of samples before snowfall but was absent after snowfall despite a high human presence (Figure 6). This waste was of various origins, including fabric, sponge, and plastic pieces. Eggshell fragments were not detected at the urban site (Figure 6).

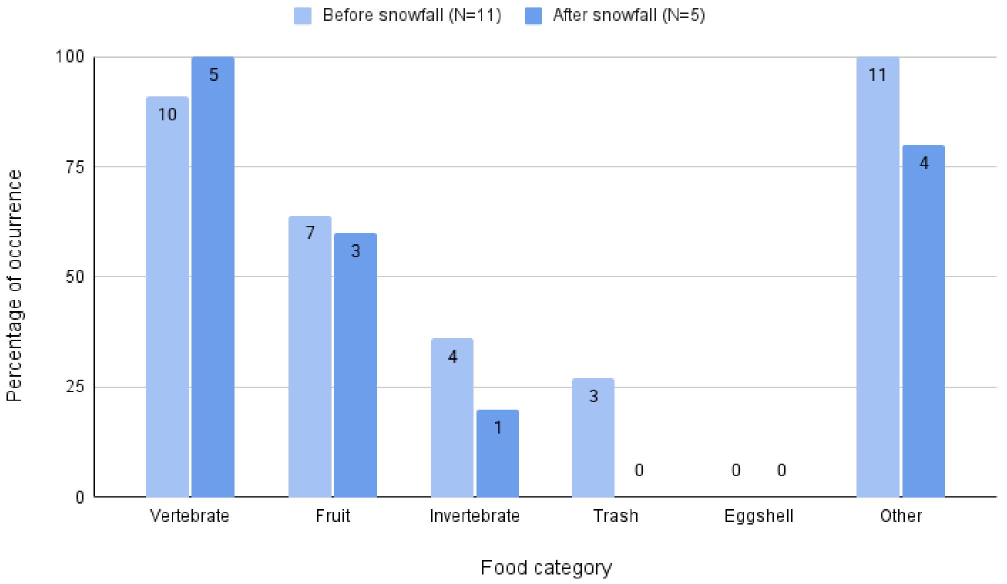


Figure 6. Occurrence of food categories in the urban site, expressed as a percentage. Numbers on the bars indicate the actual occurrences, i.e., the number of faecal samples containing at least one identifiable item of each category.

Weight Proportions

As shown in Figure 7, vertebrate prey accounted for the largest proportion of dietary remains. The mean proportion increased significantly during the season, rising from 0.20 before snowfall to 0.65 after (Appendix A, Table A1). However, the variance in winter was high (±0.40), largely due to a single faecal sample containing only hare remains, which is an unusually large prey item compared to those previously found.

Although trash was present in 27.3% of the samples collected before snowfall (Figure 6), it represented only a small proportion of the total ingested volume, with a mean of 0.098 before snowfall and 0 after.

Fruits were consumed consistently across seasons, with only minor changes in mean proportions between sample groups (Figure 7, Appendix A, Table A1). Despite the relatively high occurrence of invertebrates (31.25%, Figure 6), their contribution in terms of volume was negligible (Appendix A, Table A1). Eggshells were completely absent from urban faeces (mean = 0).

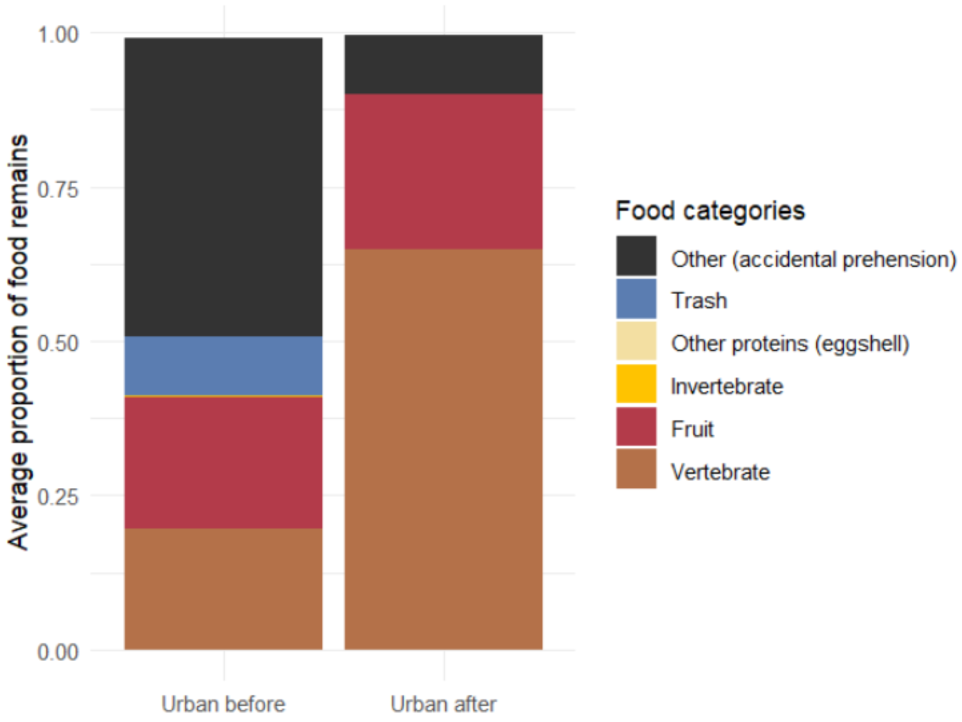


Figure 7. Diet composition of urban red foxes before and after snowfall (average weight proportion of food remains). For detailed values, see Appendix A, Table A1.

Additional Observations

The total proportion of identifiable dietary material in faeces dropped from 0.30 before snowfall to 0.20 after (Appendix B, Table B3). Despite this decrease, the total faecal mass doubled after snowfall (Appendix B, Table B1). This may be due to increased meat consumption, which contributes to faecal bulk but leaves fewer identifiable residues.

4.1.2 Semi-Urban Site

Occurrences

As shown in Figure 8, almost all faeces from the semi-urban area contained vertebrate remains, with only one instance of absence before snowfall (95.65%). Most of the prey were identified as small rodents, with eight occurrences of birds before snowfall. This equates to nearly half of the faeces containing bird remains during this period. In comparison, only one occurrence of a bird has been reported after snowfall.

Fruit was the second most consumed resource across both periods, but its value decreased by 10% after the transition to the snowy season (from 100% to 66.7%)

(Figure 8). As expected, there was a complete absence of invertebrates (i.e., insects) after snowfall.

The results in Figure 8 indicate a low and relatively stable occurrence of anthropogenic waste. However, there was a slight increase around the transition to the snowy season (11.8% before and 16.7% after), which corresponds to only two scats before and one after snowfall. The trash was varied and included paper, glass, plastic, and aluminium. An identical variation pattern was observed for eggshells (Figure 8).

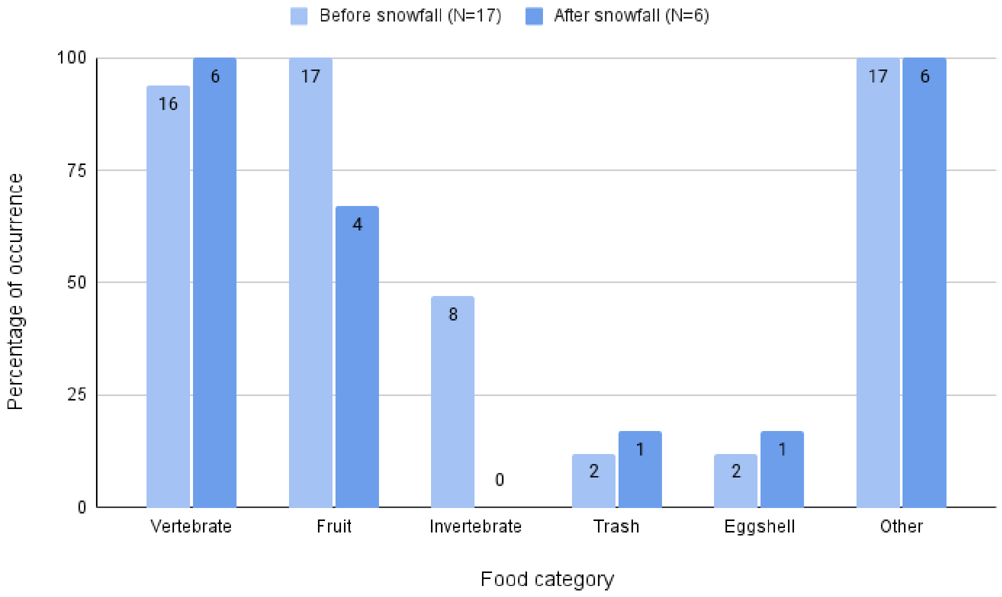


Figure 8. Occurrence of food categories in the semi-urban site, expressed as a percentage. Numbers on the bars indicate the actual occurrences, i.e., the number of faecal samples containing at least one identifiable item of each category.

Weight Proportions

As shown in Figure 9, the ingested volume of vertebrate prey was the largest, at 0.30 before and 0.40 after snowfall (Figure 9, Appendix A, Table A2), showing a slight increase in vertebrate consumption. In both periods, the variance remained stable, suggesting a consistent dietary contribution throughout the year (Appendix A, Table A2).

Before snowfall, the contribution of fruits to the diet (0.39) exceeded that of vertebrates (Figure 9). However, this proportion decreased to 0.24 after snowfall, becoming half that of vertebrates in terms of volume. As with vertebrates, the variance remained stable across both periods, indicating a consistent contribution within each season.

Invertebrates, trash, and eggshells represented only a very small proportion of the ingested volume (Figure 9, Appendix A, Table A2) compared to their calculated occurrence rates (Figure 8). The proportions are all negligible compared to the other two main categories of food remains (Appendix A, Table A2). Nevertheless, some minor changes were observed. As expected, invertebrates were completely absent after snowfall. In contrast, the proportion of trash strongly increased after snowfall (from 0.00011 to 0.04100), but with a higher variance. This is explained by one post-snowfall sample containing various small quantities of different trash remains. Finally, eggshells decreased slightly after snowfall but remained negligible overall in both periods (Figure 9, Appendix A, Table A2).

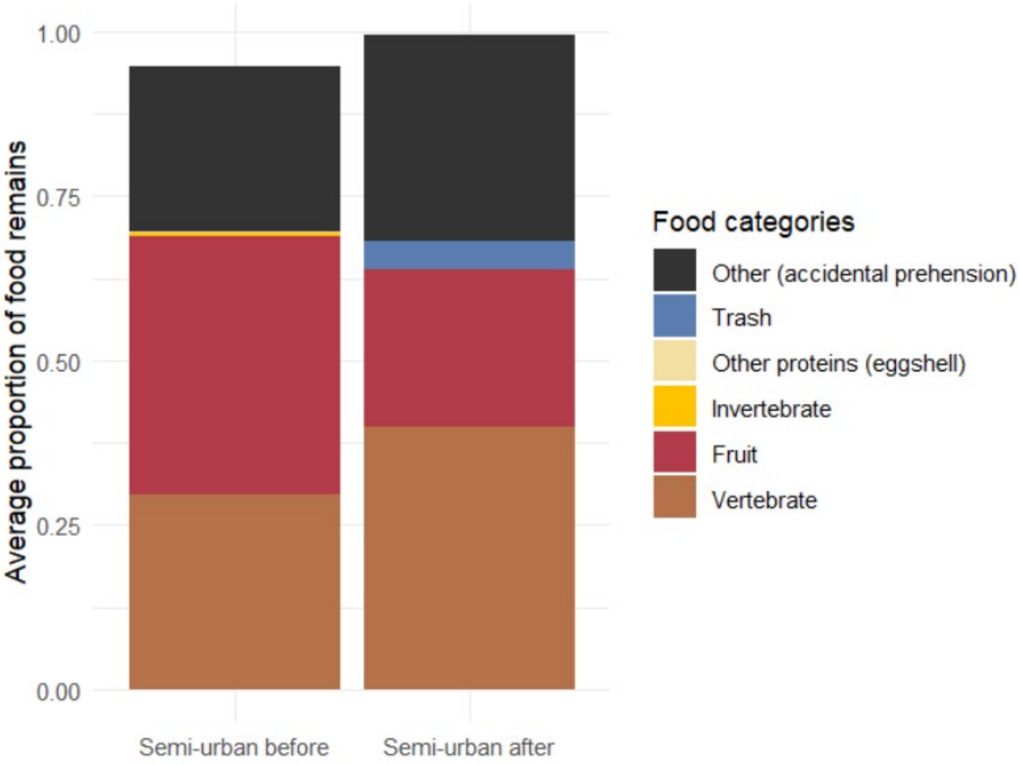


Figure 9. Diet composition of semi-urban red foxes before and after snowfall (weight proportion of food remains). For detailed values, see Appendix A, Table A2.

Additional Observations

The mean weight proportion of total food remains is very stable between the two periods, as is the average faecal mass (Appendix B, Table B1 and B2). This suggests that, after snowfall, there is no increase in faecal matter or the proportion of food remains.

4.2 Statistical Analyses

Permutation tests conducted on mean proportions reveal that almost no food remains category differs significantly between seasons or study sites (Appendix A, Table A3). Apart from the “other” category, only two comparisons are significantly different.

The first comparison concerns the mean proportion of prey in the urban area before and after the snowfall period. This proportion shows a significant increase in the volume of vertebrates after snowfall, rising from 0.20 to 0.65 ($P < 0.05$), representing a 225% increase. However, this is most likely due to the presence of unusually large prey (hares) in one of the samples, as well as the small number of samples taken during the second period (five samples from the urban site after snowfall, Table 1). This is also confirmed by the high variance observed during this period (±0.40) (Appendix A, Table A1).

The second significant comparison is the mean proportion of trash in urban and semi-urban sites before snowfall, which is roughly 1000 times higher ($P < 0.1$) in the urban site than in the semi-urban one, although these proportions remain low (Appendix A, Table A1 & A2). This may be related to the nature of the trash, which was mostly plastic and sponge in the urban area and mostly plastic and paper in the semi-urban area. In effect, the results show little difference between sites within the same season (Appendix A, Table A1 & A2). This suggests that the type and amount of trash consumed (which is probably accidental) is solely responsible for the results of this test and does not reflect an actual difference in consumption between the study sites.

While permutation tests indicated significant differences in vertebrate consumption in the urban site between pre- and post-snowfall periods, this result should be interpreted with caution. The small sample size during the post-snowfall period (N=5) and the high variance, largely driven by a single scat containing an unusually large prey item (hare), likely inflate the apparent effect. The limited number of possible permutations under such conditions may also compromise the reliability of the test. In future analyses, bootstrapped confidence intervals or effect size estimates may offer more robust insights into seasonal diet shifts. Importantly, the biological relevance of these changes should be evaluated considering the natural variability in red fox diet and the likelihood of opportunistic feeding behaviour, especially in winter.

5. Discussion

5.1 Overall Dietary Characteristics

This study provides a detailed assessment of the seasonal and spatial variations in the red fox's diet in response to winter conditions in urbanised environments. Overall, there were few drastic changes between seasons in either habitat, with a relatively stable and generalist diet maintained year-round.

5.1.1 Maintenance of a Generalist Diet

In both environments, vertebrate prey, mainly rodents, were the main food resource for red foxes. These findings align with the observations of Helldin & Danielsson (2007) and Needham et al. (2014), who demonstrated that they are consumed relatively consistently throughout the year in natural Scandinavian environments. Thus, as described by Kidawa & Kowalczyk (2011), rodents act as an essential buffer resource in the red fox's diet, which could explain why seasonal shifts are less necessary (Peterson et al., 2021).

Berries represent the second most frequent food item in the red fox's diet, showing a high reliance on fruit, especially lingonberries, independently of the level of urbanisation. By way of comparison, previous studies carried out elsewhere in Europe have shown more modest levels of consumption. In natural environments in Poland, for example, plant matter is considered a negligible component of the red fox's diet, representing up to 3.6% of its digestive content (Kidawa & Kowalczyk, 2011). However, their low-calorie and high-water content suggest that they are probably a supplementary food, possibly driven by local availability or secondary functions such as hydration, satiety, or digestive transit, rather than direct nutritional benefits (Wilson & Thomas, 2022).

Finally, invertebrates, eggshells, and trash were consumed in small quantities and sporadically across sites and periods, representing marginal dietary supplements. Although these remains were found in several samples, they did not follow a clear or consistent pattern across habitats or seasons. These results are consistent with previous findings regarding the consumption of invertebrates and lower vertebrates (e.g., reptiles, amphibians, and fish) by foxes, which have been identified as secondary consumers in the natural environment by Martsiv et al. (2021) and Rafaqat et al. (2024). However, they contrast with previous findings, which report higher invertebrate consumption in urban areas due to the scarcity of other food resources, particularly in autumn (Castañeda et al., 2020; Fletcher et al., 2025), which was not observed here.

5.1.2 Dietary Changes After Snowfall

Following snowfall, a few non-significant changes were observed: a modest increase in vertebrate prey (particularly in urban samples); persistence of berry consumption; and a decline or disappearance of invertebrates and rubbish.

Although the occurrence of vertebrate prey remained stable overall, their proportion of the total food residue mass increased after snowfall in both habitats. This shift was more intense in the urban environment but less stable, as shown by the variance. This suggests that foxes consumed more prey during this season but at a less stable rate in terms of quantity per day compared with the period before the snowfall.

Even after snowfall, fruit remained the second most consumed food in both habitats. In urban areas, the average proportion remained stable between the two periods, whereas it decreased slightly in the semi-urban area. This decline aligns with observations made in semi-natural or rural habitats, where fruit consumption decreases in winter (Helldin & Danielsson, 2007; Needham et al., 2014).

As expected, invertebrates were absent from all analysed scats after snowfall. However, the results do not support the assumption of this study concerning waste consumption, which was expected to increase in winter at the urban site. Only some semi-urban faeces contained a low occurrence of trash after snowfall. This is consistent with some other findings, for exemple, Peterson et al. (2021), who found no human-related remains in red fox scats in suburban New York.

5.2 Ecological and Behavioural Interpretation

5.2.1 Increase in Hunting Effort

An increase in the consumption of vertebrate prey suggests an adaptation to the winter diet, potentially in response to decreased availability of other food sources (Helldin & Danielsson, 2007; Needham et al., 2014).

This higher consumption could be the result of an increased hunting effort in response to harsh winter conditions, which are more energetically demanding for maintaining the metabolism of foxes. Therefore, although rodents are more difficult to hunt in winter due to their activity beneath the snow (Jędrzejewski & Jędrzejewska, 1992), they contains proteins and fats which have a higher nutritional and energetic value than berries, which are still consumed in large quantities in winter (Wilson & Thomas, 2022). This behaviour is supported by the presence of hare in the urban area, which is a bigger prey than usual and represent a greater effort to catch, but a bigger energy intake (Jędrzejewski & Jędrzejewska, 1992).

In semi-urban environments, the proportion of rodents increases more moderately after snowfall. This may be due to a more consistent availability of natural resources, reducing the need for a radical shift in dietary strategy. Nevertheless, we observe variations in prey types: bird remains are mostly found before snowfall but are absent afterwards. This is consistent with the findings of Needham et al. (2014) in Norway, who reported a winter decline in bird abundance in natural areas.The relative stability of conditions (including thicker and more consistent snow cover) could make rodent access less variable than in cities, which may explain the lower variance observed here. In contrast, the variance was high in the urban environment, which may be due to intra-seasonal variability in snow cover in urban areas. Access to rodents can be temporarily more difficult right after snowfall (Carricondo-Sanchez et al., 2016), whereas capture becomes easier on snow-free surfaces or during melting periods. Therefore, the probability of accessing rodents in urban areas may be more variable than in semi-urban areas, resulting in a more varied diet throughout the season.

5.2.2 Foraging on Residual Fruits

The persistent presence of berries appears to be strongly influenced by seasonal and human-related factors, which have different effects depending on the degree of urbanisation of the habitat. The strict stability observed in the urban area may reflect continuous availability linked to milder urban microclimates and easier access to residual fruits from the previous summer in winter. It could be due to thinner snow layers and potential access to feral or cultivated fruit trees. However, the occurrence of berries before snowfall is very low compared to in the semi-urban environment, suggesting limited access to berries in cities, even in summer. It is likely due to intensive human foraging reducing the actual availability of this resource despite its theoretical presence. In other words, the pressure humans exert on plant resources in summer has an equivalent effect to that of a harsh winter in a less urbanised setting, creating a form of 'anthropogenic seasonality'. Indeed, the average proportion of berries in urban faeces before snowfall is almost identical to that observed in semi-urban areas after snowfall, which supports this idea.

Nevertheless, the importance of fruit remains modest in terms of its relative proportion in this study. The greater variance observed in urban environments suggests variability in access to this resource over time, possibly linked to the reasons previously mentioned.

5.2.3 Opportunistic Feeding on Other Resources

Following snowfall, invertebrates become inaccessible due to hibernation or deep burrowing. Other protein sources, represented exclusively by eggshell fragments, were only found in urban environments, possibly as an opportunistic consumption of anthropogenic food waste, such as compost or discarded food. The complete absence of eggshells in semi-urban areas is surprising, but this may be due to stricter waste management practices or greater competition for such resources.

Interestingly, waste was present in 30% of urban faeces before snowfall but absent after. The high variance in proportion also suggests that, although foxes generally consume little waste, they may opportunistically rely on it. This seasonal contrast is surprising, as one might expect foxes to rely more on human-derived food in winter, when natural prey becomes scarce. One plausible explanation is that outdoor human activity, and thus the availability of directly accessible waste, is reduced in colder months (e.g., fewer outdoor meals are consumed). It is also possible that foxes focus most of their energy on hunting, as previously mentioned.

This sporadic reliance aligns with the findings of Fletcher et al. (2025), who found that the intake of anthropogenic food by urban foxes varies considerably among individuals. It is also possible that this resource was mostly consumed accidentally, as much of the rubbish found did not originally contain food, but may have picked up its smell.

5.3 Relevance to Urban Ecology

5.3.1 High Dietary Flexibility

Ultimately, the observed variations suggest that the red fox demonstrates a similar and highly flexible diet across both natural and human-modified landscapes, adjusting its foraging behaviour in response to local constraints, resource availability, and potentially, the presence of competitors. In general, semi-urban habitats have shown dietary patterns that are similar to those of foxes in natural settings, whereas urban habitats have exhibited less marked shifts due to anthropogenic pressures. Notably, the most significant differences did not arise from seasonal changes within a given habitat, but from inter-habitat comparisons before and after snowfall.

This opportunistic behaviour is reflected in the high variance observed in vertebrate proportions, indicating strong heterogeneity in the types and amounts of prey captured. Depending on available resources, the red fox can widen its predatory spectrum, as previously reported by Castañeda et al. (2020) in Paris and Helldin & Danielsson (2007) in Grimsö, Sweden.

5.3.2 Resources Diversity Depends on the Urbanism Level

The different food categories are similar on both sites, but their composition varies slightly depending on the level of urbanisation. Firstly, about vertebrates, the rodent family was not identified in this study, but differentiation was made between mammals and birds. Notably, the low occurrence of birds in urban faeces compared with the semi-urban contrasts with the results of Peterson et al. (2021) in New York, who reported birds as the most frequent prey (39% of samples), with an increased trend in winter. This difference may be due to the type of urban environment studied: our study focused on a forested urban area, whereas Peterson et al.'s study focused on a dense suburban area.

Regarding fruits, different types of seeds were found in the urban area, whereas lingonberries were predominant in the semi-urban area, suggesting a greater variety of fruits in this environment.

Finally, regarding invertebrates, semi-urban zones appear to offer greater diversity in natural microhabitats (e.g., leaf litter and open areas), favouring a wider variety of insects, as previously observed along urbanisation gradients by Moreira et al. (2024). This is reflected in the types of invertebrate remains found in the scat samples. In urban areas, the remains mostly belonged to *Carabidae*, which thrive in forest habitats. In contrast, in semi-urban areas, numerous Orthoptera were also found; this group proliferates in open and sunny habitats. However, this hypothesis would require confirmation through targeted entomological analysis.

5.3.3 Natural Prey Remains Preferred to Human Food Waste

Contrary to expectations, even in urban settings, foxes relied more on natural prey than on human food waste. However, when access to prey is sometimes limited, consuming berries may appear to be a suboptimal compensatory solution, potentially reinforced by the scarcity of alternative animal or human-provided resources. Previous studies have shown that the consumption of waste by red foxes varies considerably depending on the environment and geography. For instance, Forman (2005) found evidence of waste in 40.7% of fox droppings in natural areas of Wales, whereas Kidawa & Kowalczyk (2011) found evidence of waste in only 3.1% of fox droppings in Poland. Similarly, Castañeda et al. (2020) found that 17% of suburban foxes in Paris had consumed human-derived food. Fletcher et al. (2025) reported that it constituted 35% of the urban red fox diet in the UK. These differences highlight the complex interaction between demographic, environmental, cultural, and behavioural factors that influence the use of anthropogenic food.

5.3.4 Importance of Effective Waste Management

A possible explanation in the Swedish context may be greater public awareness regarding wildlife, combined with effective proactive measures such as wildlife-proof garbage bins and restrictions on outdoor food waste or pet access (Peterson et al., 2021). On a broader scale, although waste makes up a small proportion of total biomass consumed, its presence reflects human influence on fox diets. Notably, in summer, the proportion of waste found in urban fox scats nearly matches the deficit in vertebrate prey compared to semi-urban zones, suggesting a form of dietary compensation. However, urban foxes may rely more heavily on human leftovers to meet their energetic needs, if they have the opportunity, revealing the importance of restricting the fox's access to this resource.

5.3.5 Wildlife in Urban Areas: Interactions and Management Considerations

Winter-related ecological stress seems to manifest differently depending on habitat type. In semi-urban areas, where snow cover is less affected by human activities such as heating, traffic, or snow removal, it may represent a more substantial challenge for foxes. In addition, the potential presence of a large predator—likely a wolf, according to scat identification—could further influence fox foraging patterns through competition or spatial exclusion (Helldin & Danielsson 2007; Kidawa & Kowalczyk 2011).

By contrast, such pressures are absent in the urban area, where the only potential competitors are domestic animals that pose little threat. Prey type and availability may also vary in highly urbanised areas due to habitat fragmentation, human density, or other anthropogenic pressures. Interestingly, predation on large prey (e.g., hares) was recorded only in the urban area, suggesting that urban foxes may be more inclined to attempt hunting challenging prey. Alternatively, they might benefit from anthropogenic noise (e.g., car traffic), which could facilitate the capture of prey that would be harder to hunt in a natural environment. These observations highlight the need to consider prey population management and the ecological role of green spaces when planning urban landscapes.

5.4 Applied Value, Broader Implications, and Methodological Limitations

Scat analysis has been used in many studies to assess changes in the diet and resource use of carnivores over time. These analyses are particularly useful for considering the impact of a rapidly changing environment, such as that in Umeå, on the diets of predators. They have shown that red foxes respond flexibly to seasonal constraints, which supports their success in urban environments. This information is relevant in many areas, particularly wildlife management, where it can be used to understand and mitigate human-wildlife conflict. Secondly, it is relevant in urban planning to design green spaces that balance biodiversity with ecosystem health. It is also relevant for researchers interested in how generalist species adapt to climate and habitat change.

Nevertheless, even when combining dry mass and occurrence methods, scat analyses provide only a snapshot of the last meal, which may not be representative of the overall diet (Breuer, 2005). They also do not provide information on variation between individuals (Angerbjörn et al., 1994) or on age and sex (Helldin & Danielsson, 2007). Due to variations in food density, scat size, and inconsistent recovery rates of food items, this approach can only provide an approximate estimate of actual biomass intake (Klare et al., 2011). The digestibility rate of a given food category depends on its nature and when it was eaten (Ferreras & Fernandez-de-Simon, 2019; Peterson et al., 2021). Therefore, highly digestible elements, such as berries or anthropogenic resources, tend to be underestimated as they leave fewer solid remains than prey items (Fletcher et al., 2025).

Scat analysis can also be affected by bias arising from laboratory procedures and misidentification (Klare et al., 2011). The precision with which the different remains categories were sorted depended heavily on the time available. For instance, it was nearly impossible to separate feathers from fur within the time constraints, meaning mammals and birds could not be distinguished in the proportion calculations. However, they could be distinguished in the occurrence data.

6. Recommendations for Future Research

Although this study focuses on comparing dietary shifts between sites and periods using a methodology that is both affordable and validated by previous peer-reviewed studies, future research could improve upon this by providing a more complete description of dietary adaptations.

6.1 Detection of Scavenging and Prey Selection

Firstly, no scavenging was observed, despite it being commonly reported in Scandinavian natural habitats during winter (Needham et al., 2014). This absence may reflect lower carcass availability in the urban and semi-urban environments under study compared to more remote forested or rural areas. However, the presence of large carnivores such as wolves is to consider, notably in the semi-urban area (Helldin & Danielsson, 2007). Hence, the lack of scavenging activity detected could also be due to limited sampling or carcasses hairs that were not identified in the faeces. Some faeces may have contained hairs from large carcasses, such as roe deer or moose, which red foxes are known to scavenge in winter in Norway (Needham et al., 2014). Such hairs could be identified through medulla index calculations and cuticle pattern descriptions (Debrot et al., 1982), but this step was not performed in the present study.

A more precise identification of food remains, for example, using reference collections or classification guides, could provide a more detailed dietary description. This could also reveal prey preferences and clarify which rodent species act as a buffer, helping to determine which prey species should ideally be preserved. As the hairs and other remains were not fully identified, it is not possible to confirm scavenging behaviour or detect differences in prey preference between urban and semi-urban areas. For example, faeces from the urban area were assumed to contain hare hairs due to the high proportion of a single hair type present, whereas no hare hairs were identified in the semi-urban area, despite evidence of their presence in the environment, such as pellets and footprints in the snow. Some hairs may have been present in quantities too small to be identified. Identification is further complicated by the fact that some remains, such as bird feathers, are poorly preserved (Needham et al., 2014).

An alternative approach to confirming scavenging behaviour would be to combine faecal analysis with the use of camera traps, which could capture increased hunting activity during winter and allow the identification and comparison of prey availability with prey consumed. In this study, however, all food categories were assumed to be equally available, which may have introduced a simplification (Helldin & Danielsson, 2007).

6.2 Use Isotopes to Assess Long-Term Diet and Anthropogenic Reliance

Another analysis method could be used, such as stable isotope analysis, which is based on the ratios of stable isotopes, especially carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), within an animal's tissues. This method reveals dietary trends over the animal's lifetime (Angerbjörn et al., 1994), offering a more general picture than previously mentioned methods. It is particularly used to reveal and help quantify the intake of human-derived food, particularly C4-based processed foods, in growing urban zones (Fletcher et al., 2025). Isotopes could also reveal sex-specific differences, as female foxes may consume more anthropogenic food during periods of high energy demand, such as lactation (Fletcher et al., 2025). However, this technique requires tissue directly from the animal, which is more difficult to obtain than faeces. It is also mostly limited by its relatively high cost and reduced availability (Ferreras & Fernandez-de-Simon, 2019). It also provides a less detailed description of the diet since it cannot identify the specific species consumed, only the origin (animal, vegetable, etc.) (Peterson et al., 2021).

6.3 Enhancing Accuracy in Faecal Sampling with DNA Analyses

The identification of red fox scats involved multiple stages, each introducing potential sources of bias. Field identification was sometimes challenging due to environmental degradation (e.g., snow, rain) and the potential confusion with similarly sized dogs. Detection bias might also have occurred: scats containing brightly coloured berries were often easier to spot, possibly inflating the proportion of fruit in the dataset. This detection bias may have been stronger in winter, as evidenced by the single scat collected in February containing no fruit.

Post-filtering identification based on visual indicators, used for seven samples, may have further biased the classification. Ideally, faecal origin should be confirmed directly in the field or with DNA methods to avoid such uncertainties.

Moreover, even with better methods, absolute certainty is rare. For instance, red foxes are known to consume dog faeces (interspecific coprophagia), as revealed by DNA metabarcoding studies showing frequent domestic dog DNA in fox scats, possibly reflecting consumption of dog droppings as a fallback in winter when prey is scarce (Waggershauser et al., 2022). Conversely, some dogs, especially hunting dogs, consume berries or small prey, producing scats visually similar to foxes'. These dietary overlaps further complicate visual identification without genetic confirmation.

6.4 Improving Study Duration and Coverage

Finally, this study found no significant differences in diet between areas or periods, except for two results, which, as mentioned in the 'Results' section, are questionable in terms of reliability. As in many previous studies, the most probable explanation for this is the limited sample size: only 39 faecal samples were collected, reflecting the short duration of the study and its narrow geographical scope. For example, Fletcher et al. (2025) and Peterson et al. (2021) also report an absence of statistically significant seasonal variation, partly due to small sample sizes. This is particularly pertinent when assessing the consumption of anthropogenic materials, as this requires larger sampling efforts. According to these studies, one year of data collection is insufficient. Rafaqat et al. (2024) also confirm that a larger sample size is necessary to capture the full dietary variation (they collected 32 faecal samples over one year). The limited number of samples may have affected the reliability of the results; for example, the unusually high proportion of vertebrates (0.65) in urban post-snow samples may reflect isolated events, such as the consumption of large prey, such as hares. Such outliers can bias quantitative comparisons by strongly influencing averages.

A longer study duration could reduce sampling bias caused by seasonal constraints, such as reduced collecting success in winter due to snow cover or unexpected weather events (Peterson et al., 2021). This occurred in this study due to unstable temperatures and snow cover. Additionally, the unplanned clearance of the urban forest area between sampling periods for an urban extension project may have temporarily disturbed the local fauna, including red foxes.

Increasing the spatial coverage could improve the results by exploring a broader urban-rural gradient and and increasing the likelihood of sampling scats from multiple fox territories. In this study, each site covered approximately 2 km^2, whereas the average red fox territory in Swedish boreal forests is around 5 km^2 (Needham et al., 2014). This implies that all faeces collected at each site may have originated from a single fox, meaning the results may reflect the diet of only two foxes in total. Consequently, the generalizability of the findings is limited, as it remains uncertain whether a single fox can represent the broader population. This factor may also explain the occasional difficulty in locating scats, as the resident fox could have been elsewhere within its territory during sampling.

An alternative approach to address this limitation would have been to sample smaller but more numerous areas within each site, increasing the likelihood of detecting multiple individuals. Finally, this constraint further justifies the restrained use of statistical tests, as the samples cannot be considered independent.

6.5 Improvements in Quantitative Analysis

All the previously mentioned improvements could contribute to a larger, more comprehensive dataset, enabling more robust statistical analyses such as ANOVA tests (Breuer, 2005). Additionally, diet diversity indices (e.g., the Shannon index or niche width) could be used to quantify trophic breadth across seasons and sites. Some studies also recommend applying correction factors to convert dry mass into an estimate of the amount of fresh biomass consumed, to avoid under- or overestimation due to varying digestion rates. However, these correction factors are not always reliable as they are derived from captive animals, which may differ from wild individuals. They can also be imprecise for certain types of food (Ferreras & Fernandez-de-Simon, 2019).

Overall, this study should be considered a pilot study. It is limited in terms of both time and scope, but it is sufficient to highlight the key questions and dynamics regarding the impact of rapid urbanisation on wildlife ecology.

7. Conclusion and Perspectives

Overall, this study reveals that red foxes adapt their diet in response to the different pressures of urban and semi-urban environments. Vertebrate prey act as a buffer resource in both environments and across seasons, with consumption increasing after snowfall to meet higher energy demands. Fruit, particularly lingonberries, also plays a significant role when it is available. The two habitats respond similarly to constraints and follow a natural seasonal pattern. This applies even to urban foxes, which experience weaker climatic constraints (such as thinner snow cover due to human activity). Nevertheless, they face stronger and more unstable human-induced competition for berries during the pre-snowfall period. Conversely, semi-urban foxes face stronger competition for resources with other omnivores all year long. Ultimately, in both habitats, foxes opportunistically consume secondary foods such as invertebrates and rubbish throughout the study period. Despite these insights, limited sampling, a short study duration, and a narrow geographic scope prevent any statistical conclusions from being drawn.

In the context of global warming, shorter winters, reduced snow cover, higher temperatures, and ongoing urbanisation could alter fox foraging behaviour (Angerbjörn et al., 1994). Urban sprawl introduces new food sources, such as rubbish, compost, and garden produce (Handler et al., 2020), while increased human affluence may lead to more waste and carcasses being available (Carricondo-Sanchez et al., 2016). Extreme weather events such as winter thaw can devastate rodent populations by disrupting protective snow layers (Kleiven, 2022), thereby affecting the fox's diet. The red fox remains a keystone urban predator that is valued by the public. It is crucial for regulating rodent populations, including voles that carry the Puumala hantavirus (Khalil et al., 2019), and it influences tick dynamics (Takumi et al., 2019). Therefore, limiting wildlife access to refuse, as well as monitoring shifts in the fox's diet (including incidental parasite ingestion), is essential for public health and wildlife management, as well as for understanding how ecosystems respond to rapid environmental change.

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Popular science summary

Red foxes are among the most adaptable omnivores in Europe. They feed on a wide variety of foods, including berries, insects, and, most importantly, small mammals such as voles. This adaptability enables them to thrive in virtually any environment, from remote forests to the heart of major cities such as New York. As urbanisation continues to transform the landscape, important questions arise about the effect of the human presence on their diet and behaviour. This study investigated how red foxes exploit available food resources in Umeå, a rapidly growing municipality in Sweden, across seasons and in areas with differing levels of human activity.

Around 40 faecal samples (scats) were collected across urban and semi-urban sites during autumn and winter. Each sample was carefully examined to confirm its origin and identify the type of food remains present, including vertebrate prey, fruit, insects, and human-derived waste such as plastic. Small mammal hairs, bird feathers, insect parts, and plant material were recorded to reconstruct the composition of the foxes' diets. The proportions of each food category were then compared across sites and seasons to detect patterns of impact from snowfall and urban exploitation.

The results show that red foxes display remarkable dietary flexibility. Their diets were primarily composed of mammalian prey and fruit in both environments across both seasons. In urban and semi-urban areas alike, foxes relied heavily on small rodents in winter when other resources were scarce. They consumed a wide variety of foods, including insects and human-derived debris, although these items were present in only a small proportion of samples, highlighting their opportunistic behaviour. The presence of various waste residues, such as plastic and aluminium, in the scats illustrates the unintended role humans play in subsidising urban wildlife.

These findings demonstrate red foxes' ability to exploit human-altered landscapes but also suggest urbanisation can substantially alter their foraging ecology if not properly managed. Understanding these patterns is crucial for urban wildlife management. Ensuring proper waste management and limiting access to human food sources can reduce human–fox conflicts and mitigate health risks for both humans and animals. More broadly, our study highlights the capacity of generalist species to thrive in cities, emphasising the need for urban planning that accounts for adaptable wildlife.

Appendix A

Table A1. Average weight proportion ± standard deviation of each food remains category in the urban site.

	Before snowfall (N=11)	**After snowfall (N=5)**
Vertebrate	0.20 ± 0.23	0.65 ± 0.40
Fruit	0.21 ± 0.35	0.25 ± 0.42
Invertebrate	0.0018 ± 0.0049	1e-05 ± 2.2e-05
Trash	0.098 ± 0.29	0
Eggshell	0	0
Other	0.48 ± 0.37	0.095 ± 0.17

Table A2. Average weight proportion ± standard deviation of each food remains category in the semi-urban site.

	Before snowfall (N=17)	**After snowfall (N=6)**
Vertebrate	0.30 ± 0.31	0.40 ± 0.28
Fruit	0.39 ± 0.33	0.24 ± 0.28
Invertebrate	0.0067 ± 0.022	0
Trash	0.00011 ± 0.00035	0.041 ± 0.1
Eggshell	0.00086 ± 0.0033	0.00017 ± 0.00042
Other	0.25 ±0.25	0.31 ± 0.28

Table A3. Permutation test results comparing average weight proportions of food categories across periods (before vs. after snowfall) and sites (urban vs. semi-urban). Significant P values are marked with (**) if P <0.05 and (*) if P< 0.1.

	Category		**Average ± *SD***		**Average ± *SD***	**P**
			Before		**After**	
Urban	Vertebrate	N = 11	0.1956 ± 0.2285	N = 5	0.6479 ± 0.4013	0.0142**
	Fruit		0.2132 ± 0.3461		0.2515 ± 0.4208	0.8087
	Invertebrate		0.0018 ± 0.0049		0 ± 0	0.4907
	Trash		0.0975 ± 0.2946		0 ± 0	0.6014
	Eggshell		0		0 ± 0	1
	Other		0.4818 ± 0.3743		0.0951 ± 0.1653	0.0457**
Semi-urban	Vertebrate	N = 17	0.2958 ± 0.3099	N = 6	0.3983 ± 0.2831	0.483
	Fruit		0.3922 ± 0.3274		0.2411 ± 0.2778	0.329
	Invertebrate		0.0067 ± 0.0222		0 ± 0 (n=6)	0.316
	Trash		1e-04 ± 3e-04		0.0415 ± 0.1016	0.2567
	Eggshell		9e-04 ± 0.0033		2e-04 ± 4e-04	0.954
	Other		0.2515 ± 0.2502		0.3132 ± 0.28	0.6308
			Urban		**Semi-urban**	
Before	Vertebrate	N = 11	0.1956 ± 0.2285	N = 17	0.2958 ± 0.3099	0.3687
	Fruit		0.2132 ± 0.3461		0.3922 ± 0.3274	0.1856
	Invertebrate		0.0018 ± 0.0049		0.0067 ± 0.0222	0.7689
	Trash		0.0975 ± 0.2946		1e-04 ± 3e-04	0.0517*

	Category		**Average ± *SD***		**Average ± *SD***	**P**
	Eggshell		0		9e-04 ± 0.0033	0.7596
	Other		0.4818 ± 0.3743		0.2515 ± 0.2502	0.0575*
After	Vertebrate	N = 17	0.6479 ± 0.4013	N = 6	0.3983 ± 0.2831	0.2609
	Fruit		0.2515 ± 0.4208		0.2411 ± 0.2778	0.9905
	Invertebrate		0 ± 0		0 ± 0	0.4578
	Trash		0 ± 0		0.0415 ± 0.1016	1
	Eggshell		0 ± 0		2e-04 ± 4e-04	1
	Other		0.0951 ± 0.1653		0.3132 ± 0.28	0.1472

Appendix B

Table B1. Mean mass (g) of faeces per site and period.

	Urban	Semi-urban
Before snowfall	6.2526 *(N=11)*	6.9396 *(N=17)*
After snowfall	13.274 *(N=5)*	7.1833 *(N=6)*

Table B2. Mean mass (g) of food remains per scat, per site and period.

	Urban	Semi-urban
Before snowfall	1.3472 *(N=11)*	3.2876 *(N=17)*
After snowfall	1.6667 *(N=5)*	3.3806 *(N=6)*

Table B3. Average weight proportion ± standard deviation of food remains per site and period.

	Urban	Semi-urban
Before snowfall	0.30 ± 0.25	0.53 ± 0.15
After snowfall	0.20 ± 0.16	0.51 ± 0.22

Table B4. Mean mass (g) of food remains categories, per site and period. Masses reported for each food category were calculated relative to the total mass of food remains within a sample. The mean mass of total food remains was calculated relative to the total dry mass of the faecal sample (i.e., the total proportion of remains in the scat).

	URBAN		SEMI-URBAN	
	Before snowfall	After snowfall	Before snowfall	After snowfall
Total food remains	1.3472	1.6666	3. 2876	3.3806
Vertebrate	0.2827	1.4018	0.9231	1.1317
Fruit	0.3905	0.1764	0.8878	0.9716
Invertebrate	0.0019	0.00004	0.0092	0
Trash	0.0588	0	0.0003	0.0344
Eggshell	0	0	0.0023	0.0003
Other	0.5969	0.0805	1.3571	1.23

Table B5. Minimum and maximum recorded masses (g) of food remains categories, per site and period.

	URBAN				**SEMI-URBAN**			
	Before snowfall		**After snowfall**		**Before snowfall**		**After snowfall**	
	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX
Vertebrate	0	2,1291	0,0028	3,9615	0	3,7345	0,265	1,8835
Fruit	0	1,5784	0	0,6226	0,1077	2,7153	0	2,0859
Invertebrate	0	0,0178	0	0,0002	0	0,1158	0	0
Eggshell	0	0	0	0	0	0,0382	0	0,0018
Trash	0	0,5542	0	0	0	0,0038	0	0,2061

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