The Effects of Red Fox (*Vulpes vulpes*) Predator Scent on Winter Burrow Use by Eastern Cottontail Rabbits (*Sylvilagus floridanus*)

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Abstract

During the winter months, the Eastern cottontail (*Sylvilagus floridanus*) must simultaneously cope with freezing temperatures that impose physiological stress, while remaining vigilant for a variety of predators. Because of this, rabbits frequently use burrows around man-made structures to escape the cold and predation. To enhance their detection of predators, Eastern cottontails are also sensitive to a variety of olfactory cues. However, despite the importance of Eastern cottontails in red fox (*Vulpes vulpes*) diets, little is known about scent cues that rabbits use to detect red foxes. As such, I designed an experiment to determine whether winter burrow use by Eastern cottontails is affected by the application of red fox urine near burrows. After identifying active rabbit burrows near abandoned buildings in Ithaca, New York during winter 2017-2018, camera traps were installed to monitor their use before and after setting up scent wicks dipped in red fox urine or a water control near burrow entrances. Although no statistically significant effect was observed between burrow use before and after treatment, a variety of mammalian and avian species were seen in and around burrows over the course of the winter. This indicates that burrows may be important to a range of North American mammals and birds, knowledge which may be helpful in creating future conservation management plans for these species. This project has also provided continued evidence for the usefulness of camera traps in documenting predator-prey behavior and studying wildlife ecology.

Introduction

Prey are faced with many constraints as they attempt to maximize survival and reproduction. In the temperate northeast of North America, seasonal changes are a large source of these constraints, especially those associated with winter. Winter temperatures usually dip below freezing in the northeast (Campbell et al. 2005), which imposes significant stress on the homeothermic physiological balance of endothermic mammals, and snowfall obscures vegetation to herbivores, among a whole host of other challenges associated with the season. To cope with these physical stressors, many organisms (Watts and Jonkel 1988, Yacoe 1983, Lyman and Chatfield 1955, Fishman and Lyman 1961, Lyman and Blinks 2005, Patil et al. 2013) go into a state of dormancy to reduce metabolic energy usage. Hibernating species have become poster children for winter, which has led to the season being inaccurately labeled the "'dormant season', based on the belief that biological activity ceases during this period" (Campbell et al. 2005). This misconception has resulted in a lack of enthusiasm for studying ecological systems in winter except for in the arctic (Campbell et al. 2005), which precisely necessitates more research on winter ecology. In reality, many common northeastern prey species do not hibernate or become dormant, such as the white-tailed deer (*Odocoileus virginianus*) (Ozoga and Harger 1966), Eastern grey squirrel (*Sciurus carolinensis*) (Lyman and Blinks 2005, Brown and Yeager 1945), 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 cope with constraints imposed by climate and other stressors.

One way these species are able to cope with the snow and freezing temperatures is to find temporary shelter in spaces that are shielded from the elements. Snow itself has insulating properties that allow it to function as a temporary seasonal refuge (Palm and Tveitereid 2012, Colbeck 2012, Pomeroy and Brun 2001, Gouttevin et al. 2012). However, in areas with less snowfall or short-lived snow, less ephemeral dwellings are preferred. Favorite choices for many northeastern mammals are previously constructed woodchuck (*Marmota monax*) burrows and holes up against the exterior bases of man-made suburban structures. Eastern cottontails are among the species that use burrows (Godin 1977, Linduska 1947), though this is largely a statement of expert opinion. This has led many biologists to doubt that Eastern cottontails take shelter in places apart from small indentations in the ground used for nesting (Beule and Studholme 1942, Casteel 1966). One aim of this project is to clarify the contested extent of burrow use by Eastern cottontails.

Because prey species often remain active throughout the winter, many North American predators are similarly active such as wolves (*Canis lupus*) (Johnson et al. 2017), red foxes (*Vulpes vulpes*) (Ables 1969), gray foxes (*Urocyon cinereoargenteus*) (Harrison 1997), coyotes (*Canis latrans*) (Ozoga and Harger 1966, Gese and Grothe 1995, Neale and Sacks 2003), American martens (*Martes americana*) (Drew and Bissonette 1997), fishers (*Pekania pennanti*) (Leonard 1981), and bobcats (*Lynx rufus*) (Neale and Sacks 2003). The presence of predators presents an added challenge to the survival of prey species in winter, who 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 decision-making process of prey species as they attempt to maximize foraging and minimize multiple risks to their survival (Villen-Perez et al. 2013, Hilton et al. 1999). Prey that may use burrows to escape both predators and the weather in winter have been insufficiently studied in this context. Being able to piece apart when and why prey use burrows is valuable for understanding their behavioral ecology.

One way to solve this problem is to try and understand how prey specifically respond to predators. In the co-evolutionary game 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). By detecting cues from predators, prey can modulate their behavior to avoid capture. This manifests itself in many prey species through a fear response to fight, flee, or freeze in place (Bracha 2004, Apfelbach et al. 2005). Many mammalian fear-inducing cues are olfactory, which are 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 (Rosen et al. 2015, Lindgren et al. 1995, Apfelbach et al. 2015, Osada et al. 2014, Sullivan 1986). Widespread 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 ecosystem, as fear responses to novel predators are slow to evolve (Atkins et al. 2016). One such predator is the red fox, which 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.), and snowshoe hares (*Lepus americanus*) (Dickman and Doncaster 1984, Fanson 2010, Jedrzejewski et al. 1993, Laska et al. 2005, Lindgren et al. 1995, Navarro-Castilla and Barja 2014a, Navarro-Castilla and Barja 2014b, Orrock et al. 2004, Sullivan and Crump 1986, Takahashi et al. 2005). It is also known from the literature that "the most important prey for red foxes in the eastern US are cottontails (*Sylvilagus* spp.)" (Frey 2013). 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, not a single study exists that demonstrates the olfactory relationship between the red fox and the Eastern cottontail. Coupled with the facts that evidence for burrow use by Eastern cottontails remains largely based on expert opinion, winter ecology is comparatively understudied in relation to the ecology of other seasons, and that tradeoffs prey make to cope with the multiple constraints of the physical environment and predation pressure are of interest, this presented an exceptional opportunity to study the predator-prey interaction between the red fox and Eastern cottontail.

I designed this project with three main goals. The first was to document animal behavioral ecology at winter burrows in the suburban American northeast. This included characterizing the diversity of species that occur in and around burrows and their behavior in and around the burrows. This also included describing the physical characteristics of burrows themselves. The second goal was to experimentally test the hypothesis that Eastern cottontails exhibit a fear response to the scent of red foxes. The third goal was to experimentally determine whether this fear response could cause the frequency of burrow use to decrease despite winter cold temperatures and snowfall that originally necessitate burrow use. These goals were accomplished through an experimental design employing camera traps at burrow entrances around old buildings near Ithaca, New York in the winter of 2017-2018. For the observational part of this project, camera traps merely observed the “natural” activity at the burrows. For the other parts of this project however, a controlled experiment was designed in which red fox urine was applied to wicking devices at burrow entrances over a two week period, and the camera traps functioned to document changes (or lack thereof) in patterns of animal activity at the burrows before and after treatment, and between control and treatment burrows.

Materials and Methods

Field design

Beginning in late November 2017, large animal burrows, likely old woodchuck burrows, around old abandoned buildings on Cornell University-owned lands near Ithaca, New York were identified. Camera traps were deployed facing these burrows either screwed into a tree or on a wooden stake between 30 and 60 cm off the ground and at a distance of 120 to 180 cm from each burrow. At sites where multiple burrows were identified, only burrows that were at least 3 m apart were monitored to increase the likelihood of each burrow being independent, rather than connected underground to other burrow entrances. The camera traps used were Cuddeback brand (De Pere, WI) Model C1 or Model 11339, and were set to take 3 consecutive photo bursts for both day and night. 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 were used over the course of this project, at 6 different sites (Figure 1). Characteristics of each burrow were also documented, which included the greatest width and height (or length) of the entrance holes, the coordinates of each burrow, and a site description. All work was approved by Cornell University IACUC protocol number 2017-0123.

Site descriptions

The six sites used were: (1) East Hill barn, (2) Game Farm shack, (3) Turkey Hill beehive building, (4) Lydell Lab, (5) Stevenson Road barns, and the (6) Cornell Ecology and Evolutionary Biology (EEB) Research Pond facility.

(1) *East Hill barn* – Two cameras were set up at this site. It is characterized by an old abandoned farm animal barn that is 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. The first burrow (cam 40) was identified as a hole in the base of the wall of the building, underneath some brambles and a caving in roof. The second burrow (cam 54) was

identified under a slab of broken concrete near, but not connected to the base of the building, underneath a bush.

(2) *Game Farm shack* – Three cameras were set up at this site. It is characterized by an old wooden shack set in an empty field along Game Farm Road. Old slabs of broken concrete were strewn about the shack, remnants of a small patio, but grass, weeds, bushes, and brambles had also sprung up all around. This made the concrete unnoticeable until closer examination of the substrate when I was driving wooden stakes into the ground. The first burrow (cam 42) was identified as a hole near the base of the shack surrounded by a few small concrete slab pieces and grass. The second burrow (cam 43) was identified as a hole in the side of the wooden shack that was less covered by grass and brambles, but was still partially surrounded by concrete slab pieces. The third burrow (cam 45) was identified under a slab of broken concrete and dirt farther away from the shack, but also covered by grass and tall brambles.

(3) *Turkey Hill beehive building* – Six cameras were set up at this site. It is characterized by an old metal building about 100 m west of Turkey Hill Road. Beehives are actively kept along one side of this building during the growing season, but were absent during this project. The building itself is surrounded by tall, thick grass, shorter grass, small coniferous trees, and old metal equipment debris. The first burrow (cam 48) was identified as a hole up against one corner of the building, surrounded by thick grass. The second burrow (cam 49) was identified as a hole up against another corner of the building. It was surrounded by grass and old debris like plywood and a tire, and was partially shaded by a coniferous tree. The third and fourth burrows (cams 50 and 51) were identified as holes underneath one side of the building. They were more exposed, though some small, thin trees and short grass had sprouted nearby. The fifth burrow (cam 55) was identified as a hole up against the third corner of the building, covered by old wooden pallets

and some short grass. The sixth burrow (cam 58) was identified as a hole underneath another side of the building, and was covered by some thick grass and small, thin trees.

(4) *Lydell Lab* – Three cameras were set up at this site. It is characterized by an old wooden barn-like building in a field a few meters away from an actively maintained and used concrete research building and greenhouse. The first burrow (cam 39) was identified as a hole underneath one corner of the wooden building. The burrow was only surrounded by short lawn grass and was not covered by overhanging brambles or other forms of cover. The second burrow (cam 60) was identified as a hole underneath one side of the wooden building, similarly only surrounded by short lawn grass and no overhanging brambles or cover. The third burrow (cam 59) was identified as a hole underneath another side of the building, but this burrow was heavily covered by a dense thicket of brambles that stretched along the entire side of the building.

(5) *Stevenson Road barns* – Four cameras were set up at this site. It is characterized by a series of old barns 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 are empty, and a nearby tall, empty, cylindrical corn silo towers over these buildings. The first burrow (cam 61) was identified as a hole underneath the long side of a rectangular building. It was partially but thinly covered by small burdock bushes. The second burrow (cam 57) was identified as a hole underneath the short side of this building, near the silo, and was only slightly shaded by a few thin, dead brambles. The third burrow (cam 52) was identified as a hole underneath the same building as the first and second burrows, right near the silo. It was surrounded primarily by rocky gravel and a few small trees which had grown up through cracks in the concrete. The fourth burrow (cam 56) was identified as a hole underneath the side of another building, and was surrounded only by short grass and patches of old hay.

(6) *Cornell EEB Research Pond facility* – Three cameras were set up at this site. It is characterized by a large metal garage-like building and a nearby smaller temporary building at the end of a gravel road that are both still maintained by staff. The first burrow (cam 62) was identified as a hole in the vinyl siding of the temporary building. There was no immediate cover above or around this hole, merely short lawn-type grass. The second burrow (cam 38) was identified as a hole underneath the larger building near the pathway between the larger building and the temporary building. Some wooden siding on the large building overhung this hole, but there were no other forms of cover. The third burrow (cam 53) was identified as a hole underneath another side of the large building. It was surrounded, but not covered by some thick grass, weeds, and some short bramble bushes.

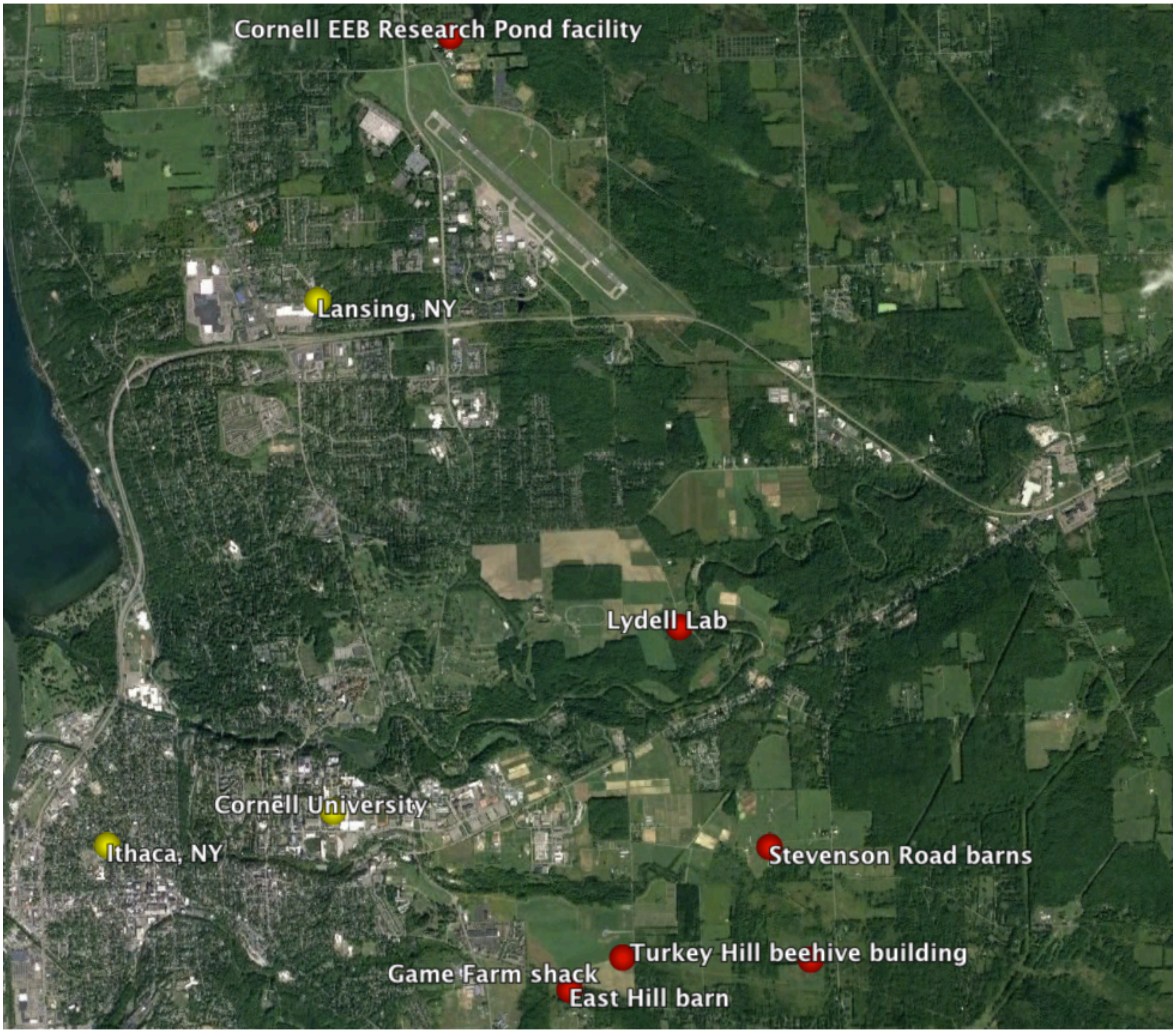

Figure 1. A Google Earth map of Ithaca, NY and surrounding towns with each of the six study sites plotted

Design of red fox urine repellent trial

During the final two weeks of this 8-week project, from 1 January to 16 January 2018, each of the 21 identified burrows was treated either with red fox urine or a water control. This was accomplished using Quik-wiks 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 brown to make them more inconspicuous from 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, because the hooks at the tops of the tubes would not fully close around the plant prop loops. 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 a bottle of Poland Spring water with no added minerals. A total of 14 burrows received red fox urine treatment (cams 38, 43, 45, 49, 50, 51, 52, 54, 56, 57, 58, 59, 60, and 62) and 7 burrows received the water control (cams 39, 40, 42, 53, 55, and 61). Each of the 6 sites had at least one burrow treated with the control, and at least one burrow treated with urine, to help eliminate site-specific interactions. The control and treatment burrows were usually spaced far apart at each site to try and eliminate potential wafting of the urine scent to the control burrows.

Because temperatures during the experimental period often dipped below freezing, the liquid-treated wicks often froze. Therefore, wicks were frequently re-dipped in their respective urine or water control 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, and off the camera itself, so as not to obscure each camera’s ability to sense movement and take photos. However, brushing off the snow was not perfect and there may have been days when the snow buried the camera and burrow, even after snow had just been cleared. This severe weather was one major limitation of the field component of this experiment. 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 collected into a single database and examined. Of the 6,466 total photos, those not containing animals were deleted. For photos that did contain animals, it was possible that the camera traps had taken multiple pictures of the same animal(s) within a short period of time. I therefore decided to document photos by event, rather than just document every single photo collected, which would have led to overrepresentation of the amount of activity at some burrows, especially during the day. Due to apparent constraints with warming up the bulb for camera flash, more photos were taken per burst during the day than at night. This delay in flash for evening pictures resulted in approximately one-minute delays between many of the night photos. Because a photo burst could have started in the last few seconds of 10:00 am and continued through 10:01 am for example, I therefore decided that each event would span a period of two minutes, and any animals documented within the same two-minute period would only be counted once. For example, if a series of photo bursts contained pictures from 10:02 through 10:09, I only counted 4 events (10:02-10:03, 10:04-10:05, 10:06-10:07, and 10:08-10:09). This eliminated overrepresentation of daytime photos which sometimes had upwards of 5 to 10 photos of the same animal within a one-minute interval, activity that cameras would not have been able to capture at night. This ultimately led to a total of 1,734 usable photo events.

Because cameras were initially set up at burrows on different dates all throughout November and December 2017, it was not possible to compare activity at each burrow from day to day. Instead, burrow activity was averaged over periods of one week. For ease of analysis, all data were eliminated before the start of the first consecutive week on 20 November 2017 at 17:01 and after the last consecutive week on 15 January 2018 at 17:00 so that individual weeks could be compared to one another. This resulted in 8 total weeks that were used for this project (Table 1).

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 cameras were assigned to a starting week that corresponded to the first day of a consecutive week, and any previous days of data were eliminated for that camera. All cameras had at least 4 total weeks of data, including the 2 treatment weeks, and at least 2 weeks before treatment. The cameras were assigned to starting weeks based on their initial deployment date (Table 2).

Table 2. Week of deployment for each camera used during the study from 20 November 2017 through 15 January 2018.

Starting week	Cameras
1	40, 42, 43, 45, 49, 51
2	48, 50, 55
3	39, 54, 58, 59, 60
4	38, 53, 62
5	52, 56, 57, 61

Cameras that started in week 1 therefore had the most weeks of data averaged, and cameras that started in week 5 had the fewest. These limitations were due to time constraints on placing cameras, and confirming whether a burrow had Eastern cottontail activity.

Weather data for each day 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). This included maximum temperature in degrees Fahrenheit, minimum temperature in degrees Fahrenheit, average temperature in degrees Fahrenheit, snowfall in inches, and snow depth in inches. Fahrenheit and inches were converted to Celsius and centimeters, respectively. Snowfall and snow depth that were marked as "Trace" were assumed to be 0 cm. Unlike the camera trap weekly dates I assigned to each of the 8 weeks of the project (which ended at 17:00 and began at 17:01), weather data were only available per day. Therefore, I assigned weather to another set of weekly dates, for which one day of the week did not completely overlap with the assigned camera trap weeks (Table 3).

Table 3. Weeks to which weather and climate data were assigned during 21 November 2017 to 15 January 2018

Weather week	Dates
1	21 November 2017 to 27 November 2017
2	28 November 2017 to 4 December 2017
3	5 December 2017 to 11 December 2017
4	12 December 2017 to 18 December 2017
5	19 December 2017 to 25 December 2017
6	26 December 2017 to 1 January 2018
7	2 January 2018 to 8 January 2018
8	9 January 2018 to 15 January 2018

Statistical Analysis

All statistical analyses were performed in program R (R Core Team 2017).

Burrow characteristics

The burrow dimensions for all 21 burrows were recorded (Table 4), which included the burrow hole size (calculated by multiplying the greatest burrow width by the greatest burrow height, or length). A plot was then created with all the individual burrow sizes, along with the mean burrow size (Figure 2).

Red fox urine repellent trial

A series of Welch Two Sample t-tests were performed to compare the means in pre-treatment and post-treatment weekly burrow visitation for the 5 most abundant mammals found at the 21 camera traps, for both control and treatment burrows. Burrow visitation was defined as the sum total number of photo events from all the cameras per week. Weeks with high burrow visitation had more photo events than weeks with low burrow visitation. The five most abundant species included the Eastern cottontail (*Sylvilagus floridanus*), mouse (*Peromyscus* spp.), striped skunk (*Mephitis mephitis*), house cat (*Felis sylvestris catus*), and Virginia opossum (*Didelphis virginiana*). T-tests were performed that included all 21 burrows, or excluded burrows for species (other than Eastern cottontail, which was observed at every burrow at least once during both pre-treatment and post-treatment weeks) that were neither observed in the pre-treatment nor the post-treatment weeks.

Analysis of variance for significant results

Because t-tests revealed statistically significant differences in mean weekly burrow visitation between pre- and post-treatment weeks for 1 of the 5 species, analysis of variance (ANOVA) was conducted in R comparing the species' weekly burrow visitation against urine treatment, maximum weekly temperature, minimum weekly temperature, average weekly temperature, average weekly snowfall, total weekly snowfall, or average weekly snow depth.

Climate variable graphs

Plots (Figures 3 and 4) were created for both Eastern cottontails and striped skunks that compared weekly burrow visitation against maximum weekly temperature, minimum weekly temperature, average weekly temperature, average weekly snowfall, total weekly snowfall, and average weekly snow depth based on the information contained in Tables 8 and 9.

Results

Observed species

Table 4. 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. Mice, weasel, shrew, and North American sparrow species were only identifiable to the genus level or higher.

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

Over the course of this project, at least 22 mammal and bird species visited the burrows (Table 4). This list includes one species that was observed on 16 January 2018, the American Crow, despite the fact that I omitted photos from that date for quantitative analysis. However, I still believe it is relevant to mention all species observed during the winter season as part of the qualitative analysis.

Of the 1,752 total animals identified from the 1,734 total individual photo events (since some photo events contained multiple individuals) from 17 November 2017 to 16 January 2018, 158 contained pictures of unknown animals (not including unknown rodents and unknown birds) that I was unable to classify. This makes my identification rate approximately 91%.

Burrow characteristics

Most of the 21 evaluated burrows were relatively rectangular so I multiplied the widest width by the highest height, or longest length, to get the total opening area (Table 5). The average burrow size is 440.5 cm^2. Burrow size ranges from 156 cm^2 to 1,148 cm^2 (Figure 2).

Table 5. Dimensions for each of the 21 burrows monitored during 17 November 2017 to 18 January 2018 near Ithaca, New York.

Cam	Location	Burrow width (cm)	Burrow height (cm)	Burrow hole size (W x H) (cm^2)
40	East Hill barn	24	14.5	348
54	East Hill barn	23	13	299
42	Game Farm shack	28	41	1148
43	Game Farm shack	9	22	198
45	Game Farm shack	30	25	750
48	Turkey Hill beehive building	17	21	357
49	Turkey Hill beehive building	22	12.5	275
50	Turkey Hill beehive building	39	10.5	410
51	Turkey Hill beehive building	30	9	270
55	Turkey Hill beehive building	21	20	420
58	Turkey Hill beehive building	28	10	280
39	Lydell Lab	20	12	240
59	Lydell Lab	25.5	18	459
60	Lydell Lab	54	12	648
52	Stevenson road barns	35	10	350
56	Stevenson road barns	11.5	30	345
57	Stevenson road barns	40	17	680
61	Stevenson road barns	51	13	663
62	Cornell EEB Research Pond facility	12.5	12.5	156
38	Cornell EEB Research Pond facility	30	11	330
53	Cornell EEB Research Pond facility	50	12.5	625

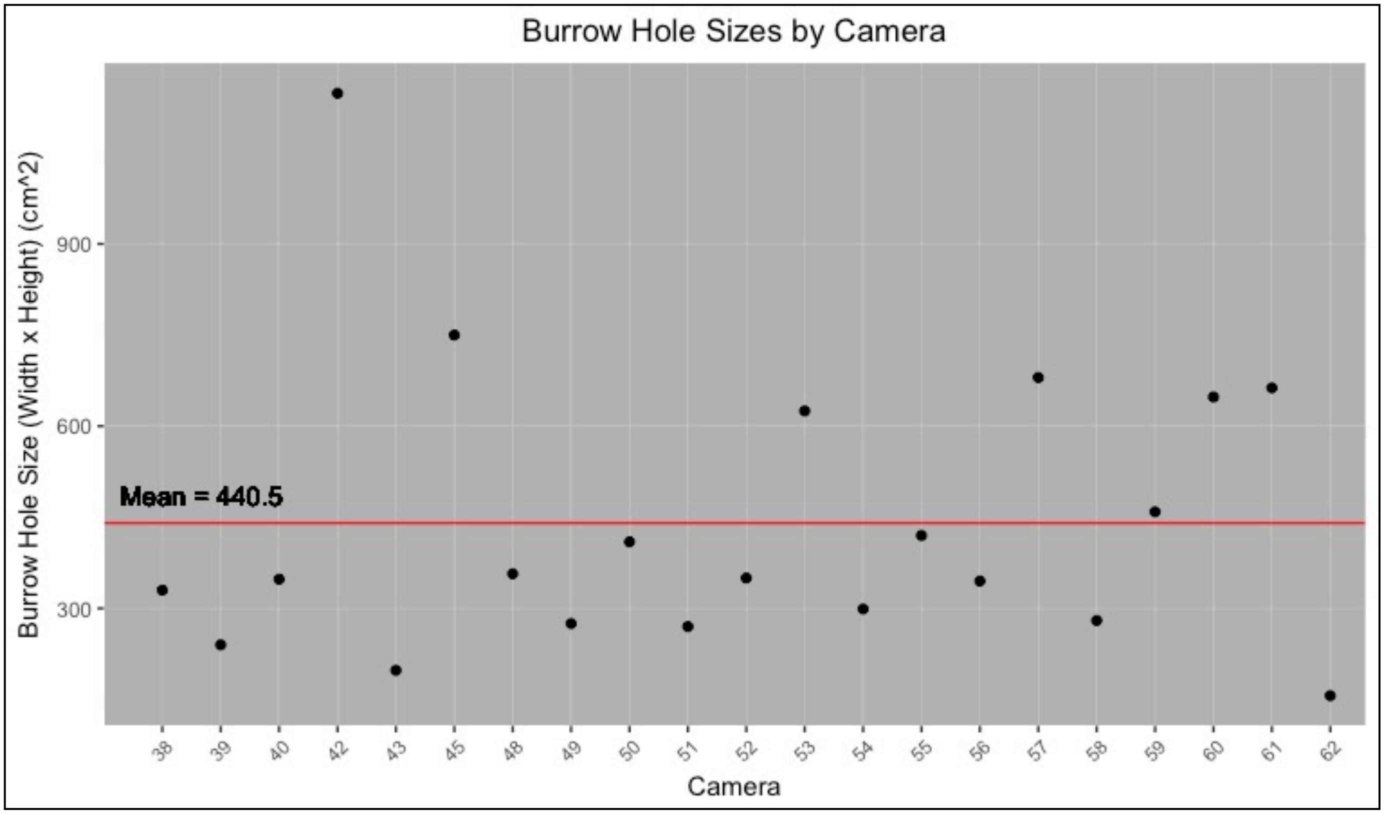

Figure 2. Plot of the calculated entrance hole sizes for the 21 evaluated burrows. The mean burrow size of 440.5 cm^2 is also marked as a red line.

Red fox urine repellent trial

Weekly burrow visitation (total number of photo events per week) was determined for each of the five most abundant species (Table 6). The eight weeks of the study were then split into "pre-treatment" and "post-treatment" groups upon which t-tests could be performed to determine statistically significant differences in weekly burrow visitation. Two t-tests were conducted for the Eastern cottontail because it was observed at all 21 burrows, while 4 t-tests were conducted for each of the other four most abundant mammal species observed (Table 7). The only statistically significant ($p < 0.05$) t-tests were ones including striped skunks observed at treatment burrows. This gives strong support that burrow visitation by skunks was different during pre- and post-treatment weeks. This warranted conducting analysis of variance to determine likely causes of this difference.

Choosing to exclude burrows that were neither visited by species during the pre-treatment nor post-treatment weeks did not make a difference in terms of finding a statistically significant result, but the specific t-test values were different than those that did not exclude any burrows.

Table 6. The average weekly burrow visits for the five most abundant mammal species.

Week	Cottontail Visits	Skunk Visits	Opossum Visits	Mouse Visits	Cat Visits
1	5.0	4.3	0.7	3.3	0.7
2	5.2	2.8	1.3	6.1	0.8
3	9.5	0.9	0.7	4.6	0.8
4	6.6	0.1	0.2	3.7	0.1
5	3.6	2.4	0.8	1.6	1.3
6	4.2	0.6	0	0.7	1.3
7	3.0	0.1	0	1.4	0.4
8	5.3	1.1	0.3	1.3	1.6

Table 7. Results of the Welch Two Sample t-tests performed in R for the five most abundant mammal species at burrows. T-tests were performed for both control and treatment groups, and using all burrows or only the subset of burrows that had at least one photo event instance either during pre-treatment or post-treatment weeks. Eastern cottontails were observed at all 21 cameras, so only 2 t-tests were needed. Statistically significant results are highlighted in bold.

Species	T-test	Result
Eastern cottontail	Control: all burrows	$t = -0.40166$, $df = 11.186$, $p = 0.6955$
	Treatment: all burrows	$t = 1.4914$, $df = 19.529$, $p = 0.1518$
Striped skunk	Control: all burrows	$t = 0.46038$, $df = 11.793$, $p = 0.6536$
	Control: 1 burrow excluded	$t = 0.49331$, $df = 9.8875$, $p = 0.6326$
	Treatment: all burrows	$t = 2.2801$, $df = 16.978$, $\mathbf{p = 0.0358}$
	Treatment: 3 burrows excluded	$t = 2.5635$, $df = 13.525$, $\mathbf{p = 0.023}$
Virginia opossum	Control: all burrows	$t = 1.342$, $df = 6.2707$, $p = 0.2261$
	Control: 3 burrows excluded	$t = 1.4799$, $df = 3.1654$, $p = 0.2309$
	Treatment: all burrows	$t = 0.29401$, $df = 20.666$, $p = 0.7717$
	Treatment: 8 burrows excluded	$t = 0.35773$, $df = 6.705$, $p = 0.7315$
House cat	Control: all burrows	$t = 0.15692$, $df = 11.79$, $p = 0.878$
	Control: 4 burrows excluded	$t = 0.3656$, $df = 3.7514$, $p = 0.7343$
	Treatment: all burrows	$t = -0.74125$, $df = 23.408$, $p = 0.4659$
	Treatment: 7 burrows excluded	$t = -0.99606$, $df = 11.229$, $p = 0.3402$
Mouse	Control: all burrows	$t = 0.42988$, $df = 11.738$, $p = 0.6751$
	Control: 3 burrows excluded	$t = 0.46245$, $df = 5.978$, $p = 0.6601$
	Treatment: all burrows	$t = 0.91024$, $df = 19.876$, $p = 0.3736$
	Treatment: 7 burrows excluded	$t = 0.99994$, $df = 9.4823$, $p = 0.3422$

Analysis of variance for significant results

The results from Table 5 indicated that there was a statistically significant difference in pre-treatment and post-treatment weekly burrow visitation by striped skunks, so analysis of variance (ANOVA) was conducted to determine likely causes of this difference. Results from ANOVA (Table 8) revealed that weekly skunk visitation to burrows was likely explained by minimum weekly temperature and average weekly temperature, because p-values for the two predictors were statistically significant ($p < 0.05$). As temperature decreased, less activity was observed around burrow entrances. There was also some evidence that maximum weekly temperature influences skunk burrow use, since the p-value from the relevant ANOVA test was marginally close to being statistically significant ($p = 0.0714$). In fact, all other predictors including average weekly snowfall, total weekly snowfall, and average weekly snow depth were closer to being significant in their ANOVA tests than urine treatment, based on their p-values. This provides support for weather and climate, especially temperature, as more important factors in determining skunk use of burrows than the presence of red fox urine.

Table 8. Results of Analysis of Variance performed in R for striped skunks weekly burrow visitation. Statistically significant results are highlighted in bold.

Model	Result
Skunk visits: Treatment	df = 1, F = 1.032, p = 0.349
Skunk visits: Max Weekly Temperature	df = 1, F = 4.78, p = 0.0714
Skunk visits: Min Weekly Temperature	df = 1, F = 11.13, **p = 0.0157**
Skunk visits: Average Weekly Temperature	df = 1, F = 10.31, **p = 0.0183**
Skunk visits: Average Weekly Snowfall	df = 1, F = 3.108, p = 0.128
Skunk visits: Total Weekly Snowfall	df = 1, F = 2.83, p = 0.143
Skunk visits: Average Weekly Snow Depth	df = 1, F = 3.873, p = 0.0966

Climate variable graphs

Weekly climate variables were obtained from the Game Farm Road weather station (Table 9). Little to no apparent correlation can be seen in graphs of Eastern cottontail weekly burrow visitation plotted against other weather and climate variables (Figure 3). This lack of observed trends is consistent with the results obtained from the t-tests for Eastern cottontails, in which there were no statistically significant differences in weekly burrow visitation during pre-treatment and post-treatment weeks. Though weekly burrow visitation appears to follow weekly snowfall variables as in Figure 3d and Figure 3e, these correlations are likely visually misleading. However, visually apparent correlations in Figure 4 for striped skunk weekly burrow visitation plotted against weather and climate variables, especially minimum weekly temperature (Figure 4b) and average weekly temperature (Figure 4c), may represent real correlations, based on the previous t-tests and ANOVAs.

Table 9. Weekly weather and climate variables

Week	Maximum Temp (˚C)	Minimum Temp (˚C)	Average Temp (˚C)	Average Snowfall (cm)	Total Snowfall (cm)	Average Snow Depth (cm)
1	13.9	-3.3	2.8	0.0	0.0	0.0
2	12.2	-6.1	1.8	0.0	0.0	0.0
3	10.6	-7.8	-0.7	0.2	1.0	0.0
4	1.1	-18.9	-6.7	1.6	10.9	4.4
5	10.0	-5.0	0.7	0.6	4.1	0.4
6	-2.2	-19.4	-12.9	1.5	10.7	4.7
7	-4.4	-19.4	-14.2	0.8	4.6	9.8
8	16.7	-22.8	-3.6	2.5	17.5	10.5

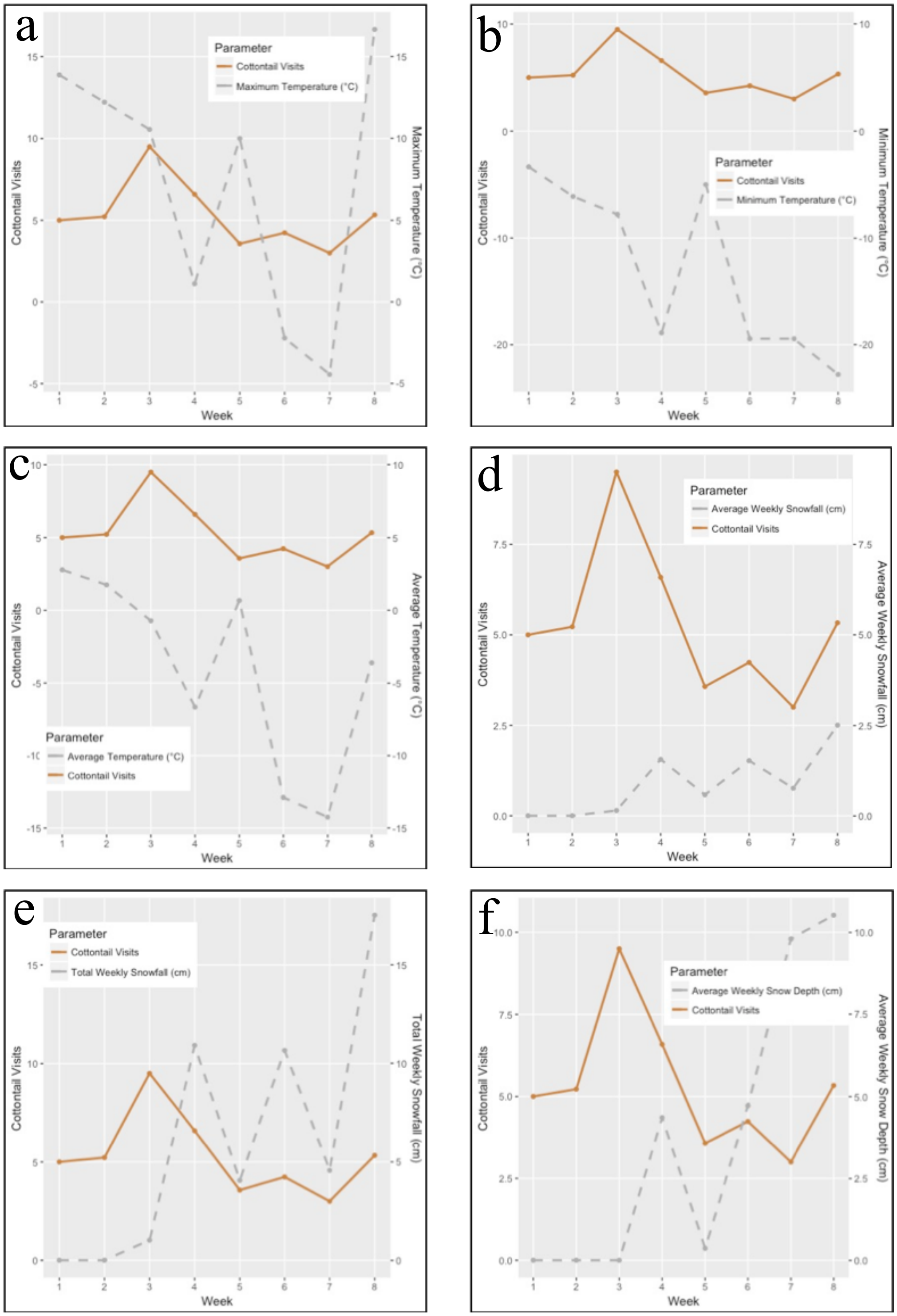

Figure 3. (a) Eastern cottontail visits and maximum temperature across weeks. (b) Eastern cottontail visits and minimum temperature across weeks. (c) Eastern cottontail visits and average temperature across weeks. (d) Eastern cottontail visits and average weekly snowfall across weeks. (e) Eastern cottontail visits and total weekly snowfall across weeks. (f) Eastern cottontail visits and average weekly snow depth across weeks.

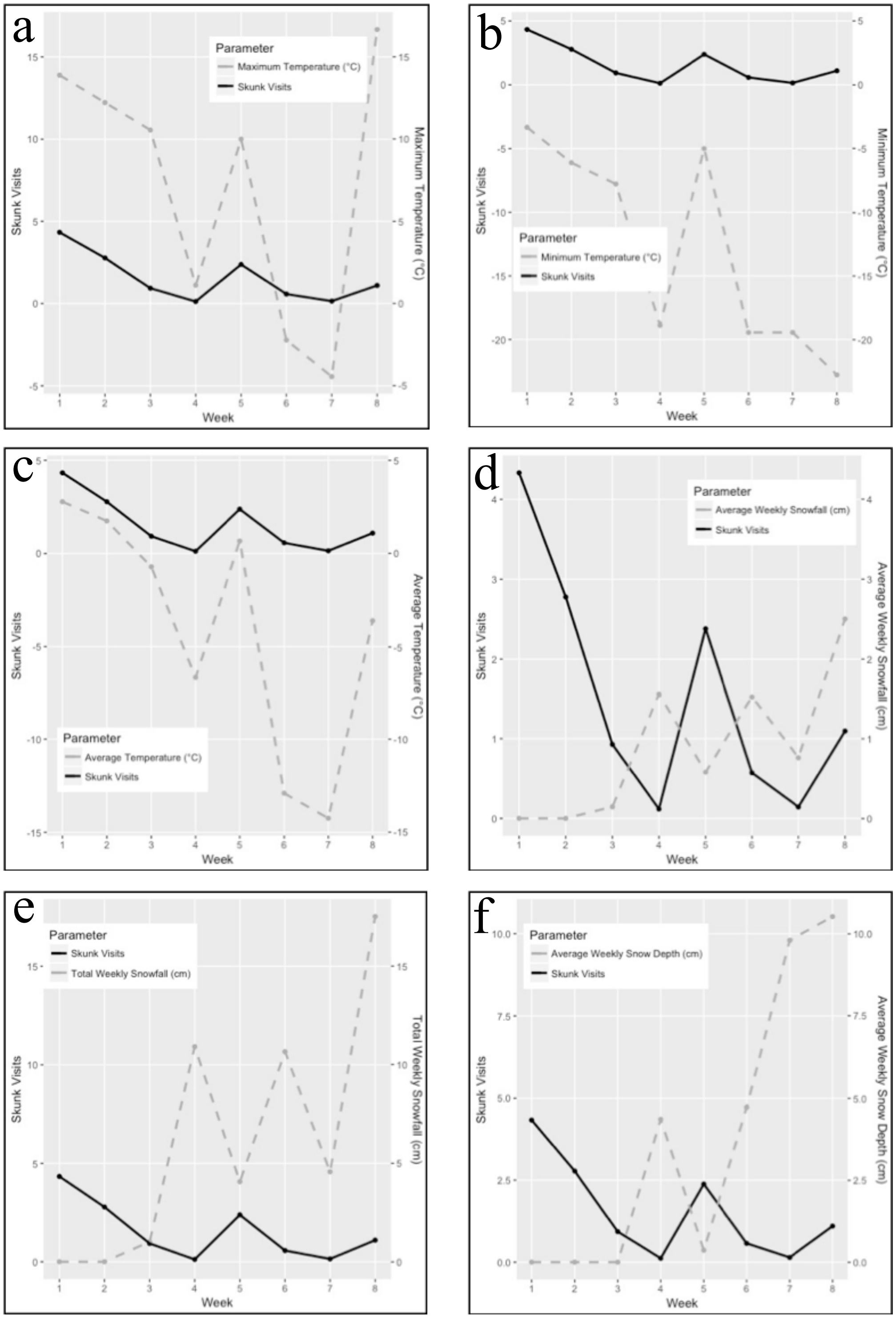

Figure 4. (a) Skunk visits and maximum temperature across weeks. (b) Skunk visits and minimum temperature across weeks. (c) Skunk visits and average temperature across weeks. (d) Skunk visits and average weekly snowfall across weeks. (e) Skunk visits and total weekly snowfall across weeks. (f) Skunk visits and average weekly snow depth across weeks.

Discussion

Observed species

The sheer diversity of animal species observed at presumptively abandoned woodchuck burrows over the course of one winter season indicates how important these burrows are to a variety of organisms, especially mammals. At least 16 mammal species were observed, in addition to at least 6 avian species (some species could not be identified to the species level). This larger mammalian diversity likely reflects how these mammals are confined to the ground, whereas many bird species spend much of their time airborne, and roosting in trees. It is also unlikely that birds actually enter the burrows and take refuge from the elements – they were merely observed around the entrances.

Although Eastern cottontails were the primary mammals using old woodchuck burrows in winter based on the number of events they were observed, a surprising number of photos documented activity of striped skunks, Virginia opossums, house cats, and mice in and around burrows. Skunk use of burrows, including those dug by woodchucks (Godin 1977), has been previously observed in Ithaca, New York dating back to at least 1937 (Hamilton 1937). Skunks are also known to enter a state of dormancy in the winter, though rather than true hibernation, the extent of their winter inactivity is better defined as a daily shallow torpor (Geiser 2013, Melvin and Andrews 2009). Other studies in Minnesota (Sunquist 1974) and Manitoba, Canada (Mutch and Aleksiuk 1977) have not found as much skunk activity around burrows, though this might be due to the severity of winters in those places, or limitations in study design, which relied on radio telemetry and visual observations. As a contrast, the camera traps used in this project have the advantage that they can continue logging data when humans are not out with radio telemetry receivers in blizzard conditions, or in the middle of the night, a time when many skunks were observed to be active during this project. Radio collars on study animals also limit observations only to those animals, whereas camera traps can uniformly capture the activity of many animals, including that of non-target individuals. Radio collars themselves may also affect the behavior of study organisms (Gibson et al. 2013), and even those that are motion-sensitive are not able to document certain animal behaviors (Gillingham and Bunnell 1985). Camera traps are not without their limitations, though. The large amounts of data collected by camera traps can often overwhelm researchers in their analysis due to problems with image processing, storage, and backup of photos (Newey et al. 2015). Technological failures such as batteries dying, motion sensors not picking up movement, or software glitches leading to incorrectly recorded dates and times may introduce false negatives and false positives (Newey et al. 2015, Caravaggi et al. 2017, Pirie et al. 2016). Camera flash or presence may also impact behavior (Meek et al. 2015, Caravaggi et al. 2017). However, many of these issues pale in comparison to the value of obtaining otherwise unavailable data on extremely rare, cryptic, or critically endangered species (Rahman et al. 2016, Jackson et al. 2006).

Virginia opossums are also known to use burrows (Godin 1977), including those of mountain beavers (*Aplodontia rufa*) (Engeman et al. 1991) and armadillos (Lay 1942). I herein document them using burrows likely dug by woodchucks, especially around man-made structures. 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 (Godin 1977, McManus 1969) in order to survive, compared to other times of the year. Mice are also known to use burrows, but are less constrained by the size of existing burrows because they are smaller mammals than woodchucks. As such, mice can nest in a variety of places, from under old stumps to mere holes in walls (Godin 1977). Their activity around the burrows in this study is less surprising.

It is of particular note that local house and feral cats frequently visited and entered burrows during winter. Although cats are not native to North America, since their introduction over 175 years ago (George 1974), the cat population in the United States may now number well over 80 million, and they are estimated to take avian and mammalian prey in the billions (Loss et al. 2013). Cats are also strong competitors with raptors for prey mice, which may implicate them in the declines of many raptor species (George 1974). Due to their abundance and ability to capture prey, their competition may exacerbate this decline in winter, when prey are much scarcer. Cats may also have significant negative impacts on burrowing species, as they have been implicated in reducing the nesting success and burrow densities of seabirds on Marion Island in South Africa (Dilley et al. 2017). Cats are apparently knowledgeable of the winter burrow habits of many mammalian species, as they were observed entering and leaving burrows many times over the course of this project that were also being used by other species, likely as they were searching for prey. Though none were captured and marked, by using the unique marking pattern observed on many of these cats, particularly the orange and grey tabby varieties, it is evident that many of these local suburban cats patrol the same areas repeatedly. In one case, a dark gray tabby cat was observed stepping in the exact same spot with the exact same foot hours after it had patrolled the burrow.

Knowledge that prey species use burrows may not be unique to house cats because bobcats, gray foxes, mink, weasels, and a coyote were also observed approaching and examining burrows during this project. This intelligence is likely characteristic of many northeastern carnivores, which provides evidence that they have search images for many different places to look for prey. Although bobcats, coyotes, and other larger predators could only examine burrow entrances, mink and weasels were observed exiting burrows, species which are known to enter the burrows of many of their prey species (Vaughan 1961, Zielinski 2000). Mink and other mustelids may even have knowledge of the circadian rhythms of their prey, as their periods of activity coincide with those of their prey (Zielinski 2000, Zielinski 1986, Gerell 1969). The finding of the bobcat at a burrow by the East Hill barn may also show that bobcats may live closer to suburban areas, and be more integrated in suburban ecosystems, than originally believed. This finding may have positive implications for the ability of bobcats to adapt to urban sprawl, but may also imply the possibility of human-wildlife conflicts or bobcat-house cat interactions.

Another important finding from this project is the fact that many different species used the same burrows within short periods of time. For example, at camera 40 between November 20 and November 28, I documented use of a single burrow by cottontails, mice, a skunk, an opossum, cats, and chipmunks. This has two important implications. First, this implies that burrow use is temporary. This means that there may be unique cues that cause specific animals to seek out or leave burrows, and that some cues may be different for different species. The usual inference that temperature and weather variables cause animals to take shelter may not be the biggest factor at play. These factors may aid in building better models of when certain species are likely to use burrows. The second implication is that multiple animals may be using the same burrow at the same time, which means there may be an increased potential for the coexistence of multiple species in a small space. For example, at camera 51 on November 23, 2017, I documented a skunk exiting a burrow only 14 minutes after a cottontail had left it (Figure 5). Though it is possible the camera failed to take a picture of the skunk or cottontail initially entering the burrow, the fact that the photos were taken greater than 1 minute apart rules out the possibility that the camera flash was still warming up for a second picture after it took the first. The two species were therefore likely to both be in the burrow at the same time. This may imply that burrows are communal havens for many species, perhaps in the same way as communal watering holes in Africa may function for the various predators and prey of the Serengeti. Alternatively, the presence of multiple chambers within burrows (Grizzell 1955) may allow for burrow use by multiple species with little to no interaction between them.

It is apparent that burrows are important to the diversity of species observed using them. Because most of these burrows were likely dug out by woodchucks, the value of woodchucks as suburban ecosystem engineers is likely immense. Although woodchucks may often be seen as pests to humans (indeed one monitored burrow in this study had been dug next to a pipe that fed water into a horse trough, which allowed cold air in, and subsequently caused the water to freeze, restricting water to the horses), they may actually be helping facilitate the coexistence of many mammalian species in suburban areas. Additionally, because a majority of the monitored burrows in this project were underneath or around older man-made structures often in disrepair, humans may indirectly be helping animals to survive the winter. In this way, humans might even be considered useful ecosystem engineers. However, humans undoubtedly have also contributed many problems, especially as it concerns the introduction of non-native species, as was the case with the cats observed at several sites. Also, a non-native Ring-necked Pheasant was seen at cameras 49, 50, and 51 near the Turkey Hill beehive building, which likely escaped from the nearby New York State Department of Environmental Conservation pheasant farm operation.

Figure 5. A skunk was seen leaving a burrow only 14 minutes after an Eastern cottontail had exited in photos taken by camera 51 set up at the Turkey Hill beehive building on 23 November 2017.

Burrow characteristics

The size of the burrow is the main limitation of the species that are able to use the burrow. However, Eastern cottontails occupied burrows from as small as 156 cm^2 to as large as

1,148 cm^2. This likely reflects the Eastern cottontail's adaptability as a species to occupying unused spaces, rather than requiring spaces of specific dimensions. The 156 cm^2 burrow was used exclusively by Eastern cottontails, while the burrow that was 1,148 cm^2 was used by Eastern cottontails, skunks, and mice. It is interesting to note that the largest burrow was not used the most by different species. This provides evidence that just because a burrow is large enough for a specific species, other characteristics of the burrow may not make it optimal. Other such factors might include the amount of cover above and around the burrow, the availability of foraging sites nearby, the presence of competitor species already occupying the burrow, or the thermoregulatory and insulating properties of the burrow, among others.

Effect of red fox urine on burrow activity

The results of t-tests do not give support for an effect of red fox urine on the change in Eastern cottontail burrow use in winter. However, because of the importance of Eastern cottontails to the red fox diet, and predator scent cues to many mammalian prey species, it is unlikely that the possibility of an olfactory relationship between red foxes and Eastern cottontails can be ruled out. One reason is because Eastern cottontails may have habituated to the scent of red fox urine by their burrows, even within 1 day of treatment (Figure 6).

Another reason may be that urine may not modulate behavior around previously colonized shelters. The scent of a predator may be information an Eastern cottontail uses to avoid following a novel path in a forest, but a cottontail may be comfortable with scents around familiar areas where it may know of a variety of holes into which it can quickly escape from a fox. This might also suggest that the physical characteristics of winter are more of an immediate threat to Eastern cottontails than the rare or even occasional encounter with a fox. 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 fox). As a result, olfactory cues from nearby predators may not be paid much attention in the winter by Eastern cottontails. The cost of moving to a new burrow and risking exposure to the elements or predation may be too high in comparison to any inconvenience from a predator's smell at the current burrow. The lack of a statistically significant difference between burrow use before and after urine treatment in this experiment provides strong support for this conclusion.

Lastly, although there was no observed effect of urine treatment on cottontail burrow use, there may have been short-term changes in behavior. For example, Eastern cottontails may have frozen in place, run away, or had some other alteration in behavior on the first day of treatment, when the urine scent was novel. However, this behavior may not have been observed for at least three reasons. The first is that 1 January 2018, the date the urine treatment first went out, was a particularly cold day, with an average temperature of -16.3 ˚C. This may have possibly confounded observing any change in behavior, as little activity in general was observed that day (9 total photo events across all burrows, only 5 of which were cottontails). Eastern cottontails may have hunkered down in their burrows for the day. The second reason is that the settings of the camera traps used in this experiment were not able to capture behavior on short time scales. By the time all the urine treatments had been set out that day at 17:00, it was beginning to get dark. This meant that camera traps were likely switching to their evening functions that used flash. And as discussed earlier, there were often delays greater than 1 minute between photos taken at night. To capture and accurately document behaviors that may have lasted only a few seconds or more, camera traps would better have been set on video-taking mode rather than 3-picture bursts. Regardless, camera traps were still effective at capturing a range of behaviors for many species. Thirdly, Eastern cottontails may actually have sensed and responded to the urine and stayed in or away from burrows, which would explain the lack of observed activity.

The small sample sizes in this project and high variability in burrow visits among burrows likely contributed to the lack of statistical significance found at urine treatment burrows between pre-treatment and post-treatment weeks. However, there was a reduction in Eastern cottontail burrow visitation between pre- and post-treatment weeks at urine-treated burrows, from a mean of 6.2 to 3.3 weekly visits. There was also less of a difference between the visitation means at control burrows (4.7 in pre-treatment weeks and 5.9 visits in post-treatment weeks). Taken together, this suggests that a statistically significant pattern might have been observed if there had been a larger sample size. Additionally, because the start of some weeks did not coincide with the deployment date of camera traps towards the beginning of the project, the initial effect of having camera traps set up at burrows was not adequately taken into account. However, if Eastern cottontails are able to rapidly habituate to the urine of their predators, they may show a similar trend in habituating to foreign objects like camera traps. Indeed if this was not the case, it is unlikely that 789 photo instances would have been observed.

Throughout the entire experiment, no red foxes were observed at burrows, though a gray fox was, along with other mammalian carnivores known to use scent marking (e.g., bobcats and a coyote). Scent marking by carnivores is an incredibly important behavior; 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 (Henry 1977). Therefore, there are a few plausible reasons why no red foxes were observed at burrows, apart from red foxes not responding to scent marking cues, which is unlikely (but see Banks et al. 2016). First, there may have been no red foxes denning near to, or patrolling the vicinity of the 6 study sites. Indeed the Cornell EEB Research Pond facility is gated off with a tall, barbed wire metal fence, so red foxes may not have been physically able to enter the facility grounds. Second, red foxes might also not prefer to be around more suburban areas such as the 6 sites in this project. Third, the red fox urine treatment may actually have been an effective cue which caused red foxes to stay clear of treated burrows to avoid intraspecific competitive fights in an already challenging winter environment. However, previous research has demonstrated that red foxes are actually attracted to conspecific scent cues, rather than avoiding them, which makes this absence of red foxes in this project even more perplexing (Arnold et al. 2011, but see Banks et al. 2016). Therefore, more research is needed to document the effects of red fox urine on red fox behavior.

Though there was a statistically significant difference in burrow visitation by striped skunks at red fox urine-treated burrows, this is more likely due to the effects of Northeastern winter temperatures (specifically, minimum and average weekly temperatures) than urine. Figure 4b and Figure 4c help reveal how closely skunk appearance at burrows is correlated with temperature. Skunks do hibernate to some degree, and this correlation likely reflects how they try to conserve energy in particularly cold weeks. Additionally, small sample sizes, especially for the water control treatment (only 7 burrows), may be contributing to false statistically significant t-test results, or a lack thereof.

Figure 6. An Eastern cottontail was observed at a burrow being treated with red fox urine only one day after the treatment was set up on 1 January 2018. This image was taken by camera 38 at the Cornell EEB Research Pond facility on 2 January 2018. The urine-treated scent wick can be seen in the background.

Other behavioral observations

It is generally believed that Eastern cottontails forage on woody plants in winter, girdling tree bark and causing damage to both wild and native plants in suburban regions (Baker et al. 2015, Dalke and Sime 1941, Kellner and Swihart 2017). However, cottontails were observed foraging through snow on more herbaceous vegetation in this project (Figure 7).

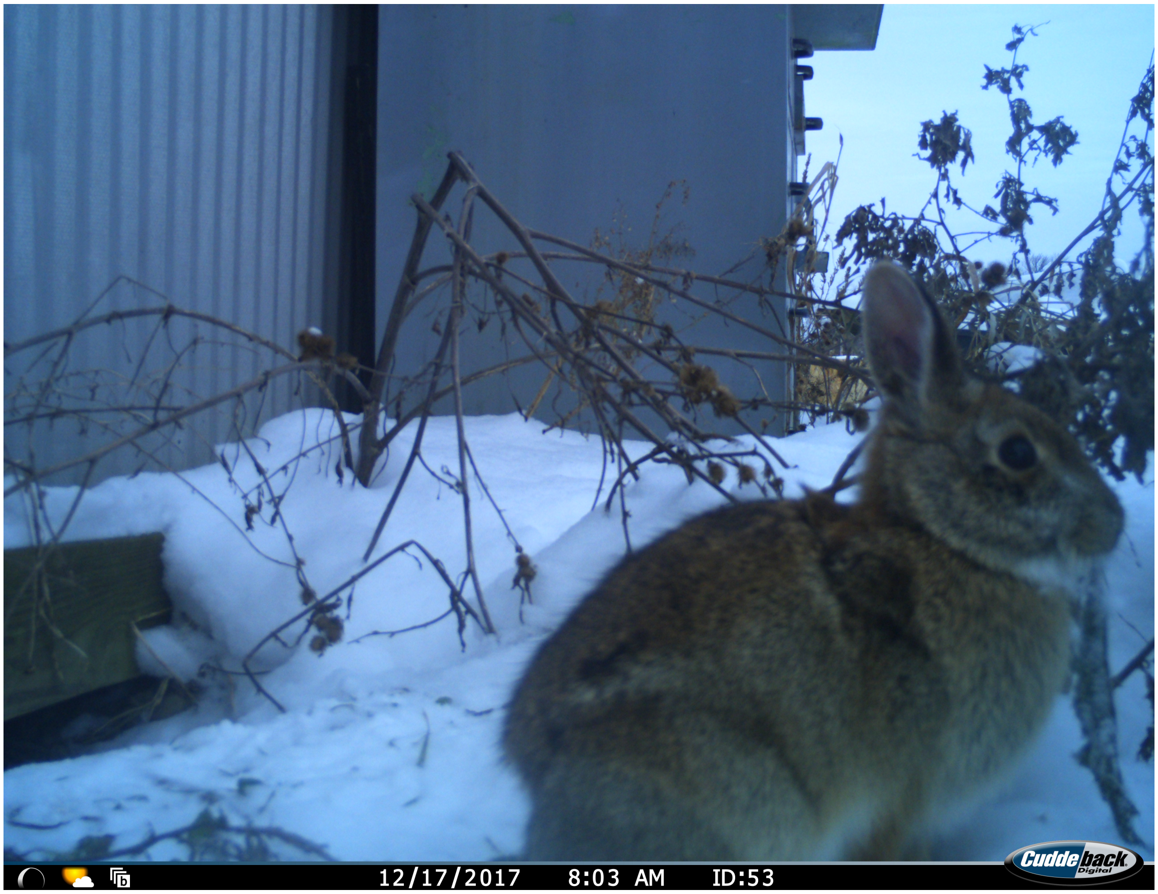

Figure 7. An Eastern cottontail was observed eating herbaceous vegetation in the snow on 17 December 2017 by camera 53 at the Cornell EEB Research Pond facility.

Conclusions

Though this project did not provide evidence that red fox urine can modulate Eastern cottontail burrow use in winter, there were many important implications of conducting this quasi-study-experiment. This project is a testament to the value of camera traps in wildlife ecology research, as they can document a range of animal behavior during times that are challenging for humans to record data (e.g., during winter, late at night, and during inclement weather). This project was also able to clearly document that Eastern cottontails use burrows, likely dug by woodchucks, under and around abandoned man-made structures during the winter months. Expert opinion on the burrow habits of cottontails is now a proven fact, at least in New York

State. North American rabbit burrow use is also known from Michigan (Linduska 1947), and in Europe by European rabbits (*Oryctolagus cuniculus*) who dig their own burrows (Kolb 1985). The winter burrow use by Eastern cottontails documented in this project also has implications for the conservation of other North American lagomorphs, notably the New England cottontail (*Sylvilagus transitionalis*), which is listed as a species of special concern in New York State (New York Natural Heritage Program 2017). Knowledge from this project may aid in future conservation management plans aimed at protecting habitat containing potential burrows that New England cottontails may use during the winter months.

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