



The effects of red fox scent on winter activity patterns of suburban wildlife: evaluating predator-prey interactions and the importance of groundhog burrows in promoting biodiversity

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Abstract

During winter, prey species in suburban areas of the northeastern United States must consider trade-offs in maximizing survival while they are simultaneously constrained by predators and climatic conditions associated with winter such as snow and low temperatures. Many mammalian prey mitigate the physiological stress from the cold by taking refuge in burrows. Some have also developed olfactory sensitivity to predator scent cues as they attempt to avoid predation in the landscape of fear and co-evolutionary arms race between predators and prey. The Eastern cottontail (*Sylvilagus floridanus*) is one of these species that both uses burrows in winter and is sensitive to scents. However, despite the importance of cottontails in the diet of Red foxes (*Vulpes vulpes*), one of their major predators, little is known about scent cues that cottontails use to detect foxes. Eastern cottontails and other suburban wildlife that occupied burrows dug by Groundhogs near Ithaca, New York, USA were exposed to scent wicks treated with Red fox urine during the winter of 2017–2018 to determine if the frequency of burrow use would decrease because of a perceived heightened risk of predation. We observed no response to the predator odor by cottontails and the other burrow-utilizing species. This lack of a behavioral response by prey may be due to the attenuation of fear in suburban environments. A surprising variety of mammalian and avian taxa ($n = 22$) were recorded at burrows, including Striped skunks, mice, Domestic cats, Virginia opossums, Bobcats, White-tailed deer, Weasels, a Coyote, and a Gray fox. Surprisingly we did not observe a single Red fox, for whom intraspecific scent cues are also important. We also documented daily patterns of activity around burrows of the five most commonly observed taxa. Our investigation reveals that Groundhogs are notable ecosystem engineers whose burrows function as important landscape features and local hotspots of biodiversity during the winter in a suburban ecosystem.

Keywords Behavioral ecology · Predator-prey · Landscape ecology · Landscape of fear · Sensory ecology · Ecosystem engineering · Olfaction · Winter · Red fox · Carnivore · Burrows

Introduction

Prey species are faced with many constraints as they attempt to maximize survival and reproduction. In temperate northeastern North America, seasonal changes associated with winter are one of these constraints. Winter temperatures involve sustained periods below freezing (Campbell et al. 2005), imposing significant stress on

the homeothermic physiological balance of endothermic mammals. Snowfall also obscures vegetation, restricting herbivore diets. To cope with these physical stressors, some organisms go into a state of dormancy to reduce metabolic energy usage (Fishman and Lyman 1961; Lyman and Blinks 1959; Lyman and Chatfield 1955; Patil et al. 2013; Watts and Jonkel 1988; Yacoe 1983). However, many common mammalian prey species do not hibernate or become dormant including the White-tailed deer (*Odocoileus virginianus*) (Ozoga and Harger 1966), Eastern gray squirrel (*Sciurus carolinensis*) (Brown and Yeager 1945; Lyman and Blinks 1959), and Eastern cottontail (*Sylvilagus floridanus*), which remain active throughout the winter (Chapman and Litvaitis 2003). These species continue foraging, or otherwise draw from hoarded food caches as they actively contend with the constraints imposed by climate and other stressors.

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One way these species are able to cope with the snow and freezing temperatures is to find shelter in spaces that are shielded from the elements. Snow itself has insulating properties that allow it to function as a temporary refuge (Colbeck 1983; Gouttevin et al. 2012; Palm and Tveitereid 1979; Pomeroy and Brun 2001), as in the case of Ruffed Grouse (*Bonasa umbellus*) snow roosting (Blanchette et al. 2007; Thompson and Fritzell 1988; Whitaker and Stauffer 2003) and Meadow vole (*Microtus pennsylvanicus*) snow tunneling (Madison et al. 1984). However, in areas with less snowfall or short-lived snow, less ephemeral refuges are preferred. Favorite choices for many mammals in northeastern North America are previously-constructed Groundhog/Woodchuck (*Marmota monax*) burrows and holes near the foundations of human-made structures. Eastern cottontails are among the species that use these burrows (Godin 1977; Linduska 1947; Nelson 1982; Swihart and Picone 1995). Factors that may determine a preferred burrow for cottontails or other animals during winter might include the habitat and cover type around burrows (Beule and Studholme 1942; Bond et al. 2002; Swihart and Yahner 1982), the availability of foraging sites nearby (Abu Baker et al. 2015), the location of the burrow in relation to local predator density (Glebskiy et al. 2018), or the thermoregulatory and insulating properties of the burrow (Buffenstein 1984), among others. As Eastern cottontails are the most widely distributed species in the genus *Sylvilagus*, occupying diverse habitats from fields to forests, from Canada through northern South America (Chapman et al. 1980), burrow use is not likely a localized phenomenon, especially in those parts of their ranges that are sympatric with burrow-digging commensal species like Groundhogs. In fact, burrow use by rabbits like the European rabbit (*Oryctolagus cuniculus*) (Kolb 1985, 1994), Pygmy rabbit (*Brachylagus idahoensis*) (Wilson et al. 2012), and even convergent forms like the Springhare (*Pedetes capensis*) (Butynski and Mattingly 1979) occurs all across the planet.

Burrows are important ecological landscape features for many species in a variety of biomes, from desert owls (Estabrook 1999) and grassland toads (Jansen et al. 2001), to coastal crabs (Aspey 1978) and savannah mongooses (Waterman and Roth 2007). Groundhogs and other ground squirrels use them to escape predators, rear young, and as hibernation chambers during the winter (Lehrer and Schooley 2010; Lehrer et al. 2011; Patil et al. 2013). Burrows are not just important for the burrow-digger, but for a variety of other commensal species as well. For example, burrows constructed by Gopher tortoises (*Gopherus polyphemus*) may host over 300 commensal species (Alexy et al. 2003; Kinlaw and Grasmueck 2012; McHugh et al. 2019; Potash et al. 2020; Vaughan 1961), and over 100 species of vertebrates have been observed on the colonies of burrowing Black-tailed prairie dogs (Witmer et al. 2006). Burrows dug by marmots are even reported to be important

to the ecology of foxes specifically (Murdoch et al. 2009). Therefore burrow diggers like Gopher tortoises, Black-tailed prairie dogs, and Groundhogs may act as important keystone ecosystem engineers for a variety of species in the ecosystems in which they are present, and may be underappreciated for their promotion of biodiversity.

Because mammalian prey species often remain active throughout the winter, many North American predators are similarly active such as Red foxes (*Vulpes vulpes*) (Ables 1969), Gray foxes (*Urocyon cinereoargenteus*) (Harrison 1997), Wolves (*Canis lupus*) (Johnson et al. 2017), Coyotes (*Canis latrans*) (Gese and Grothe 1995; Neale and Sacks 2001; Ozoga and Harger 1966), American martens (*Martes americana*) (Drew and Bissonette 1997), Fishers (*Pekania pennanti*) (Leonard 1981), and Bobcats (*Lynx rufus*) (Neale and Sacks 2001). The presence of predators is an added challenge to the survival of prey species in winter, which must now consider tradeoffs in foraging due to the constraints of both the physical environment and predation pressure. There is considerable interest in understanding the strategies and decision-making processes that prey species use to maximize foraging and minimize multiple risks to their survival, especially by predation (Brown and Kotler 2004; Hilton et al. 1999; Hughes and Ward 1993; Lima 1998; Lima and Dill 1990; Lima et al. 1985; Smith et al. 1997; Villén-Pérez et al. 2013). The use of burrows by prey species to escape both predators (Wilson et al. 2012) and winter climatic conditions has been insufficiently studied in this context. Being able to tease apart when and why prey species use burrows is valuable for understanding their behavioral ecology.

One way to investigate this problem is to split the question into its component pieces, and look directly at how prey species respond specifically just to predators. In the co-evolutionary arms race between predators and prey, as predators increase their efficiency of capturing prey, prey respond by increasing their ability to detect and discriminate among predators (Atkins et al. 2016), as in the case of the Red Queen effect (Dieckmann et al. 1995; Marrow et al. 1992; Schaffer and Rosenzweig 1978; Van Valen 1973). By detecting cues from predators, prey can change their behavior to avoid capture. This manifests itself in many prey species through an anti-predator fear response to fight, flee, or freeze in place (Apfelbach et al. 2005; Brown and Kotler 2004; Brown et al. 1999; Lingle and Pellis 2002; Monclús et al. 2009). Many important mammalian fear-inducing cues are olfactory (Sullivan et al. 2015), sensed from predator odors. It has been shown that these scent cues can powerfully affect the behavior of prey in a myriad of predator-prey systems (Apfelbach et al. 2015; Lindgren et al. 1995; Nielsen et al. 2015; Osada et al. 2014; Rosen et al. 2015; Sullivan 1986). Predators may induce fear responses in a variety of prey species, which may be an indicator of how importantly integrated they have become in an ecological community, as fear responses to novel predators

are slow to evolve (Atkins et al. 2016). One such predator, the Red fox, is known to induce fear responses in mice (*Apodemus sylvaticus*, *Peromyscus leucopus*, and *P. polionotus*), rats (*Rattus norvegicus*), voles (*Clethrionomys glareolus* and *Microtus agrestis*), shrews (*Sorex* spp.), Fox squirrels (*Sciurus niger*), and Snowshoe hares (*Lepus americanus*) (Dickman and Doncaster 1984; Fanson 2010; Jędrzejewski et al. 1993; Laska et al. 2005; Lindgren et al. 1995; Navarro-Castilla and Barja 2014a, b; Orrock et al. 2004; Sullivan and Crump 1986; Takahashi et al. 2005; Thorson et al. 1998). It has also been reported that “the most important prey for Red foxes in the Eastern US are cottontails (*Sylvilagus* spp.)” (Frey 2013), and that rabbits are of particular importance to foxes during the winter months (Cook and Hamilton 1944). The dietary importance of Eastern cottontails to Red foxes in the northeastern United States continues to be confirmed (Peterson et al. 2020), and is further demonstrated by the fact that introducing cottontails to a novel area (such as Italy) causes Red foxes to immediately specialize on them (Balestrieri et al. 2005).

Eastern cottontails and other rabbits are sensitive and responsive to a variety of olfactory cues (Baldwin et al. 2006; Mella et al. 2016), including an attraction both to those of other rabbits (Young and Henke 1999) and surprisingly to those of coyotes (Drew et al. 1988), and an aversion to many commercial wildlife repellents (Mason et al. 1999; Williams and Short 2014). This may be explained by the fact that predation pressure on cottontails is intense (Boland and Litvaitis 2008), including during the winter. However, despite the importance of cottontails to the diet of Red foxes, and the prevalence of research on how predator scents induce fear responses in prey, no study exists to our knowledge that demonstrates an olfactory relationship between the Red fox and the Eastern cottontail. Consequently, we examined the response of Eastern cottontails to Red fox urine at burrows in winter, and through our experimental design were also able to observe the behavioral dynamics of many other species of wildlife that used these same burrows.

We developed this project with three main goals. The first was to experimentally test the hypothesis that Eastern cottontails exhibit a fear response to the scent of Red foxes. We hypothesized that Eastern cottontail rabbits would display such a response. The second goal was to experimentally determine whether this fear response, if it existed, could cause the frequency of burrow use to decrease despite low winter temperatures and snowfall. We hypothesized if there was at first a fear response by Eastern cottontail rabbits, then the frequency would decrease over time. The third goal was to document the diversity and behavioral ecology of species that occur in and around burrows in a suburban region of northeastern North America in winter. We hypothesized that Eastern cottontail rabbits would be active at burrows, but there

might be activity by other species there as well, such as Red foxes.

Methods

Field design

We employed a dual observational-experimental design using camera traps at burrow entrances around old buildings near Ithaca, New York, during the winter of 2017–2018. For the observational part of this investigation, camera traps merely recorded the activity of wildlife at the burrows. For the experimental portion, Red fox urine was applied to wicking devices at burrow entrances over a two-week period, and camera traps functioned to document changes (or lack thereof) in patterns of animal activity at the burrows before and after treatment, between control and treatment burrows.

Beginning in late November 2017, we opportunistically identified burrows most likely excavated by Groundhogs around old abandoned and/or isolated buildings on Cornell University-owned lands near Ithaca, New York. Camera traps were deployed facing these burrows either screwed onto a tree or on a wooden stake between 30 and 60 cm above ground, and at a distance of 120 to 180 cm from each burrow. Human disturbance at these sites was minimal to none because they were on private university property. Burrows were located at several derelict buildings covered with brush, or were at buildings otherwise not actively used during winter. For sites that were normally operational during other seasons (e.g., the Cornell EEB Research Pond facility), the building managers were made aware of the cameras and left them alone. However, we posted clearly visible warnings to stay away on all camera stakes in the event someone would happen upon them. At sites where multiple burrows were identified, only burrow entrances that were at least 3 m apart were monitored to increase the likelihood of each being independent and unconnected to other entrances underground. The camera traps used were Cuddeback Model C1 or Model 11339 (De Pere, WI), and were set to take 3 consecutive photo bursts for both day and night, with a “fast as possible” (less than one second) setting for delay time between bursts. A few days after initial set up, cameras were checked to see if any photos had been taken of Eastern cottontails. If not, the camera was removed and placed at another identified burrow. In this way, 21 separate burrows occupied by Eastern cottontails were used over the course of this project, at 6 different sites (Figs. 1 and 2). Characteristics of each burrow were also documented, which included the GPS coordinates of each burrow and a site description. All work was approved by Cornell University Institutional Animal Care and Use Committee, protocol number 2017–0123.

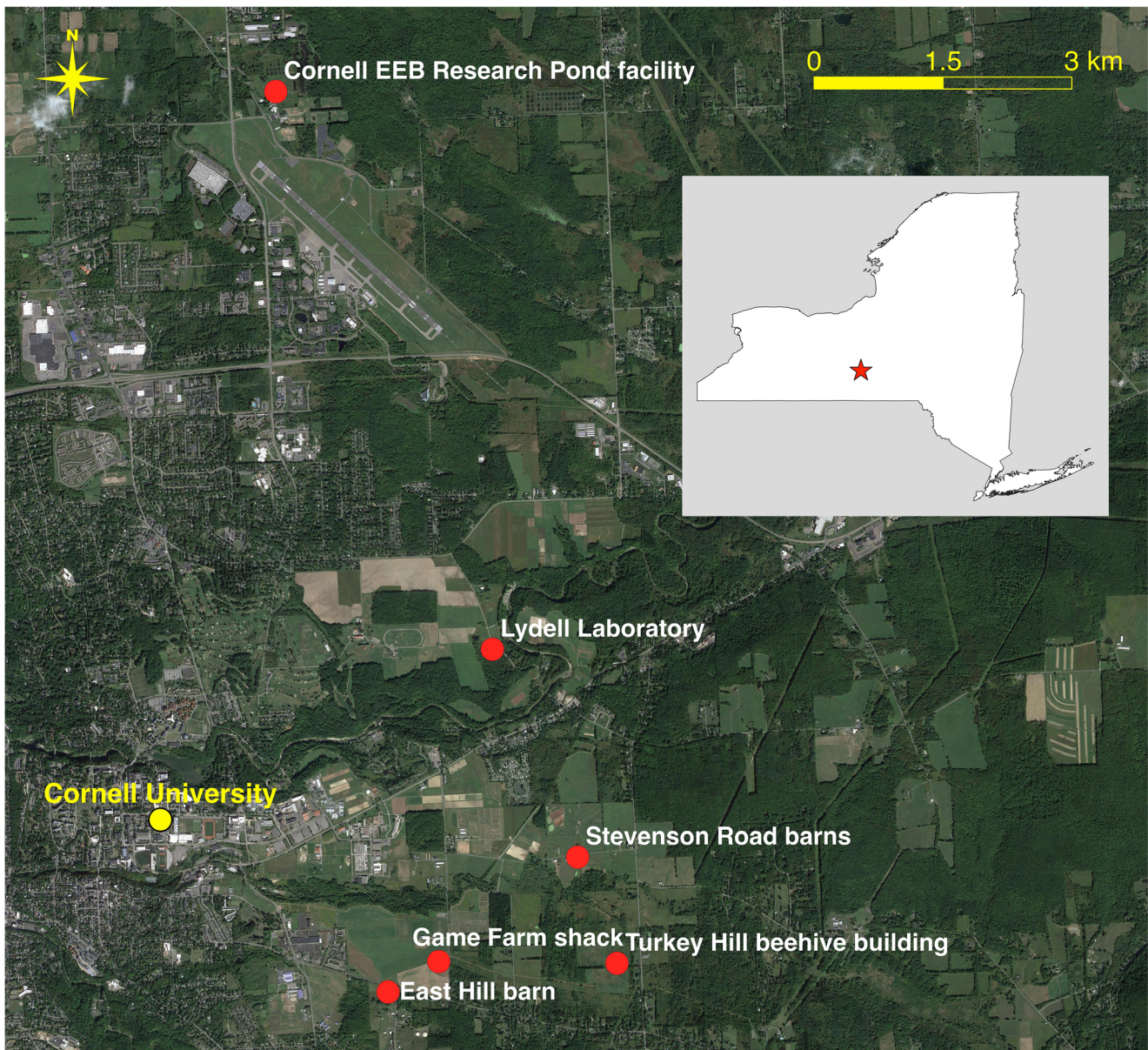


Fig. 1 The locations of the 6 opportunistically-chosen study sites around Ithaca, NY, mapped with QGIS (QGIS Development Team 2020)

Field site descriptions

The six sites used were: (1) East Hill barn, (2) Game Farm shack, (3) Turkey Hill beehive building, (4) Lydell Laboratory, (5) Stevenson Road barns, and the (6) Cornell Ecology and Evolutionary Biology (EEB) Research Pond facility (Fig. 1). The locations of Groundhog burrows at each of these sites (examples can be seen in Fig. 3) were field-mapped and marked.

(1) *East Hill barn* (two burrows): This site was characterized by an old abandoned farm animal barn surrounded by a broken concrete patio. Sparse vegetation, weeds, and thorny brambles had sprouted between the cracks of the concrete or around the base of the building. (2) *Game Farm shack* (three

burrows): This site was characterized by an old wooden shack set in an empty field along Game Farm Road. Old slabs of broken concrete were scattered about the shack, remnants of a small patio, but grass, weeds, bushes, and brambles had also grown up all around them. (3) *Turkey Hill beehive building* (six burrows): This site was characterized by an old metal building about 100 m west of Turkey Hill Road. Beehives were active along one side of this building during the previous growing season, but were absent during winter. The building itself was surrounded by tall, thick grass, shorter grass, small coniferous trees, and old metal equipment debris. (4) *Lydell Laboratory* (three burrows): This site was characterized by an old wooden barn-like building in a field a few meters away from an actively maintained and used concrete research

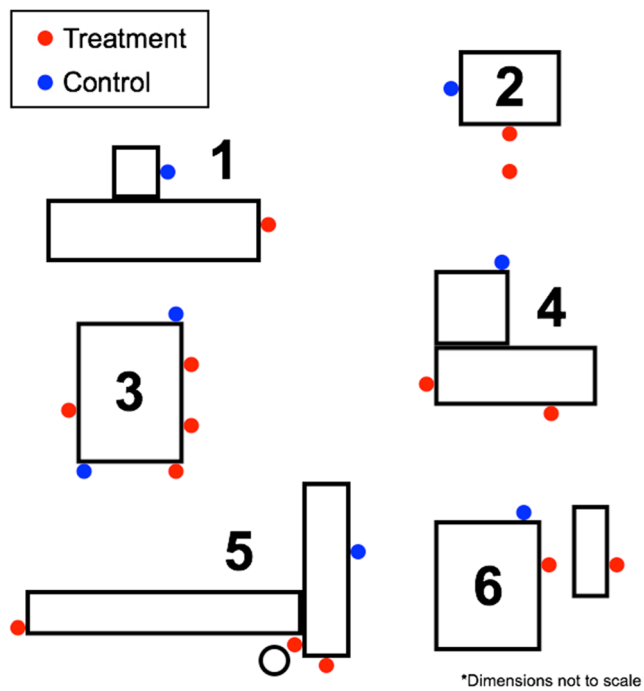


Fig. 2 Relative positioning of the treatment and control burrows around the six sites and their associated buildings. (1) East Hill barn, (2) Game Farm shack, (3) Turkey Hill beehive building, (4) Lydell Laboratory, (5) Stevenson Road barns, and (6) Cornell Ecology and Evolutionary Biology (EEB) Research Pond facility. See Fig. 1 for site locations

building and greenhouse. One side was adjacent to a large brambly hedge, and the other sides were along a neatly mown lawn without any cover. (5) *Stevenson Road barns* (four burrows): This site was characterized by a series of old barns and an empty corn silo along Stevenson Road that are still somewhat maintained by staff who tend to horses that are kept behind the barns. However, many of these buildings were empty. Burrows were along broken concrete walkways or dug into the soil along the building foundation with little overhanging cover. (6) *Cornell EEB Research Pond facility* (three burrows): This site was characterized by a large metal garage-like building and a smaller temporary building nearby, both of which were still maintained by staff. The sides of the buildings were mostly exposed, with only a few short brambles and weeds remaining.

Red fox urine repellent trial design

The camera-trap data for the 8-week field season were collected in two phases. For the first 6 weeks, cameras passively recorded all wildlife activity at burrows. However, during the final 2 weeks (1 to 15 January 2018), each of the 21 identified burrows was treated either with a Red fox urine- or water-dipped (control) wick. This was accomplished using Quik-wicks brand scent dispensers (Wildlife Research Center, Inc., Ramsey, MN), which are small plastic tubes that hang upside down as a felt tip dipped in liquid hangs out from the

bottom of the tubes. The wicks were spray-painted a dark matte brown to make them more inconspicuous than their original neon-orange color. These wicks were hung from the loops of green 45-cm metal plant props with the help of thin galvanized steel wire and duct tape. The plant props with the hanging wicks were then placed within 30 cm of the burrow entrances for each of the 21 identified burrows, and the felt wick tips were dipped in either Red fox urine, which was purchased in 473 mL bottles from the Trap Shack Company (Arcadia, WI), or bottles of Poland Spring water with no added minerals. A total of 14 burrows received Red fox urine treatment and 7 burrows received the water control, chosen arbitrarily (Fig. 2). Each of the 6 sites had at least one burrow treated with the control, and at least one burrow treated with urine, to reduce site-specific interactions. The control and treatment burrows were spaced far apart at each site to try and eliminate potential drifting of the urine odor to the control burrows.

Because temperatures during the experiment frequently fell below freezing, the liquid-treated wicks often froze. Therefore, wicks were re-dipped in their respective urine or water treatment every three days (January 1, 4, 7, 10, and 13). Snow also piled up on the burrows and in front of the cameras during this 2-week period. Therefore, on the days that the wicks were being treated, snow was brushed off in the path in front of the camera to the burrow entrance, and off the camera itself, so as not to obscure each camera's ability to sense movement and take photos. However despite this maintenance, snowfall may occasionally have influenced the visibility of burrows. Cameras were checked once per week for battery levels and to replace SD cards.

Data selection criteria

After the field component of this project concluded, all photos were organized into a single database and examined. Of the 6466 total photos, those not containing animals ($n = 4732$) were deleted. For photos that contained animals, it was possible that the camera traps had taken multiple pictures of the same animal(s) within a short period of time because of the 3-picture burst setting. We therefore decided to concatenate photos into events, rather than document every single photo collected, to reduce overrepresentation of activity at burrows. An event was defined as all pictures taken within 2 min of each other, a similar interval to that of Jacques et al. (2016), and any animals documented within that interval would only be counted once. This ultimately led to a total of 1734 photo events. However, independence may have been violated between consecutive events because the 2-min interval cut-off was decided arbitrarily, and individual animals were not marked for identification.

Because cameras were set up at burrows on different dates throughout November and December 2017 while

Fig. 3 Examples of burrows at each of the 6 sites. TL Two mice at East Hill barn. TR Striped skunk at Game Farm shack. CL Gray fox at Turkey Hill beehive building. CR Eastern cottontail at Lydell laboratory. BL Virginia opossum at Stevenson Road barns. BR Eastern cottontail at the Cornell EEB Research Pond facility



determining cottontail activity, it was not possible to compare activity at each burrow from day-to-day. Instead, burrow activity was summed over periods of one week, and weeks were compared to each other. All data from the few days before the start of the first week on 20 November 2017 at 17:01, and the day after the last consecutive week on 15 January 2018 at 17:00 were eliminated so that each study week had exactly 7 operating days for ease of comparison across weeks and cameras. This resulted in 8 total weeks that were used for analysis of the experimental treatment (Table 1). The study cameras at all 21 active burrows had at least 4 total weeks of camera monitoring data, including the 2 treatment weeks, and at least the final 2 weeks pre-treatment. Cameras that started in week 1 therefore had the most weeks of summed photo events to average, and cameras that started in week 5 had the fewest.

Table 1 Start and end dates and times for each week during the study from 20 November 2017 through 15 January 2018

Week	Start date	End date
1	20 November 2017 at 17:01	27 November 2017 at 17:00
2	27 November 2017 at 17:01	4 December 2017 at 17:00
3	4 December 2017 at 17:01	11 December 2017 at 17:00
4	11 December 2017 at 17:01	18 December 2017 at 17:00
5	18 December 2017 at 17:01	25 December 2017 at 17:00
6	25 December 2017 at 17:01	1 January 2018 at 17:00
7 (treatment)	1 January 2018 at 17:01	8 January 2018 at 17:00
8 (treatment)	8 January 2018 at 17:01	15 January 2018 at 17:00

All burrows in week 7 and 8 week were treated with Red fox urine or a water control

Statistical analysis

All statistical analyses were performed in program R (R Core Team 2020). Weekly burrow visitation (total number of photo events per week) was determined per burrow for each of the five most commonly observed taxa, which were the Eastern cottontail (*Sylvilagus floridanus*), mouse (*Peromyscus* spp.), Striped skunk (*Mephitis mephitis*), Domestic cat (*Felis silvestris catus*), and Virginia opossum (*Didelphis virginiana*), respectively. We then employed a hybrid approach for the analysis, first using a Before-After Control-Impact (BACI) analysis with a series of t-tests, and then by regressing linear mixed effect models to the data.

Before-After Control-Impact/Treatment designs are common analyses used to assess the effects of perturbations on ecosystems, either naturally or human-induced (Conner et al. 2016). To employ the BACI method for this investigation specifically, the eight weeks of the study were split into “pre-treatment” and “treatment” groups upon which a series of Welch Two-Sample t-tests could be performed (pre-treatment vs. treatment, and treatment vs. control). T-tests were performed using all 8 weeks (6 pre-treatment, 2 treatment) and with a subset of the data using only the final 2 weeks of pre-treatment (weeks 5 and 6) and the 2 treatment weeks. Because t-tests revealed statistically significant differences in mean weekly burrow visitation between pre-treatment and treatment weeks only for Striped skunks at urine treatment burrows, analysis of variance (ANOVA) was conducted in R comparing skunk weekly burrow visitation against urine treatment, weekly temperature (max., min., avg.), weekly snowfall (avg. and total), or average weekly snow depth.

Burrow visits for each of the five most commonly observed taxa were then analyzed using linear mixed-effects models, with fixed effects of week, group (treatment or control), and week by group, and random effects of site, camera, and site by week. Significance of the fixed effects was tested using F-tests with the Satterthwaite approximation for degrees of freedom, and burrow visitation between treatment and control burrows was compared using Tukey’s adjustment for multiple comparisons (Bates et al. 2015; Kuznetsova et al. 2017; Lenth 2020). Diagnostic plots were used to check the assumptions of normality of the residuals and homogeneity of variance. For the five most commonly observed taxa, the correlation between burrow visitation and six weather variables was examined to possibly determine if the individual climatic variation between weeks better explained significant differences in burrow visitation than urine treatment. These variables included temperature (max., min., and avg.), snowfall (avg. and total), and average snow depth. Weather data was compiled from the Northeast Regional Climate Center’s web page for Ithaca, New York using their Game Farm Road Weather Station

(<http://www.nrcc.cornell.edu/wxstation/ithaca/ithaca.html>). Snowfall and snow depth records that were marked as “Trace” were assumed to be 0 cm.

Results

Observed species

A combined total of at least 22 mammal and bird taxa visited the burrows (Table 2) over the 8 weeks of camera trap photography. This list includes the American Crow, despite the fact that it was observed on 16 January 2018 immediately after the treatment trial had officially ended (Table 1), and all photos from that date were omitted from the quantitative analysis. Of the 1752 individual detections of animals identified from the 1734 total photo events (some photo events contained multiple individuals) from 17 November 2017 to 16 January 2018, 158 contained pictures of unknown animals

Table 2 All species encountered at burrows from 17 November 2017 to 16 January 2018 near Ithaca, New York, and the number of photo events documented per species

Common name	Scientific name	Number of events
Eastern cottontail	<i>Sylvilagus floridanus</i>	789
Mouse	<i>Peromyscus</i> spp.	317
Striped skunk	<i>Mephitis mephitis</i>	181
Domestic cat	<i>Felis silvestris catus</i>	125
Virginia opossum	<i>Didelphis virginiana</i>	56
Eastern gray squirrel	<i>Sciurus carolinensis</i>	28
American red squirrel	<i>Tamiasciurus hudsonicus</i>	13
Unknown rodent	Various	10
Weasel	<i>Mustela</i> spp.	5
White-tailed deer	<i>Odocoileus virginianus</i>	3
Eastern chipmunk	<i>Tamias striatus</i>	3
Shrew	<i>Blarina</i> spp.	3
Raccoon	<i>Procyon lotor</i>	2
Bobcat	<i>Lynx rufus</i>	2
American mink	<i>Neovison vison</i>	2
Coyote	<i>Canis latrans</i>	1
Gray fox	<i>Urocyon cinereoargenteus</i>	1
Sparrow	Various	12
Unknown bird	Various	12
Blue Jay	<i>Cyanocitta cristata</i>	11
Ring-necked Pheasant	<i>Phasianus colchicus</i>	8
Dark-eyed Junco	<i>Junco hyemalis</i>	7
American Crow	<i>Corvus brachyrhynchos</i>	2
Northern Cardinal	<i>Cardinalis cardinalis</i>	1

Mice, weasels, shrews, and sparrows were only identifiable to the genus level or higher

that we were unable to classify even to the level of “unknown rodent” or “unknown bird.” This makes our identification rate approximately 91%.

Red fox urine repellent trial

We examined burrow visitation over time for each of the five most commonly observed taxa (Fig. 4). From the pre-treatment to treatment weeks, the average number of visits at urine-treated burrows for cottontails went from 6.8 to 3.3, mice went from 0.802 to 0.214, skunks went from 1.9 to 0.321, cats went from 0.775 to 0.964, and opossums went from 0.925 to 0.215 (Table 3).

BACI analysis and the t-tests revealed no statistically significant ($p < 0.05$) differences between Eastern cottontail activity at burrows before and after Red fox urine was applied at treatment burrows, nor that of mice, cats, or opossums (Table 4). The analysis did reveal a difference ($p < 0.05$) for Striped skunks between treatment and control burrows in both the full 8-week and truncated 4-week datasets. However, ANOVA revealed that these differences were more likely explained by minimum ($F = 11.13$, $p = 0.0157$) and average ($F = 10.31$, $p = 0.0183$) weekly temperatures. As temperature decreased, less Striped skunk activity was observed around burrow entrances (Fig. 5). There was also some evidence from the ANOVA that maximum weekly temperature influenced skunk burrow use ($F = 4.78$, $p = 0.0714$). All other predictors (i.e., average weekly snowfall, total weekly snowfall, and average weekly snow depth) were also closer to being significant than urine treatment.

The regression analysis revealed similar results. Estimated marginal means showed significant differences between

control and treatment burrow use for cottontails at week 3, skunks at week 8, mice at weeks 2, 3, and 4, and opossums at week 5 (marked with asterisks in Fig. 4). Our best interpretation of any significant differences seen between groups in the pre-treatment weeks is random variation, as we did not measure other variables during those weeks (e.g., food abundance). The t-tests between burrows during pre-treatment weeks from the BACI analysis also revealed no statistically significant differences, so the significant differences from the regression models are likely artifacts. F-tests conducted on the models for each of the five taxa were statistically significant for the cottontail week*group interaction term (Sum sq. = 295.767, $F = 3.0315$, $p = 0.0073$); the mouse week (Sum sq. = 289.174, $F = 3.3297$, $p = 0.0032$), group (Sum sq. = 66.159, $F = 5.3326$, $p = 0.0316$), and week*group interaction terms (Sum sq. = 279.319, $F = 3.2163$, $p = 0.0042$); and the skunk week term (Sum Sq = 109.268, $F = 6.3249$, $p = 0.00013$) (Table 5). Given that the “week” term is a reasonable proxy for differences in weekly weather, subsequent correlation tests revealed weekly skunk and opossum visitation to burrows was likely dependent on both temperature and snow depth (Figs. 5 and 6). Activity around burrow entrances increased as temperature increased, and decreased as snow depth increased, for both skunks and opossums.

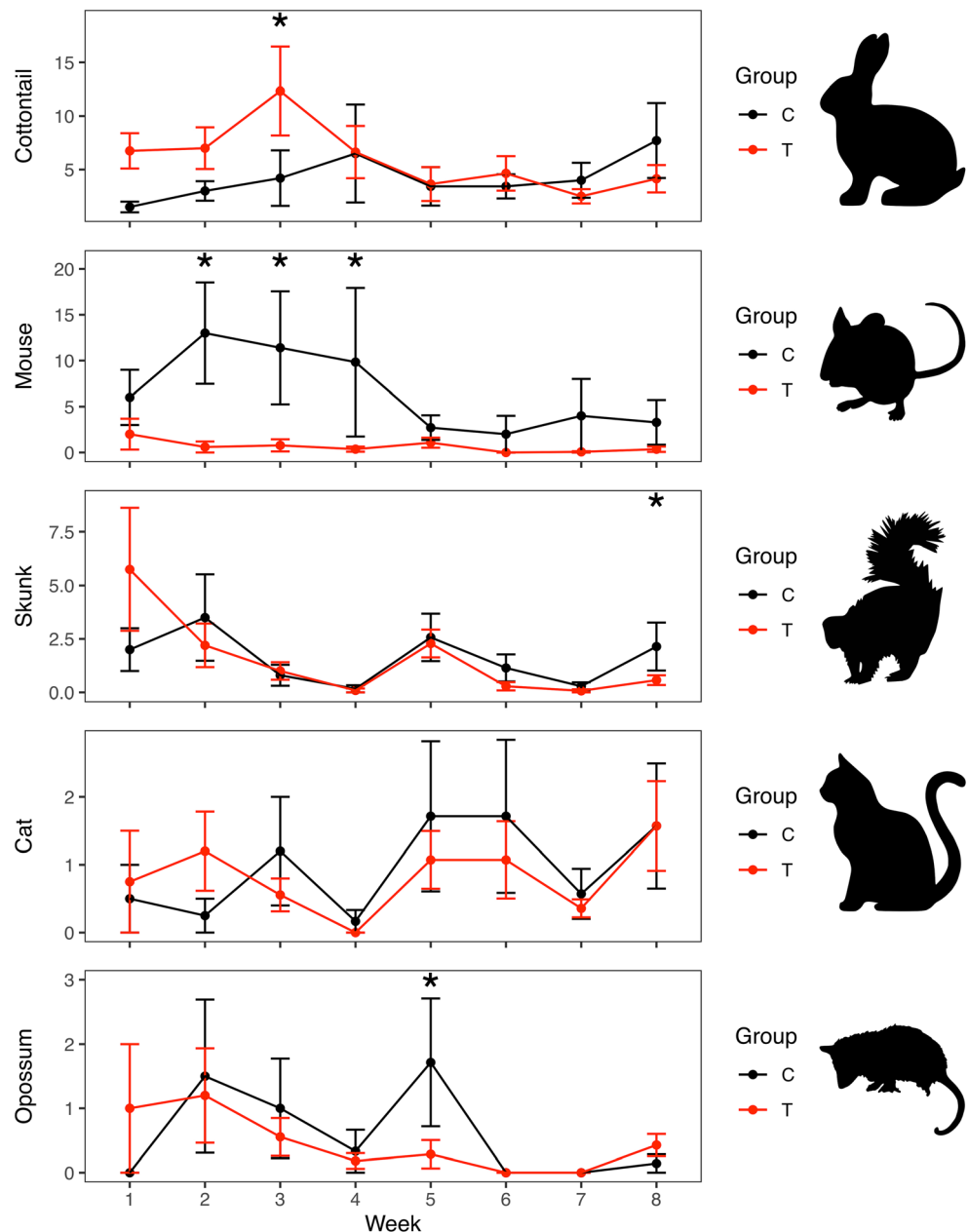
Discussion

One of the most central questions to the ecology of predator-prey interactions is whether communities are structured from the top-down by predators, or from the bottom-up by the resources available to primary producers (Barbosa and

Table 3 The average weekly visits for the five most commonly observed taxa, with the summed averages of Pre-treatment (Weeks 1-6) and Treatment (Weeks 7-8) shown in bold

Week	Cottontail visits		Mouse visits		Skunk visits		Cat visits		Opossum visits	
	Treat	Control	Treat	Control	Treat	Control	Treat	Control	Treat	Control
1	6.8	1.5	2.0	6.0	5.8	2.0	0.8	0.5	1.0	0.0
2	7.0	3.0	0.6	13.0	2.2	3.5	1.2	0.3	1.2	1.5
3	12.3	4.2	0.8	11.4	1.0	0.8	0.6	1.2	0.6	1.0
4	6.6	6.5	0.4	9.8	0.1	0.2	0.0	0.2	0.2	0.3
5	3.6	3.4	1.1	2.7	2.3	2.6	1.1	1.7	0.3	1.7
6	4.6	3.4	0.0	2.0	0.3	1.1	1.1	1.7	0.0	0.0
7	2.5	4.0	0.1	4.0	0.1	0.3	0.4	0.6	0.0	0.0
8	4.1	7.7	0.4	3.3	0.6	2.1	1.6	1.6	0.4	0.1
Pre-treatment 1-6	6.8	3.7	0.8	7.5	1.9	1.7	0.8	0.9	0.9	0.8
Treatment 7-8	3.3	5.9	0.2	3.6	0.3	1.2	1.0	1.1	0.2	0.1

Fig. 4 Burrow visitation over time for each of the five most commonly observed taxa between treatment and control groups. T = Red fox urine treatment group, C = water control group. Note that treatment or control wicks were not stationed at burrows until weeks 7 and 8. Asterisks are marked above the weeks for which there was a statistically significant difference between treatment and control groups



Castellanos 2005; Laundré et al. 2014). From the top-down perspective, predators can affect species assemblages directly through predation, or indirectly such as through the modification of prey behavior due to perceived predation risk and fear (Brown 1999; Wilson et al. 2012). This phenomenon is often referred to as the “landscape of fear” (Laundré et al. 2010). In the present experiment, we sought to evaluate how strongly Eastern cottontails (and other common suburban wildlife) perceived their risk of predation by Red foxes through the lens of olfaction. Contrary to our hypothesis, application of Red fox urine had no measurable effect on burrow use by Eastern cottontails in winter. Therefore, our data appear to suggest predation risk is not as important in determining cottontail behavior at burrows as other factors.

However, while not statistically significant, we did observe a trend toward lower burrow visitation by Eastern cottontails from pre-treatment to treatment weeks at urine-treated burrows, from a mean of 6.8 to 3.3 weekly visits (Table 3). The mean rabbit visitation at control burrows followed an opposite trend (3.7 in pre-treatment weeks and 5.9 visits in treatment weeks). Taken together, it is possible that a statistically significant pattern might have been observed had there been a larger sample size of burrows, the urine trial been conducted over multiple years, and the urine trial lasted longer than 2 weeks. As in the present study, Jacques et al. (2016) also noted no statistically significant response by many mammals to a variety of scents, including the urine of Red foxes, even though other studies have shown that such responses do occur,

Table 4 Results of the BACI Welch Two Sample t-tests comparing burrow visitation between pre-treatment weeks and treatment weeks for the five most commonly observed taxa at burrows

Taxa	T-test	Result (all 8 weeks)	Result (truncated dataset)
Eastern cottontail	Control	$t = -0.40166, df = 11.186, p = 0.6955$	$t = -0.88389, df = 9.4516, p = 0.3987$
	Treatment	$t = 1.4914, df = 19.529, p = 0.1518$	$t = 0.47665, df = 21.117, p = 0.6385$
Striped skunk	Control	$t = 0.46038, df = 11.793, p = 0.6536$	$t = 0.6445, df = 10.642, p = 0.5329$
	Treatment	$t = 2.2801, df = 16.978, p = \mathbf{0.0358}$	$t = 2.4029, df = 16.53, p = \mathbf{0.02832}$
Virginia opossum	Control	$t = 1.342, df = 6.2707, p = 0.2261$	$t = 1.5661, df = 6.2482, p = 0.1664$
	Treatment	$t = 0.29401, df = 20.666, p = 0.7717$	$t = -0.5099, df = 24.584, p = 0.6147$
Domestic cat	Control	$t = 0.15692, df = 11.79, p = 0.878$	$t = 0.5328, df = 8.8199, p = 0.6073$
	Treatment	$t = -0.74125, df = 23.408, p = 0.4659$	$t = 0.17906, df = 24.741, p = 0.8593$
Mouse	Control	$t = 0.42988, df = 11.738, p = 0.6751$	$t = -0.36289, df = 8.8062, p = 0.7252$
	Treatment	$t = 0.91024, df = 19.876, p = 0.3736$	$t = 1.0339, df = 19.769, p = 0.3136$

T-tests were performed for both control and treatment groups, and by using all 8 weeks (6 pre-treatment, 2 treatment) or by using a truncated set of the last 2 weeks pre-treatment and the 2 treatment weeks. Statistically significant results are highlighted in bold

including in lagomorphs (e.g., Sullivan and Crump 1986; Thorson et al. 1998). Therefore there may be other context-specific factors that modulate fear responses. For example, cottontails may use urban environments specifically to mitigate predation risk from carnivore predators (Jones et al. 2016), given that predation pressure is lower on prey in urban areas (Eötvös et al. 2018).

Because Eastern cottontails are sensitive to olfactory cues (Baldwin et al. 2006), their lack of an observed response begs the question of whether animals behave differently in urban versus rural environments. Indeed, there is a healthy body of evidence that prey fear responses to predators and humans are attenuated in urban areas, or other behavioral modifications are made (Lowry et al. 2013). For example, passerines have shorter flight escape distances in urban areas (Gliwicz et al. 1994; Møller 2012). White-tailed deer may display no foraging patch abandonment in urban sites despite predatory coyotes also using those same patches to hunt (Magle et al. 2014). Corvids display less neophobia to human-made objects in urban than in rural areas (Greggor et al. 2016). Gray and

Fox squirrels also have reduced wariness with increased abundance, and reduced fleeing distances in urban zones (Bateman and Fleming 2014; McCleery 2009; Parker and Nilon 2008). With regard to burrowing species, European rabbits invest less time to hiding in their burrows and displaying anti-predator behavior in more urban areas (Ziege et al. 2016), and urban Burrowing Owls (*Athene cunicularia*) are more fearless and perceive humans as lower risk than their rural counterparts (Carrete and Tella 2017; Cavalli et al. 2016). We suspect a similar reduction in fear response may at least partially explain the behavior of the Eastern cottontails in our investigation.

Other explanations for a lack of an observed response by cottontails may include that picture-taking mode, rather than using video on our camera traps, was not able to capture split-second responses like approach behaviors, as in Jacques et al. (2016). Alternatively, fox urine may simply not affect rabbit behavior around previously-colonized safe shelters. The scent of a predator may be information an Eastern cottontail uses in unfamiliar territory, but a cottontail may be comfortable with scents near familiar areas where it may know of several

Fig. 5 Striped skunk burrow visitation compared to (a) average weekly temperature and (b) snow depth

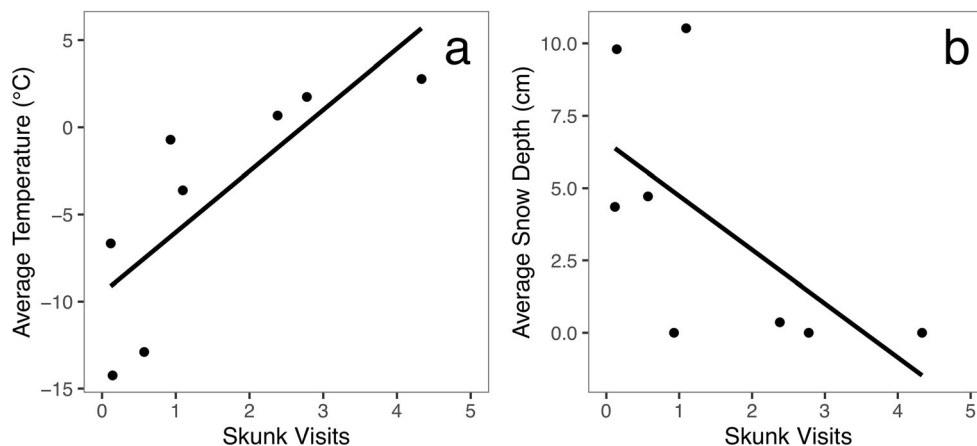


Table 5 Results from the F-tests of the linear mixed models for burrow visitation by each of the five most commonly observed taxa, testing the fixed effects of week (Table 1) and treatment group (urine/water treatment; see text), and their interaction. Statistically significant results are in bold

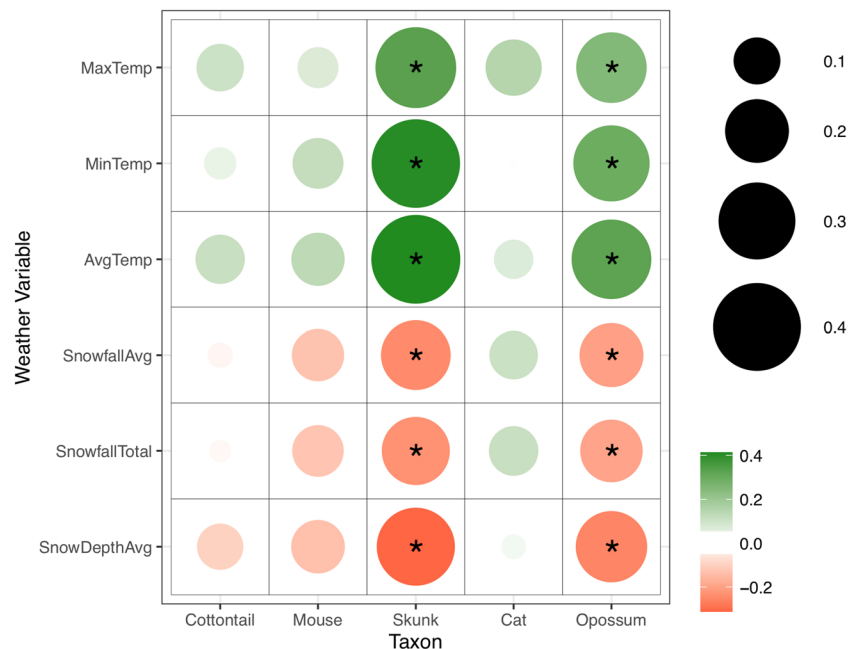
Species	Effect	Sum Sq	Mean Sq	numDF	denDF	F-value	<i>p</i> value
Cottontail	Week	78.525	11.218	7	27.115	0.805	0.591
	Group	30.956	30.956	1	17.179	2.221	0.154
	Week:Group	295.767	42.252	7	75.792	3.032	0.00728
Mouse	Week	289.174	41.311	7	95.995	3.330	0.00323
	Group	66.159	66.159	1	20.188	5.332	0.0316
	Week:Group	279.319	39.903	7	95.995	3.216	0.00418
Skunk	Week	109.268	15.610	7	29.992	6.325	0.000131
	Group	0.807	0.8069	1	19.069	0.327	0.574
	Week:Group	20.493	2.9276	7	80.809	1.186	0.320
Cat	Week	10.032	1.433	7	31.963	1.164	0.350
	Group	0.356	0.356	1	16.754	0.289	0.598
	Week:Group	4.256	0.608	7	79.223	0.494	0.836
Opossum	Week	9.419	1.346	7	38.680	2.186	0.0570
	Group	0.477	0.477	1	19.681	0.775	0.389
	Week:Group	8.876	1.268	7	85.846	2.060	0.0566

refuges into which it can quickly escape from a predator. Severe winter weather may pose more of an immediate threat to Eastern cottontails than the rare, or even occasional encounter with a fox, especially given that species dedicate more time to optimizing foraging in the winter because there is more of a thermoregulatory cost (Avery 1985; Belovsky 1984; Fortin et al. 2005; Holmes and Laundré 2006; Turner et al. 1993; Villén-Pérez et al. 2013). Cold temperatures can persist from hours to weeks, while an encounter with a fox may last from seconds to minutes. Therefore, it would be more advantageous to seek shelter from an almost certain stressor (e.g., low winter

temperatures) than one that has a lower probability of occurring (e.g., an encounter with a Red fox).

Another perhaps more interesting explanation for not seeing any effect of fox urine treatment on Eastern cottontail behavior is the “olfactory concealment theory,” which deals with the physical processes of air currents. It suggests that animals should hide from olfactory predators by positioning themselves where updrafts and turbulence occur since they disperse and dissipate scents, which last longer on colder and less sunny days (Conover 2007). It also may imply animals position

Fig. 6 Degree of correlation between burrow visitation of the five most commonly observed taxa and six weather variables. Green and red indicate positive and negative correlations, respectively. Color of the circles becomes sharper and darker, and size of the circles becomes larger with stronger correlations. Statistically significant correlations are marked with an asterisk



themselves in areas where there are fewer turbulent air currents. Burrows, or the areas immediately adjacent to burrows covered by vegetation, may be conducive to cottontail scent concealment because an individual's scent may collect in isolation, or is otherwise shielded from strong, less-turbulent air currents. Indeed Eastern cottontails preferentially forage in urban environments under cover, particularly low-lying shrubs (Abu Baker et al. 2015; Linduska 1947), a landscape feature we often associated with our own burrows.

We observed a surprisingly higher number of species ($n = 22$) at burrows than we had expected. The high diversity of animal species photographed at burrows by camera traps over the course of a single winter season indicates how important these burrows are to a variety of organisms in suburban areas. At least 16 mammal species were photographed as well as at least 6 bird species (some individuals could not be identified to the species level).

One of our most interesting findings was that not a single Red fox was observed at any of the burrows we monitored in our investigation, even though we observed other mammalian carnivores known to use scent marking (e.g., Bobcats, a Gray fox, and a Coyote). Scent marking is an important behavior with many functions for carnivores (Erlinge et al. 1982; Gorman and Trowbridge 1989; Rodgers et al. 2015; Rothman and Mech 1979), including for Red foxes specifically (Arnold et al. 2011; Henry 1977, 1980; Jorgenson et al. 1978; MacDonald 1979). Indeed, it is speculated that urination alone serves at least 11 distinct functions in mammals including territory marking, dominance displays, trail following, and synchronizing the reproductive physiology of females (Gosling and Roberts 2001; Henry 1977; Johnson 1973). There are many possible reasons why no Red foxes were observed at burrows apart from that Red foxes failed to respond to scent-marking cues from conspecifics (as in Banks et al. 2016). Red foxes may be less active during November through January. Foxes may have more difficulty detecting scents leading to burrows (as in the “olfactory concealment theory”). They might also have an aversion to the amount of human activity in suburban areas near Ithaca, NY specifically, although they usually integrate well in such habitats (Adkins and Stott 1998; Červinka et al. 2014; Kamler and Ballard 2002; Lombardi et al. 2017; Stark et al. 2019). It was unlikely that Red foxes were absent in the study area because they have been commonly seen on camera traps around Ithaca as part of other research projects (P. Curtis, pers. obs.), and we were able to document a similarly-sized Gray fox and Coyote. It is also unlikely our camera traps failed to photograph them if they were in the field of view, as they have been adequately studied with camera traps (e.g., Sarmiento et al. 2009).

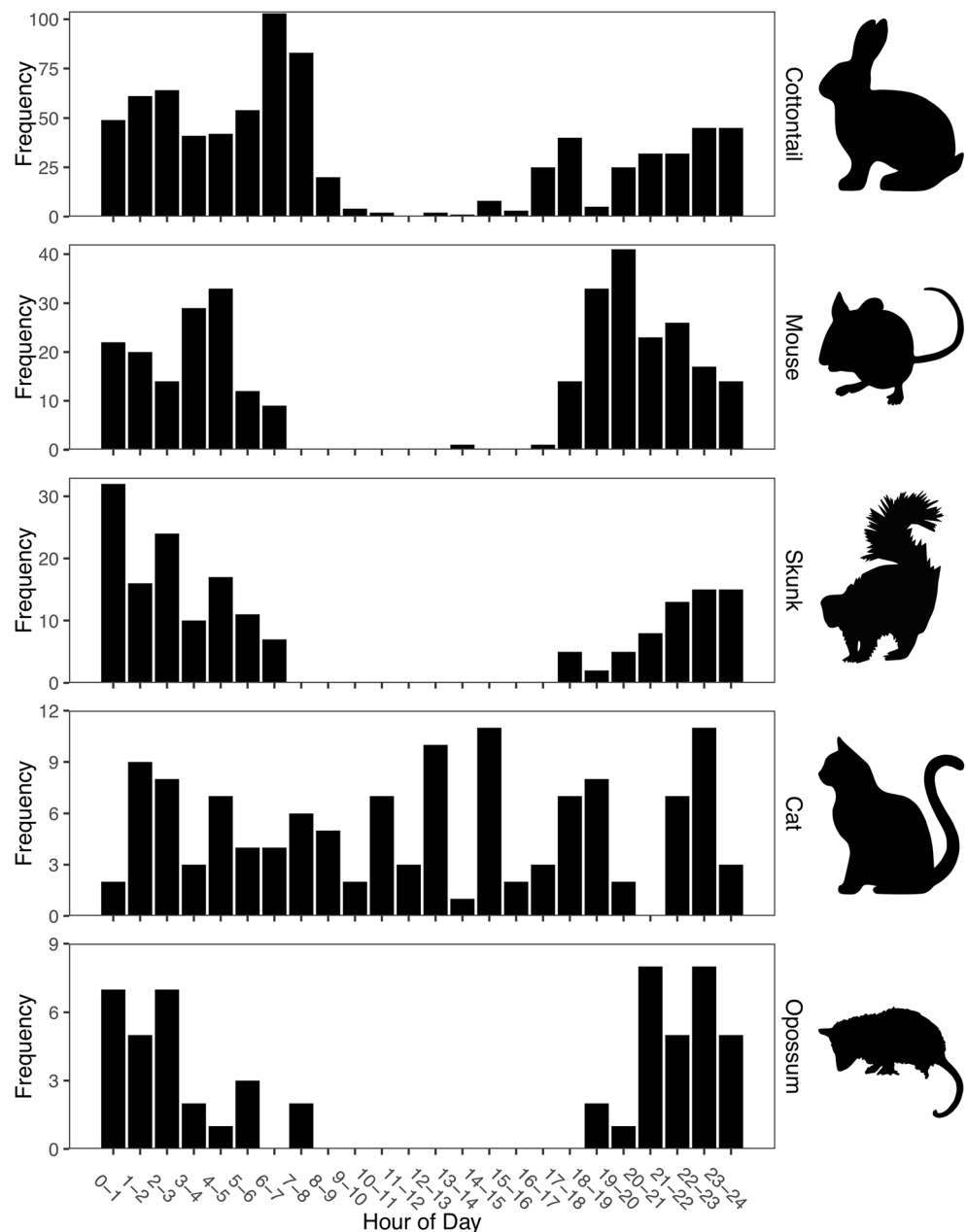
Although Eastern cottontails were the most commonly observed mammals using Groundhog burrows in winter, a surprising number of photos documented activity of Striped

skunks, Virginia opossums, Domestic cats, and mice in and around burrows. Striped skunk use of burrows, including those dug by Groundhogs (Godin 1977), has been previously observed in Ithaca, New York, dating back to at least the 1930s (Hamilton 1937). Skunks are known to enter a state of dormancy in winter, though rather than true hibernation, their winter inactivity is better defined as a daily shallow torpor (Geiser 2013; Melvin and Andrews 2009), or “carnivoran lethargy” (Aleksiuk and Stewart 1977; Mutch and Aleksiuk 1977), which helps explain their reduced activity at burrows during particularly cold weeks. Our analysis of skunk activity and climatic variables (Figs. 5 and 6) corroborates this aspect of their natural history. Previous work on Striped skunk daily activity (Mutch and Aleksiuk 1977) also corroborates why we saw the skunks in our own investigation mostly active at night (Fig. 7). Eastern cottontails displayed a similar nocturnal or otherwise crepuscular pattern of activity (Fig. 7), which is also previously known (Pinger and Rowley 1975).

During our study, Domestic cats frequently visited and entered burrows, and likely competed with native predators as they searched for prey. Domestic cats may have significant negative impacts on burrowing species in particular, for example they are implicated in reducing the nesting success and burrow densities of seabirds on Marion Island in South Africa (Dilley et al. 2017). Although Domestic cats are not native to North America, since their introduction over 190 years ago (George 1974), the Domestic cat population in the United States may now number well over 80 million, and they are estimated to annually take avian and mammalian prey in the billions (Loss et al. 2013). Though Domestic cats may exhibit a high degree of flexibility in diet composition, they have recently been implicated as potential competitors with Red foxes, specifically in suburban areas (Castañeda et al. 2020). Domestic cats and Striped skunks have also been known to display interspecific aggression towards foxes (Harrison et al. 2011), which might have partially contributed to the lack of Red fox observations in this study. Due to the abundance and ability of cats to capture prey, their competition with native predators for food resources may be particularly detrimental in winter when prey are much scarcer. This is compounded by the fact that Domestic cats were observed to be active at nearly all times of the day (Fig. 7). Horn et al. (2011) found similar patterns of activity by radio-tracked Domestic cats in Illinois, noting more activity in colder seasons by feral cats. Cat activity has also been previously shown to coincide with that of Virginia opossums (Hernandez et al. 2018), one of the five most commonly observed taxa in our study.

Apart from Domestic cats and Striped skunks, other mammalian carnivores including Bobcats, American mink, Weasels, a Gray fox, and a Coyote were photographed approaching and examining burrows during our investigation. Although Bobcats, Coyotes, and other larger predators cannot enter burrows, American mink and

Fig. 7 Daily activity histograms of burrow visitation for the five most commonly observed taxa: Eastern cottontail rabbits, mice, Striped skunks, Domestic cats, and Virginia opossums



Weasels were observed exiting burrows in our study. Mustelids are known to enter the burrows of many of their prey (Vaughan 1961; Zielinski 2000), and may even match their periods of activity with the circadian rhythms of their prey (Gerell 1969; Zielinski 1986; Zielinski 2000). Coyotes are also known to match their foraging and activity patterns with lagomorphs specifically (Arias-Del Razo et al. 2011).

Virginia opossums have been reported to use burrows (Godin 1977), including those of Mountain beavers (*Aplodontia rufa*) (Engeman et al. 1991), armadillos (Lay 1942), and the dens of cottontails (Linduska 1947). Their activity in and around burrows in winter may be explained by

the fact that opossums spend almost twice as much time foraging and nest building during this season compared to other times of the year (Godin 1977; McManus 1969). They were mostly active at night in our investigation (Fig. 7), as has been shown previously (Cone and Cone 1968; Holmes 1991; Kanda et al. 2005). Mice have also been known to use burrows, including those of Groundhogs and rabbits (Linduska 1947; Swihart and Picone 1995), but they may also nest in a variety of other places, including cavities under old stumps and in walls (Godin 1977). In the present study they were mostly active at night (Fig. 7), as expected of mice in the genus *Peromyscus* (Bruseo and Barry 1995; Owings and Lockard 1971), but contrary to what is known about urbanized

Field mice *Apodemus agrarius*, which are more diurnal in town parks (Gliwicz et al. 1994).

Many different species used the same burrows within short periods of time. For example, at a single camera during the week of 20 to 28 November, we documented use of a single burrow by Eastern cottontails, mice, Domestic cats, Eastern chipmunks, a Striped skunk, and a Virginia opossum. Multiple animals may even be using a single burrow simultaneously, which may imply an increased potential for the coexistence of multiple species in these engineered habitat features. For example, at another camera on 23 November, we observed a skunk exiting a burrow only 14 min after a cottontail had left it (Fig. 8). Though it is possible the camera failed to take a picture of the second individual initially entering the burrow, this was unlikely given the fact that the photos were taken greater than 1 min apart. These two species were therefore likely both in the burrow at the same time. Concurrent burrow use by mixed species assemblages is also surprisingly known between rodents and carnivores, as with Cape ground squirrels (*Xerus inauris*), Suricates (*Suricata suricatta*), and Yellow mongooses (*Cynictis pencilatus*) (Waterman and Roth 2007). However, interspecific interactions between simultaneous burrow users need not be frequent if there are multiple chambers or tunnels within burrow complexes (Grizzell 1955; Sherrod et al. 2019).

Burrows dug by Groundhogs can be found across a gradient of urbanization (Lehrer and Schooley 2010) given that Groundhogs are widely distributed across all of North America (Cassola 2016). Therefore, they are likely important features for commensal species in both natural (more rural) and human-modified landscapes. In an agricultural landscape, fewer Groundhog burrows may be found in more urbanized areas (Lehrer and Schooley 2010), which might lead to higher concentrations of species using the more limited number of burrows. This may explain the wide diversity of species seen at the burrows in our investigation. Unlike Groundhog burrows however, higher densities of European rabbit burrows

are found in more urbanized areas (Ziege et al. 2015). Should Eastern cottontails in North America display a similar pattern of burrow use to European rabbits, though there may be fewer Groundhog burrows in urban areas, more rabbits may seek to use those in urban as opposed to those in rural areas. More research is needed to fully test this hypothesis however.

Because most of the burrows in this investigation were likely excavated by Groundhogs, the value of Groundhogs as keystone ecosystem engineers is likely immense. Although often seen as pests to humans because they damage building foundations and trees within orchards for example (Swihart and Picone 1994), Groundhogs may actually be facilitating the coexistence of many species in suburban areas. This is also the case for other burrow diggers such as gopher tortoises, which act as ecosystem engineers for the benefit of over 300 commensal species (Alexy et al. 2003; Kinlaw and Grasmueck 2012; McHugh et al. 2019; Potash et al. 2020; Vaughan 1961), Black-tailed prairie dogs which help support biodiversity in urban-suburban areas specifically (Witmer et al. 2006), and even lagomorphs like the European rabbit (Bravo et al. 2009). The attention being paid to commensalism in anthropogenic environments is becoming increasingly important and relevant in order to find ways for wildlife to integrate with human civilization (Hulme-Beaman et al. 2016). As the human population grows and urban sprawl continues its geographical expansion, it is important to consider the evolving dynamics of wildlife in urbanized regions, and their adaptability to a changing landscape. Many aspects of their biology will, and already have become, increasingly dependent on our influence (Ditchkoff et al. 2006; Gallo and Fidino 2018; Gallo et al. 2017). In many cases, such as for Field mice, Blackbirds, and Groundhogs, survival is much higher in urban than rural areas during the challenging months of winter (Gliwicz et al. 1994; Lehrer et al. 2011). Therefore if people want to appreciate and encounter wildlife in their daily routines, we have a responsibility as stewards of the environment to maintain and manage it. Managing species like Groundhogs that promote



Fig. 8 A Striped skunk exits a burrow 14 min after an Eastern cottontail rabbit on 23 November 2017 around 23:00

biodiversity will only make the task easier, especially for the conservation of rare species. The New England cottontail (*Sylvilagus transitionalis*) for example, which is listed as a species of special concern in New York State (New York Natural Heritage Program 2017), may benefit from using burrows given its similarities in natural history to the Eastern cottontail. Specific actions that can be taken to help these species include leaving out brush piles for Groundhogs to use when constructing burrows (Linduska 1947), and by not filling in or collapsing burrows when their destruction is not essential. Given that Groundhogs are killed more by vehicle collisions than predation in urban environments (Lehrer et al. 2011), more care must also be taken by humans not to directly harm them. Management would do well to incorporate principles such as landscape ecology, sensory ecology, predator-prey dynamics, and the value of ecosystem engineers into future approaches to understanding animal behavior in suburban ecosystems.

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Data availability Not applicable.

Compliance with ethical standards

Conflicts of interest/competing interests None declared.

Ethics approval All work was approved by Cornell University Institutional Animal Care and Use Committee Protocol Number 2017–0123.

Consent to participate Not applicable.

Consent for publication Not applicable.

Code availability Not applicable.

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