# Building urban predator-prey networks using camera traps

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A B S T R A C T

Loss of interspecific interactions often precedes extinction events. Therefore, knowledge of species interactions is important to inform conservation strategies aimed at maintaining biodiversity in a changing world. Collecting data on species interactions can, however, be logistically challenging and costly. Hence, alternative data collection and processing methods are needed, and camera traps potentially represent a cost-effective way to identify the predator-prey interactions needed to generate trophic networks. Here, we compare two types of datasets, derived from camera traps, and test their effectiveness to build bipartite predator-prey networks: one based on predation events (prey observed within a predator's jaws), and one based on potential encounter events (i.e., predator and prey species detected within a defined time threshold). Our analyses focused on two predators, coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*), in an urbanized area (Toronto, Canada). Our findings suggest the two datasets provided complementary information on the bipartite networks' structure: predation events underestimated large mammal prey, and potential encounter events underestimated small mammal prey. Together, the predator-prey interactions that we found reflected previous literature on dietary analysis. To improve the information provided by camera traps on trophic interactions, we suggest taking into account site-specific conditions (e.g., presence of birdfeeders or microhabitat differences), as these may alter both predation events and potential encounter events detected. Furthermore, to improve the accuracy of the predator-prey interactions obtained with potential encounter events, time interval threshold and detection sequence (i.e., prey or predator detected first) should be taken into account when defining a potential encounter event. Potential encounter events provide a promising complementary method for assessing predator-prey interactions from camera traps, in particular when predator photos from camera traps are not available. Future research should devise strategies to estimate and include predator-prey predation likelihood in bipartite networks derived from potential encounter events.

## 1. Introduction

Interspecific interactions are a bellwether of species ecology, as interaction loss often precedes extinction events, thereby influencing biodiversity, community stability, and ecosystem functioning (Bregman et al., 2015; Simmons et al., 2020; Valiente-Banuet et al., 2015). In particular, trophic interactions play a significant role in shaping ecological communities (Faurby and Svenning, 2016; Gravel et al., 2011). Therefore, trophic interactions have been widely studied through network analysis, especially for aquatic organisms and soil invertebrates (Bossier et al., 2020; Creamer et al., 2016; Niquil et al., 1999). However, studies on trophic networks involving mammals are mostly limited to marine and freshwater mammals, tropical bats, African herbivores, and large wild felids and canids from temperate regions (Boyi et al., 2022; Clare et al., 2019; Kartzinel et al., 2015; Meyer et al., 2020; Pansu et al.,

2019). To the best of our knowledge, trophic networks including urban mammals have not yet been analyzed, and predation datasets for mammals in urban areas remain underrepresented (Eötvös et al., 2018; Herrera et al., 2022). Yet, urban areas represent a noteworthy study environment as predator-prey systems in these areas are tenuous, given the extirpation of larger predators, and the remaining predator and prey species incur behavioral changes following anthropogenic presence (Gallo et al., 2019; Lima et al., 2021; Magle et al., 2014; Ritzel and Gallo, 2020) and anthropogenic food sources (Fischer et al., 2012).

Enhancing knowledge about predator-prey interactions in urban areas relies on the accurate and reliable collection of new data or the exploitation of available datasets cataloging species interactions in situ (Pringle and Hutchinson, 2020). Typically, empirical pairwise predator-prey interactions are recorded in a food web when evidence of a feeding interaction is obtained via field observations (Dormann et al., 2017),

through gut content analyses or DNA techniques (McLeod et al., 2021). However, this represents a high-cost barrier for most researchers to achieve in order to adequately characterize species interactions in an ecological community (Poisot et al., 2021). Moreover, constructing food webs using field observations has a high likelihood of missing in situ trophic interactions when an observer is not present to record such observations (Pringle and Hutchinson, 2020). Thus, alternative methods like camera traps for monitoring communities that do not rely on human observations are needed. Indeed, camera traps are an emerging cost-effective approach for continuously recording species interactions (Smith et al., 2020; Suraci et al., 2020) without directly handling or disturbing wildlife, however their potential for building food webs is still relatively unknown.

In terms of mammalian trophic interactions, camera traps so far have been used for recording predator and prey behavior using baited traps (Palmer et al., 2022; Smith et al., 2020), to analyze predator avoidance (Gallo et al., 2019) and predator-prey co-occurrence (Magle et al., 2014). Nonetheless, camera traps can also be used to opportunistically record predation events when capturing carrying behavior (Wagnon and Serfass, 2017; Windell et al., 2019) and these recorded predation events can then be used to model predator-prey networks. Furthermore, additional information on species interactions can be inferred from camera traps using the difference in time between the occurrence of predators and prey (i.e., waiting time). These waiting times so far have been used for analyzing spatio-temporal avoidance between species and overlap in their daily activity patterns (Niedballa et al., 2019) and for estimating the probability of predator co-occurrence (Gilbert et al., 2022), but may also have the potential to predict and quantify predator-prey encounters.

We propose that by setting a waiting time threshold, we can quantify the number of instances in which two species have had the highest likelihood of encountering each other, defining a potential encounter event. Some of these potential encounters may result in predation events, depending on how close in time these predator-prey pairs occur, the species' movement, defense and attack capabilities, and their social behavior (Suraci et al., 2020). Presence, absence, and frequency of such potential encounter events may be useful to further understand trophic interactions and complement the predation events detected using camera traps when building networks.

Here, we characterize an urban predator-prey network using camera traps by incorporating both predation events and potential predator-prey encounters. We used 33 cameras deployed throughout Toronto (Ontario, Canada), focusing on two predators: red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*). These mesocarnivores are increasingly present in urban areas across North America (Gese et al., 2012) and are thought to play an important role in regulating herbivore populations and distribution in urban and suburban areas (Jones et al., 2016).

## 2. Methods

### 2.1. Study area

We conducted our study in the Toronto region, a dense urban region (4334 people/km², 2016 census) with over 1500 urban landscaped-green areas scattered throughout (e.g., cemeteries, orchards, golf courses, parks, yards) and five forested river valleys. Our sampling design covers three transects running from the most urban core area, downtown Toronto, to the three least-populated neighborhoods in the region (Fig. 1). The surroundings of our study region are characterized by a comparatively low-density human population (<300 people/km²), wood areas, and agricultural land.

### 2.2. Focal species

The largest predators in our study area are red foxes and coyotes. Both species are generalist, have opportunistic diets, and are highly adapted to urban areas (Bateman and Fleming, 2012; Lukasik and Alexander, 2011; Watts et al., 2015). Foxes have been documented feeding primarily on birds, lagomorphs [e.g., eastern cottontail rabbits (*Sylvilagus floridanus*)], eastern grey squirrels (*Sciurus carolinensis*), and small rodents (Peterson et al., 2021; Rosatte and Allan, 2009) but may also prey on young raccoons (*Procyon lotor*) and cats (*Felis catus*) (Davis et al., 2015; Wagnon and Serfass, 2017). Coyotes have been found to prey on small rodents, such as deer mice (*Peromyscus maniculatus*), meadow voles (*Microtus pennsylvanicus*), eastern cottontail rabbits and other lagomorphs, groundhogs (*Marmota monax*), and eastern grey squirrels, and more rarely on raccoons and domestic cats, opossums (*Virginia opossum*), and striped skunks (*Mephitis mephitis*) (Duncan et al., 2020; Larson et al., 2015; Morey et al., 2007; Peterson et al., 2021; Poessel et al., 2017; Thompson, 2014). No records of coyotes feeding on white-tailed deer (*Odocoileus virginianus*) in Toronto have been documented in the literature, however large ungulates have been found to be
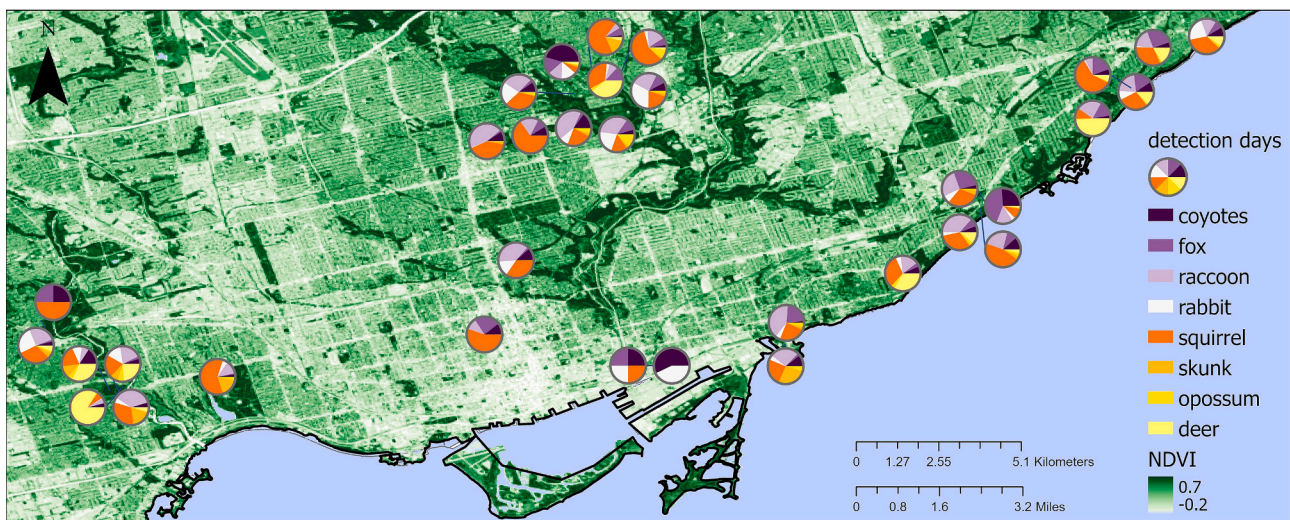


**Fig. 1.** Locations of the 33 camera traps in Toronto (Ontario), the occurrences of the two predators (coyotes *Canis latrans*, and red foxes *Vulpes vulpes*), and prey species. Pie charts represent the relative abundance of the selected predator and prey species (daily presence/absence) for each site, from September 2020 to October 2021. Base map represents the normalized vegetation index (NDVI), estimated from Landsat 8, on July 9th, 2021, where higher values (darker green) represent greater vegetation density.

a major portion of the diet of coyotes in other landscapes (Balluffi-Fry et al., 2020; Morey et al., 2007; Peterson et al., 2021). In three cases, fox material has been found in coyote scat, albeit at a very low occurrence (Dowd and Gese, 2012; Liccioli et al., 2015; Poessel et al., 2017).

### 2.3. Data collection

We used 33 motion-triggered cameras (Bushnell 16MP Trophy Cam HD Essential E3 Trail Camera) to record the presence of mammals in our study area. The camera traps were located at knee-height level on trees or lamp posts throughout our transects, either in parks, natural areas, or along roadsides. Our cameras collected photos for one full year from October 2020 to September 2021, recording one photo per motion trigger, with a 30-s period where cameras could not be further triggered. Every photo with >2 species was then inspected for predation events, defined as a predator (i.e., coyote or fox) that contained another species within their jaws. In instances where prey were not clearly recognizable, we classified prey according to their size and shape.

As potential encounter events, we considered every instance where a prey and a predator were detected less than five minutes apart at one same site. To measure waiting times (i.e., time difference between each species recorded), we used the combn() function from the *utils* R package. We aimed at the smallest threshold possible considering the sample number in order to have at least 50 potential encounter events. However, the time interval can be chosen to vary depending on predator-prey vigilance behavior and permanence duration when detecting a prey nearby, and prey-specific predator-avoidance behavior and escape ability (e.g., use of trees) (Andrewartha et al., 2021; Parsons et al., 2022; Sunde et al., 2022).

### 2.4. Network analysis

To represent the predator-prey interactions in our system, we generated bipartite networks. In our network representation, nodes depicted a community's species while edges connecting pairwise nodes were their trophic interactions (Delmas et al., 2019). We generated bipartite networks from the predation events detected on camera, and from the potential encounter events estimated from the capture time. While we included in our networks every mammal within the capture range of our camera traps, we excluded dogs as a prey in the network analysis since the likelihood of a dog becoming prey is dependent on their size and whether they were leashed, and we did not have that information in our dataset. The bipartite networks were generated with frame2webs() and plotweb() functions from the *bipartite* package in R (version 4.0.3) (Dormann et al., 2008). We then generated an incidence matrix using the computeModules() and plotModuleWeb() functions in the *bipartite* package (Dormann et al., 2008).

## 3. Results

### 3.1. Predation events

We detected 2361 instances of foxes and 1195 instances of coyotes diversely distributed across the 33 camera sites, with a mean of 221 trap nights (Fig. 1, Table S1). Within these detections, we found 43 predation events, where either a fox ($n = 21$) or a coyote ($n = 22$) were carrying a prey within their jaws. From these 43 predation events, 41 events contained mammals, of which 14 could be identified to the species level. These included eastern grey squirrels, eastern cottontail rabbits, raccoons and domestic cats (Figs. 2a and 3). Those instances where we could not identify the mammal prey to the species level, we categorized prey based on size and shape, and defined them as either "rodent-like"
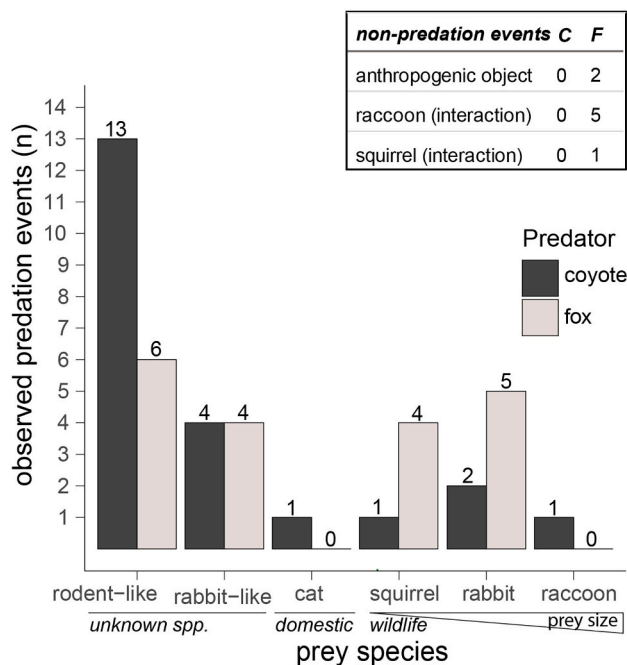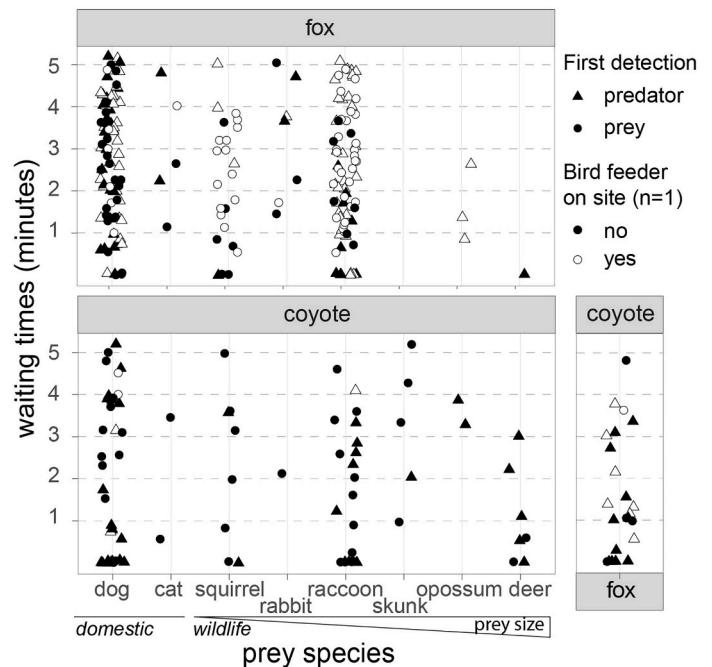


**Fig. 2.** Predation events observed and potential encounter events estimated from camera traps. (a) Number of predation events detected for each prey species by each predator (coyote (dark), fox (light)). Prey species include instances where prey was unidentifiable, these are separated following size and shape, domestic species, and wild species ordered by size. Additional table includes non-predation events, i.e. anthropogenic objects held or when a potential prey occurred in the same frame as a coyote (C) or a red fox (F), but prey was not held by the predator. (b) Potential encounter events dissected by waiting time interval (y-axis) between predators and potential prey detected. The latter distinguished between domestic (left) or wild (right), ordered by size, and between the predators (bottom right). Symbol shape identifies potential encounter events where predator species occurred first (triangles), and where prey species occurred first (circle), and empty symbols identify potential encounter events from the site with a bird feeder. Potential encounter events between our two focal predators are shown in the bottom left box.
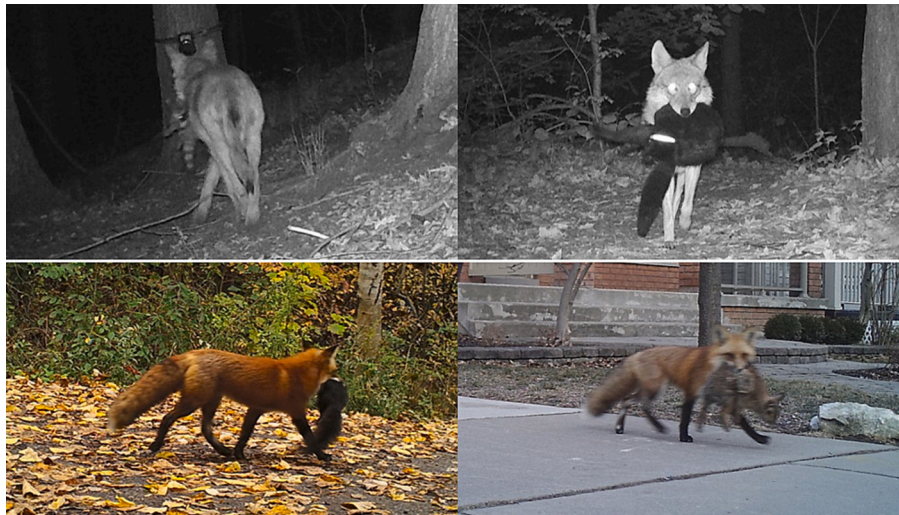
**Fig. 3.** Examples of predation events detected: coyote with a juvenile raccoon (top-left), coyote with a domestic cat (top-right), red fox with a squirrel (bottom-left), red fox with a rabbit (bottom-right).

(coyotes: $n = 13/22$, fox: $n = 6/19$) or "rabbit-like" (coyotes: $n = 4/22$, fox: $n = 4/19$) (Fig. 2a). Additionally, we observed eight non-predation events from which two anthropogenic objects being carried by foxes and six instances where the potential prey was not being carried (Fig. 2a). The latter were all observed at the site with a bird-feeder and included five interaction events between foxes and raccoons not apparently trophic, and one interaction event between a fox and a squirrel, where the fox was actively hunting the squirrel (Fig. S1).

### 3.2. Potential encounter events

We found 299 potential encounter events between predators and prey (fox: $n = 210$, coyotes: $n = 89$). From the potential encounter events between our focal predators and potential prey, 131 involved dogs (fox: $n = 89$, coyotes: $n = 42$). Excluding dogs reduced the number of potential encounter events to 168 (fox: $n = 121$, coyotes: $n = 47$), of which in 75 events the first animal detected was a predator (fox: $n = 55$, coyotes: $n = 20$) and in 93 events the first animal detected was a prey (fox: $n = 66$, coyotes: $n = 27$).

Prey species found in potential encounter events included domestic animals (cats) and wildlife (squirrels, rabbits, raccoons, skunks, opossums, and deer; Fig. 2b). While during the sampling year we also detected mink, groundhogs, and chipmunks (Table S1), these detections did not yield any potential encounter events with our two focal predators.

Interestingly, at one site, the camera was coincidentally facing a bird feeder, resulting in a noticeable higher interaction rate between squirrels, raccoons, opossums, and our focal predators, in particular foxes, yielding for the latter $2.5\times$ more potential encounter events than all other camera sites combined (fox: $n = 84$, coyotes: $n = 1$, excluding dogs, Fig. 2b). Therefore, to ensure commensurability, this site was removed from the subsequent network analysis. As a result, the potential encounter events included in the network analysis were reduced to 77 events (fox: $n = 32$, coyotes: $n = 45$).

In terms of potential interactions between our focal predators, we found 26 potential encounter events, where in five events foxes were detected first and in 18 events foxes were detected shortly after coyotes. However, we did not consider foxes as potential prey of coyotes in the subsequent network analysis given the low occurrence rate of fox material in coyote scat analyzed in previous literature, mentioned above.
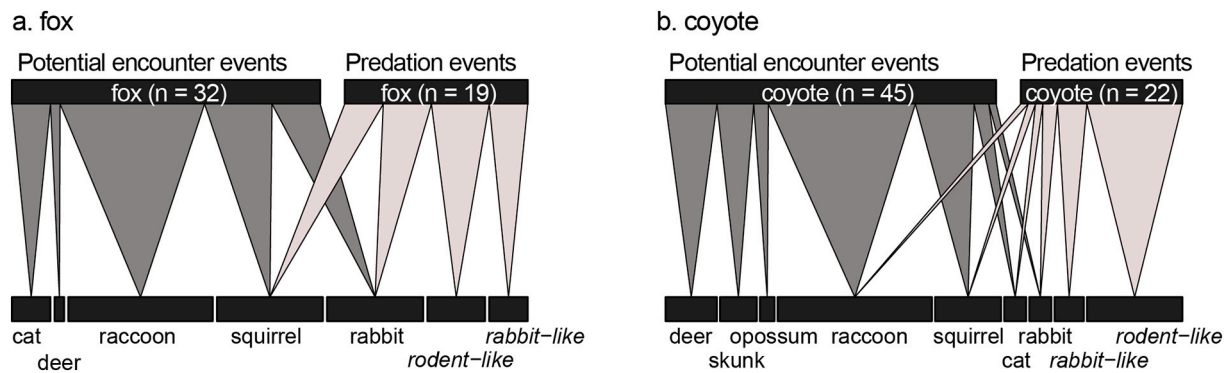
### 3.3. Bipartite networks

When comparing predator-prey interactions obtained from both types of data, all interactions observed in the predation events networks also occurred in the potential encounter events networks. The predator-prey interactions included squirrels and rabbits as fox prey (Fig. 4a), and raccoons, cats, squirrels, and rabbits as coyote prey (Fig. 4b). However, some predator-prey interactions appeared exclusively in the potential encounter events networks, i.e., cats, deer, and raccoons with foxes (Fig. 4a), and deer, skunk, and opossums with coyotes (Fig. 4b). Furthermore, a large portion of the predator-prey interactions included in the predation events network were unidentifiable prey species, especially for rodent-like mammals with coyotes and foxes (coyotes: $n = 13/22$, fox: $n = 6/19$) (Fig. 4a), and to a lesser extent rabbit-like mammals with both our focal predators (coyotes: $n = 4/22$, fox: $n = 4/19$) (Fig. 4a).

When comparing predator-prey niches we found differences between the networks generated using different types of data (Fig. 5). Specifically, in the predation events network, raccoon and cat were prey exclusive to coyotes. Yet, common to both were the predator-prey interactions with squirrels, rabbits, and unknown rabbit-like and rodent-like mammals. Instead, in the potential encounter events network, there was a high level of coyote-fox niche overlap resulting from shared potential interactions with raccoons, squirrels, cats, rabbits, and to a lesser extent deer (Fig. 5b). This bipartite network additionally included larger mammals as potential prey that were not included in the predation events networks, such as raccoon and deer for foxes, and opossums, skunks, and deer for coyotes.
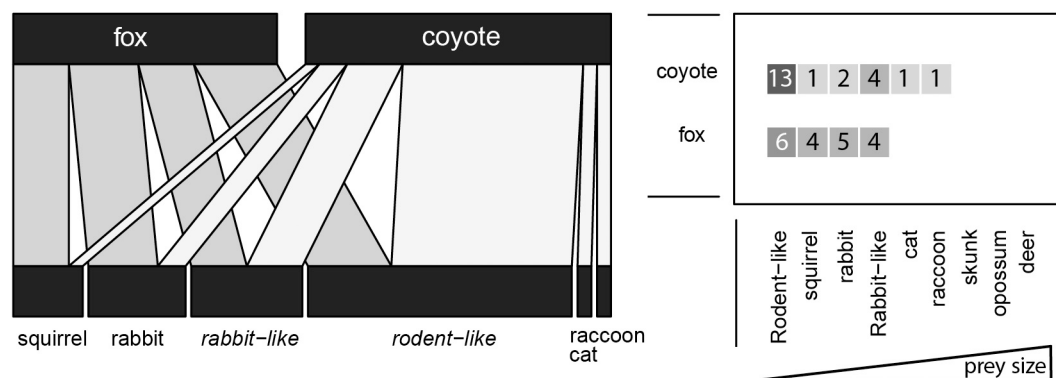
## 4. Discussion

The bipartite networks we generated, from both observed and potential predation events, provided complementary information. On one hand, networks created from observed predation events suggested that coyotes and foxes favoured predominantly small- and medium-sized mammals as prey, while likely underestimating the predation of larger mammals, where prey-carrying behavior may be less frequent (Windell et al., 2019). On the other hand, networks built from potential encounter events underestimated smaller prey items that were not within the body size range detected by the camera angle (i.e., rodents), as ours were set at a height level which predominantly detected medium to large mammals (i.e., mammals with a body size larger than chipmunks). However, generating networks from potential encounter events allowed for the
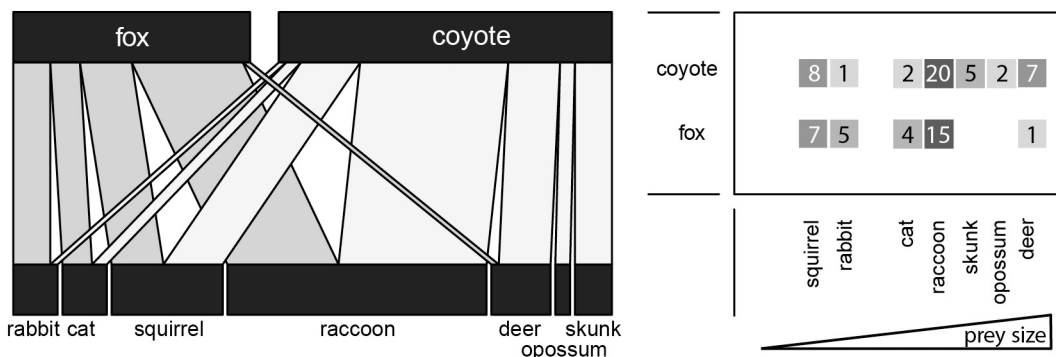
**Fig. 4.** Bipartite network showing overlapping prey species between the predation events and the potential encounter events datasets, for (a) foxes and (b) coyotes. Number of events observed in each dataset (*n*).



**Fig. 5.** Left: Predator-prey bipartite networks showing prey overlap between predator species, generated using predation events (a) and potential encounter events (b). Right: Incidence matrices for each network showing prey, or potential prey, species counts, ordered by prey size.

inclusion and identification of prey animals that were difficult to identify when carried by predators, e.g., due to blur or lack of species-specific markings, and identified the feasibility of predation for those larger mammals for which predation success or prey-carrying behavior is less likely. Potential encounter events thus provide a promising complementary method for assessing predator-prey interactions, in particular when predator photos from camera traps are not available, for example when using repository camera trap datasets without stored photos.

Our findings in terms of prey species were consistent with previous literature on dietary analysis for both coyotes and foxes. In our urban study area, we observed in our predation events dataset that the main prey of coyotes were small prey items like rodents or birds, while the main prey of foxes were medium-sized mammals, like rabbits. Bipartite networks generated from these observations suggested an overlap in

prey size for both predators, including squirrels and rabbits, while cats and raccoons remained exclusively the prey of coyotes. These findings are consistent with our bipartite networks generated from potential encounter events, which additionally suggested that larger mammal species (e.g., deer) may potentially serve as prey for both coyotes and foxes. Together, the results from both analyses coincide with previous urban dietary analyses. For example for coyotes, rodents and lagomorphs were the most prevalent prey species in high-density housing areas of Denver (Poessel et al., 2017), similar to our findings in Toronto, a densely built urban area. Furthermore, consistent with our results for coyote predator-prey interactions based on potential encounter events, deer have been found in coyote scat analysis in urban areas in Illinois (Morey et al., 2007) and Alabama (Randa et al., 2009); however, this was attributed to roadkill scavenging rather than predation events. The

latter may further explain the absence of large ungulate predation events and the low number of potential encounter events between deer and coyote in our dense urban study area, as deer presence in coyote scat may be independent of predation events and potential encounters. For foxes, our results also coincided with previous dietary analyses, as foxes have been found to feed primarily on birds and small rodents in rural and suburban areas (Contesse et al., 2004; Peterson et al., 2021), but on medium-sized mammals like rabbits (as well as anthropogenic waste) in heavily urbanized zones (Herrera et al., 2022; Lavin et al., 2003; Randa et al., 2009; Rosatte and Allan, 2009; Soe et al., 2017). The consistency between our findings and previous research suggests predation events and potential encounter events are both highly efficacious ways of collecting information on predator-prey interactions.

However, to improve the accuracy of networks using potential encounter events obtained from camera traps a lower waiting time threshold is optimal. This may be achieved via a higher sampling effort by increasing the number of sampling sites which may allow for a reduction in the threshold without losing statistical power. The threshold may also be fine-tuned to specific predator-prey pairs of interest in order to reflect better on the predation likelihood arising from their species-specific travel speed and movement patterns. For example, from our camera trap data, rabbits tended to stay for extended periods of time at one site, given the number of consecutive photos triggered when they appear. Therefore, a larger time interval would be relevant for interactions such as the predator-lagomorph, where prey might remain close to the site for a longer duration, increasing the likelihood of encounter at longer waiting times. Additionally, the predator-prey sequence of appearance, i.e., which species is recorded first, might also be important for certain predator-prey pairs, in particular for prey with predator-avoidance behavior increasing waiting times between predators and subsequent prey captures (Ferrero et al., 2011; Monclús et al., 2009; Sunde et al., 2022). Lastly, an attack-frequency parameter may be included when building the network, with the purpose of correcting predator-prey pairs where the probability of a destructive encounter is low. For example, where prey are only generally preyed upon when young or sick, such as foxes on raccoons, deer, and cats (Davis et al., 2015; Epstein et al., 1983; Wagnon and Serfass, 2017) and coyotes on skunks and opossums (Duncan et al., 2020; Larson et al., 2015; Murray et al., 2015). Nevertheless, since these predator-prey pair attack probabilities are likely constant and pair-specific, it should not affect pair-specific trophic comparisons across sites. Instead, particular attention should be paid to site-specific detection parameters, such as camera angle view and microhabitat included in the frame, as these may influence predator-prey detection rates and the likelihood of capturing predation events. Additionally, camera trap settings such as capture delay period and burst mode may also influence the possibility of including the closest predator-prey encounters.

When comparing trophic interactions across camera sites, it is important to consider whether the camera sites include the use of lures or the presence of bird feeders or other wildlife attractants, as these can increase the frequency of interactions, in particular for omnivorous mesopredators which may feed on fallen seeds, such as foxes and raccoons. These attractants may be a source of bias either by increasing the sampling unit area when considering occupancy (Burton et al., 2015), by unbalancing the presence of predator and prey in the site (Fidino et al., 2020; Holinda et al., 2020), or by increasing the encounter rate between predator and prey species, as suggested by our findings (Fig. 2b). An increased encounter rate between mesopredators, due to bird feeders, water fountains, or fruiting trees (Hansen et al., 2020) can also have social and ecological implications, such as increased human wildlife conflict, and an accelerated spread of diseases, as mammalian predator-prey pairs are usually compatible disease hosts (Malmberg et al., 2021). Further research should investigate changes in encounter rates following anthropogenic wildlife attractants to provide relevant information for predicting introduced sampling bias on camera trap studies and adequate policy suggestions with the aim of mitigating conflict and disease spread in urban areas.

The datasets here analyzed can be used to understand species interactions beyond the identification of predator-prey links. Potential encounter events derived from predator-prey occurrences can be used to quantify encounter rates across different landscape types and environmental conditions. Furthermore, in combination with predation event observations, these potential encounter events can be used to estimate predation/attack likelihood between predator-prey pairs (Suraci et al., 2022). Encounter rates and predation likelihood are both valuable estimates for the parametrization of individual-based models and epidemiological models. Additionally, potential encounter rates derived from camera traps may be used to understand the effects of human presence in predator-prey avoidance (Van Scoyoc et al., 2023) and as a complement to other mathematical metrics for estimating encounter rates (Carroll et al., 2019).

## 5. Conclusion

Overall, based on our findings, camera trap datasets can serve as a valuable tool for estimating predator-prey interactions, using both predation events and potential encounter events as they provide complementary information. However, it is important to note the strengths and limitations of the datasets obtained from camera traps, as each may underestimate specific prey size classes, and be subject to sensitivity differences following camera trap settings. Furthermore, ways in which potential encounter events may be fine-tuned should be considered to better reflect predation likelihood between predator-prey pairs. Future research should focus on devising strategies to estimate predation likelihood for predator-prey pairs following an encounter event, and further analyzing the effect of wildlife attractants on encounter rates.

## CRediT authorship contribution statement

**Tiziana A. Gelmi-Candusso:** Conceptualization, Formal analysis, Visualization, Data curation, Funding acquisition, Methodology, Project administration, Writing – original draft, Writing – review & editing. **Chris Brimacombe:** Formal analysis, Validation, Writing – original draft, Writing – review & editing. **Germain Collinge Ménard:** Data curation, Investigation, Writing – original draft, Writing – review & editing. **Marie-Josée Fortin:** Funding acquisition, Resources, Supervision, Writing – review & editing.

## Declaration of Competing Interest

None.

## Data availability

Code and data can be found in github repository at tgelmi-candusso/predator_prey_networks

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2023.e00305.

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