Prey Dynamics Before, During, and After Red Foxes Den on an Urban University Campus

Maximilian L. Allen and Remington J. Moll

Volume 10, 2023 Urban Naturalist No. 66

♦ The *Urban Naturalist* is an open-access, peer-reviewed, and edited interdisciplinary natural history journal with a global focus on urban and suburban areas (ISSN 2328-8965 [online]).
♦ The journal features research articles, notes, and research summaries on terrestrial, freshwater, and marine organisms and their habitats.
♦ It offers article-by-article online publication for prompt distribution to a global audience.
♦ It offers authors the option of publishing large files such as data tables, and audio and video clips as online supplemental files.
♦ Special issues - The *Urban Naturalist* welcomes proposals for special issues that are based on conference proceedings or on a series of invitational articles. Special issue editors can rely on the publisher's years of experiences in efficiently handling most details relating to the publication of special issues.
♦ Indexing - The *Urban Naturalist* is a young journal whose indexing at this time is by way of author entries in Google Scholar and Researchgate. Its indexing coverage is expected to become comparable to that of the Institute's first 3 journals (*Northeastern Naturalist*, *Southeastern Naturalist*, and *Journal of the North Atlantic*). These 3 journals are included in full-text in BioOne.org and JSTOR.org and are indexed in Web of Science (clarivate.com) and EBSCO.com.
♦ The journal's editor and staff are pleased to discuss ideas for manuscripts and to assist during all stages of manuscript preparation. The journal has a page charge to help defray a portion of the costs of publishing manuscripts. Instructions for Authors are available online on the journal's website (http://www.eaglehill.us/urna).
♦ It is co-published with the *Northeastern Naturalist*, *Southeastern Naturalist*, *Caribbean Naturalist*, *Eastern Paleontologist, Journal of the North Atlantic*, and other journals.
♦ It is available online in full-text version on the journal's website (http://www.eaglehill.us/urna). Arrangements for inclusion in other databases are being pursued.

Cover Photograph: A red fox parent and puppy interacting outside of their den on the University of Illinois campus. Photograph © Maximilian Allen.

The ***Urban Naturalist*** (ISSN # 2328-8965) is published by the Eagle Hill Institute, PO Box 9, 59 Eagle Hill Road, Steuben, ME 04680-0009. Phone 207-546-2821 Ext. 4. E-mail: office@eaglehill.us. Webpage: http://www.eaglehill.us/urna. Copyright © 2023, all rights reserved. Published on an article by article basis. **Special issue proposals are welcome**. The *Urban Naturalist* is an open access journal. **Authors**: Submission guidelines are available at http://www.eaglehill.us/urna. **Co-published journals:** The *Northeastern Naturalist*, *Southeastern Naturalist*, *Caribbean Naturalist*, and *Eastern Paleontologist*, each with a separate Board of Editors. The Eagle Hill Institute is a tax exempt 501(c)(3) nonprofit corporation of the State of Maine (Federal ID # 010379899).

Prey Dynamics Before, During, and After Red Foxes Den on an Urban University Campus

Maximilian L. Allen[1*] and Remington J. Moll[2]

Abstract - Many mammals use dens seasonally to protect neonatal young from weather and predators. Carnivores often become central place foragers during denning, which can influence the local abundance of prey. We began monitoring a site with camera traps on the University of Illinois campus in Urbana, Illinois in February 2021, which a pair of *Vulpes vulpes* Linnaeus (Red Fox) started using for a den in March 2022. This provided a natural study to determine how the relative abundance of prey changed in relation to Red Foxes denning. Red Fox use of the camera trap site sharply increased when they began denning, with a peak of 17.2 visits/day in April 2022 compared to an average of 0.7 visits/day during non-denning months. *Sylvilagus floridanus* Allen (Eastern Cottontail) relative abundance was relatively steady from July 2021 through March 2022 (average of 0.9 visits/day), when their relative abundance decreased to no visits during April and May 2022 as Red Fox relative abundance peaked. *Sciurus carolinensis* Gmelin (Eastern Gray Squirrel) exhibited a similar pattern, with high abundance from September 2021 through March 2022 (average of 6.9 visits/day) before a substantial decrease to the minimum of 0.4 visits/day in May 2022 when Red Foxes were denning. Thus, Red Fox denning coincided with strong decreases in the relative abundance of Eastern Gray Squirrels and Eastern Cottontails – both key prey species of Red Foxes in the Midwestern USA. The pattern of prey dynamics at the den site resembled that at two nearby reference sites, but the fluctuations were stronger, especially for Eastern Gray Squirrels which exhibited a significant ($p < 0.05$) reduction at the den site but not at reference sites. Our study supports previous studies indicating that when animals shift their habits to become central place foragers, they can change the activity patterns of other wildlife species in the vicinity. Our results also suggest that denning activity could act as a localized pulse of predation risk that modifies prey dynamics in urban systems.

Introduction

Seasonal use of dens when raising neonatal young is an integral aspect of the ecology of many mammals. Survival is often lower for dependent, neonatal young than other life stages (Trapp et al. 2008), and mammals employ a variety of behavioral adaptations to reduce neonate mortality risk. Particularly notable among these adaptations is the use of dens, which provide protection from inclement weather and predators (Storm et al. 1976, Yovovich et al. 2020). The variety of different species that use dens to increase survival of young highlights the importance of this strategy for mammals.

Denning by carnivores often leads to intensive use of a site as they temporarily shift their habits to become central place foragers (Yovovich et al. 2020). The intensive use of sites can have changes on the vegetative structure (Gharajehdaghipour et al. 2016, Obidzinski and Gleogowski 2005, Schmitz et al. 1997) and on the abundance of prey and other wildlife (Kujawa and Łęcki 2008, Ruiz-Olmo et al. 2003). Dens are often located in areas with cover that are inconspicuous to predators, but also in areas rich in food resources to meet the high

[1]Illinois Natural History Survey, Prairie Research Institute, University of Illinois, 1816 S. Oak Street, Champaign, IL 61820, USA. [2]Department of Natural Resources and the Environment, 56 College Road, University of New Hampshire, Durham, NH 03824, USA. [*]Corresponding author: maxallen@illinois.edu.

Associate Editor: Michael McKinney, University of Tennessee.

energetic demands of neonatal young (Trapp et al. 2008, Yovovich et al. 2020). During this time when dens become the center of animals' activity, the parents make forays around and away from the den site to secure food and other resources. In theory, prey that are found closer to the den are more prone to predation due to their proximity to the home range center of the carnivore. As such, prey populations in the immediate area may become depleted (Kujawa and Łęcki 2008, Ruiz-Olmo et al. 2003), leading to increasingly longer foraging bouts by parents, which may result in decreasing energetic gains and lower survival for young.

Vulpes vulpes Linnaeus (Red Fox) are diet generalists that are widespread across northern latitudes (Frey 2013). In the midwestern USA, Red Foxes generally pair bond starting in December or January and mate in January or early February (Storm et al. 1976). Females give birth to one litter of an average of three to four (range one to twelve) kits each year in spring (Storm et al. 1976). Kits are born inside the den in late March or April (Storm et al. 1976) and emerge from dens at 3–5 weeks of age (Macdonald 1980, Seton 1925). Kits are initially restricted in movements to the immediate area of the den for about a month (Storm et al. 1976), but continue to expand their activity away from the den until dispersal (Robertson et al. 2000) which often occurs in late September or October (Storm et al. 1976). Red Fox dens are usually in burrows, either dug into the ground (sometimes dug by marmots or other burrowing mammals) or under buildings (Marks and Bloomfield 2006). Red Foxes will sometimes move dens when disturbed (Storm et al. 1976) or for other reasons. Red Foxes will den in developed urban areas, but tend to select areas away from roads (Zaman et al. 2020); they also avoid properties with *Canis lupus familiaris* Linnaeus (Domestic Dog) (Marks and Bloomfield 2006) or dominant carnivores such as *Canis latrans* Say (Coyote) (Voigt and Earle 1983). Red Foxes tend to feed on small mammalian prey, including mice, voles, cottontails, and squirrels, as well as fruit, nuts, and snakes (Murie 1936). As a diet generalist, Red Foxes often eat the food or prey that is most abundant and easiest to acquire (Murie 1936). During denning and kit-rearing, the male fox will typically bring prey back to the den, and excess prey may be cached for later consumption (Seton 1925). It follows that items brought and cached at the den site by Red Foxes tend to reflect their availability in the proximate landscape. Given that denning occurs in late winter and early spring, these items tend to be composed of a higher proportion of animal matter compared to other seasons such as fall when non-animal matter (e.g., fruit) plays a larger role in Red Fox diets (Korschgen 1959, Seton 1925).

As part of a long-term project with the Urban Wildlife Information Network (Magle et al. 2019), we began monitoring a site on the University of Illinois campus in Urbana, Illinois in February 2021. A pair of Red Foxes started using a nearby barn as a den in March 2022, providing a natural study to determine if the relative abundance of prey changed over time at the den site. While this change in prey availability has been shown with songbirds (Kujawa and Łęcki 2008) and waterfowl (Ruiz-Olmo et al. 2003), Red Foxes have a variable diet based on abundance of prey, thus it is less known whether Red Foxes produce a similar effect on mammalian prey. We therefore sought to 1) quantify the relative abundance of Red Fox prey before, during, and after the denning period, and 2) compare the patterns at the den site to nearest neighbor sites to make inferences regarding the potential for Red Foxes to impact local prey communities near den sites.

Materials and Methods

Study area

Our study area was located in Champaign County, Illinois, USA (2,580 km^2). This area is typical of the landscape in central Illinois with small deciduous woodlots dominated by oak (*Quercus* spp.) and grasslands surrounded by large amounts of predominately corn, soybean, and wheat row crop agriculture (Bauder et al. 2022). The major urban areas in the county are the adjoining cities of Champaign and Urbana (combined human population of ~220,000), which surround the campus of the University of Illinois. The region has a continental climate, with cold winters and warm summers, and annual precipitation of about 100 cm. The mammalian wildlife community of this area is comprised of species typical of the midwestern USA, including many small rodents (e.g., Microtine voles and *Peromyscus* spp.), squirrels (*Sciurus* spp.), and lagomorphs, as well as medium and larger bodied species such as Coyotes and *Odocoileus virginianus* Zimmermann (White-tailed Deer).

Field methods

We deployed a series of camera traps in Champaign County, Illinois along a transect line as part of the Urban Wildlife Information Network (Magle et al. 2019). We placed a single camera trap at sites within 2 km of the transect line and at least 1 km from any other camera trap. We used standardized procedures (i.e., camera traps set 0.4–0.75 m off the ground and 3–7 m away from the target site, with a northerly orientation; Kays et al. 2022a) and opportunistically targeted areas likely to be used by mammals (e.g., trails) to maximize detections of wildlife. We programmed camera traps to take a series of 3 photos when they detected motion with a 1 min refractory period between trigger events. We serviced camera traps (downloading memory cards and checking batteries) approximately every 5 to 7 weeks. We placed one of the camera traps (model: Campark T80, Hong Kong) in a mixed-use landscape comprised of livestock, agricultural, and athletic fields near the Veterinary Medicine complex at the University of Illinois (2001 S Lincoln Ave, Urbana, IL 61802) on February 21, 2021, and continually monitored the area until October 31, 2022. Because of the short period of monitoring in February 2021, we removed this from analyses; leaving us with 10 months of monitoring in each year.

Data analyses

We used program R version 4.2.2 (R Core Team 2022) for statistical analyses. To avoid pseudo-replication, we considered consecutive photo captures of the same species within 30 minutes to be the same visit (Wang et al. 2015). We totaled the number of independent visits for each species and determined their relative abundance (*RAB*) at the camera trap by dividing the number of visits by the trap nights the camera trap was operational in a given month. The camera traps did not appear to be sensitive enough to accurately detect the frequency of visits by birds or small rodents (Kays et al. 2022b), so we did not consider these taxa in our analyses. Rather, we focused on the two most abundant prey species in the area that were amenable to camera trap sampling, namely, *Sylvilagus floridanus* Allen (Eastern Cottontail) and *Sciurus carolinensis* Gmelin (Eastern Gray Squirrel). We tested for differences in prey RAB at the fox den site during the five months period to denning and the five months following denning using a nonparametric Mann-Whitney test.

To compare data from the fox den site with baseline sites lacking Red Foxes, we calculated RABs at two neighboring camera sites (1.3 km and 1.5 km away, respectively), which had 5 total Red Fox detections during the 21-month period of interest (compared to >1,000 detections at the fox den site; see below). We tested for differences in prey RAB between the den site and reference sites across the 20-month study period, again using a nonparametric Mann-Whitney test.

Results

The activity of Red Foxes at our camera trap site changed substantially (Fig. 1) when they started using a den under the unused barn adjacent to the site in 2022. While the camera did not include den entrances in its viewshed, the foxes regularly used the area in front of the camera – likely because it was the protected side of the barn with thicker vegetation and away from vehicle traffic. The den itself had multiple entrances, primarily dug inside and outside the lowest level of the abandoned barn. We found incidental prey items around the den during camera checks, including Eastern Gray Squirrels, Eastern Cottontails, and waterfowl.

At the den site, Red Fox annual visitation (n_{2021} = 22, n_{2022} = 1,203) and monthly patterns of relative abundance varied across time. In 2021, we did not document Red Foxes in March, then we recorded 0.1 visits/day in April, 0.1 visits/day in May, and 0.2 visits/day in June, before all visitation stopped until November. Starting in November, visitation increased each month (Fig. 1) until a substantial increase in March (4.8 visits/day) and peak in April (17.2 visits/day). Visitation then declined to pre-denning levels in June (0.8 visits/day) and July (0.9 visits/day) before increasing in August (2.8 visits/day) and September (4.3 visits/day; Fig. 1).

Among prey species, both Eastern Cottontail (n_{2021} = 289, n_{2022} = 114) and Eastern Gray Squirrel (n_{2021} = 1424, n_{2022} = 1057) were more frequent visitors at the den site in 2021 than in 2022. Eastern Cottontails exhibited a peak in relative abundance in March (2.0 visits/day) and April 2021 (1.9 visits/day) before decreasing to no visits in June 2021. Cottontail relative abundance was then relatively steady (between 0.7 and 1.3 visits/day) from July 2021 through March 2022, when their relative abundance decreased to no visits during April and May 2022 when Red Fox relative abundance was highest (Fig. 1). Eastern Gray Squirrels exhibited a similar pattern (Fig. 1), with a peak in relative abundance in March 2021 (8.8 visits/day) before a substantial decrease to lows (ranging from 1.2 to 1.5 visits/day) from June to August 2021. Squirrel relative abundance was then relatively high from September 2021 through March 2022 (ranging between 3.7 to 9.9 visits/day) before a substantial decrease to the minimum 0.4 visits/day in May 2022 when Red Foxes were using the area for a den. Both Eastern Gray Squirrel and Eastern Cottontail RAB was on average higher in the five-month period prior to denning (7.7 and 0.9 visits/day,

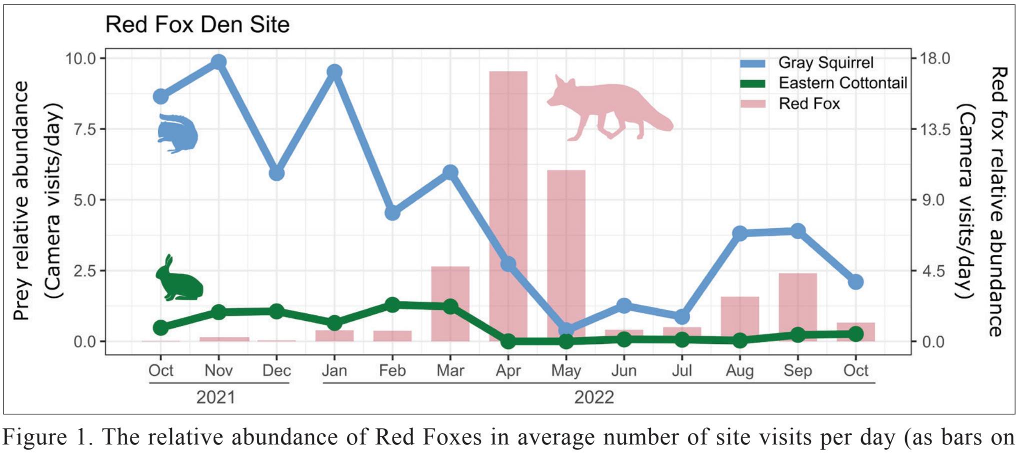

Figure 1. The relative abundance of Red Foxes in average number of site visits per day (as bars on the secondary y-axis) and their two frequent prey: Eastern Cottontails and Eastern Gray Squirrels (as lines on the primary y-axis) at the fox den site in Illinois, USA.

respectively) compared to the five-month period following denning (2.4 and 0.1 visits/day, respectively; $p < 0.01$ for both comparisons).

Red Foxes were only detected at 1 of the 2 neighboring sites (with 3 detections in May 2021, and 1 each in April and August 2022). For prey species, we also documented more Eastern Cottontail and Eastern Gray Squirrels in 2021 than 2022 at the neighboring sites ($n_{2021} = 217$, $n_{2022} = 88$ for cottontail; $n_{2021} = 1{,}230$, $n_{2022} = 734$ for squirrels). The patterns of RAB for these 2 species at the neighboring sites generally followed their patterns at the fox den site, with 2 distinctions. First, Eastern Gray Squirrel RAB was less variable and lower overall at the neighboring sites, with an average of 0.6 visits/day compared to an average of 2.0 visits/day at the den site, a difference that was statistically significant ($p = 0.01$). Squirrels also exhibited a more pronounced peak and subsequent steeper decline at the den site in winter 2021 and spring 2022 (Fig. 2). Second, Eastern Cottontail RAB was approximately 3 times higher at the fox den site in spring and summer 2021, but then the RABs of all sites became similar during the last year of the study (October 2021 to October 2022; Fig. 2) and there was no difference in overall Easter Cottontail RABs between the den and reference sites during the study period ($p = 0.16$).

Discussion

The advent of Red Foxes using an urban den site around the University of Illinois coincided with a substantial decrease in the relative abundance of Eastern Gray Squirrels and Eastern Cottontails – both key prey species of Red Foxes in the Midwestern USA (Murie 1936). While this pattern is suggestive, it is difficult to prove causation, especially as there was also a notable drop in relative abundance for both prey species at the same time the previous year. The pattern of prey dynamics at the den site was similar to that documented at two nearby reference sites, but the fluctuations were much more dramatic, especially for Eastern Gray Squirrels (Fig. 2).

Red Foxes are increasingly common in developed urban areas in the Midwest (Cervantes et al. 2023), such as our study site on the University of Illinois campus, even when denning and raising young. This is thought to be partly due to avoiding larger and dominant Coyotes

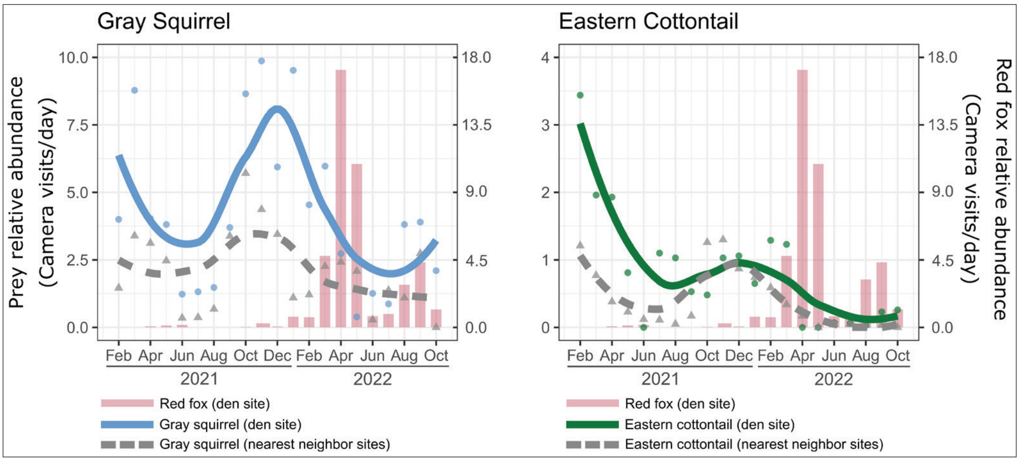

Figure 2. Smoothed lines fit using local polynomial regression of prey at the fox den site (colored lines) and the two nearest neighboring sites (gray dashed lines) at study sites in Illinois, USA. The background points are the raw data points, colored to match each species with shapes mapping to sites (circles for the den site and triangles for the reference sites). All relative abundances are average visits/day during a given month, and the relative abundance of Red Foxes at the den site is on the secondary axis.

(Moll et al. 2018, Mueller et al. 2018, Cervantes et al. 2023), which are less likely to use heavily developed areas and instead prefer larger natural areas within cities (Gehrt et al. 2009, Mueller et al. 2019), and partly due to the greater availability of resources in cities (Mueller et al. 2018, Cervantes et al. 2023). Red Foxes tend to select areas away from roads (Zaman et al. 2020) and properties with Domestic Dogs (Marks and Bloomfield 2006) and Coyotes (Voigt and Earle 1983) for their dens. Coyotes were very infrequent visitors to the camera trap site before the intensive use of the Red Foxes for a den (one visit in March 2021 and another in January 2022). However, Coyotes made 6 visits in April 2022 at the peak of Red Fox activity and another in May 2022. During the 2022 visits, the Coyotes appeared to be scavenging from food scraps left around the area by the denning Red Fox family. In fact, the Red Fox use of the den may have attracted Coyotes to the area by unintentionally provisioning them with food. Despite their potential for conflict, we did not document any antagonistic encounters between the Coyotes and Red Foxes.

Besides small mammals (e.g., mice and voles), Eastern Gray Squirrels are likely the most abundant prey species for Red Foxes across the contiguous USA (Kays et al. 2020a). Despite their abundance, Eastern Gray Squirrels are often consumed by Red Foxes at a lower frequency than rabbits and small mammals (e.g., Brown and Yeager 1945, Hockman and Chapman 1983). Given that Red Foxes are opportunistic predators, it is possible that the Red Fox den site was an exception to this pattern, possibly due to the high abundance of squirrels at the site. An alternative explanation for the strong decline in Eastern Gray Squirrel activity during denning is a behavioral antipredator modification in response to increased local predation risk. Eastern Gray Squirrels respond with behavioral avoidance to Red Fox scent cues (Rosell 2001) and can strongly alter their movement and refuge habitat use in response to perceived predation risk (Dill and Houtman 1989). Therefore, rather than being depredated, Eastern Gray Squirrels might have modified their activity or space use near the den site to reduce predation risk during the denning period.

Understanding the denning ecology of species is helpful for understanding aspects of their natural and life histories. When animals start denning and shift their habits to become central place foragers, they can change the environment and other wildlife species in the den vicinity (Gharajehdaghipour et al. 2016, Kujawa and Łęcki 2008, Obidzinski and Gleogowski 2005, Ruiz-Olmo et al. 2003). Similar to other research on prey species, we documented a substantial decrease in the relative abundance of prey species when Red Foxes started intensively using an urban area as a den. Although this study could not determine whether this was a numerical or behavioral response of Eastern Gray Squirrels to Red Fox predation risk, it suggests that denning activity could act as a localized pulse of risk that modifies prey abundance or behavior. As species like Red Foxes continue to adapt to urbanizing environments, future work could reveal how human-modified landscape features (e.g., barns as in this study) might attract predators seeking den sites, with implications for the surrounding prey communities.

Acknowledgements

We thank the Illinois Natural History Survey, and the University of Illinois for their support.

Literature Cited

Bauder, J.M., M.L. Allen, T.J. Benson, A. Ahlers, C. Miller, and K. Stodola. 2022. Long-term data reveal equivocal evidence for intraguild suppression among sympatric canids. Biodiversity and Conservation 31:2965–2979.

Brown, L.G. and L.E. Yeager. 1945. Fox squirrels and gray squirrels in Illinois. Illinois Natural History Survey Bulletin 23:449-536.

Cervantes, A.M., R.L. Schooley, E.W. Lehrer, T. Gallo, M.L. Allen, M. Fidino, S.B. Magle. 2023. Carnivore coexistence in Chicago: Niche partitioning of Coyotes and Red Foxes. Urban Ecosystems.

Dill, L. M., and R. Houtman. 1989. The influence of distance to refuge on flight initiation distance in the gray squirrel (*Sciurus carolinesis*). Canadian Journal of Zoology 67:233-235.

Frey, J.K. 2013. Re-evaluation of the evidence for the importation of Red Foxes from Europe to colonial America: Origins of the southeastern Red Fox (*Vulpes vulpes fulva*). Biological Conservation 158:74–79.

Gharajehdaghipour, T., J. Roth, P. Fafard, and J.H. Markham. 2016. Arctic foxes as ecosystem engineers: Increased soil nutrients lead to increased plant productivity on fox dens. Scientific Reports 6:24020.

Gehrt, S.D., C. Anchor, and L.A. White. 2009. Home range and landscape use of Coyotes in a metropolitan landscape: Conflict or coexistence? Journal of Mammalogy 90:1045–1057.

Hockman, J.G. and J.A. Chapman. 1983. Comparative feeding habits of Red Foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) in Maryland. American Midland Naturalist 110:276–285.

Kays, R., M. Cove, and 151 others. 2022a. SNAPSHOT USA 2020: A second coordinated national camera trap survey of the United States during the COVID-19 pandemic. Ecology 103:e3775.

Kays, R., M. Lasky, M.L. Allen, R. Dowler, M. Hawkins, A. Hope, B. Kohli, V. Mathis, B. McLean, L. Olson, C. Thompson, D. Thornton, J. Widness, and M.V. Cove. 2022b. Which mammals can be identified from camera traps and crowdsourced photographs? Journal of Mammalogy 103:767–775.

Korschgen, L.J. 1959. Food habits of the Red Fox in Missouri. Journal of Wildlife Management 23:168–176.

Kujawa, K., and R. Łęcki. 2008. Does Red Fox *Vulpes vulpes* affect bird species richness and abundance in an agricultural landscape? Acta Ornithologica, 43:167–178.

Macdonald, D.W. 1980. Social factors affecting reproduction by the Red Fox. *In*: E. Zimen (Ed.). The Red Fox. Biogeographica. Springer, Dordrecht, Netherlands.

Magle, S.B., M. Fidino, E.W. Lehrer, T. Gallo, M.P. Mulligan, M.J. Ríos, A.A. Ahlers, J. Angstmann, A. Belaire, B. Dugelby, A. Gramza, L. Hartley, B. MacDougall, T. Ryan, C. Salsbury, H. Sander, C. Schell, K. Simon, S. St Onge, and D. Drake. 2019. Advancing urban wildlife research through a multi-city collaboration. Frontiers in Ecology and the Environment 17:232–239.

Marks, C.A., and T.E. Bloomfield. 2006. Home-range size and selection of natal den and diurnal shelter sites by urban Red Foxes (*Vulpes vulpes*) in Melbourne. Wildlife Research 33:339–347.

Moll, R.J., J.D. Cepek, P.D. Lorch, P.M. Dennis, T. Robison, J.J. Millspaugh, and R.A. Montgomery. 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosystems 21:765–778.

Murie, A. 1936. Following fox trails. University of Michigan Museum of Zoology Miscellaneous Publications 32: 66 p.

Mueller, M.M., D. Drake, and M.L. Allen. 2018. Coexistence of Coyotes (*Canis latrans*) and Red Foxes (*Vulpes Vulpes*) in an urban landscape. PLoS One 13:e0190971.

Mueller, M.M., D. Drake, and M.L. Allen. 2019. Using citizen science to inform urban canid management. Landscape and Urban Planning 189:362–371.

Obidzinski, A., and R. Gleogowski. 2005. Changes of forest flora composition in vicinity of dens of Red Fox and setts of Eurasian badger. Polish Journal of Ecology 53:197–213.

R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Robertson, C.P., P.J. Baker, and S. Harris. 2000. Ranging behaviour of juvenile Red Foxes and its implications for management. Acta Theriologica 45:525–535.

Rosell, F. 2001. Effectiveness of predator odors as gray squirrel repellents. Canadian Journal of Zoology 79:1719–1723.

Ruiz-Olmo, J., F. Blanch, and F. Vidal. 2003. Relationships between the Red Fox and waterbirds in the Ebro Delta Natural Park, NE Spain. Waterbirds 26:217–225.

Schmitz, O.J., A.P. Beckerman, and K.M. O'Brien. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. Ecology 78:1388–1399.

Seton, E.T. 1925. Lives of game animals Volume I: Cats, wolves, and foxes. Doubleday, Doran & Company, Inc. Garden City, New York, USA.

Storm, G.L., R.D. Andrews, R.L. Phillips, R.A. Bishop, D.B. Siniff, and J.R. Tester. 1976. Morphology, reproduction, dispersal, and mortality of midwestern Red Fox populations. Wildlife Monographs 49:3–82.

Trapp, J.R., P. Beier, C. Mack, D.R. Parsons, and P.C. Paquet. 2008. Wolf, *Canis lupus*, den site selection in the Rocky Mountains. Canadian Field-Naturalist 122:49–56.

Voigt, D.R., and B.D. Earle. 1983. Avoidance of Coyotes by Red Fox families. The Journal of Wildlife Management 47:852–857.

Yovovich, V., M.L. Allen, L. Macauley and C.C. Wilmers. 2020. Using spatial characteristics of apex carnivore reproductive behaviors to inform conservation planning. Biodiversity and Conservation 29:2589–2603.

Wang, Y., M.L. Allen, and C.C. Wilmers. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biological Conservation 190:23–33.

Zaman, M., B.A. Tolhurst, M. Zhu, and G. Jiang. 2020. Den-site selection at multiple scales by the Red Fox (*Vulpes vulpes subsp. montana*) in a patchy human-dominated landscape. Global Ecology and Conservation 23:e01136.