

University of Groningen

## Gray squirrels consume anthropogenic food waste most often during winter

Rimbach, Rebecca; Butler, Gabrielle; Gupte, Pratik R.; Jäger, Jörg; Parker, Claire; Pontzer, Herman

*Published in:*  
Mammalian Biology

*DOI:*  
[10.1007/s42991-022-00326-3](https://doi.org/10.1007/s42991-022-00326-3)

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2023

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Rimbach, R., Butler, G., Gupte, P. R., Jäger, J., Parker, C., & Pontzer, H. (2023). Gray squirrels consume anthropogenic food waste most often during winter. *Mammalian Biology*, 103, 69-81. Advance online publication. <https://doi.org/10.1007/s42991-022-00326-3>

**Copyright**

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

**Take-down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

*Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.*



# Gray squirrels consume anthropogenic food waste most often during winter

Rebecca Rimbach<sup>1,2</sup> · Gabrielle Butler<sup>1</sup> · Pratik R. Gupte<sup>3</sup> · Jörg Jäger<sup>1,2</sup> · Claire Parker<sup>1</sup> · Herman Pontzer<sup>1,4</sup>

Received: 12 April 2022 / Accepted: 24 October 2022 / Published online: 4 November 2022

© The Author(s) under exclusive licence to Deutsche Gesellschaft für Säugetierkunde 2022, corrected publication 2022

## Abstract

Urban habitats provide wildlife with predictable, easily accessible and abundant food sources in the form of human food waste. Urban eastern gray squirrels (*Sciurus carolinensis*) are commonly observed feeding in trash bins, but we lack data regarding the type, quantity and seasonal changes in food waste usage. We observed five trash bins on an urban university campus during four different observation periods. We recorded the time squirrels spent on and inside trash bins and type of retrieved food items. We also recorded ambient temperature, human presence and trash bin filling. Moreover, we determined changes in squirrel population density in a natural and three anthropogenic habitats during the same periods. Trash bins were fuller when human presence was higher. The higher human presence, the more squirrels went on and inside the bin, but there was no effect on number of retrieved food items. Trash bin usage by squirrels decreased when ambient temperature and bin filling increased. Most food items were retrieved during the coldest observation period, a period of high human presence, and the majority of retrieved food items were starchy foods (e.g., bread, French fries). The relationship between the number of squirrels observed along transects and a measure of urbanization, the normalized difference built-up index, was negative in periods with high ambient temperatures and positive in periods with low ambient temperatures, indicating winter may be less challenging in urban areas, likely facilitated by the availability of anthropogenic food sources, allowing a higher level of activity throughout winter.

**Keywords** Anthropogenic food sources · Population density · Garbage · Trash bin · Urbanization · Waste

## Introduction

Urban development is a major form of land change, and can result in local extinction of native species and their replacement with non-native species (McKinney 2006, 2008; Grimmer 2007; Grimm et al. 2008). While some species, such as many carnivores (Ordeñana et al. 2010), avoid urban

environments, synanthropic species, for example, many bird and rodent species, manage to reproduce and persist in anthropogenically modified habitats (McKinney 2006; Hansen et al. 2020). However, numerous sub-lethal effects on behavior, communication, metabolism, nutrition, stress hormone levels and health have been described (Birnie-Gauvin et al. 2016). A species' response to urbanization can be region-specific and vary with landscape-scale metrics such as human population density and the availability of green space (Plaza and Lambertucci 2017; Murray et al. 2019; Fidino et al. 2020).

Urban habitats differ in many aspects from more natural habitats. Importantly, they often present animals with predictable and abundant anthropogenic food subsidies in the form of bird feeders, nuts provided for rodents, backyard resources, composts, human food waste or refuse (Oro et al. 2013; Plaza and Lambertucci 2017; Hansen et al. 2020). Numerous urban populations of birds, mammals, reptiles and amphibians are known to consume anthropogenic food sources (Contesse et al. 2004; Oro et al. 2013; Birnie-Gauvin et al. 2016; Plaza and Lambertucci 2017; Katlam et al. 2018; Schulte-Hostedde

Handling editor: Adam J Munn.

✉ Rebecca Rimbach  
rrimbach@gmail.com

<sup>1</sup> Evolutionary Anthropology, Duke University, Durham, NC, USA

<sup>2</sup> School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

<sup>3</sup> Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands

<sup>4</sup> Duke Global Health Institute, Duke University, Durham, NC, USA

et al. 2018; Lenzi et al. 2019). Nutrient content of anthropogenic food differs from natural food. Human food waste typically has a higher fat and carbohydrate content, and its consumption can result in a reduced intake of dietary protein, antioxidants and vitamins (Murray et al. 2015b, a; Andersson et al. 2018; Schulte-Hostedde et al. 2018). Both positive and negative health outcomes have been reported from wildlife species that ingest anthropogenic food waste (Plaza and Lambertucci 2017), but we lack data regarding the type, quantity and seasonal changes in food waste usage for many species.

Eastern gray squirrels (*Sciurus carolinensis*) are commonly found in anthropogenic environments in North America [and Europe] (van der Merwe et al. 2005; Benson 2013; Engel et al. 2020). In hardwood forests, they primarily feed on tree nuts and samara fruits of deciduous trees and shrubs (Moller 1983). They are scatter hoarders and rely on stored food items during winter (Koprowski 1994). In urban habitats, they also raid gardens, bird feeders and composts (Hansen et al. 2020), and although gray squirrels are commonly observed feeding in dumpsters and trash bins, this behavior has only been noted anecdotally in the scientific literature (van der Merwe et al. 2005). Gray squirrels are diurnal and easy to spot. Urban populations become habituated to human presence and show reduced flight initiation distances, which are used to measure perceived predation risk (Cooper et al. 2008; Bateman and Fleming 2014; Engel et al. 2020). These characteristics make gray squirrels an excellent model species to study human food waste consumption. Gray squirrel population density varies between different habitat types and is often elevated in urban environments (Hein 1997; Parker and Nilon 2008; Engel et al. 2020). But few studies have determined and compared seasonal changes in population density in different habitat types. For this study, we conducted a total of 161.5 h of observations of five different trash bins situated on an urban university campus. We assumed that trash bins would be fuller when more people were present on campus, and thus, predicted that squirrels would use trash bins more often during periods of high human presence. Further, we predicted that trash bin usage would vary seasonally. In winter, natural food availability is low and squirrels rely on previously stored food items (Koprowski 1994). Thus, we expected that squirrels would consume more anthropogenic food items during the winter, and especially so at the end of winter, when natural food availability is lowest. We also assessed how squirrel population density changes throughout the year in a natural and three anthropogenic habitats.

## Materials and methods

### Study species

The eastern gray squirrel (*S. carolinensis*) is a medium sized (300–710 g) tree squirrel native throughout eastern

North America (Koprowski 1994). It is commonly found in both deciduous forests and anthropogenic environments, such as parks and residential areas, and it has been successfully introduced to Europe and South Africa (Benson 2013). They frequently descend to the ground to forage and cache food (Koprowski 1994). Their peak activity period occurs in summer or fall (Bakken 1959; Thompson 1977); their activity pattern is bimodal from spring to fall, with morning and afternoon peaks, and unimodal in winter, with one peak occurring around midday (Koprowski 1994; Koprowski et al. 2016). Gray squirrel food consumption peaks in summer or fall and decreases in winter, and body mass is largest in fall or winter and decreases in the spring (Knee 1983; Koprowski 1994). Home range size varies between 0.5 and 20.2 ha, but home ranges are usually smaller than 5 ha (Doebel and McGinnes 1974; Koprowski 1994; Tounzen et al. 2012).

Gray squirrel population density differs between different habitats. In forest habitats, population densities around or below 3/ha have been reported (Barkalow et al. 1970; Healy and Welsh 1992). In contrast, population densities can be much higher in urban environments (Hein 1997; Engel et al. 2020), although area-specific differences have been reported (Parker and Nilon 2008). An average population density of 32/ha has been reported in urban parks in St. Louis, Missouri (Engel et al. 2020). The same study reported lower population densities in urban forests (6/ha), residential neighborhoods (5/ha) and cemeteries (4/ha), and very low densities at golf courses (< 1/ha) (Engel et al. 2020). Population density at an urban university campus has been reported as 4.7/ha (Hein 1997).

### Trash bin observations

We observed five different metal trash bins (Fig. 1) on Duke University campus, North Carolina, USA (36.001596, – 78.940459). The average distance between trash bins was 343 m ( $\pm$ SD = 169 m). We observed each bin for at least 8 h each during four different observation periods, resulting in 40 h of observation per period and a total of 161.5 h of observation. Observation periods lasted for 36–42 days during July–August 2020 (summer), September–October 2020 (fall), November–December 2020 (transition fall–winter) and February–March 2021 (transition winter–spring). All bins were situated on Duke West campus (2.9 km<sup>2</sup>), which contains a heterogeneous mixture of buildings, sparsely treed grass lawns and several small forested areas which contain several tree species that offer natural food sources to the squirrel population (e.g., oak, maple, hickory, pine). The majority of residential quads are situated on Duke West campus and the campus population comprised ~ 16,170 students in the academic year



**Fig. 1** Eastern gray squirrel (*Sciurus carolinensis*) eating a piece of bacon it retrieved from one of the five trash bins used for observations

2020–2021. No lectures occurred between November 16th 2020 and January 20th 2021. We chose trash bins that were located in areas which are frequently used by people. Three bins were in close proximity to food courts and restaurants, one was situated in front of a building that contains a cafe and is highly frequented by students, and the fifth bin was located next to a small forested area which is used by students and staff to relax and eat on benches near the trash bin. During the first Covid-19 lockdown in North Carolina (between July and August 2020), very few people were

present on Duke university campus and most restaurants were closed. However, trash bin filling in July was similar to November 2020 and February 2021 (Table 1) because trash bins were emptied less regularly (every 2–3 days) compared to every 1–2 days outside of the lockdown (pers. comm. with refuse collectors). We did not note any bird feeders on campus, but squirrels are occasionally intentionally fed with anthropogenic food by people, for example, on food courts (pers. obs.). In all but the February sampling period, we conducted half of the observations in the mornings and half in the afternoons, and we adjusted the observation windows to the changes in daylength and activity of squirrels (July: 7:45–10:15 and 15:00–19:00; September: 8:15–10:15 and 15:00–18:00; November: 8:30–11:00 and 14:00–17:00). Squirrels show a unimodal pattern of activity in winter, and thus, in February we conducted observations between 12:00 and 17:00 when they are most active. During observations, we sat at a distance of approximately 10 m from trash bins and recorded the date, start and end time of the observation, weather condition (sunny, cloudy, windy), bin ID and how full the bin was at the beginning of the observation (0–100%; 125% was used for overflowing bins), whether the bin was in the shade or sun, time a squirrel climbed on a bin and left it, time a squirrel went inside and when it came out of the bin. We also noted whether squirrels retrieved food items and the type of food item. Although we are unable to test this, we deem it likely that squirrels consumed the vast majority of food items outside of trash bins. The majority of squirrels (84% of individuals) spent less than one minute inside the trash bin and only 8% spent more than 2 min inside. When inside a bin, we would hear squirrels go through the trash, looking for food which they then consumed while sitting on the bin or a nearby tree. During each observation, we counted how many people used trash bins and the number of people walking past bins within 2 m. Specifically, we counted each disturbance at a bin, meaning that we counted a group of people passing by a bin as a single disturbance. We also extracted average ambient temperature during each observation from a

**Table 1** Overview of the observation hours and variation in ambient temperature, time squirrels spent on and inside trash bins, the number of times they retrieved food items, trash bin filling, the total number of people walking past a bin, the number of people walking past a bin per minute during observations in the four sampling periods and the total number of people using a bin (values are mean  $\pm$  SD)

Observation period	July 2020	September 2020	November 2020	February 2021
Observation hours	40.7	40.8	40	40
Average ambient temperature during observations ( $^{\circ}$ C)	30.2 $\pm$ 4.8	21.3 $\pm$ 5.9	13.4 $\pm$ 5.2	10.4 $\pm$ 3.3
Total time on bin (min)	38	99.5	63.5	128.5
Total time in bin (min)	10	40	22.5	49.4
Total number of food items	5	24	12	60
Trash bin filling (%)	46.2 $\pm$ 36.8	63.8 $\pm$ 33.3	42.8 $\pm$ 29.1	41.6 $\pm$ 26.4
Total number of people walking past bin per observation period	875	4585	2470	9765
People walking past bin/min	0.22 $\pm$ 0.23	0.96 $\pm$ 1.03	0.51 $\pm$ 0.57	1.16 $\pm$ 1.11
Total number of people using bin	19	42	26	70

weather station (<https://www.wunderground.com/dashboard/pws/KNCDURHA275>) situated on Duke West campus (36.007000, -78.937000), with a maximum distance from a study bin of 930 m.

### Squirrel abundance

Gray squirrels are readily detectable when moving slowly along a line transect (Healy and Welsh 1992). We conducted surveys on six transects during July, September and November 2020, and in February 2021. We sampled three transects on Duke University West campus (one along Chapel Drive: C\_C, one along Science Drive: C\_S, one between Research Drive and Erwin Road: C\_R), one in Duke Forest (F; Korstian Division), one in downtown Durham (DT; along Foster Street) and one in a cemetery (Maplewood Cemetery, CE; Fig. 4). The transects on Duke campus were close to each other (0.7–0.8 km, measured from the middle of one transect to the middle of the other transect). The study trash bins were at an average distance of 153 m to the C\_C transect (measured at nearest point between bin and transect; min: 3 m; max: 310 m), 265 m to the C\_S transect (min: 3 m; max: 650 m) and 448 m to the C\_R transect (min: 270 m; max: 700 m). The distance between the transects on Duke campus to the transect in Duke Forest was 7.3 km, 3.3 km to the downtown transect and 1.1 km to the cemetery transect. The distance between the cemetery transect and the Duke Forest transect was 8 km, 2.5 km between the cemetery transect the downtown transect, and 10.5 km between the downtown transect and the Duke Forest transect. We chose these transects to determine squirrel population density across a range of urbanized and natural habitats. Average transect length was 1212 m ( $\pm$  SD = 669 m). We followed established sidewalks or walking trails at each site, walking as straight as possible, and we did not revisit any portions of the transect. We walked each transect four times each during each period. In 2020, we walked each transect twice in the morning and twice in the afternoon, to match peak activity times of squirrels. In February 2021, we walked all transects 4 times during midday (12:00–17:00) due to their unimodal pattern of activity in winter (Koprowski 1994). We did not walk transects on rainy days, and we walked a total distance of 93.2 km.

During each walk, we recorded the start and end time of the walk and number of squirrels and people observed along the transect. We also recorded the average ambient temperature during the walk using the weather station closest to each transect (using the same weather station for the 3 transects on Duke campus and 4 different stations in total; [www.underground.com](http://www.underground.com)). We calculated a relative abundance of squirrels (per ha) by dividing number of squirrels observed on a given transect by the sampling area for this transect.

### Landscape analysis

We obtained two landscape metrics for each transect, the NDVI (normalized difference vegetation index; Pettorelli 2013), and NDBI (normalized difference built-up index; Zha et al. 2003). NDVI is a commonly used and widely informative metric of natural resource availability and ecological integrity (Pettorelli 2013). In contrast, NDBI relies on the specific spectral reflectance characteristics of human-made materials such as concrete to indicate the level of urbanization (Zha et al. 2003). We buffered each transect by two different buffer sizes. We used a 40 m radius based on the minimum reported adult home range size for gray squirrels of 0.5 ha (Doebel and McGinnes 1974), a buffer size previously used for the species (Engel et al. 2020). We also used a 90 m radius based on more commonly observed home range sizes below 5 ha (Koprowski 1994). We extracted the mean of summer NDVI and NDBI.

We used Google Earth Engine (Gorelick et al. 2017) to process Sentinel-2, Level-1C snapshots taken between April 01, 2020 and October 01, 2020 into NDVI and NDBI values, using band 8 (near infra-red; 835.1 or 833 nm) and band 4 (red; 664.5 nm or 665 nm) to calculate NDVI, and band 11 (short-wave infra-red 1613.7 nm or 1610.4 nm) and band 8 to calculate NDBI, translating Zha et al.'s (2003) approach with LANDSAT snapshots for use with Sentinel 2 data. We further transformed the NDBI values in the range 0–1, with higher values indicating greater urbanization. The snapshots comprised of data from the individual satellites S2A and S2B, hence the minor differences in band wavelengths.

### Statistical analyses

We conducted all analyses in R 4.0.5 (R Core Team 2021). Ambient temperature, the number of people walking past a bin, the number of people using a bin per observation, bin filling, and time squirrels spent on and inside a bin did not follow a normal distribution. Therefore, we used Kruskal–Wallis rank sum tests to examine if these variables differed between observation periods. Subsequently, we conducted pairwise comparisons using Wilcoxon rank sum tests to determine during which observation periods these variables differed. We corrected *P* values for multiple testing using the Holm method (Holm 1979). We used Pearson's product-moment correlations to assess if bin filling correlated with the number of people walking past trash bins.

### Trash bin usage

We used three different types of trash bin usage data: number of squirrels on a bin, number of squirrels inside a bin and number of squirrels that retrieved a food item per observation. All three types of data were zero-inflated count data,

and thus, we fitted zero-inflated generalized linear mixed models (GLMMs) using the function ‘glmmTMB’ from the R package glmmTMB (Brooks et al. 2017). We used the type of bin usage as response variable and included average ambient temperature during the observation, bin filling, number of people walking past the bin and whether the bin was in the sun or shade as explanatory variables. We included the natural log transformed duration (minutes) of each observation as an offset term to account for duration differences (mean  $\pm$  SD = 66.6  $\pm$  35.3 min). We included bin identity as a random effect. We derived variance inflation factors (VIFs) using the function ‘vif’ of the car package (Fox and Weisberg 2019), which did not indicate collinearity (all VIFs  $\leq$  2). We used the R package DHARMA (Hartig 2020) to assess model fit using the function ‘simulateResiduals’ and tested for overdispersion using the function ‘testDispersion’.

### Retrieved food items

We used a Kruskal–Wallis rank sum test to examine if the number of food items retrieved during an observation differed between sampling periods, and subsequently, we conducted pairwise comparisons using Wilcoxon rank sum tests. We assessed whether there were differences in broad categories of food items (starchy foods [e.g., French fries, bread, pizza, pasta, rice, chips], meat and poultry, vegetable, fruit, sugar-sweetened beverage and non-food items) that squirrels retrieved from bins between observation periods using a Fisher’s Exact Test.

### Squirrel abundance

The number of squirrels observed along a transect was zero-inflated count data, and thus, we fitted a zero-inflated GLMM using the function ‘glmmTMB’ from the R package glmmTMB (Brooks et al. 2017). We used the number of squirrels observed per transect walk as response variable and included transect ID, study period and average ambient temperature as explanatory variables. We included the natural log transformed duration (minutes) of each transect walk as an offset term to account for duration differences. We included observer identity as a random effect. To assess the effect of urbanized habitat on squirrel abundance, we fitted a second model, and included average ambient temperature, average NDBI of a transect, study period and an interaction between NDBI and study period as explanatory variables, and we used natural log transformed speed (distance walked per minute) as offset term and observer identity as a random effect. We did not include interaction terms because this resulted in convergence issues. VIFs did not indicate collinearity (all  $\leq$  2). We assessed model fit using the function ‘simulateResiduals’ and tested for overdispersion using the function ‘testDispersion’.

## Results

Average ambient temperature (Kruskal–Wallis  $\chi^2 = 232.48$ ,  $df = 3$ ,  $P < 0.0001$ ), number of people walking past a bin per minute observation ( $\chi^2 = 122.42$ ,  $df = 3$ ,  $P < 0.0001$ ), number of people using a bin per observation ( $\chi^2 = 63.37$ ,  $df = 3$ ,  $P < 0.0001$ ), bin filling ( $\chi^2 = 29.71$ ,  $df = 3$ ,  $P < 0.0001$ ), time squirrels spent on bins ( $\chi^2 = 13.78$ ,  $df = 3$ ,  $P = 0.003$ ) and time squirrels spent inside bins ( $\chi^2 = 13.94$ ,  $df = 3$ ,  $P = 0.002$ ) differed between observation periods (Table 1). All pairwise comparisons between the four observation periods were significant regarding ambient temperature and number of people walking past a bin (Pairwise comparisons using Wilcoxon rank sum test; all  $P < 0.0001$ ). More people used bins per observation in September compared to November ( $P = 0.005$ ) and more people used bins in February compared to all other periods (all  $P < 0.0001$ ). Bins were fuller in September compared to July ( $P = 0.022$ ), November ( $P < 0.0001$ ) and February ( $P < 0.0001$ ; Table 1).

In all periods except July (during the first Covid-19 lockdown in North Carolina, USA), the more people walked past a bin per minute of observation, the fuller bins were (Pearson’s product-moment correlation: July:  $t = 0.30$ ,  $df = 57$ ,  $P = 0.764$ ,  $r = 0.040$ ; September:  $t = 4.89$ ,  $df = 87$ ,  $P < 0.0001$ ,  $r = 0.465$ ; November:  $t = 6.18$ ,  $df = 81$ ,  $P < 0.0001$ ,  $r = 0.566$ ; February:  $t = 8.46$ ,  $df = 123$ ,  $P < 0.0001$ ,  $r = 0.606$ ). Squirrels spent less time on bins in November (mean  $\pm$  SD = 1.92  $\pm$  2.49 min) compared to February (4.41  $\pm$  4.49 min;  $P = 0.003$ ), but there were no differences between the other periods (July: 2.52  $\pm$  2.03 min; September: 2.73  $\pm$  2.71 min). The duration squirrels spent inside bins was shorter in February (0.67  $\pm$  0.35 min) compared to September (0.98  $\pm$  0.61 min;  $P = 0.002$ ), but there were no other differences (July: 0.71  $\pm$  0.43 min; November: 0.75  $\pm$  0.41 min).

### Trash bin usage

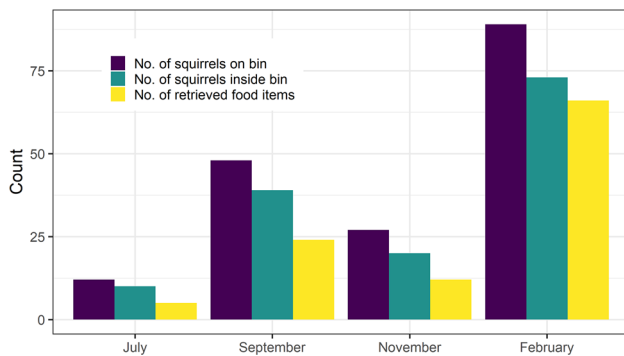
The three types of trash bin usage were positively correlated to each other (Pearson’s product-moment correlations: number of squirrels that went on and inside a bin:  $t = 45.74$ ,  $df = 177$ ,  $P < 0.0001$ ,  $r = 0.960$ ; number of squirrels that went on a bin and number of food items retrieved:  $t = 25.33$ ,  $df = 177$ ,  $P < 0.0001$ ,  $r = 0.885$ ; number of squirrels that went inside a bin and number of food items retrieved:  $t = 34.56$ ,  $df = 177$ ,  $P < 0.0001$ ,  $r = 0.933$ ; Fig. 2).

Ambient temperature and bin filling had a negative effect on all three types of trash bin usage (Table 2). The more people walked past a bin, the more squirrels went on and inside a bin (Table 2), but the number of food items squirrels retrieved from bins was not related to the number of people

walking past bins (Table 2). Whether a bin was in the sun or in the shade did not affect trash bin usage (Table 2).

## Retrieved food items

Squirrels retrieved and consumed a total of 101 food items during all four observation periods combined (Fig. 3). Squirrels retrieved 59.4% of food items during February and 5% in July (Fig. 3; Table 1). The number of food items retrieved differed between sampling periods ( $\chi^2 = 12.52$ ,  $df = 3$ ,  $P = 0.006$ ). Squirrels retrieved more food items in February (mean  $\pm$  SD =  $1.74 \pm 4.85$  per observation) compared to July ( $0.11 \pm 0.48$  per observation; Pairwise comparisons using



**Fig. 2** Seasonal changes in the number of eastern gray squirrels (*Sciurus carolinensis*) observed on and inside a trash bin, and the number of food items squirrels retrieved from trash bins

**Table 2** Results of the zero-inflated generalized linear mixed models to test for an association between ambient temperature, whether a bin was in the sun or shade, number of people walking past a bin, bin fill-

Predictors	Squirrels on bin			Squirrels in bin			Number of food items		
	Estimate $\pm$ SE	<i>z</i>	<i>P</i>	Estimate $\pm$ SE	<i>z</i>	<i>P</i>	Estimate $\pm$ SE	<i>z</i>	<i>P</i>
<i>Conditional model</i>									
(Intercept)	-2.68 $\pm$ 0.45	-5.90	<0.0001	-3.24 $\pm$ 0.60	-5.45	<0.0001	-2.99 $\pm$ 0.97	-3.07	0.002
Temperature	-0.03 $\pm$ 0.01	-3.79	<b>0.0001</b>	-0.03 $\pm$ 0.01	-2.93	<b>0.003</b>	-0.07 $\pm$ 0.02	-3.86	<b>0.0001</b>
Sun or shade[sun]	-0.24 $\pm$ 0.18	-1.33	0.184	-0.39 $\pm$ 0.27	-1.43	0.152	-0.60 $\pm$ 0.35	-1.71	0.088
People	0.00 $\pm$ 0.00	3.95	<b>0.0001</b>	0.01 $\pm$ 0.00	4.13	< <b>0.0001</b>	0.00 $\pm$ 0.00	0.27	0.789
Bin filling	-0.01 $\pm$ 0.00	-4.18	< <b>0.0001</b>	-0.01 $\pm$ 0.00	-2.66	<b>0.008</b>	-0.01 $\pm$ 0.00	-2.39	<b>0.017</b>
<i>Zero-inflation model</i>									
(Intercept)	-0.45 $\pm$ 0.23	-1.93	0.053	0.09 $\pm$ 0.25	0.37	0.711	-0.36 $\pm$ 0.27	-1.37	0.172
<i>Random effects</i>									
$\sigma^2$	0.89			1.44			2.45		
ICC	0.47			0.47			0.59		
Marginal $R^2$ /conditional $R^2$	0.123/0.535			0.094/0.520			0.083/0.621		

Ln-transformed duration (minutes) of each observation was used as an offset term and bin identity as a random effect. Factors in bold type indicate significant predictors

$\sigma^2$  = variance of the random effect 'bin ID'; ICC = Intraclass coefficient of variation

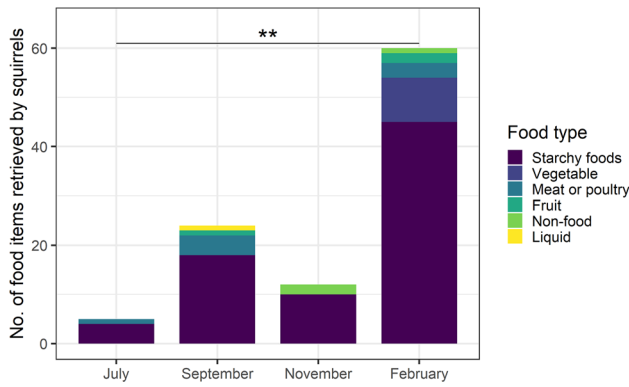
The marginal  $R^2$  considers only the variance of the fixed effects, while the conditional  $R^2$  takes both the fixed and random effects into account

Wilcoxon rank sum test:  $P = 0.006$ ), but there were no further differences between observation periods (September:  $0.48 \pm 1.15$ ; November:  $0.27 \pm 1.08$ ). The majority (76.2%) of retrieved food items were starchy foods (e.g., French fries, bread, pizza, pasta, rice, chips), 8.9% were vegetables (e.g., salad, tomato, cucumber), 7.9% were red meat and poultry (e.g., chicken, bacon), 3.0% were fruit (e.g., banana, grape), 3.0% were non-food items (e.g., paper bag or napkin) and 1.0% was a sugar-sweetened beverage, a soft drink, which the squirrel licked out of a plastic cup. Which food categories squirrels retrieved from bins did not differ between sampling periods (Fisher's Exact Test:  $P = 0.079$ ; Fig. 3).

## Squirrel abundance

The six transects differed in NDVI (0.26–0.87) and NDBI (0.11–0.64; Table 3; Fig. 4). NDVI and NDBI were highly correlated at both the 40 m buffer (Pearson's product-moment correlation:  $t = -64.401$ ,  $df = 22$ ,  $P < 0.0001$ ,  $r = -0.997$ ) and the 90 m buffer ( $t = -80.01$ ,  $df = 22$ ,  $P < 0.0001$ ,  $r = -0.998$ ). We observed a total of 294 squirrels across all transects and sampling periods (Table 3). Average relative squirrel abundance ranged from 0 to 6.85 ind/ha (Table 3). The observation period with the most squirrel sightings was November 2020 with 95 individuals, followed by September 2020 with 87 individuals, July 2020 with 79 squirrels and 33 squirrels in February 2021. The zero-inflated GLMM showed that the number of squirrels observed per time walked differed between transects

ing and the number of eastern gray squirrels (*Sciurus carolinensis*) that went on a trash bin, inside a trash bin and the number of food items they retrieved from a trash bin



**Fig. 3** Number of food items and food types that eastern gray squirrels (*Sciurus carolinensis*) retrieved from trash bins during the four different observation periods. Food types are ordered by total number of observations in descending order (Significant differences between observation periods are illustrated (\* $p \leq 0.05$ ; \*\* $p \leq 0.01$ , \*\*\* $p \leq 0.001$ ))

( $\chi^2 = 64.76$ ,  $df = 5$ ,  $P < 0.0001$ ) and study periods ( $\chi^2 = 55.20$ ,  $df = 3$ ,  $P < 0.0001$ ), whereas ambient temperature ( $\chi^2 = 1.40$ ,  $df = 1$ ,  $P = 0.238$ ) had no influence.

The number of squirrels observed per time walked at the cemetery transect was lower compared to all other transects (C\_R: Estimate  $\pm$  SE:  $3.84 \pm 0.54$ ,  $z = 7.13$ ,  $P < 0.0001$ ; F:  $2.56 \pm 0.52$ ,  $z = 4.88$ ,  $P < 0.0001$ , DT:  $2.16 \pm 0.54$ ,  $z = 4.00$ ,  $P < 0.0001$ ; C\_C:  $2.74 \pm 0.54$ ,  $z = 5.03$ ,  $P < 0.0001$ ; C\_S:  $2.98 \pm 0.52$ ,  $z = 5.68$ ,  $P < 0.0001$ ). The C\_R transect on Duke campus had higher numbers of squirrels observed per time walked than most other transects (F:  $1.28 \pm 0.26$ ,  $z = 4.91$ ,  $P < 0.0001$ ; DT:  $1.68 \pm 0.32$ ,  $z = 5.21$ ,  $P < 0.0001$ ; C\_C:  $1.10 \pm 0.29$ ,  $z = 3.83$ ,  $P < 0.0001$ ; C\_S:  $0.86 \pm 0.21$ ,  $z = 4.16$ ,  $P < 0.0001$ ). There was also a difference between DT and C\_S ( $0.82 \pm 0.29$ ,  $z = 2.83$ ,  $P = 0.005$ ). In February 2021, fewer squirrels were observed per time walked compared to all other periods (September  $1.85 \pm 0.28$ ,  $z = 6.71$ ,  $P < 0.0001$ ; November:  $1.87 \pm 0.26$ ,  $z = 7.11$ ,  $P < 0.001$ ; July:  $1.83 \pm 0.41$ ,  $z = 4.48$ ,  $P < 0.0001$ ; Table 3; Fig. 5).

The interaction between NDBI and study period ( $\chi^2 = 42.02$ ,  $df = 3$ ,  $P < 0.0001$ ; Fig. 6) influenced the number of squirrels observed along a transect. The relationship between the number of squirrels observed and NDBI was

negative in July and September, and positive in November and February (Fig. 6). Ambient temperature ( $\chi^2 = 0.70$ ,  $df = 1$ ,  $P = 0.404$ ) did not influence the number of squirrels observed along a transect.

## Discussion

Human food waste can be an important food subsidy for urban wildlife. Although we know that many species make use of this abundant and readily available resource, limited data are available on the extrinsic factors that influence when animals use these resources and which food items they are feeding on. Such knowledge would offer insights into the effects that human food waste consumption can have on animal behavior and health, and would contribute to our understanding of how human-wildlife coexistence can be improved (Plaza and Lambertucci 2017).

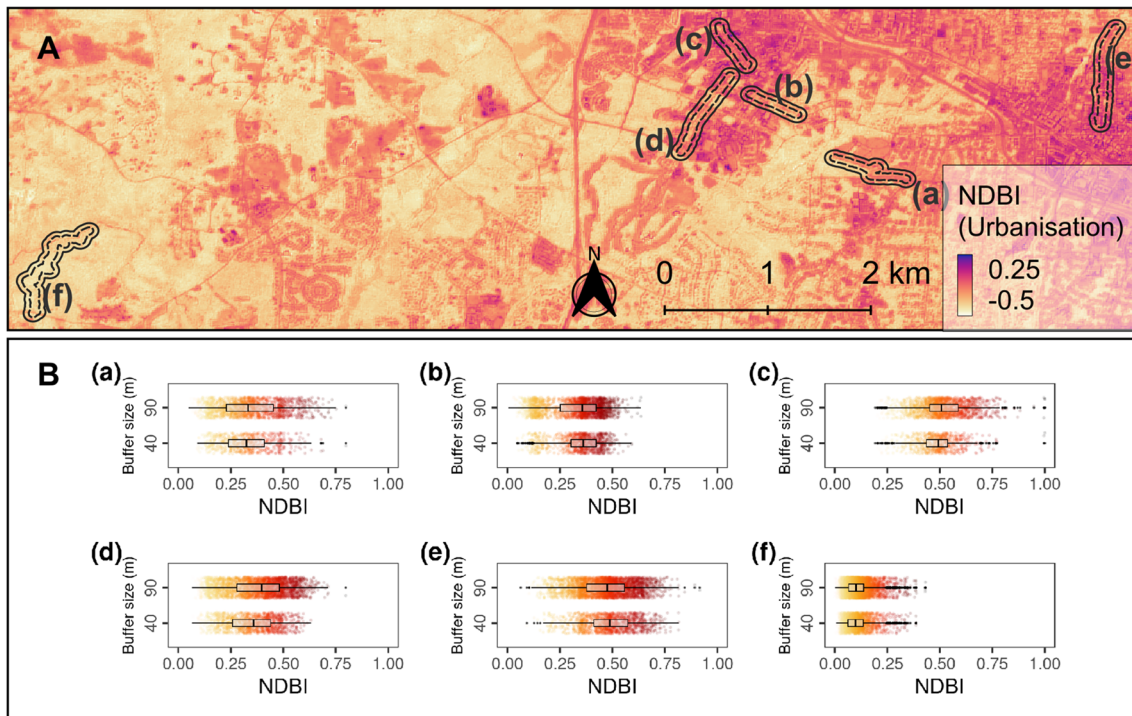
### Trash bin usage

Trash bins were fuller during periods of high human presence and human presence positively influenced how many squirrels went on and inside a bin. Urban squirrels experience a reduced predation pressure and are less wary of humans compared to squirrels from rural habitats (Cooper et al. 2008; Parker and Nilon 2008; Bateman and Fleming 2014; Engel et al. 2020). Decreased wariness may explain why a higher level of disturbance, via high human presence at trash bins, did not have a negative effect on trash bin usage. Our results indicate that ambient temperature and bin filling negatively influence all three types of trash bin usage. When ambient temperatures increased, less squirrels were observed on and inside trash bins and they retrieved less food items. Squirrels are usually less active during periods of the day with high ambient temperatures (Skibieli et al. 2002; Parker et al. 2014), likely explaining the negative relationship between temperature and trash bin usage. Another explanation for this finding might be that squirrels likely have a lower requirement for high caloric food when ambient temperatures are high (i.e., summer), due to decreased energy requirements for thermoregulatory heat production

**Table 3** Overview of differences between transects in NDVI and NDBI (calculated from the 40 m buffer), total number of squirrels observed and the relative squirrel abundance during each study period (values are mean  $\pm$  SD)

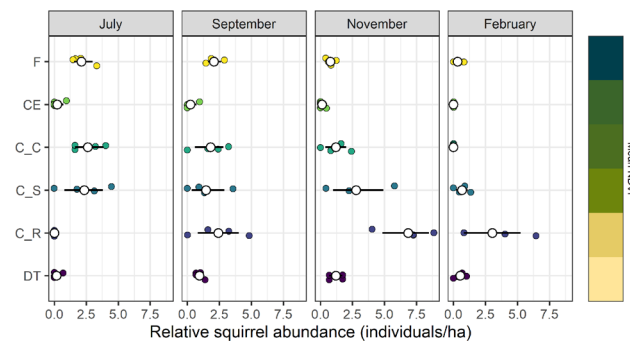
Transect	NDVI	NDBI	Squirrels	Squirrel abundance (individuals/ha)			
				July'20	Sept'20	Nov'20	Feb'21
Duke Forest (F)	0.87	0.11	102	$2.12 \pm 0.83$	$2.07 \pm 0.61$	$0.78 \pm 0.35$	$0.31 \pm 0.36$
Cemetery (CE)	0.58	0.39	5	$0.24 \pm 0.47$	$0.24 \pm 0.47$	$0.12 \pm 0.24$	0
Duke Chapel Drive (C_C)	0.53	0.41	28	$2.62 \pm 1.21$	$1.81 \pm 1.38$	$1.21 \pm 1.04$	0
Duke Science Drive (C_S)	0.45	0.47	65	$2.34 \pm 1.91$	$1.45 \pm 1.52$	$2.79 \pm 2.23$	$0.67 \pm 0.58$
Duke Research Drive (C_R)	0.30	0.62	61	0	$2.42 \pm 2.08$	$6.85 \pm 2.03$	$3.02 \pm 2.74$
Downtown Durham (DT)	0.26	0.64	33	$0.17 \pm 0.34$	$0.95 \pm 0.33$	$1.21 \pm 0.60$	$0.52 \pm 0.45$





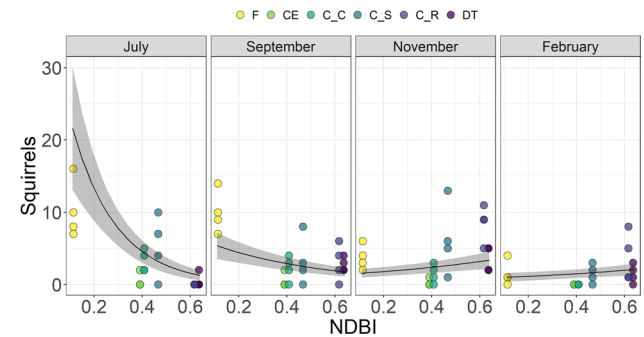
**Fig. 4** (A) Location of the study transects (a–f) in the Durham area. NDBI values are reflected in the coloration, light coloration (yellow) indicates rural areas with a low NDBI and dark coloration (red to purple) indicates urban areas with a high NDBI. The lower panels

show boxplots, with median values as well as 1st and 3rd quartiles, for the 40 m and the 90 m buffer around the transects (a=cemetery; b=C\_C, c=C\_R, d=C\_S, e=Durham downtown, f=Duke Forest)



**Fig. 5** Changes in eastern gray squirrels (*Sciurus carolinensis*) abundance (individuals/ha) from July 2020 to February 2021. Data points indicate squirrel abundance determined during each of the four walks of each transect in each of the four sampling periods. The white circle shows the average value and the bars show the 95% CI. The bar on the right side depicts the mean NDVI of the 6 transects and transects are ordered from the highest NDVI (transect forest) to the one with the lowest index (transect downtown; F=Duke Forest; CE=cemetery; C\_C, C\_S and C\_R=transects on Duke campus; DT=Durham downtown)

to maintain body temperature at high ambient temperatures (Heldmaier et al. 1990). In addition, it is also possible that squirrels consumed less anthropogenic food items at high ambient temperatures because food items, such as red meat,



**Fig. 6** The interaction effect of NDBI, a measure of urbanization, and study period on the number of eastern gray squirrels (*Sciurus carolinensis*) observed along six transects. Model estimates (lines) and confidence bands (shaded areas) for the fitted values based on standard errors computed from the covariance matrix of the fitted regression coefficients are shown. Colors indicate the different transects (F=Duke Forest; CE=cemetery; C\_C, C\_S and C\_R=transects on Duke campus; DT=Durham downtown)

poultry and starchy foods, spoil faster at high temperatures compared to cooler temperatures. One limitation of this study is that we did not examine food composition or directly measure food availability inside trash bins, instead we used trash bin filling as a proxy for food availability. However, trash inside bins did not solely consist of food items, but also

consisted of inedible trash such as cardboard, newspaper, plastic containers and foam packaging. Moreover, very full bins could hinder a squirrel's ability to locate and access food items, potentially explaining the negative relationship between bin filling and all types of trash bin usage.

We found that squirrels consume more anthropogenic food items during the coldest period of our study (here February), likely because natural food availability is lowest and they rely on fat reserves and stored food items in winter (Koprowski 1994; Pereira et al. 2002). Similarly, rooks (*Corvus frugilegus*), grizzly bears (*Ursus arctos*), Malayan sun bears (*Helarctos malayanus*) and wolves (*Canis lupus*) rely more heavily on human food waste when natural food availability is low (Meriggi and Lovarit 1996; Te Wong et al. 2004; Peirce and Van Daele 2006; Olea and Baglione 2008). Foraging and food caching peaks in fall, and they accumulate fat stores in preparation for winter (Koprowski 1994; Spritzer 2002). Thus, it is likely that squirrels spent a large proportion of their time storing food items in November, resulting in less retrieved food items in the late fall. Similar to wildlife that adjusts caloric intake between seasons, people show an increased intake of total calories, especially carbohydrates, in the fall (de Castro 1991) and favor food items they deem high in calories when exposed to winter cues (Folwarczny et al. 2022). Although this finding does not seem to be universal and some studies find no seasonal differences in the intake of energy, food groups and macronutrients in people (Bernstein et al. 2016). Thus, if the eating habitats of trash bin users changed between seasons, it is conceivable that the composition of anthropogenic food items in trash bins also varied between seasons (e.g., higher availability of calorically dense items in fall and winter), likely making bins especially attractive to squirrels in the winter.

Squirrels retrieved a diverse array of food items from trash bins, including starchy foods (e.g., bread, fries, pasta; 76%), vegetables (9%), red meat and poultry (8%), and fruit (3%). Gray squirrels living in forest habitats also have a diverse diet and consume fruit, small vertebrates, bird eggs and hatchlings (Koprowski 1994). In urban habitats, they are also known to raid gardens, bird feeders and composts (Hansen et al. 2020). Therefore, their consumption of meat, fruit and vegetable is not surprising, and other urban mammals are also known to have a more diverse diet compared to rural populations (Murray et al. 2015a). Carbohydrates are an important source of energy (Jéquier 1994) and thus, consumption of calorically dense foods, such as starchy foods, may sustain populations during winter when they rely on stored food and fat reserves. We observed several cases of aggression and chasing between squirrels, where one individual actively defended access to a trash bin against others squirrels (pers. obs.),

indicating that trash bins resemble an important food source for them. Similarly, other species experience high aggression rates or competition at trash bins (Plaza and Lambertucci 2017). One limitation of our study is that we were unable to distinguish between individuals that visited trash bins and consumed anthropogenic food items. Thus, we cannot rule out that individuals visited trash bins repeatedly. Our study provides first insights into the importance of anthropogenic food waste and trash for squirrels. Long-term effects, for example regarding body condition, health and population trends are not well studied (Oro et al. 2013; Plaza and Lambertucci 2017), and should be a focus for future studies. Trash bins and dumpsters could potentially also negatively affect or harm individuals, for example by exposing animals to contact with potentially hazardous items such as plastic (Katlam et al. 2018). We observed squirrels that opened plastic bags and foam packaging to access food items and that licked plastic food wrapping (pers. obs.), a behavior that could result in the ingestion of the packaging and wrapping material. Ingestion of plastic has been reported for several species, but physiological impacts of plastic ingestion, especially for mammals (Plaza and Lambertucci 2017; Puskic et al. 2020) are not well studied.

Preventing wildlife from accessing trash bins, and anthropogenic food and wrapping items inside bins, may be a low-cost and easy to implement conservation measure which could help control the population of gray squirrels for example in the UK and northern Italy, where gray squirrels are invasive and displace the native Eurasian red squirrel (*Sciurus vulgaris*) (Okubo et al. 1989; Gurnell et al. 2004). Restricting access to trash bins could be one way to reduce the success of invasive gray squirrels in urban habitats, especially since they are more terrestrial than red squirrels (Kenward and Holm 1989), and thus may be more likely to descend to trash bins during foraging. Gray squirrels often occur at high population densities (Hein 1997; Engel et al. 2020), but it is currently unclear whether this is caused by the consumption of anthropogenic food resources which then results in increased reproductive success or increased survival rates. In fact, urban gray squirrels show differences in health parameters from rural squirrels which could reflect physiological stress in urban individuals (Schmidt et al. 2022).

### Changes in squirrel abundance

Gray squirrel population densities are often higher in urban habitats compared to rural habitats (Hein 1997; Parker and Nilon 2008; Engel et al. 2020), and anthropogenic food sources have been suggested as the main reason for elevated abundances (Bowers and Breland 1996; Parker and Nilon 2008; Bonnington et al. 2014).

Here we did not determine availability of natural and anthropogenic food items along the transects, but instead determined NDBI as a measure of urbanization and we assumed that more urbanized transects would also offer more anthropogenic food items. Our results show that relative squirrel abundance differed between transects and study periods. Overall, squirrel abundance was lowest at the cemetery (0.00–0.24 squirrels/ha), the transect with the second lowest NDBI value. Only one side of the transect had trees while the other sides consisted of grassland and graves. Gray squirrels are known to avoid open grassy areas (Tounzen et al. 2012), likely explaining low abundances observed at this transect. Similarly, low squirrel abundance (1–9 squirrels/ha) have been reported in cemeteries in St. Louis, Missouri (Engel et al. 2020). Squirrel abundance was also relatively low at the most urban transect, downtown Durham (0.17–1.21 squirrels/ha). In all periods but in November, squirrel abundance in Duke Forest (0.31–2.12 squirrels/ha) was higher than abundances at the downtown Durham transect. The transect in Duke Forest had the densest vegetation, and thus, it is possible that we underestimated abundances compared to the other more open transects. However, population densities around or below 3/ha have previously been reported in forest habitats (Barkalow et al. 1970; Healy and Welsh 1992). Squirrel abundances in the forest habitat were lowest in February, when there was little foliage in the forest and visibility was greatest. We noted the highest squirrel abundances in the transects on Duke campus (0.00–6.85 squirrels/ha), although variation existed between transects and study periods. A previous study reported comparable abundances (4.7 squirrels/ha) at another urban university campus (Hein 1997). Squirrel abundances changed between study periods and changes differed between transects. For example, squirrel abundance decreased throughout the study along the forest and cemetery transects but increased until November in several urban transects and then decreased in February (the period of highest consumption of anthropogenic food items), the period with the lowest ambient temperatures. The changes throughout the study period likely reflect changes in the activity of squirrels which are busy foraging and caching food the fall and are less active in the winter (Koprowski 1994). Trash bins are unevenly distributed in space and resemble clumped food resources which can offer high caloric food items and can attract several squirrels simultaneously (we observed up to 8 squirrels simultaneously at a close distance to a single trash bin). Thus, it may be that in February the squirrels on the urban transects did not evenly distribute in space, but rather showed a clumped distribution pattern, resulting in lower observations along these transects. However, this is rather speculative and

should be tested, for example, using telemetry or GPS loggers fitted on squirrels to track changes in their movements and space use, especially around trash bins.

The relationship between the number of squirrels observed and NDBI was negative in July and September, but positive in November and February. Thus, during the two warmer study periods, more squirrels were observed in less urbanized areas (e.g., Duke Forest) with a low NDBI, whereas during the two colder study periods, more squirrels were observed in the urban areas with a high NDBI. This result suggests that winter conditions may be less challenging in urban areas compared to more rural areas. This may be due, to some extent, to the ‘urban heat island effect’, where air temperatures are higher in urban compared to surrounding areas (Imhoff et al. 2010), allowing animals, especially small bodied species, to remain active for prolonged periods in winter. For example, gray squirrels start foraging earlier in the day in areas with high impervious surface cover (i.e., urban areas) compared to in areas with low impervious surface cover (Larson and Sander 2022), potentially because of warmer ambient temperatures caused by impervious surfaces which would reduce some of the metabolic costs associated with activity at low ambient temperatures. Moreover, anthropogenic food sources are readily available in urban habitats (Oro et al. 2013; Plaza and Lambertucci 2017), and access to these resources has generally been reported to positively affect body condition via increases in body mass (Andrzejewski et al. 1978; Oтали and Gilchrist 2004; Schulte-Hostedde et al. 2018). Thus, urban gray squirrels may be less energy limited during the cold period compared to rural squirrels, allowing them to remain more active during the colder study periods. Some small mammals also show higher winter survival rates in urban habitats compared to natural habitats, likely due to a combination of several factors such as increased ambient temperatures, high availability of anthropogenic food sources and reduced predation rates from natural predators (Andrzejewski et al. 1978; Babińska-Werka et al. 1981; McCleery 2009; Rosatte et al. 2010; Rodewald et al. 2011; Eötvös et al. 2018). Our bin observations showed that indeed, squirrels consumed more anthropogenic food items during the coldest period of our study. Anthropogenic food sources are known to reduce starvation and positively influence abundances and survival of wildlife, particularly during the winter (Brittingham and Temple 1988; Robb et al. 2008; Plaza and Lambertucci 2017; Szala et al. 2020). Alternatively, squirrels in urban habitats may not be able to store sufficient food sources in preparation for winter and therefore, may need to actively search for food throughout winter. However, we did not observe any obviously sick or malnourished squirrels during the study.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s42991-022-00326-3>.

**Acknowledgements** The authors want to thank Nickolas Amato, Hannah Chen, Jerry Fu, Bailey Griffen, Christi Mela, Charles Veronee, Janya Wiley and Ellen Zhang for their support and assistance during data collection.

**Author contributions** Conceptualization: R.R. and H.P.; methodology and resources: R.R. and H.P.; data collection: R.R., G.B, P.R.G., J.J. and C.P.; formal analysis: R.R. and P.R.G.; writing—original draft: R.R.; writing—review and editing: G.B, P.R.G., J.J., C.P. and H.P.; funding acquisition: H.P.

**Funding** This study was funded by the Duke University.

**Data and code availability** The datasets used in formal analysis as part of the current study and R code used in analysis are available as supplementary information. Code for urbanization (NDBI) and vegetation cover (NDVI) around Durham can be found at <https://github.com/pratikunterwegs/bin-squirrels>.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethics approval** All animal use and methods were approved by the Duke University Institutional Animal Care and Use Committee (Protocol #: A057-20-02).

## References

- Andersson MN, Nilsson J, Nilsson JÅ, Isaksson C (2018) Diet and ambient temperature interact to shape plasma fatty acid composition, basal metabolic rate and oxidative stress in great tits. *J Exp Biol* 221:jeb.186759. <https://doi.org/10.1242/jeb.186759>
- Andrzejewski R, Babińska-Werka J, Gliwicz J, Goszczyński J (1978) Synurbanization processes in population of *Apodemus agrarius*. I. Characteristics of populations in an urbanization gradient. *Acta Theriol (Warsz)* 23:341–358. <https://doi.org/10.4098/at.arch.78-24>
- Babińska-Werka J, Gliwicz J, Goszczyński J (1981) Demographic processes in an urban population of the striped field mouse. *Acta Theriol (Warsz)* 26:275–283. <https://doi.org/10.4098/at.arch.81-23>
- Bakken A (1959) Behavior of gray squirrels. In: Proceedings of the annual conference, Southeastern Association of Game and Fish Commissioners, pp 393–406
- Barkalow FS, Hamilton RB, Soots RF (1970) The vital statistics of an unexploited gray squirrel population. *J Mammal* 34:489–500
- Bateman PW, Fleming PA (2014) Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? *J Zool* 294:93–98. <https://doi.org/10.1111/jzo.12156>
- Benson E (2013) The urbanization of the eastern gray squirrel in the United States. *J Am Hist* 100:691–710. <https://doi.org/10.1093/jahist/jat353>
- Bernstein S, Zambell K, Amar MJ et al (2016) Dietary intake patterns are consistent across seasons in a cohort of healthy adults in a metropolitan population. *J Acad Nutr Diet* 116:38–45. <https://doi.org/10.1016/j.jand.2015.08.008>
- Birnie-Gauvin K, Peiman KS, Gallagher AJ et al (2016) Sublethal consequences of urban life for wild vertebrates. *Environ Rev* 24:416–425. <https://doi.org/10.1139/er-2016-0029>
- Bonnington C, Gaston KJ, Evans KL (2014) Squirrels in suburbia: influence of urbanisation on the occurrence and distribution of a common exotic mammal. *Urban Ecosyst* 17:533–546. <https://doi.org/10.1007/s11252-013-0331-2>
- Bowers MA, Breland B (1996) Foraging of gray squirrels on an urban-rural gradient: use of the gud to assess anthropogenic impact. *Ecol Appl* 6:1135–1142. <https://doi.org/10.2307/2269597>
- Brittingham MC, Temple SA (1988) Impacts of supplemental feeding on survival rates of black-capped chickadees. *Ecology* 69:581–589
- Brooks ME, Kristensen K, van Benthem KJ et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400
- Contesse P, Hegglin D, Gloor S et al (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. <https://doi.org/10.1078/1616-5047-00123>
- Cooper CA, Neff AJ, Poon DP, Smith GR (2008) Behavioral responses of eastern gray squirrels in suburban habitats differing in human activity levels. *Northeast Nat* 15:619–625. <https://doi.org/10.1656/1092-6194-15.4.619>
- de Castro JM (1991) Seasonal rhythms of human nutrient intake and meal pattern. *Physiol Behav* 50:243–248. [https://doi.org/10.1016/0031-9384\(91\)90527-U](https://doi.org/10.1016/0031-9384(91)90527-U)
- Doebel JH, McGinnes BS (1974) Home range and activity of a gray squirrel population. *J Wildl Manage* 38:860–867
- Engel LD, Carlen EJ, Losos JB, Winchell KM (2020) Eastern gray squirrels (*Sciurus carolinensis*) differ in abundance and response to humans across urban habitats of St. Louis Urban Nat 33:1–16
- Eötvös CB, Magura T, Lövei GL (2018) A meta-analysis indicates reduced predation pressure with increasing urbanization. *Landscape Urban Plan* 180:54–59. <https://doi.org/10.1016/j.landurbplan.2018.08.010>
- Fidino AM, Gallo T, Lehrer EW et al (2020) Landscape-scale differences among cities alter common species' responses to urbanization. *Ecol Appl* 31:e02253. <https://doi.org/10.1002/eap.2253>
- Folwarczny M, Otterbring T, Sigurdsson V, Gasiorska A (2022) Seasonal cues to food scarcity and calorie cravings: winter cues elicit preferences for energy-dense foods. *Food Qual Prefer* 96:104379
- Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. Sage Publications, Thousand Oaks
- Gorelick N, Hancher M, Dixon M et al (2017) Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sens Environ* 202:18–27
- Grimm NB, Faeth SH, Golubiewski NE et al (2008) Global change and the ecology of cities. *Science* 319:756–760. <https://doi.org/10.1126/science.1150195>
- Grimmond S (2007) Urbanization and global environmental change: local effects of urban warming. *Geogr J* 173:83–88. [https://doi.org/10.1111/j.1475-4959.2007.232\\_3.x](https://doi.org/10.1111/j.1475-4959.2007.232_3.x)
- Gurnell J, Wauters LA, Lurz PWW, Tosi G (2004) Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. *J Anim Ecol* 73:26–35. <https://doi.org/10.1111/j.1365-2656.2004.00791.x>
- Hansen CP, Parsons AW, Kays R, Millsbaugh JJ (2020) Does use of backyard resources explain the abundance of urban wildlife? *Front Ecol Evol* 8:570771. <https://doi.org/10.3389/fevo.2020.570771>
- Hartig F (2020) DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.3.0
- Healy WM, Welsh CJE (1992) Evaluating line transects to monitor gray squirrel populations. *Wildl Soc Bull* 20:83–90

- Hein EW (1997) Demonstration of line transect methodologies to estimate urban gray squirrel density. *Environ Manage* 21:943–947. <https://doi.org/10.1007/s002679900078>
- Heldmaier G, Klaus S, Wiesinger H (1990) Seasonal adaptation of thermoregulatory heat production in small mammals. Thermoreception and temperature regulation. Springer, Berlin, pp 235–243
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70
- Imhoff ML, Zhang P, Wolfe RE, Bounoua L (2010) Remote sensing of the urban heat island effect across biomes in the continental USA. *Remote Sens Environ* 114:504–513. <https://doi.org/10.1016/j.rse.2009.10.008>
- Jéquier E (1994) Carbohydrates as a source of energy. *Am J Clin Nutr* 59:682S–685S. <https://doi.org/10.1093/ajcn/59.3.682S>
- Katlam G, Prasad S, Aggarwal M, Kumar R (2018) Trash on the menu: patterns of animal visitation and foraging behaviour at garbage dumps. *Curr Sci* 115:2322–2326. <https://doi.org/10.18520/cs/v115/i12/2322-2326>
- Kenward RE, Holm JL (1989) What future for British red squirrels? *Biol J Linn Soc* 38:83–89
- Knee C (1983) Squirrel energetics. *Mamm Rev* 13:113–122. <https://doi.org/10.1111/j.1365-2907.1983.tb00272.x>
- Koprowski J (1994) *Sciurus carolinensis*. *Mamm Species* 480:1–9
- Koprowski JL, Munroe KE, Edelman AJ (2016) Gray not grey: the ecology of *Sciurus carolinensis* in their native range in North America. In: Craig S, Lurz P, Gurnell J (eds) Grey squirrels: ecology and management of an invasive species in Europe. European Squirrel Initiative, pp 1–17
- Larson RN, Sander HA (2022) Seasonal activity patterns of sympatric eastern gray squirrels (*Sciurus carolinensis*) and fox squirrels (*Sciurus niger*) in a Midwestern metropolitan region. *Urban Ecosyst* 25:1527–1539. <https://doi.org/10.1007/s11252-022-01245-4>
- Lenzi J, González-Bergonzoni I, Machín E et al (2019) The impact of anthropogenic food subsidies on a generalist seabird during nestling growth. *Sci Total Environ* 687:546–553. <https://doi.org/10.1016/j.scitotenv.2019.05.485>
- McCleery RA (2009) Reproduction, juvenile survival and retention in an urban fox squirrel population. *Urban Ecosyst* 12:177–184. <https://doi.org/10.1007/s11252-008-0074-7>
- McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biol Conserv* 127:247–260. <https://doi.org/10.1016/j.biocon.2005.09.005>
- McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst* 11:161–176. <https://doi.org/10.1007/s11252-007-0045-4>
- Meriggi A, Lovarit S (1996) A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? *J Appl Ecol* 33:1561–1571
- Moller H (1983) Foods and foraging behaviour of red (*Sciurus vulgaris*) and grey (*Sciurus carolinensis*) squirrels. *Mamm Rev* 13:81–98. <https://doi.org/10.1111/j.1365-2907.1983.tb00270.x>
- Murray M, Cembrowski A, Latham ADM et al (2015a) Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human-wildlife conflict. *Ecography (cop)* 38:1235–1242. <https://doi.org/10.1111/ecog.01128>
- Murray M, Edwards MA, Abercrombie B (2015b) Poor health is associated with use of anthropogenic resources in an urban carnivore. *Proc R Soc B* 282:20150009. <https://doi.org/10.1098/rspb.2015.0009>
- Murray M, Sánchez CA, Becker DJ et al (2019) City sicker? A meta-analysis of wildlife health and urbanization. *Front Ecol Environ* 17:575–583. <https://doi.org/10.1002/fee.2126>
- Okubo A, Maini PK, Williamson MH, Murray JD (1989) On the spatial spread of the grey squirrel in Britain. *Proc R Soc B* 238:113–125
- Olea PP, Baglione V (2008) Population trends of Rooks *Corvus frugilegus* in Spain and the importance of refuse tips. *Ibis (Lond 1859)* 150:98–109. <https://doi.org/10.1111/j.1474-919X.2007.00751.x>
- Ordeñana MA, Crooks KR, Boydston EE et al (2010) Effects of urbanization on carnivore species distribution and richness. *J Mammal* 91:1322–1331. <https://doi.org/10.1644/09-MAMM-A-312.1>
- Oro D, Genovart M, Tavecchia G et al (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecol Lett* 16:1501–1514. <https://doi.org/10.1111/ele.12187>
- Otali E, Gilchrist JS (2004) The effects of refuse feeding on body condition, reproduction, and survival of banded mongooses. *J Mammal* 85:491–497. <https://doi.org/10.1644/BRG-021>
- Parker TS, Nilon CH (2008) Gray squirrel density, habitat suitability, and behavior in urban parks. *Urban Ecosyst* 11:243–255. <https://doi.org/10.1007/s11252-008-0060-0>
- Parker TS, Gonzales SK, Nilon CH (2014) Seasonal comparisons of daily activity budgets of gray squirrels (*Sciurus carolinensis*) in urban areas. *Urban Ecosyst* 17:969–978. <https://doi.org/10.1007/s11252-014-0371-2>
- Peirce KN, Van Daele LJ (2006) Use of a garbage dump by brown bears in Dillingham, Alaska. *Ursus* 17:165–177. [https://doi.org/10.2192/1537-6176\(2006\)17\[165:UOAGDB\]2.0.CO;2](https://doi.org/10.2192/1537-6176(2006)17[165:UOAGDB]2.0.CO;2)
- Pereira ME, Aines J, Scheckter JL (2002) Tactics of heterothermy in eastern gray squirrels (*Sciurus carolinensis*). *J Mammal* 83:467–477. [https://doi.org/10.1644/1545-1542\(2002\)083%3c0467:TOHIEG%3e2.0.CO;2](https://doi.org/10.1644/1545-1542(2002)083%3c0467:TOHIEG%3e2.0.CO;2)
- Pettorelli N (2013) The normalized difference vegetation index. Oxford University Press, Oxford
- Plaza PI, Lambertucci SA (2017) How are garbage dumps impacting vertebrate demography, health, and conservation? *Glob Ecol Conserv* 12:9–20. <https://doi.org/10.1016/j.gecco.2017.08.002>
- Puskic PS, Lavers JL, Bond AL (2020) A critical review of harm associated with plastic ingestion on vertebrates. *Sci Total Environ* 743:140666. <https://doi.org/10.1016/j.scitotenv.2020.140666>
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Robb GN, McDonald RA, Chamberlain DE, Bearhop S (2008) Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front Ecol Environ* 6:476–484. <https://doi.org/10.1890/060152>
- Rodewald AD, Kearns LJ, Shustack DP (2011) Anthropogenic resource subsidies decouple predator–prey relationships. *Ecol Appl* 21:936–943
- Rosatte R, Sobey K, Dragoo JW, Gehrt SD (2010) Striped skunks and allies (*Mephitis* spp.). In: Gehrt SD, Riley SPD, Cypher BL (eds) Urban carnivores. The John Hopkins University Press, Baltimore, pp 99–106
- Schmidt C, Treberg JR, Kinnunen RP, Garroway CJ (2022) Serum biochemistry suggests a physiological response to environmental stress in a native urban eastern gray squirrel (*Sciurus carolinensis*) population. *Can Field-Nat* 136:20–29
- Schulte-Hostedde AI, Mazal Z, Jardine CM, Gagnon J (2018) Enhanced access to anthropogenic food waste is related to hyperglycemia in raccoons (*Procyon lotor*). *Conserv Physiol* 6:1–6. <https://doi.org/10.1093/conphys/coy026>
- Skibieli A, Superka B, Swan C (2002) Is squirrel foraging activity associated with temperature? *J Ecol Res* 4:5–8
- Spritzer MD (2002) Diet, microhabitat use and seasonal activity patterns of gray squirrels (*Sciurus carolinensis*) in hammock and upland pine forest. *Am Midl Nat* 148:271–281. [https://doi.org/10.1674/0003-0031\(2002\)148\[0271:DMUSAJ\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2002)148[0271:DMUSAJ]2.0.CO;2)
- Szala K, Dylewski Ł, Tobolka M (2020) Winter habitat selection of Corvids in an urban ecosystem. *Urban Ecosyst* 23:483–493. <https://doi.org/10.1007/s11252-020-00942-2>
- Te Wong S, Servheen CW, Ambu L (2004) Home range, movement and activity patterns, and bedding sites of Malayan sun bears

- Helarctos malayanus* in the Rainforest of Borneo. Biol Conserv 119:169–181. <https://doi.org/10.1016/j.biocon.2003.10.029>
- Thompson DC (1977) Diurnal and seasonal activity of the grey squirrel (*Sciurus carolinensis*). Can J Zool 55:1185–1189. <https://doi.org/10.1139/z77-153>
- Tounzen MR, Epperson D, Taulman JF (2012) Home range and habitat selection of eastern gray squirrels (*Sciurus carolinensis*) in a small urban hardwood forest. Trans Kansas Acad Sci 115:89–101. <https://doi.org/10.1660/062.115.0301>
- van der Merwe M, Brown JS, Jackson WM (2005) The coexistence of fox (*Sciurus niger*) and gray (*S. caroliniensis*) squirrels in the Chicago metropolitan area. Urban Ecosyst 8:335–347
- Zha Y, Gao J, Ni S (2003) Use of normalized difference built-up index in automatically mapping urban areas from TM imagery. Int J

Remote Sens 24:583–594. <https://doi.org/10.1080/01431160304987>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.