

**Influence of North American red squirrel caches on vertebrate foraging activity at the
northern treeline**

by

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Abstract

Resource patches create cost-effective foraging opportunities, particularly in marginal habitats such as the northern treeline. Red squirrels (*Tamiasciurus hudsonicus*) aggregate resources by caching cones in middens, which serve as strategic foraging patches for pilfering granivores and predators. At the northern treeline, caches are smaller and dispersed throughout squirrel home ranges. Using camera traps deployed in treeline habitat near Churchill, Manitoba (2020–2025), I examined vertebrate activity and diversity at caches. Wildlife activity should reflect resource abundance at caches: seed availability should facilitate granivore pilferage, thereby attracting predators. Seasonal patterns in activity should reflect resource-driven dynamics when caches are at peak food abundance, or demand-driven dynamics associated with temporal variability in consumer energetic requirements. Although cache presence did not affect species diversity, caches exhibited taxon-specific effects. Taxa with the greatest foraging behaviour at caches were most common in autumn, when caches are fullest. Red-backed voles (*Clethrionomys gapperi*) showed the strongest evidence for kleptoparasitism of caches. Snowshoe hares (*Lepus americanus*) and spruce grouse (*Canachites canadensis*) exploit large caches, but cache presence had little effect on broader space use, suggesting opportunism. Other browsing birds generally showed weak associations with cache presence, except for willow ptarmigan (*Lagopus lagopus*), which showed high foraging engagement. Red fox (*Vulpes vulpes*) detections were strongly seasonal but weakly coupled with pilfering prey activity, suggesting a temporally driven response to localized peak prey availability. In contrast, martens (*Martes americana*) foraged at caches with greater red squirrel activity. I found no evidence that other carnivorans or raptors reliably sought caches as foraging opportunities. These findings imply

caches act as localized, seasonally constrained foraging hotspots for a subset of the treeline vertebrate community. My study highlights the constrained, context-dependent role of resource patches in shaping ecosystem dynamics in marginal treeline habitats.

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Introduction

Animals have developed diverse foraging strategies (Schoener 1971), and their resource-acquisition strategies may depend on their niche, life history, and role in the dynamics of their ecosystem (Claireaux *et al.* 2018; Segev *et al.* 2021; Zumpano *et al.* 2021; Harris *et al.* 2023). Optimal foraging theory, a foundational framework in behavioural ecology used to explain how animals ultimately develop effective foraging strategies (Stephens & Krebs 2019), suggests that a successful foraging method is one in which energetic or fitness-related benefits outweigh energetic costs and other associated risks (Flower *et al.* 2013).

Maximizing nutritional gain per unit of foraging time is among the most essential components of what makes a food acquisition strategy optimal, especially when a desired resource is distributed within discrete patches (Charnov 1976; Calcagno *et al.* 2014a). The marginal value theorem, an extension of optimal foraging theory, predicts an individual's foraging effort within a resource patch before moving on to another (Charnov 1976; Stephens & Krebs 1986; Brown 1988; Calcagno *et al.* 2014b). The theorem states that when a forager's capture rate of a food item within a patch equals the average rate of capture for that same resource in the surrounding habitat, the individual will concentrate effort by traveling to new foraging grounds (Charnov 1976; Brown 1988). At this point, searching for a new patch is more energetically favourable to the consumer than continued foraging at the same patch, which would provide diminishing returns (Brown 1988). Therefore, food density, the quality of resource patches and their spatial distribution all contribute to movement patterns and net fitness of animals in an ecosystem. These influences on food-acquisition strategies may also be affected by interspecific interactions.

Within an ecosystem, some species can disproportionately modify these patch dynamics, thereby facilitating cost-effective foraging strategies across various realized niches and ecological guilds (Hale & Koprowski 2018; Gable *et al.* 2020; Losapio 2024). The mechanisms by which one species promotes optimal foraging strategies in another are diverse. Resource aggregation is one mechanism that can promote optimal foraging opportunities for other species through kleptoparasitism. Kleptoparasitism is the process by which an organism steals resources that another has procured, and it is a form of direct resource competition (Brockmann & Banard 1979; Iyengar 2008). For an interaction to be considered a form of kleptoparasitism, the animal that has procured the resource must experience a net energetic loss through a decrease in nutrient availability, and the kleptoparasite must receive a net energetic benefit (Iyengar 2008). Alternatively, a species can promote optimal foraging opportunities for others by modifying its habitat (i.e., creating structures), which can both directly and indirectly facilitate the growth or aggregation of food items (Posthumus *et al.* 2015; Gable *et al.* 2020).

The degree to which a species that facilitates resource aggregation affects community-wide dynamics likely varies with several key factors, including its realized niche and its environment. Resource aggregations and patch interactions, according to the marginal value theorem, may be especially important in marginal habitats, areas at the periphery of a species' range, often characterized by a transition in vegetation assemblages (Hester & Harrison 2007; Ferrari *et al.* 2022). For a given species, essential resources are more sparsely distributed or less readily available in marginal habitats than in their corresponding core environments (Aldridge *et al.* 2008; Beers & Frey 2022; Ferrari *et al.* 2022). In accordance with the centre-periphery hypothesis, which predicts marginal habitat at the edge of a species' distribution, periphery

populations may need to employ unique strategies to cope with harsher environmental conditions that limit occupancy and reproduction (Brown 1984; Pinon *et al.* 2017; Sultaire *et al.* 2023).

The boreal forest-tundra ecotone, the transitional zone between the boreal forest and Arctic tundra, otherwise known as the northern treeline, is one environment that represents ecologically marginal habitat for many of its inhabitants, namely forest-adapted species. The northern treeline generally has fewer resources for forest species relative to the core boreal forest (Kambo & Danby 2018; Benjamin *et al.* 2024). Forest-adapted species may alter their foraging behaviour at the treeline to compensate for the environment's short growing season and relatively low nutrient abundance (Windsor 2025).

A notable resource-aggregating species, and one that alters its foraging behaviours at the treeline, is the North American red squirrel (*Tamiasciurus hudsonicus*) (Windsor 2025). Though they display a high degree of dietary plasticity, red squirrels heavily rely on cached conifer cones, containing seeds, as a reliable winter and early spring food source (Steele 1998; Posthumus *et al.* 2015). Caching behaviour usually begins in late summer to early autumn, depending on the region (Steele 1998). The timing of caching behavior not only allows red squirrels to survive periods of food scarcity, but also to achieve reproductive success during the mating season, which occurs between late winter to early spring, when available resources on the landscape are low (Steele 1998; Haines *et al.* 2022). Caches are typically within aggregations of conifer cone scales that accumulate through squirrel feeding activity (Steele 1998). Red squirrel caches provide a cool, enclosed environment that prevents cones from opening, thereby limiting seed germination (Smith 1968; Steele 1998). Throughout most of the red squirrel's distribution, over 50% of all procured seed-bearing cones are stored within a central, large larder, commonly referred to as a midden (Smith 1981; Hurly & Lorie 1997; Steele 1998; Posthumus *et al.*

2015). Red squirrels are territorial and typically have a home range of 0.22-0.91 hectares, depending on habitat type, but home ranges can extend up to 4.8 hectares during periods of low resource availability (Smith 1968; Gurnell 1984 in Steele 1998). The high degree of territoriality exhibited by red squirrels means that middens are only used and contributed to by one individual at a time (Windsor 2025). Middens are reused over multiple years and can be inherited by other individuals across multiple generations of territorial ownership (Boutin & Larsen 1993; Windsor 2025).

Despite a widespread trend of creating large, centralized larders, red squirrels at the treeline often adopt a different strategy, creating a series of significantly smaller, partially subterranean caches dispersed throughout their home range (Windsor 2025; personal observation). These squirrels also show a preference for creating burrow nests rather than the tree and drey nests they typically occupy in other habitats (Windsor 2025). The burrows of red squirrels at the treeline likely consist of multiple chambers, some containing cached food or a nest, connected by a series of tunnels (Windsor 2025). On top of a burrow network, there is typically an aggregation of cone scales and other feeding debris created by the resident squirrel or its predecessors (Windsor 2025; personal observation). These feeding sites signify the presence of a cache and resemble miniature middens. True middens also occur in treeline habitat, but they are not the dominant caching method, and their frequency of construction is lower relative to other portions of the red squirrel's range (Windsor 2025; personal observation). This spatial variation in caching behaviour may result from predation risk intensified by low tree density or the relatively harsh winter conditions at the treeline (Kambo & David 2013; Mendes *et al.* 2019; Benjamin *et al.* 2024; Windsor 2025).

At the treeline, squirrel diets consist of ~70% fungi, likely because the region's cone and seed production from conifers is relatively poor (Windsor 2025). However, fungi, a protein-rich resource, lacks substantial lipid content. Despite a primarily fungivorous diet, red squirrels at their northern range periphery still rely on lipids of conifer seeds for overwinter survival (Windsor 2025). The importance of lipids in the winter diet of red squirrels implies that at the treeline, red squirrels are still caching cones when they are available, which is reflected by the aggregations of cone scale debris at cache sites (Windsor 2025; personal observation).

Red squirrel caches serve a diverse array of community-wide effects. Middens are considered hotspots for kleptoparasitic interactions with other squirrels and other species (Edelman *et al.* 2005). Among heterospecifics, red squirrel caches can serve as valuable pilfering sites for granivores (Pearson & Ruggiero 2001; Edelman *et al.* 2005; Posthumus *et al.* 2015; Put *et al.* 2017). Granivorous small mammals, namely Arvicoline rodents, pilfer seeds knocked loose during red squirrel feeding activity, placing them into a cache's associated cone-scale pile and the surrounding area (Pearson & Ruggiero 2001; Edelman *et al.* 2005; Posthumus *et al.* 2015). Ground-foraging passerines use caches in a manner like granivorous small mammals, feeding directly from the contents of a squirrel's feeding debris (Posthumus *et al.* 2015). Large-bodied facultative granivores, such as grizzly bears (*Ursus arctos horribilis*) and American black bears (*Ursus americanus*), directly excavate red squirrel caches to access lipid-rich seeds in preparation for winter torpor (Mattson 1997; Kendall 1983; Edelman *et al.* 2005; Hamer 2017; Put 2017). Other direct community effects are associated with the structure of the midden itself, providing woody nesting material for various rodent species (Edelman *et al.* 2005).

In addition to the direct effects of red squirrel caches on the facultative granivore guild, they also can serve indirect effects to granivore predators (Pearson & Ruggiero 2001; Edelman *et*

al. 2005; Windsor 2025). Red squirrels and many other granivores that use their caches are regular prey items for various mesocarnivores throughout the boreal forest (Pearson & Ruggiero 2001; Edelman *et al.* 2005; Posthumus *et al.* 2015; Windsor 2025). Squirrel caching behaviour makes the general midden vicinity an ideal hunting ground for squirrel predators (Posthumus *et al.* 2015; Windsor 2025). Similarly, pilfering heterospecific granivore species at caches can also attract their associated predators to the area (Pearson & Ruggiero 2001; Endelman & Koprowski 2005; Posthumus *et al.* 2015). For example, in winter, American martens (*Martes americana*) use middens to access subnivean spaces, which they use both for hunting small mammals and for thermoregulation (Buskirk 1984; Sherburne 1993; Posthumus 2015). Other examples include increased mesocarnivore diversity and abundance at active red squirrel caches relative to patches of forest without prominent squirrel activity, attributed to pilfering small mammal activity (Posthumus *et al.* 2015).

Despite being widely regarded as important foraging sites for various species, few, if any, studies have examined the ecosystem-wide role of these caches in marginal treeline habitat, where conifer cone production is poor and red squirrels do not typically create large, central larders (Pearson & Ruggiero 2001; Villegas *et al.* 2013; Posthumus *et al.* 2015; Windsor 2025; Personal observation). Since cone production is lower at the treeline than in more centralized boreal forest habitats (Vilgas *et al.* 2013; Benjamin *et al.* 2024), granivores at their northern range periphery may heavily rely on squirrel caches as resource aggregations, even if these caches are relatively small. Granivore predators at the treeline may therefore find cost-effective foraging opportunities within the vicinity of red squirrel caches. Additionally, few, if any, studies have examined temporal variation in the use of squirrel caches. Given the timing of cache construction, ecological guilds may respond differently at varying points throughout the year.

The aim of this study was to quantify intraguild and species-specific activity at red squirrel caches as a function of cache size, seasonality, foraging engagement, and habitat characteristics at the treeline of northern Manitoba. Firstly, because of the resource's that caches provide granivores, there may be more wildlife activity at caches than at non-cache sites, particularly by facultative granivores, and by extension, their associated predators. I also predict that cache sites will have greater species richness compared to cache-less areas. I propose two hypotheses to explain the relationship between wildlife foraging activity and circannual average food item abundance at cache sites, one for granivores and one for their predators. My granivore hypothesis suggests that a cache's surface area reflects aggregated seed abundance, thereby influencing granivore foraging effort (Edelman *et al.* 2005; Posthumus *et al.* 2015). I predict that as the cache area increases, so too will granivore activity. My predator hypothesis suggests a relationship between prey species abundance and predator activity at cache sites. This hypothesis is predicated on the notion that red squirrel caches facilitate granivore pilferage, thereby making the cache vicinity cost-effective hunting grounds for carnivores (Edelman *et al.* 2005; Posthumus *et al.* 2015). Under the predator hypothesis, I predict a positive relationship between predator activity and prey abundance at cache sites. To understand the seasonal influence of caches on wildlife activity, I propose two competing hypotheses, one based on resource availability and the other based on the consumer's energetic requirements. My resource-driven hypothesis posits a relationship between the time of year and foraging activity, driven by seasonal variability in cache contents (Steele 1998). Under this hypothesis, I predict that wildlife activity will peak in autumn, when caches are at their fullest (Steele 1998; Mendes *et al.* 2019), and decrease in proportion to cached food abundance. My demand-driven seasonal hypothesis posits a relationship between wildlife activity at caches and the consumer's energetic needs. Under this

hypothesis, I predict that wildlife activity at caches will increase in periods of high endotherm energy requirements associated with overwintering (Liu *et al.* 2003; Churchfield *et al.* 2012; Desforges 2020). Due to the expected influence of caches on the facilitation heterospecific foraging opportunities, I also predict that species richness at these resource patches will be proportional to the vertebrate community's responses to cache quality and seasonality.

Methods

Study area

Our study area was located in the forest-tundra ecotone near Churchill, MB, Canada (Figure 1), on the north-western periphery of the Hudson Bay lowlands. This region represents marginal, northern treeline habitat for red squirrels and other forest-adapted species and is heavily fragmented by swaths of fen and tundra (Harper *et al.* 2011; Harper *et al.* 2018; Dredge and Dyke 2020; Windsor 2025). Tree diversity and density in this region are low, a characteristic common throughout treeline habitats worldwide (Lafleur 1999; Mamet & Kershaw 2011; Windsor 2025). Despite the high degree of regional habitat heterogeneity, all sampling within our immediate study area was conducted within upland, dry patches of forest. Tree density in our study area averages 484 trees per hectare, leading to a relatively low canopy coverage of approximately 25% (Lafleur 1999; Windsor 2025). Tamarack (*Larix laricina*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*) are the only conifer species present (Lafleur 1999; Windsor 2025), and white spruce is the dominant tree within our field site. Here, white spruce cone production and embryo-bearing seeds per cone are significantly lower than in core boreal habitat (Windsor *et al.* 2025). Dominant taxa of the understory community consist of large

shrubs such as Labrador teas (*Rhododendron sp.*) and willows (*Salix sp.*); smaller Ericacean shrubs; herbaceous perennial forbs; and Sphagnum mosses (*Sphagnum sp.*), among other bryophytes; and reindeer lichens (*Cladonia spp.*) (Dredge 1992; Windsor 2025; personal observation).

Data collection and processing

We installed trail cameras to examine wildlife activity at red squirrel caches between August 2020 and September 2025. We used 7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025. We used three trail camera models: Browning Strike Force Full HD, Browning Strike Force HD Pro X and Browning Strike Force Full HD Extreme (Browning Trail Cameras, Birmingham, Alabama, USA). We set the cameras' operation mode to "Trail", so they only took pictures, adjusted their multi-shot settings to 3 images (3 images per independent motion-triggered event), set their trigger speed to "fast," and calibrated their picture delay (cool-down period) to 1 second. We placed cameras approximately 1.5 meters above the ground and angled them approximately 75 degrees downward from their stand. We serviced trail cameras, swapping memory cards and changing batteries, when necessary, every April, June and August, with additional camera checks in January 2021 and 2022 and July 2025. The minimum straight-line distance between two neighbouring caches with cameras deployed was 172 m.

In August of 2024 and June, July and August of 2025, I measured the surface area of each cache by taking a top-down image next to a 1-m measuring tape for reference. I measured each cache digitally using the software ImageJ (Schneider *et al.* 2012). For each photo, I measured the length of the 1-m reference object in pixels using ImageJ's straight-line tool and entered that value in the software's Set Scale feature. I used ImageJ's freehand selection tool to trace the

perimeter of each squirrel cache and then used the Measure function to obtain the total surface area in m².

In April 2025, we implemented a paired experimental design to compare wildlife activity between caches and paired reference sites. We placed cameras at 10 selected red squirrel caches, determined from the measurements taken in August 2024, and at 10 accompanying reference sites located 50 m either north or south of each, determined by a coin flip unless the habitat in one direction differed noticeably from the corresponding treatment site (i.e. in canopy coverage, or had a fen or pond). We faced reference cameras away from their respective treatment cameras to minimize the risk of capturing an animal on its way to or from a cache site. For this second experiment, we used the same three aforementioned Browning models. We matched camera models at each pair of treatment and reference sites. Again, we set the cameras to "Trail" mode, trigger speed to "fast", multi-shot to 3 images, and picture delay to 1 second.

I processed all trail camera images using Timelapse, an image-analyzing software for camera traps, and TimelapseTemplateEditor, a software tool for creating a template to record desired data within Timelapse (Greenberg *et al.* 2019). Using TimelapseTemplateEditor, I created a template containing three count data fields, each representing a different level of engagement with the squirrel cache, for each species observed on the trail cameras (Table 1). The engagement levels are as follows:

- 1: unengaged with the cache, defined as any individual greater than one body length from the cache site.
- 2: engaged with the cache, defined as any individual at or within one body length of the cache but not actively feeding.

3: showing obvious signs of foraging activity at the cache, defined as any individual with their nose or beak directly in the cache or with prey items in their mouth.

I did not consider engagement level 3 for boreal red-backed voles (*Clethrionomys gapperi*), as it was too difficult to distinguish whether they are actively feeding or just walking through the cache sites on the trail camera images.

To ensure the independence of observations, I created a data field within my template to denote a specific event and filled it with data collected using Timelapse's episode function. In Timelapse, an episode is a set of images captured over a specified time interval. Using episode data, I distinguished different foraging events. For this study, I set my event threshold to 5 minutes. After extracting count data from Timelapse, I used the event data field to flag repeated observations of individuals and removed them from the dataset. For each event, I only kept the count of an individual's highest level of engagement. I also created a date-and-time field in Timelapse, enabling me to capture information on event seasonality.

Statistical analysis

I completed all statistical analyses using R Studio and R, version 4.5.2 (R Core Team 2025). Along with using R's base functions, I implemented the use of several packages into my analysis: tidyr and dplyr to execute dataset manipulation techniques, to prepare data for subsequent analysis (Wickham *et al.* 2023; Wickham *et al.* 2024); glmmTMB to create taxon-specific and diversity models (Brooks *et al.* 2017); DHARMA to check model diagnostics; car to check Wald-type statistical tests (Fox & Weisberg 2019), and variance inflation factors along with the lme4 package (Bates *et al.* 2015); MuMin to examine model-specific random effect variance, and both marginal and conditional R^2 values (Barton 2025); Stringr for data string

parsing (Wickham 2025); influence.ME to calculate Cook's distance to examine analytical outliers (Nieuwenhuis *et al.* 2012); and ggplot2 to generate figures (Wickham 2016).

Engagement level 3 was generally low across all species (Table 1), so I combined levels 2 and 3 into a single "engaged" category for all analyses in which engagement level was a predictor variable. Additionally, for each analysis, I aggregated counts of each species per event into counts of each species per month. To account for variability in observational effort, typically due to camera failures (e.g., loss of battery power, full SD cards, or the camera becoming buried under snow), I created a variable to record the number of observational days per camera per month. I assumed that a camera became inactive one day after its final photo was taken, prior to its subsequent servicing day. For analyses regarding migratory species, I only included observations from May to October for passerines and observations between April and November for raptors to control for seasonal patterns when no individuals were present on the landscape.

Using data from my paired experimental design, I used a generalized linear mixed effect model (GLMM) fitted with a Poisson link function to test the relationship between species richness and cache presence. Within the model, species richness was the dependent variable, site type (i.e. cache or reference) was a categorical predictor, month was a discrete numeric predictor, and site ID was a random effect. I included an interaction term between both fixed effects. To account for observational effort differences between sites, I used the log of the number of operational days per month as an offset variable. The offset term was log-transformed to account for the log-link function associated with Poisson and negative binomial GLMMs (Breslow 1984). Due to camera failure throughout my study period, my pairwise analyses include 7 operational pairs in May, 10 from June to August and 9 in September.

To quantify the relationship between cache presence and wildlife activity (number of observations), I created a GLMM, with a negative binomial link function to account for overdispersion, for each taxon with >10 total observations (Table 2). I only considered engaged counts at treatment sites for this analysis. Within each model, month and site type were once again included as predictors, plus an interaction to examine whether seasonal variation in treatment and reference sites differed. To account for differences in observation effort, I included the same offset variable included in the species richness model in each taxon-specific model. For these taxon-specific models, I once again included site ID as a random effect. I split passerines into three distinct groups for this analysis: primarily granivorous songbirds, primarily insectivorous songbirds, and Robins (*Turdus migratorius*), the most abundant and dietarily plastic passerine that I observed (Whitmer 1996; Table 2). If a camera was operational for > 3 days in a given month, I excluded that site for that month. Since reference cameras were established in late April, I also excluded April entirely from these analyses. To ensure model assumptions were not violated, I examined DHARMA residuals vs expected values and ran overdispersion, uniformity, zero inflation and outlier tests. All random effect standard deviations, conditional and marginal R^2 values for these models can be found in Table 3.

To address my seasonal and food-abundance hypotheses, I analyzed observations at caches from August 2020 to September 2025. For each of these hypotheses, I used a single GLMM for each taxon, fitted using a negative binomial link function to account for overdispersion. For each model, species count was the dependent variable. Fixed effects for taxon-specific models consist of food item prevalence, engagement level (if applicable) and month. I also included tree density (number of trees per hectare) as an environmental covariate to control for habitat variation between sites. For resident taxa, I treated month as a discrete,

second-order polynomial term to account for seasonal variability, enabling the models to capture annual peaks and declines in species activity at caches that a linear trend would miss. As in the paired design, I used the log of the number of operational days per month as an offset term to account for camera-specific, seasonal observational effort. Within each model, I included cache site ID and year as random-effect variables. As with pairwise analysis, I verified the assumptions for each GLMM by plotting DHARMA residuals against predicted values and performing residual tests for overdispersion, zero inflation, uniformity, and outliers.

For my long-term analysis (2020-2025), all facultatively granivorous species (Table 1) used the same general global model. I assumed cache area reflects food availability for granivores. Since I did not measure the cache area prior to August 2024, I assumed that each cache has maintained its relative ordered peak surface area throughout the study period. To test this assumption, I performed three Pearson's correlation coefficients (r) calculations between the measurements I took in August 2024 and the repeated measurements I took in June, July and August 2025. There was a high degree of heteroskedasticity in cache areas in all months that I took measurements in, so I $\log_{10}$ transformed both variables for each correlation to achieve bivariate normality. The results of this test revealed that cache measurements in August 2024 were strongly positively correlated with the repeated measurements taken the following June ($r = 0.97, p < 0.001$), July ($r = 0.98, p < 0.001$) and August ($r = 0.97, p < 0.001$). Within each granivore model, I included an interaction effect between engagement level and cache area to test whether the effect of cache size differed between actively foraging animals and those merely passing through the site. I also included an interaction between engagement level and month to test seasonal variation in granivore foraging effort at caches. For these analyses, I once again divided migratory passerines into primarily insectivorous and primarily granivorous with the

exception of robins, placed into their own group due to high abundance and a broad dietary niche (Whitmer 1996; Table 1). I modeled predominantly insectivorous passerines using the same functional framework as granivores because caches may attract insects and create localized resource patches at small spatial scales.

For the predator guild in my long-term study (2020-2025; Table 2), I included engaged detection rates of prey taxa (number of prey observations at engagement levels two and three, per camera, per number of operational days per month) as predictors in each predator model, selecting species observed at caches at least 10 times and known to be reliably consumed by the respective carnivore. The red fox (*Vulpes vulpes*) model used boreal red-backed vole, Canada goose (*Branta canadensis*) and snowshoe hare (*Lepus americanus*) visitation rates as predictors (Small & Keith 1992; Needham *et al.* 2014; Johnson-Bice *et al.* 2025). The American marten model included red-backed voles and snowshoe hare rates as predictor terms (Martin *et al.* 2025; Windsor 2025). Short-tailed weasels (*Mustela erminea*) and least weasels (*Mustela nivalis*), which display a high degree of dietary overlap, were aggregated into a single weasel category (Edwards *et al.* 2003; Sundell & Ylonen 2008). The weasel model includes vole visitation rates as the only prey predictor term (Edwards *et al.* 2003; Sundell & Ylonen 2008). To model predatory avian activity, I aggregated all birds of prey into a single raptor category (Table 1). Raptors of the boreal forest regularly prey on red-backed voles, snowshoe hares, and Phasianids, so the visitation rates of these groups were included in the raptor model (Tornberg 1997; Tornberg 2001; Whiteman 2009; Feierabend and Kiellán 2015). For the raptor model, I combined willow ptarmigan (*Lagopus lagopus*) and spruce grouse (*Canachites canadensis*) counts into a single category to derive a single Phasianid rate. To account for periods when raptors are not present on the landscape, due to migration, but their prey species are still

detectable, I only used data between April and October and dropped the polynomial seasonal term for this taxonomic group. Red foxes, American martens, and boreal forest *Accipiter* species are also red squirrel predators (Poole & Graf 1996; Bull 2000; Edwards & Forbes, Smith *et al.* 2023; Windsor 2025); so engaged squirrel activity was used a prey predictor term in each respective model. I did not include engagement level as a fixed effect in predator models because predators likely respond to prey availability surrounding caches rather than to caches themselves. Additionally, predators typically hunt across larger spatial scales, whereas small herbivores often forage within localized, sessile resource patches (Anderson *et al.* 2016).

To assess multi-year diversity patterns from 2020–2025, I created two species richness models: one for resident taxa and the other for migratory taxa. I separated these models to account for richness biases when migratory cohorts are not present in the area. Both long-term richness models were GLMMs fitted with a Poisson link function. Month, tree density, and cache area were included as fixed predictors, while log-transformed operational days per camera per month was included as an offset term. Once again, site ID and year were included as random intercepts. The models differed only in the cohort used to calculate species richness and the duration of the sampling period. The resident model included taxa present year-round, whereas the migratory model included migratory bird richness during the May–October period. Reflecting taxon-specific models, month was treated as a quadratic term for residents and a linear term for migrants.

Results

Paired comparisons

Overall species richness did not differ between caches and reference sites ($\chi^2 = 0.05$, $df = 1$, $p = 0.82$). Though species richness appears to be increasing from May to September (Figure 2), the overall linear influence of month on total species richness was also not significant ($\chi^2 = 0.34$, $df = 1$, $p = 0.56$), and the interaction between treatment and month was also not significant ($\chi^2 = 0.30$, $df = 1$, $p = 0.58$).

Snowshoe hare detections did not significantly differ between treatment and reference sites ($\chi^2 = 0.61$, $df = 1$, $p = 0.44$). Counts showed significant monthly variation ($\chi^2 = 9.14$, $df = 1$, $p = 0.0025$), with a negative seasonal trend ($\beta = -0.33 \pm 0.16$ SE). However, the interaction effect indicated little seasonal variability between site types ($\chi^2 = 0.02$, $df = 1$, $p = 0.88$; Figure 3).

Boreal red-backed vole counts significantly differed between site types ($\chi^2 = 9.23$, $df = 1$, $p = 0.0024$), with more frequent detections at caches ($\beta = 2.47 \pm 2.60$ SE; Figure 3). The effect of month on vole counts was also significant ($\chi^2 = 8.61$, $df = 1$, $p = 0.0033$), with a positive seasonal trend ($\beta = 0.77 \pm 0.47$ SE), but no interaction between treatment and month ($\chi^2 = 0.10$, $df = 1$, $p = 0.75$).

Robins and other primarily insectivorous or granivorous migratory passerines did not strongly differ between the two site types (robin: $\chi^2 = 0.24$, $df = 1$, $p = 0.62$; other insectivorous passerines: $\chi^2 = 0.82$, $df = 1$, $p = 0.36$; granivorous passerines: $\chi^2 = 0.00$, $df = 1$, $p = 0.98$). Detections for all migratory songbirds displayed a significant degree of monthly variability (robin: $\chi^2 = 14.04$, $df = 1$, $p < 0.001$; other insectivorous passerines: $\chi^2 = 10.29$, $df = 1$, $p = 0.0013$; granivorous passerines: $\chi^2 = 8.06$, $df = 1$, $p = 0.0045$) with a positive seasonal trend (robin: $\beta = 0.72 \pm 0.22$ SE; other insectivorous passerines: $\beta = 0.22 \pm 0.18$ SE; granivorous passerines: $\beta = 0.19 \pm 0.19$ SE). Detections at both treatment and reference sites did not

significantly differ in their response to seasonal changes, indicated by the interaction term between site type and month (robin: $\chi^2 = 0.48$, $df = 1$, $p = 0.49$; other insectivorous passerines: $\chi^2 = 2.50$, $df = 1$, $p = 0.11$; granivorous passerines: $\chi^2 = 3.77$, $df = 1$, $p = 0.052$; Figure 3).

Non-migratory avian facultative granivores, Canada jays (*Perisoreus canadensis*) and willow ptarmigan, showed no significant differences in overall detections between both site types (Canada jay: $\chi^2 = 0.58$, $df = 1$, $p = 0.44$; willow ptarmigan: $\chi^2 = 0.50$, $df = 1$, $p = 0.48$). Neither species followed the predicted monthly trend (Canada jay: $\chi^2 = 1.64$, $df = 1$, $p = 0.20$; willow ptarmigan: $\chi^2 = 2.59$, $df = 1$, $p = 0.11$), nor was the interaction between month and site type significant (Canada jay: $\chi^2 = 0.80$, $df = 1$, $p = 0.37$; willow ptarmigan: $\chi^2 = 0.33$, $df = 1$, $p = 0.57$; Figure 3). Likewise, Canada goose counts did not differ significantly between treatment and reference sites ($\chi^2 = 0.26$, $df = 1$, $p = 0.61$), did not follow a linear monthly trend ($\chi^2 = 0.00$, $df = 1$, $p = 0.95$), nor was the interaction between site type and month significant ($\chi^2 = 0.07$, $df = 1$, $p = 0.80$; Figure 3).

Predator detections at site types differed in their response to seasonal progression. The interaction between site type and month was a significant predictor of marten counts ($\chi^2 = 7.09$, $df = 1$, $p = 0.0077$), with detections at treatment sites decreasing ($\beta = -0.97 \pm 0.36$ SE) throughout the study period, relative to reference sites (Figure 3). However, the main effects for these respective variables were not significant for this species (Site type: $\chi^2 = 1.18$, $df = 1$, $p = 0.28$; Month: $\chi^2 = 1.58$, $df = 1$, $p = 0.21$). For red foxes, counts were not significantly predicted by site type ($\chi^2 = 0.80$, $df = 1$, $p = 0.37$) or a linear seasonal pattern ($\chi^2 = 0.03$, $df = 1$, $p = 0.86$; Figure 3), but the interaction between site type and month was marginal ($\chi^2 = 3.81$, $df = 1$, $p = 0.051$).

Season, engagement and resource abundance

On a circannual scale, species richness for resident treeline taxa was predicted by a negative monthly seasonal curve ($\chi^2 = 41.90$, $df = 2$, $p < 0.001$, $\beta = -5.86$, $SE = 0.91$). Resident diversity was highest in spring, with a secondary peak in early autumn, and was lowest throughout winter (Figure 4). Migratory species richness was also significantly affected by monthly variation, increasing from spring to autumn ($\chi^2 = 7.21$, $df = 1$, $p = 0.0072$, $\beta = 0.14$, $SE = 0.05$). For both resident and migratory groups, cache area had no effect on species richness (resident: $\chi^2 = 3.42$, $df = 1$, $p = 0.064$; migratory: $\chi^2 = 2.07$, $df = 1$, $p = 0.15$; Figure 4). Tree density, however, had a significant, positive effect on species richness of residents ($\chi^2 = 10.80$, $df = 1$, $p = 0.0010$, $\beta = 0.26$, $SE = 0.08$) but not migratory species ($\chi^2 = 2.37$, $df = 1$, $p = 0.12$).

Snowshoe hare counts were influenced by the main effect of month ($\chi^2 = 8.24$, $df = 2$, $p = 0.016$), with overall detections showing positive seasonal curvature ($\beta = 3.17 \pm 1.80$ SE). Engagement levels also varied significantly ($\chi^2 = 10.72$, $df = 1$, $p = 0.0011$), with unengaged individuals being less abundant than engaged ones ($\beta = -0.31 \pm 0.10$ SE). Both engagement levels appear to follow a similar seasonal pattern; however, engaged counts were comparatively higher throughout seasonal peaks in spring and autumn (Figure 5). Hare counts were also influenced by the significant interaction between engagement level and cache area ($\chi^2 = 6.28$, $df = 1$, $p = 0.012$; Figure 6). This interaction effect revealed that the cache area response was weaker for events containing unengaged individuals compared with those consisting of engaged individuals ($\beta = -0.21 \pm 0.08$ SE). The main effects for these two respective variables were significant for engagement level ($\chi^2 = 10.72$, $df = 1$, $p = 0.0011$), but not cache area ($\chi^2 = 2.66$, $df = 1$, $p = 0.10$). Tree density, an environmental covariate, positively predicted localized hare abundance ($\chi^2 = 3.96$, $df = 1$, $p = 0.047$; $\beta = 0.42 \pm 0.21$ SE). For this model, the main effect of

cache area ($\chi^2 = 2.66$, $df = 1$, $p = 0.10$), and the interaction between engagement level and month ($\chi^2 = 4.55$, $df = 2$, $p = 0.10$) were not significant.

Overall boreal red-backed vole counts were significantly influenced by the main effect of month ($\chi^2 = 25.23$, $df = 2$, $p < 0.001$), with detections showing a strong, negative quadratic curvature ($\beta = -54.54 \pm 13.30$ SE), peaking in the autumn months (Figure 5). The significant main effect of engagement level shows that overall vole detections varied between engaged and unengaged counts ($\chi^2 = 5.57$, $df = 1$, $p = 0.018$). Unengaged detections were less common than detections with engaged individuals ($\beta = -0.20 \pm 0.47$ SE). Cache area was not a significant predictor of vole activity ($\chi^2 = 0.72$, $df = 1$, $p = 0.39$; Figure 6), nor was tree density ($\chi^2 = 1.36$, $df = 1$, $p = 0.24$). There were no significant interactions between engagement level and month ($\chi^2 = 4.00$, $df = 2$, $p = 0.14$) or between engagement level and cache area ($\chi^2 = 0.88$, $df = 1$, $p = 0.35$).

All migratory passerines included in the study were significantly influenced by the main effect of month when present on the landscape from May to October (robin: $\chi^2 = 10.92$, $df = 1$, $p < 0.001$; insectivorous passerines: $\chi^2 = 17.90$, $df = 1$, $p < 0.001$; granivorous passerines: $\chi^2 = 19.44$, $df = 1$, $p < 0.001$). When accounting for their absence throughout the winter months, all songbirds displayed a positive seasonal increase, from the onset of arrival to the onset on southern migration (robin: $\beta = 0.41 \pm 0.18$ SE; insectivorous passerines: $\beta = 0.84 \pm 0.27$ SE; granivorous passerines: $\beta = 1.12 \pm 0.32$ SE). Migratory passerine detections increased throughout the summer, peaking in early Autumn before a sharp drop-off later in the season (Figure 5). However, Canada geese, another migratory facultative granivore, did not exhibit a significant seasonal trend ($\chi^2 = 0.08$, $df = 1$, $p = 0.77$). Goose detections occurred only during summer and early Autumn, with no detections recorded at the beginning or end of the sampling

season (Figure 5). For all migratory birds, engagement level was not a significant predictor of count (robin: $\chi^2 = 2.44$, $df = 1$, $p = 0.12$; insectivorous passerines: $\chi^2 = 0.13$, $df = 1$, $p = 0.72$; granivorous passerines: $\chi^2 = 0.01$, $df = 1$, $p = 0.93$; Canada goose: $\chi^2 = 0.49$, $df = 1$, $p = 0.48$), nor was tree density (robin: $\chi^2 = 1.39$, $df = 1$, $p = 0.24$; insectivorous passerines: $\chi^2 = 1.93$, $df = 1$, $p = 0.165$; granivorous passerines: $\chi^2 = 1.28$, $df = 1$, $p = 0.258$). Robins and other primarily granivorous taxa also do not respond to cache area (robin: $\chi^2 = 2.01$, $df = 1$, $p = 0.16$; granivorous passerines: $\chi^2 = 3.14$, $df = 1$, $p = 0.076$; Figure 6). Insectivorous passerines, however, exhibited a significant interaction between cache area and engagement level ($\chi^2 = 4.07$, $df = 1$, $p = 0.0436$). This interaction implies that the relationship between cache size and insectivore detections differed between engaged and unengaged observations, with the interaction coefficient suggesting that insectivore activity increased less strongly with cache size at unengaged detection events than at events consisting of engaged individuals ($\beta = -0.47 \pm 0.23$ SE; Figure 6). For insectivores, the main effects for these two respective variables were significant for engagement level ($\chi^2 = 17.90$, $df = 1$, $p < 0.001$), but not cache area ($\chi^2 = 0.51$, $df = 1$, $p = 0.48$). Engaged Canada goose detections were more prevalent at sites with smaller cache sizes ($\beta = -9.96 \pm 5.39$ SE, $\chi^2 = 6.40$, $df = 1$, $p = 0.011$; Figure 6) and with higher tree density ($\beta = 2.16 \pm 0.74$ SE, $\chi^2 = 8.53$, $df = 1$, $p = 0.0035$). Interactions between engagement level and month (robin: $\chi^2 = 0.01$, $df = 1$, $p = 0.93$; insectivorous passerines: $\chi^2 = 0.0004$, $df = 1$, $p = 0.985$; granivorous passerines: $\chi^2 = 0.22$, $df = 1$, $p = 0.64$; Canada goose: $\chi^2 = 0.01$, $df = 1$, $p = 0.92$) and engagement level and cache area (robin: $\chi^2 = 0.77$, $df = 1$, $p = 0.38$; granivorous passerines: $\chi^2 = 0.04$, $df = 1$, $p = 0.84$; Canada goose: $\chi^2 = 0.07$, $df = 1$, $p = 0.79$) were not significant. These non-significant interaction terms indicate that the effect of engagement did not differ across months or cached content abundance.

Resident avian granivores, Canada jays and willow ptarmigan, were significantly influenced by month (Canada jay: $\chi^2 = 35.12$, $df = 2$, $p < 0.001$; willow ptarmigan: $\chi^2 = 17.37$, $df = 2$, $p < 0.001$), with both species displaying a negative seasonal curve (Canada jay: $\beta = -64.32 \pm 14.37$ SE; willow ptarmigan: $\beta = -9.59 \pm 4.77$ SE). Canada jay counts peaked in spring and were absent in mid-winter (Figure 5). Ptarmigans were detected year-round, with the lowest number of detections early in winter and the highest engaged detections occurring in August (Figure 5). Spruce grouse, another resident bird, detections were not explained by a quadratic monthly trend ($\chi^2 = 3.41$, $df = 2$, $p = 0.18$), instead showing a bimodal pattern, with counts peaking in spring and autumn, and decreasing throughout summer and winter (Figure 5). Spruce grouse were the only resident bird species influenced by the main effect of cache area (Canada jay: $\chi^2 = 0.58$, $df = 1$, $p = 0.45$; willow ptarmigan: $\chi^2 = 0.09$, $df = 1$, $p = 0.76$; spruce grouse: $\chi^2 = 7.56$, $df = 1$, $p = 0.0059$; Figure 6), with engaged individuals showing a positive association with larger caches ($\beta = 0.60 \pm 0.21$ SE). However, the main effect of engagement level did not significantly influence spruce grouse, nor Canada jay counts (Canada jay: $\chi^2 = 0.96$, $df = 1$, $p = 0.33$; spruce grouse: $\chi^2 = 0.0012$, $df = 1$, $p = 0.97$). Engagement level, however, did differ significantly for ptarmigan counts ($\chi^2 = 10.65$, $df = 1$, $p = 0.0011$), with unengaged detection events being lower overall relative to engaged ones ($\beta = -0.82 \pm 0.30$ SE). All resident birds showed no preference for tree density (Canada jay: $\chi^2 = 2.96$, $df = 1$, $p = 0.085$; willow ptarmigan: $\chi^2 = 1.08$, $df = 1$, $p = 0.30$; spruce grouse: $\chi^2 = 0.81$, $df = 1$, $p = 0.37$). Model interaction terms between engagement level and month (Canada jay: $\chi^2 = 5.58$, $df = 2$, $p = 0.06$; willow ptarmigan: $\chi^2 = 0.960$, $df = 2$, $p = 0.62$; spruce grouse: $\chi^2 = 2.33$, $df = 2$, $p = 0.31$) and engagement level and cache area (Canada jay: $\chi^2 = 0.29$, $df = 1$, $p = 0.59$; willow ptarmigan: $\chi^2 = 0.98$, $df = 1$, $p = 0.32$; spruce grouse: $\chi^2 =$

1.77, $df = 1$, $p = 0.18$) were not significant. Once again, these non-significant interaction terms indicate that the effect of engagement did not differ across presumed patch quality or seasons.

Among mammalian carnivores, red foxes were the only species to respond significantly to the main effect of month ($\chi^2 = 23.88$, $df = 2$, $p < 0.001$). Overall fox detections displayed a negative seasonal curve ($\beta = -20.46 \pm 4.19$ SE), with activity peaking throughout summer and autumn and significantly less activity in winter (Figure 7). Mustelid activity, however, was not influenced by the predicted seasonal quadratic effect (American marten: $\chi^2 = 1.09$, $df = 2$, $p = 0.58$; weasel: $\chi^2 = 1.26$, $df = 2$, $p = 0.53$). Weasel activity showed sharp, but highly variable, peaks in spring, with smaller peaks in autumn and early winter, and multiple long periods without detection (Figure 7). American marten activity showed greater temporal consistency, with modest peaks in Autumn and secondary peaks in spring and early winter, creating a multimodal pattern (Figure 7). Engaged rates of pilfering granivores were poor predictors of overall carnivoran detections. Engaged Canada goose rates did not predict red fox activity ($\chi^2 = 0.82$, $df = 1$, $p = 0.36$), snowshoe hare engagement did not predict American marten or red fox activity (American marten: $\chi^2 = 1.19$, $df = 1$, $p = 0.28$; red fox: $\chi^2 = 1.96$, $df = 1$, $p = 0.16$); and boreal red-backed vole engagement did not predict activity of any carnivoran (weasel: $\chi^2 = 0.02$, $df = 1$, $p = 0.89$; American marten: $\chi^2 = 1.72$, $df = 1$, $p = 0.19$; red fox: $\chi^2 = 0.10$, $df = 1$). Red squirrel activity, however, influenced overall marten detections ($\chi^2 = 6.47$, $df = 1$, $p = 0.011$) but did not influence the detection rate of other predators (red fox: $\chi^2 = 2.65$, $df = 1$, $p = 0.10$; weasels: $\chi^2 = 1.55$, $df = 1$, $p = 0.21$; Figure 8). Marten activity increased with red squirrel cache use, as indicated by the positive relationship between the two variables ($\beta = 0.32 \pm 0.13$ SE; Figure 8). Throughout my study area, tree density was not an influential variable for any

mammalian carnivore (red fox: $\chi^2 = 2.87$, $df = 1$, $p = 0.09$; American marten: $\chi^2 = 2.69$, $df = 1$, $p = 0.10$; weasel: $\chi^2 = 0.17$, $df = 1$, $p = 0.68$).

The overall activity of the raptor functional group, when present on the landscape, did not respond linearly to month ($\chi^2 = 1.92$, $df = 1$, $p = 0.17$). Prey coupling for Accipiters at caches was poor, as the model revealed raptor detections to be unaffected by red squirrel, snowshoe hare, boreal red-backed vole and Phasianid engaged rates (red squirrel rate: $\chi^2 = 1.55$, $df = 1$, $p = 0.21$; snowshoe hare rate: $\chi^2 = 0.06$, $df = 1$, $p = 0.81$; boreal red-backed vole rate: $\chi^2 = 0.52$, $df = 1$, $p = 0.47$; Phasianid rate: $\chi^2 = 0.03$, $df = 1$, $p = 0.86$). Tree density also did not affect raptor counts ($\chi^2 = 0.17$, $df = 1$, $p = 0.68$).

Discussion

The results of my study suggest that, within marginal northern treeline habitat, North American red squirrel caches function as important resource patches. However, their effects on the vertebrate community are highly taxon specific. Within this ecotone, squirrel caches do not act as biodiversity hotspots; rather, their ecosystem-wide impact on heterospecific foraging activity is largely temporally driven. This seasonal effect is supported across both analyses: localized wildlife abundance is strongly associated with periods of peak squirrel caching activity (Steele 1998; Mendes et al. 2019), with few exceptions. Together, these results provide strong evidence for my resource-driven seasonal hypothesis. My energetic demand-driven hypothesis was supported less at the vertebrate community scale. Willow ptarmigans, however, may represent an exception, showing secondary peaks and plateaus in winter and early spring, suggesting increased pilferage during periods of high homeotherm energy requirements

associated with overwintering and reproduction (Andreev, 1991; Wilson *et al.* 2007). Snowshoe hares and spruce grouse were the only species that responded to our granivore-specific patch-quality index, cache area. Similarly, American martens were the only carnivorous species to show direct coupled activity with prey-cache engagement, specifically with red squirrels themselves. These three species are therefore the only examples supporting my circannual average food-item aggregation hypotheses. My pairwise and long-term experiments indicate that boreal red-backed voles are particularly frequent kleptoparasites of squirrel caches during peak cache abundance in autumn. Additionally, my paired study suggests that martens may preferentially forage near caches while snow is present on the landscape, with detections declining toward autumn despite increasing red squirrel caching activity. This pattern may reflect transient use of caches, possibly associated with subnivean vole availability or thermoregulatory refuge (Sherburne 1993; Pearson & Ruggiero 2001). Together, vole and marten use of treeline caches provides the strongest support for my cache presence hypothesis.

This study incorporates two experimental approaches to model wildlife activity at caches. Though other studies have quantified small-scale, localized wildlife abundance and diversity at North American red squirrel middens (Posthumus *et al.* 2015), my study is one of the few, if any, to incorporate pairwise, phenological, and patch quality approaches. Additionally, quantifying wildlife behaviour at caches through engagement level provides a functional comparison between granivores present in the area and those actively seeking pilferage opportunities. In this way, engagement level serves as a behavioural control variable, denoting cache-driven effects from general space use, in lieu of designated treatment and reference sites. Together, the two experimental approaches that I implemented provide complementary lines of evidence for the community-wide effects of red squirrel cache use: the paired design tests foraging trends at the

cache level, whereas the long-term experiment (2020-2025) highlights the causal mechanisms of those responses.

Diversity, taxon-specific and ecosystem-wide effects

My results indicate that species richness was not significantly different at caches relative to the surrounding forest. Though paired comparisons suggest that species richness was not seasonally driven in 2025, circannual richness from 2020 to 2025 reveals peaks in autumn for migrant taxa and spring for treeline residents (Figure 2; Figure 4). However, my analysis suggests that my localized measurements of vertebrate richness may be better explained by environmental covariates, such as tree density (Cardinal *et al.* 2012; Wagner *et al.* 2023). Posthumus *et al.* (2015) found that in more temperate regions of the red squirrel's distribution, caches do not serve as widespread drivers of localized diversity. My pairwise study reaffirms this result at the northern range periphery of this species.

In southern portions of the red squirrel's distribution, caches serve as taxon-specific hotspots of foraging activity (Pearson & Ruggiero 2001; Edelman *et al.* 2005; Posthumus *et al.* 2015; Put *et al.* 2017). My findings indicate that, despite regional differences in caching behaviour based on habitat quality (Mendes *et al.* 2019; Windsor 2025), treeline caches still provide foraging opportunities to a wide array of vertebrates throughout this marginal habitat. However, the overall effect that caches have on wildlife foraging patterns is highly taxon- and environmental context-specific.

Of all wildlife quantified, boreal red-backed voles were the most strongly associated with cache use, with detections being most frequent in late summer and autumn, when caches presumably reach their peak resource abundance (Steele 1998; Mendes *et al.* 2019; Figure 3;

Figure 5). This relationship suggests that at the treeline, voles are frequent pilferers of cached contents, likely consuming both conifer seeds and fungi (Amaranthus *et al.* 1994; Hoffmeister 1986, cited in Posthumus *et al.* 2015). Pearson & Ruggiero (2001) describe red-backed vole abundance at middens as the result of the habitat type in which middens are usually built (i.e., areas with abundant woody debris in the forest understory). However, my study took place within a single homogeneous forest, with treatment and corresponding reference sites located 50 meters apart, and I found that tree density, a habitat feature that likely predicts understory composition, was not influential for vole counts within my study area. My findings insinuate that red-backed detections in autumn are heavily influenced by cache presence rather than by general habitat use. Therefore, there is strong support for my hypotheses regarding the presence of cache and seasonal resource abundance in this species. The lack of observations throughout winter was likely an artifact of voles being primarily located in subnivean spaces during this time (Jolly *et al.* 2024), making it impossible to fully quantify my demand-driven seasonal hypothesis for this species. Voles also showed no preference for a specific cache area, possibly due to their small body size. Their size may indicate that even small caches provide ample resources, so that food items within a given patch remain significantly higher than in surrounding habitat, thereby satisfying an individual's energetic requirements (Charnov 1976; Calcagno *et al.* 2014a; Oatway & Morris 2007; Mortelliti & Boitani 2008).

My pairwise analysis suggests that, despite observations being highly seasonal, snowshoe hare counts did not differ between treatment and reference sites. These results imply that between May and September 2025, hares did not heavily pilfer from red squirrel caches, and detections at caches were likely the result of general habitat use. Contrary to these findings, long-term trends from 2020 to 2025 indicate that hare engagement is associated with large caches,

reflecting high resource abundance. Additionally, I found that the starkest difference between engaged and unengaged hare detections was in autumn (Figure 5), once again, reflecting a period when caches are at their fullest (Steele 1998, Mendes *et al.* 2019), thereby supporting my resource-driven seasonal hypothesis. Despite consistent high activity in spring, detections were similar across site types (i.e., treatment vs. reference) and engagement levels, which may reflect movement patterns and territory exploration associated with the early breeding season (Burt *et al.* 2016), rather than supporting my demand-driven seasonal hypothesis. Alternatively, these detection patterns may reflect seasonal habitat preferences, with snowshoe hares favoring dense low vegetation during summer and taller vegetation during winter, which may partially explain the positive association that I observed between hare detections and tree density (Kawaguchi & Desroches 2017). Though facultatively granivorous, snowshoe hare diets are diverse and vary drastically both spatially and temporally (Bryant 2003; Seccombe-Hett & Turkington, 2008; Olnes & Kielland 2017). In general, woody conifer material makes up most of their winter diet (Ellesworth *et al.* 2013). The high degree of dietary plasticity displayed by snowshoe hares, combined with their high engagement at large caches (Figure 6), insinuates that they may opportunistically exploit caches when resources exceed a certain threshold. This opportunistic explanation may account for the discrepancy in foraging patterns I observed between the two experiments. The combined results suggest that hares do not selectively occupy areas with caches but may preferentially engage with them when they provide significant foraging opportunities relative to the surrounding landscape (Charnov 1976; Calcagno *et al.* 2014a; Holbrook *et al.* 2017), thus supporting my predictions under the circannual food abundance hypothesis for this species. To my knowledge, this is the first analysis examining the direct effects of red squirrel caching behaviour on a lagomorph taxon. Given the spatial plasticity of

snowshoe hare diets (Bryant 2003; Seccombe-Hett & Turkington, 2008; Olnes & Kielland 2017), my study suggests that at the treeline, where resources are sparser than in core boreal forest habitat (Lafleur 1999; Mamet & Kershaw 2011; Windsor 2025), hares may seek supplementary nutrition from caches when opportunistically beneficial to do so.

I found that resident avian facultative granivores, Canada jays and willow ptarmigans, were not more active at caches relative to corresponding areas of open forest. However, when examining trends from 2020 to 2025, detections of both species displayed significant seasonal patterns. Jay detections were highest in spring. Though caches can still contain cones at the onset of the snow-free season (Windsor 2025), aggregated resources are presumably at their lowest abundance during this time. Like red squirrels, Canada jays also create caches that serve as overwintering food sources (Martin *et al.* 2022). Therefore, at the treeline in northern Manitoba, Canada jays rely on their own cached food items and may have less need to engage in kleptoparasitic interactions. My study revealed no significant relationship between Canada jay cache engagement and count, further suggesting a lack of theft of squirrel caches from this species. My results are consistent with findings from other portions of the red squirrel's range, where generalist, scatter-hoarding boreal-dwelling corvids do not engage in midden pilferage (Kalinowski *et al.* 2014; Posthumus *et al.* 2015). Conversely, willow ptarmigan engagement with caches varied significantly on a circannual scale; once again, the greatest difference was observed in fall, thereby supporting the resource-driven seasonal hypothesis for this species (Figure 5). Ptarmigan also exhibited high engagement throughout winter, a period associated with particularly high thermoregulatory requirements for this species (Andreev 1991; Wilson *et al.*, 2007). Alternatively, this relationship may be explained by woody plant material commonly associated with cache sites (Pearson & Ruggerio 2001), an important winter food source for

willow ptarmigan (Thomas 1984; Andreev 1991). Unlike other resident birds, spruce grouse did not follow a predicted monthly pattern. Instead, they followed a bimodal pattern, peaking both in spring and autumn (Figure 5). Once again, there may be evidence of a seasonally driven effect; however, my model for this species did not capture this pattern. Also, unlike other resident avian facultative granivores, spruce grouse were more commonly associated with larger caches (Figure 6). Though spruce grouse hold the capacity to eat seeds, they primarily eat spruce needles and fungi (Franceschi *et al.* 1991). Since treeline red squirrels cache fungi (Windsor 2025; personal observation), larger caches may indicate an abundance of this preferred food item for grouse, thereby supporting my food-aggregation hypotheses for this species.

All migratory birds included in my analysis followed a similar pattern. When present in the study area, counts of migratory species were generally highest in autumn, except for Canada geese, which showed a more sporadic activity pattern (Figure 3; Figure 5). However, counts generally did not significantly differ between site types or engagement levels. Ground-foraging passerines feed from middens in more temperate portions of the red squirrel's distribution (Posthumus *et al.* 2015). This relationship is likely still occurring within my study area, indicated by the high magnitude of engaged detections. However, there is no evidence to suggest that prominent seed-eating passerines preferentially seek out caches on the landscape of treeline environments to forage from. The high number of overall detections that coincide with peak cache resource abundance (Steele 1998; Mendes *et al.* 2019) may result from higher individual abundance during late summer (Figure 3; Figure 5). In contrast with other songbirds, insectivorous species exhibited a significant interaction between cache area and engagement level, suggesting preferential exploitation of larger caches, which may provide valuable habitat

for arthropod prey. However, few, if any, studies have quantified invertebrate use of squirrel caches.

The predator guild displayed varying responses to red squirrel caching activity. Red foxes were the only members of the predator guild to support my resource-driven seasonal hypothesis (Figure 7), with detections coinciding with periods of predicted peak granivore activity (Steele 1998; Mendes et al. 2015). Windsor (2025) found a similar result, reinforcing fox engagement with caches when presumed prey abundance is high. However, this conclusion was not supported by the American marten models in my study. Windsor (2025) also reported significant peaks in marten abundance during late summer and autumn, a pattern that was not observed in my analysis. My pairwise study's significant interaction effect between site type and month for martens revealed that individuals of this species present at caches declined from spring to autumn (Figure 3), providing some support for a demand-driven response, coinciding with marten gestation (Zerbe *et al.* 2012; Heldstab 2021). However, this conclusion was not supported by the American martens' long-term model (Figure 7). This higher visitation frequency in spring, observed in the pairwise study, may therefore suggest a transient use of caches, possibly reflecting subnivean prey abundance (Buskirk 1984; Sherburne 1993; Pearson & Ruggiero 2001). Martens were also the only carnivorous taxon that showed evidence of prey coupling, whereby a predator's abundance is closely linked to the availability of a specific prey species, specifically with red squirrels (Figure 8). Although snowshoe hares are the primary prey items of martens within this ecotone (Windsor 2025), my results suggest that martens may supplement this calorically dense resource by feeding on red squirrels, a common prey species throughout much of the martens' range (Raine 1987), at predictable cache sites.

In contrast, raptors and weasels showed no evidence of seasonal variation or prey coupling in this study. The lack of a detectable relationship likely reflects differences in foraging strategies across varying spatial scales. For example, weasels temporally specialize on hunting small prey in the subnivean zone during winter (Sundell & Ylönen 2008; Jensvoll *et al.* 2015). Though my long-term analysis revealed no significant seasonal trend in mustelid counts, Windsor (2025) found that weasel abundance at caches may peak in winter, highlighting the importance of subnivean foraging for this taxon. Therefore, weasels may respond more strongly to fluctuations in vole populations beneath the snow or within subterranean spaces than to localized prey concentrations on surface structures (Sundell & Ylönen 2008). Similarly, raptors typically hunt over larger spatial scales and may respond to regional prey abundance rather than to small, discrete resource patches (Tornberg 1997; Tornberg 2001; Soutullo *et al.* 2012). Given the weak predator–pilfering prey coupling observed in this study, the indirect effects that granivorous resource theft has on the predator guild documented in more southern habitats may not extend to the treeline (Buskirk 1984; Sherburne 1993; Pearson & Ruggiero 2001; Posthumus *et al.* 2015).

Together, these results suggest that North American red squirrel caches at their northern range periphery generally act as temporally dynamic resource patches throughout for the terrestrial vertebrate community. Seasonal pulses in cached resource abundance, associated with the onset of red squirrel caching behaviour (Steele 1998; Mendes *et al.* 2019), facilitate increased opportunistic pilfering by many of the boreal forest’s small- to mid-sized facultative granivores and mesocarnivores. In contrast, weaker or inconsistent wildlife responses during periods of high energetic demand, such as reproduction or homeotherm overwintering demands (Liu *et al.* 2003; Churchfield *et al.* 2012; Desforges 2020), do not drive cache exploitation at the community

scale. Although caches can serve as broad resource hotspots for consumers within this ecotone, larger caches may disproportionately provide cost-effective foraging opportunities for larger-bodied herbivores, consistent with their energetic requirements and the predictions of the marginal value theorem (Charnov 1976; Stephens & Krebs 1986; Brown 1988; Calcagno *et al.* 2014b). In contrast, small-bodied consumers obtain sufficient resources from caches, despite the proportionally smaller size of these patches at the treeline relative to the large middens observed further south (Edelman *et al.* 2005; Calcagno *et al.* 2014b; Oatway & Morris 2007; Mortelliti & Boitani 2008). Within the forest-predator guild, I found no strong evidence that caches serve as valuable foraging sites for predators hunting prey species other than red squirrels themselves. Direct predator-prey coupling was observed for American martens, while red foxes showed inferred coupling through seasonal increases in activity coinciding with peak granivore cache use (Steele 1998; Mendes *et al.* 2019). These findings contrast with results from regions in more central portions of the red squirrel's distribution, where heterospecific pilferer activity increases localized predator abundance (Buskirk 1984; Sherburne 1993; Posthumus *et al.* 2015).

Overall, within marginal treeline environments, where conditions are generally sub-optimal for forest-adapted inhabitants, and resource patches can be highly discrete, squirrel caches do facilitate cost-effective foraging opportunities for the vertebrate community, despite the spatial plasticity in squirrel caching behaviour (Lafleur 1999; Mamet & Kershaw 2011; Posthumus *et al.* 2015; Windsor 2015). However, general community-wide exploitation of cached contents within this ecotone is highly temporally driven and largely taxon- and context-specific. This study, therefore, emphasizes the importance of resource phenology and discrete patch dynamics in shaping vertebrate community structure at peripheral ecosystem boundaries. Ecotones can represent a marginal habitat where environmental constraints intensify resource

limitations (Sultaire *et al.* 2023). Within these habitats, discrete resource-patch dynamics may be especially important for individual fitness. Examining the ecosystem-wide role of these resource aggregations thereby offers insight into how species may adapt to ecologically harsh conditions.

Limitations and directions for future research

When interpreting the results of this study, several limitations should be considered. In a camera-trap experiment, the detectability of wildlife when present should be considered. Cameras are motion-triggered; however, the size of the individual in question and their movement patterns are all factors that contribute to a camera's likelihood of being triggered. For example, small-bodied animals may become harder to detect when foliage or understory structures obstruct the camera's field of view. In this study, animals that could realistically be obscured by vegetation or other objects (i.e. boreal red-backed voles and small-bodied browsing passerines) were more likely to be under-detected relative to larger, more mobile species. Therefore, detectability varies seasonally, with the most prominent reductions in winter. During winter, some resident taxa, such as weasels and voles, use subnivean spaces (Sherburne 1993; Pearson & Ruggiero 2002; Jensvoll *et al.* 2015; Windsor 2025). This variability in taxon-specific detectability means that my results should be interpreted as an index of activity rather than as direct, localized species abundance at a cache site or a corresponding reference site.

Another potential limitation of this study is the use of the cache area as a proxy for patch quality. At the treeline, most of a squirrel's cached food items are located within a subterranean burrow (Windsor 2025) as opposed to within a large, centralized midden (Smith 1981; Hurly & Lorie 1997; Steele 1998; Posthumus *et al.* 2015). Despite this plasticity in caching behaviour, a squirrel at the treeline still produces feeding debris piles, which resemble miniature middens (Personal observation). As a squirrel feeds, some seeds are knocked loose and fall into the

associated cone-scale pile (Edelman *et al.* 2005; Posthumus *et al.* 2015). These seeds that have been knocked loose during feeding serve as the dominant form of small- to mid-sized granivore pilferage at middens in centralized core boreal forest habitat (Pearson & Ruggiero 2002; Edelman *et al.* 2005; Posthumus *et al.* 2015). Therefore, though we could not measure true cache abundance, a cache's associated feeding debris area serves as a metric for surface-accessible seed abundance and for cache content prevalence over time.

Future studies should therefore examine these aforementioned limitations: exploring small-scale subniveal heterospecific cache activity and quantifying wildlife foraging patterns as a function of direct cached content abundance. Additionally, my study examined only the vertebrate community, but future research should examine a broader range of animal taxa, such as Arthropods, providing valuable insight into causal mechanisms for insectivore cache engagement. Alternatively, future studies should also examine how caches influence floral communities, and the role red squirrels play as a seed disperser.

Conclusion

This study examined the influence of North American red squirrel caches on vertebrate foraging behaviour in marginal treeline habitat in Northern Manitoba. Here, red squirrel caching behaviour is markedly different from that in core boreal forest environments (Windsor 2025). My results suggest that, within this marginal habitat, caches facilitate foraging activity within the vertebrate community; however, their overall influence is largely taxon- and season-specific.

Many facultatively granivorous terrestrial vertebrates across the sub-Arctic treeline exploited red squirrel caches during seasonal pulses of peak resource abundance. This period

falls in late summer and autumn, when squirrels are gathering conifer cones and other food in preparation for winter (Steele 1998; Mendes *et al.* 2019). Of all taxa examined, boreal red-backed voles showed the highest temporally driven response, suggesting that this species acts as a prominent kleptoparasite of red squirrels during periods of peak cache-resource abundance. Other resident herbivores, such as snowshoe hares and willow ptarmigan, also opportunistically capitalize on foraging opportunities provided by caches during seasonal pulses. Like with these resident species, migratory passerine activity peaks in abundance during periods of presumed high cached content abundance. However, this pattern likely reflects broader seasonal increases in passerine abundance rather than a direct response to caches, suggesting opportunistic use. Red foxes, a dominant mesocarnivore throughout the boreal forest, are also driven by this seasonal pattern, which coincides with the onset of caching behaviour, reflecting a period of presumed prey concentration.

Snowshoe hares and spruce grouse were the only facultative granivores that responded to cache area, indicating these relatively larger-bodied granivores may rely on more resource-dense patches to make cache pilferage energetically worthwhile (Charnov 1976; Calcagno *et al.* 2014a; Holbrook *et al.* 2017). In contrast, smaller-bodied pilferers may obtain sufficient resources from even small patches, thereby reducing their dependence on cached resource abundance beyond a specific threshold (Charnov 1976; Calcagno *et al.* 2014a; Oatway & Morris 2007; Mortelliti & Boitani 2008). Among the forest-predator guild, American martens were the only carnivorous species to show direct foraging engagement associated with circannual food availability, reflecting predation on red squirrels themselves and highlighting the role that caches serve as valuable foraging grounds for this mid-sized carnivore (Raine 1987).

My study emphasizes the importance of patch dynamics in ecologically marginal environments. Although red squirrel caching behaviour at the treeline is markedly different from that in core boreal forest habitats (Windsor 2025), treeline caches share many community-wide ecological similarities with middens further south. At the northern range periphery of red squirrels, caches do not act as general drivers of broad-scale habitat use throughout the vertebrate community; however, they influence localized abundance and foraging behaviour of certain taxa. Species that capitalize on these resource patches appear to do so in a manner proportional to seasonal resource dynamics or the consumer's overall energetic demands. Given the treeline's low cone production (Lafleur 1999; Mamet & Kershaw 2011; Windsor 2025) and sub-optimal conditions for forest-adapted species, the caches of North American red squirrel represent important resource patches for many taxa in otherwise resource-limited environments.

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Figures and Tables

Table 1: Tally of all independent wildlife observations by trail cameras at red squirrel caches near Churchill, MB from 2020-2025 (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025). Counts for each species or taxon were recorded at three different levels of engagement with the squirrel cache (unengaged with the cache, present at cache and feeding at the cache). No effort was made to distinguish red-backed vole counts in the “Present at cache” category from the eating at cache category. Red squirrel counts were only recorded when present at a cache. taxa denoted with an asterisk (*) were selected for statistical modeling.

Taxa	Unengaged	Present at cache	Feeding at cache
*Canada goose (<i>Branta canadensis</i>)	44	22	2
*American robin (<i>Turdus migratorius</i>)	315	363	54
*Other insectivorous passerines (Passeriniiformes)			
American pipit (<i>Anthus rubescens</i>)	19	11	3
Blackpoll warbler (<i>Setophaga striata</i>)	0	2	0
Boreal Chickadee (<i>Poecile hudsonicus</i>)	2	1	0
Bohemian waxwing (<i>Bombycilla garrulus</i>)	0	1	0
Fox Sparrow (<i>Passerella iliaca</i>)	25	30	4
Gray-cheeked thrush (<i>Catharus minimus</i>)	8	13	0
Lincoln sparrow (<i>Melospiza lincolnii</i>)	8	9	0
Orange crowned warbler (<i>Leiothlypis celata</i>)	0	2	0
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	1	3	0
White-crowned sparrow (<i>Zonotrichia leucophrys</i>)	24	14	0
Yellow-rumped warbler (<i>Setophaga coronata</i>)	5	6	0
Lapland longspur (<i>Calcarius lapponicus</i>)	2	0	1
Song sparrow (<i>Melospiza melodia</i>)	3	2	0
Alder flycatcher (<i>Empidonax alnorum</i>)	1	0	0
Swamp sparrow (<i>Melospiza georgiana</i>)	3	2	0
Northern mockingbird (<i>Mimus polyglottos</i>)	1	0	0
Rusty blackbird (<i>Euphagus carolinus</i>)	2	3	0
Palm warbler (<i>Setophaga palmarum</i>)	1	0	0
Red-breasted nuthatch (<i>Sitta canadensis</i>)	0	1	0
*Other insectivorous passerines (Passeriniiformes)			
American pipit (<i>Anthus rubescens</i>)	19	11	3
Blackpoll warbler (<i>Setophaga striata</i>)	0	2	0
Boreal Chickadee (<i>Poecile hudsonicus</i>)	2	1	0
Bohemian waxwing (<i>Bombycilla garrulus</i>)	0	1	0
Fox Sparrow (<i>Passerella iliaca</i>)	25	30	4
Gray-cheeked thrush (<i>Catharus minimus</i>)	8	13	0
Lincoln sparrow (<i>Melospiza lincolnii</i>)	8	9	0
Orange crowned warbler (<i>Leiothlypis celata</i>)	0	2	0
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	1	3	0

White-crowned sparrow (<i>Zonotrichia leucophrys</i>)	24	14	0
Yellow-rumped warbler (<i>Setophaga coronata</i>)	5	6	0
Lapland longspur (<i>Calcarius lapponicus</i>)	2	0	1
Song sparrow (<i>Melospiza melodia</i>)	3	2	0
Alder flycatcher (<i>Empidonax alnorum</i>)	1	0	0
Swamp sparrow (<i>Melospiza georgiana</i>)	3	2	0
Northern mockingbird (<i>Mimus polyglottos</i>)	1	0	0
Rusty blackbird (<i>Euphagus carolinus</i>)	2	3	0
Palm warbler (<i>Setophaga palmarum</i>)	1	0	0
Red-breasted nuthatch (<i>Sitta canadensis</i>)	0	1	0
Unidentified passerines	108	96	11
Hoary woodpecker (<i>Dryobates villosus</i>)	2	0	0
Northern flicker (<i>Colaptes auratus</i>)	1	3	2
*Canada jay (<i>Perisoreus canadensis</i>)	92	75	7
Raven (<i>Corvus corax</i>)	0	6	0
Sandhill crane (<i>Antigone canadensis</i>)	4	2	0
*Raptors (Accipitriformes)			
Snowy owl (<i>Bubo scandiacus</i>)	1	0	0
Northern harrier (<i>Circus hudsonius</i>)	0	2	0
American goshawk (<i>Accipiter atricapillus</i>)	5	10	3
*Willow ptarmigan (<i>Lagopus lagopus</i>)	38	103	15
*Spruce grouse (<i>Canachites canadensis</i>)	9	13	3
*Snowshoe hare (<i>Lepus americanus</i>)	1716	2042	317
*Red-backed vole (<i>Clethrionomys gapperi</i>)	87	335	-
Moose (<i>Alces alces</i>)	0	1	0
Caribou (<i>Rangifer tarandus</i>)	1	2	0
Wolverine (<i>Gulo gulo</i>)	1	0	0
*American marten (<i>Martes americana</i>)	27	82	30
Mink (<i>Neovision vision</i>)	4	8	3
*Weasels			
Short-tailed weasel (<i>Mustela erminea</i>)	12	35	12
Least weasel (<i>Mustela nivalis</i>)	1	5	0
Gray wolf (<i>Canis lupis</i>)	2	3	1
American black bear (<i>Ursus americanus</i>)	1	3	1
*Red fox (<i>Vulpes vulpes</i>)	62	172	18
Red squirrels (<i>Tamiasciurus hudsonicus</i>)	-	5,920	-

Table 2: Tally of all wildlife observations by trail cameras at red squirrel cache sites and reference sites, placed 50 m away and facing the opposite direction from their corresponding cache, near Churchill, MB from May to September 2025 (7 paired sites in May, 10 from June to August and 9 in September). Species or functional groups denoted with an asterisk (*) were selected for statistical modeling.

Species or functional group	Cache sites	Reference sites
*Canada goose (<i>Branta canadensis</i>)	6	7
*American robin (<i>Turdus migratorius</i>)	101	133
*Predominantly insectivorous passerines (Passeriniiformes)		
American pipit (<i>Anthus rubescens</i>)	3	0
Blackpoll warbler (<i>Setophaga striata</i>)	0	4
Boreal Chickadee (<i>Poecile hudsonicus</i>)	2	7
Bohemian waxwing (<i>Bombycilla garrulus</i>)	1	0
Fox Sparrow (<i>Passerella iliaca</i>)	38	12
Gray-cheeked thrush (<i>Catharus minimus</i>)	3	7
Lincoln sparrow (<i>Melospiza lincolnii</i>)	6	0
Northern rough-winged swallow (<i>Stelgidopteryx serripennis</i>)	0	1
Orange crowned warbler (<i>Leiothlypis celata</i>)	2	2
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	3	5
White-crowned sparrow (<i>Zonotrichia leucophrys</i>)	25	4
Yellow-rumped warbler (<i>Setophaga coronata</i>)	0	1
*Predominantly granivorous passerines (Passeriniiformes)		
Brown headed cow bird (<i>Molothrus ater</i>)	1	0
White-winged crossbill (<i>Loxia leucoptera</i>)	1	0
Dark-eyed junco (<i>Junco hyemalis</i>)	35	16
Snow bunting (<i>Plectrophenax nivalis</i>)	0	1
Tree sparrow (<i>Spizelloides arborea</i>)	9	14
*Gray jay (<i>Perisoreus canadensis</i>)	19	26
Raven (<i>Corvus corax</i>)	2	3
*Raptors (Accipitriiformes)	6	2
*Willow ptarmigan (<i>Lagopus lagopus</i>)	15	7
Spruce Grouse (<i>Canachites canadensis</i>)	5	0
*Snowshoe hare (<i>Lepus americanus</i>)	623	567
*Redback vole (<i>Clethrionomys gapperi</i>)	133	5
Moose (<i>Alces alces</i>)	1	0
Caribou (<i>Rangifer tarandus</i>)	0	2
*American marten (<i>Martes americanus</i>)	22	10
*Short-tailed weasel (<i>Mustela erminea</i>)	3	0
Gray wolf (<i>Canis lupis</i>)	0	1
American black bear (<i>Ursus americanus</i>)	1	1
*Red fox (<i>Vulpes vulpes</i>)	27	22

Table 3: Random effect SD, marginal R^2 and conditional R^2 , for paired design wildlife counts models near Churchill, MB from May to September 2025 (7 paired sites in May, 10 from June to August and 9 in September).

Model	Random effect: Site ID (SD)	Marginal R^2	Conditional R^2
Species richness	0.10	0.011	0.043
Snowshoe hare	1.25	0.069	0.516
Red-backed vole	1.52	0.188	0.446
American robin	0.92	0.176	0.385
Granivorous passerines	0.76	0.111	0.208
Insectivorous passerines	0.96	0.071	0.230
Canada jay	0.82	0.029	0.168
Willow ptarmigan	0.60	0.092	0.154
Red fox	0.48	0.037	0.085
American marten	0.58	0.100	0.161

Table 4: Random effect SD, marginal R^2 and conditional R^2 , for wildlife count models created from trail camera data collected near Churchill, MB from August 2020 to September 2025 (a maximum of 7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 12 and between 12 2025).

Model	Random effect: site ID (SD)	Random effect: year (SD)	Marginal R^2	Conditional R^2
Resident species richness	0.28	0.08	0.25	0.36
Migrant species richness	0.64	0.14	0.11	0.56
Snowshoe hare	0.92	0.70	0.10	0.58
Granivorous passerines	1.41	1.11	0.23	0.69
Insectivorous passerines	0.90	0.70	0.21	0.50
American robin	0.95	0.16	0.13	0.45
Red-backed vole	2.22	≈ 0	0.43	0.83
Willow ptarmigan	0.88	0.29	0.17	0.38
Spruce grouse	≈ 0	≈ 0	0.72	0.72
Canada jay	0.59	≈ 0	0.63	0.68
Canada goose	0.89	≈ 0	0.96	0.97
Red fox	0.54	0.33	0.16	0.28
American marten	0.30	0.48	0.09	0.19
Weasel	0.56	0.75	0.01	0.18
Raptors	≈ 0	≈ 0	0.08	0.08

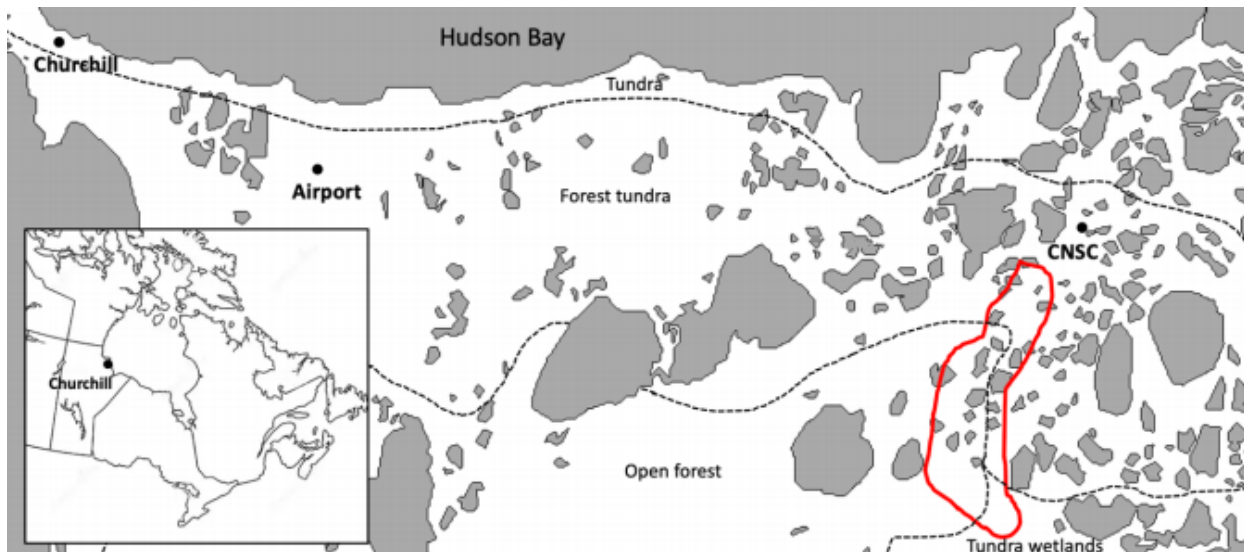


Figure 1: Map of my study area, in the Churchill region of Northern Manitoba, Canada. The red outline marks the area in which we monitored red squirrel (*Tamiasciurus hudsonicus*) caches. The dashed lines denote different habitat types. This figure was adapted from Windsor (2025), originally adapted from Corkery *et al.* (2019).

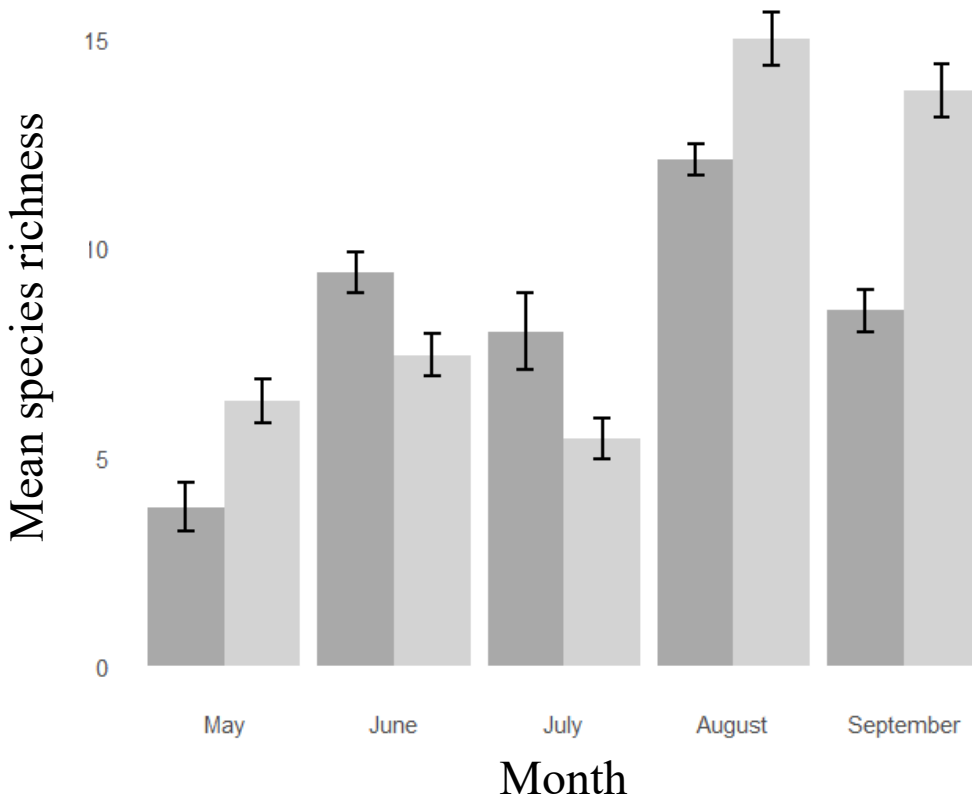
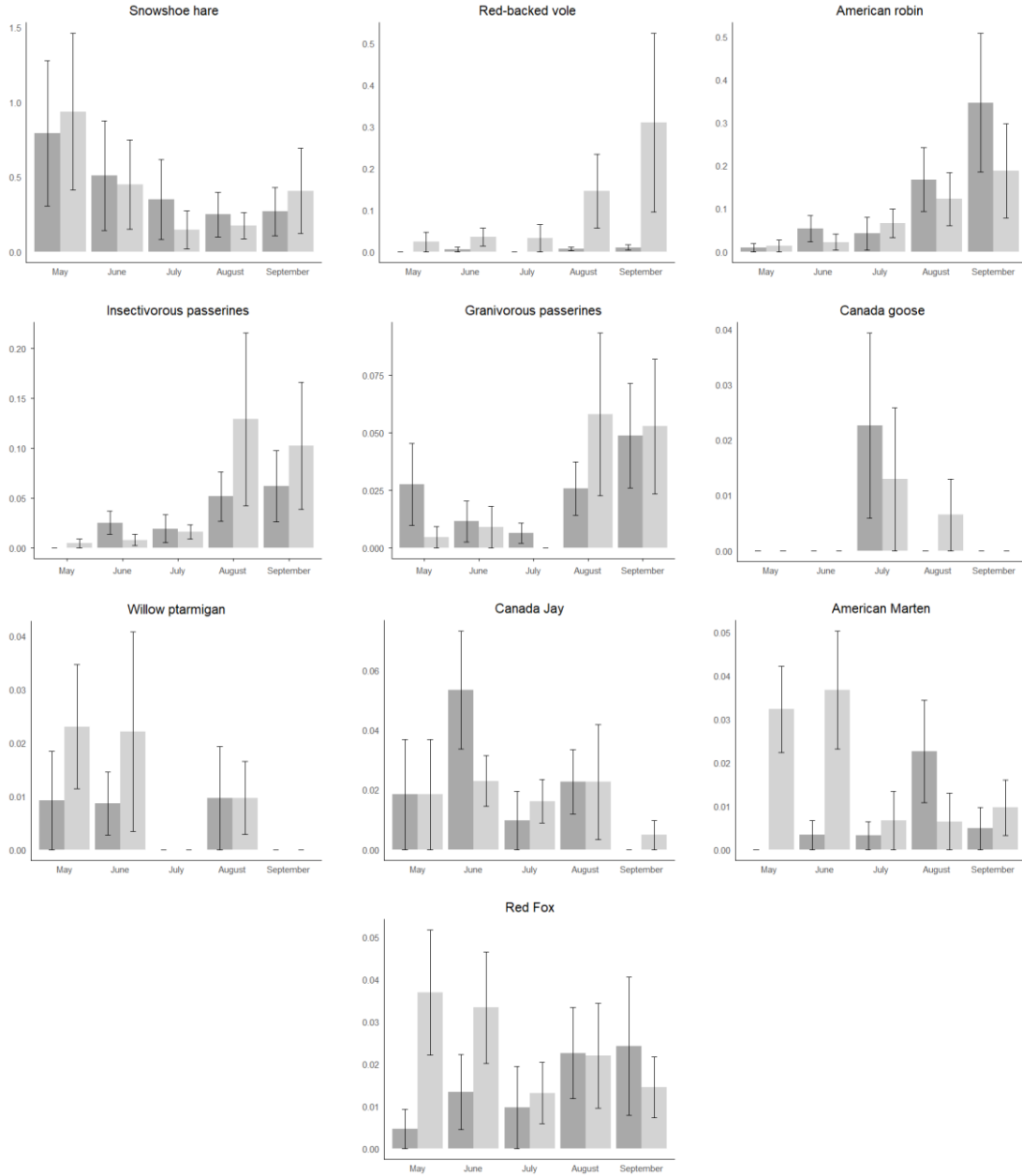


Figure 2: Species richness (mean $\pm$ SE) at red squirrel caches (light grey) and corresponding control sites (dark grey) assessed by trail cameras near Churchill, MB, from May to September 2025 (7 paired sites in May, 10 from June to August, and 9 in September).

Detection rate (observations per day)



Month

Figure 3: Monthly mean detections rates (observations per functioning camera day; $\pm$ SE) of focal species and functional groups at red squirrel caches (light gray) and corresponding control sites (dark gray), assessed through trail camera imagery near Churchill, MB, from May to September 2025 (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025).

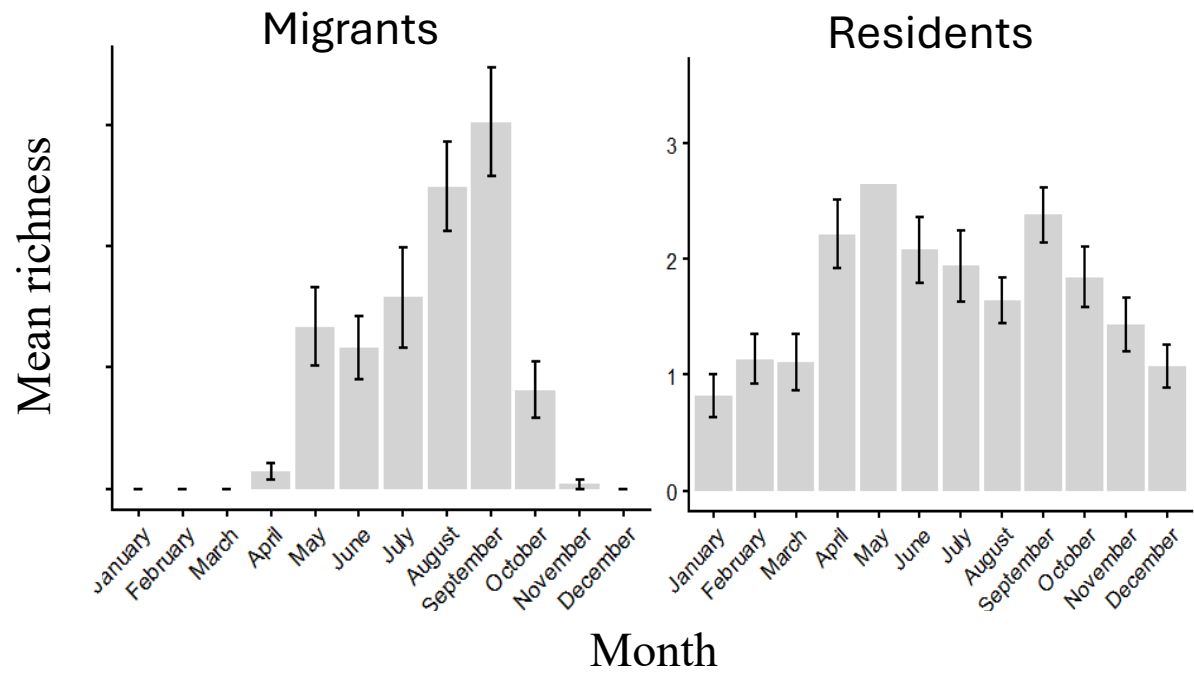


Figure 4: Species richness (mean $\pm$ SE) of resident and migrant species at red squirrel caches in sub-Arctic treeline habitat in northern Manitoba from August 2020 to September 2025 assessed through trail camera imagery (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025).

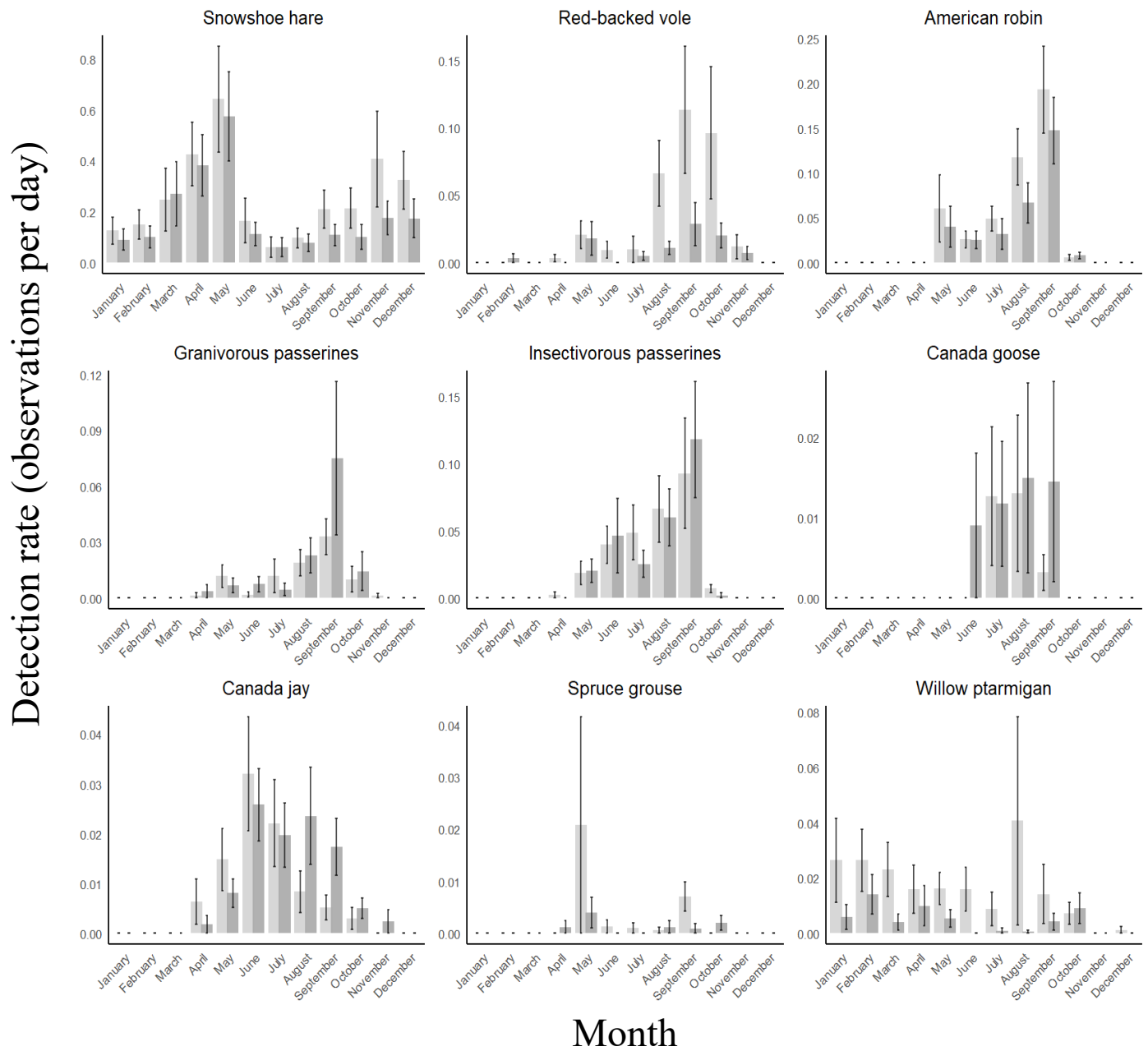


Figure 5: Monthly detection rates (observations per functioning camera day; mean $\pm$ SE) of pilfering species at red squirrel caches, assessed through trail camera imagery near Churchill, MB, from August 2020 to September 2025 (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025). The detection rate for each focal species or functional group is divided between engaged (at a squirrel cache; light grey) and unengaged (>1 body length away from a squirrel cache; dark grey) individuals.

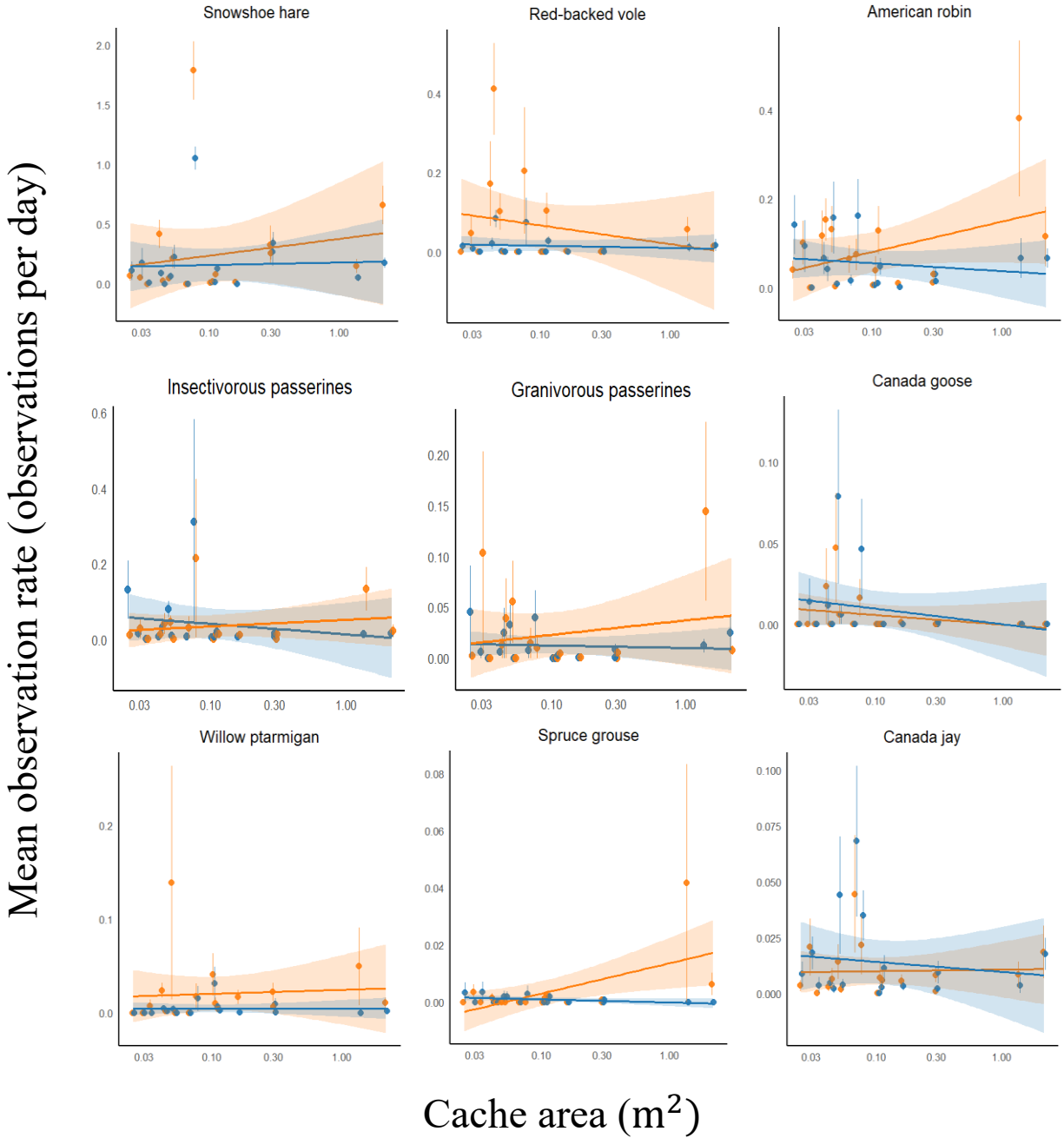


Figure 6: Relationship between red squirrel cache area (m²) and observation rate (observations per camera day; mean $\pm$ SE) of facultative granivores captured on remote camera trap images in treeline habitat near Churchill, MB (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025). Cache areas (n = 17) were measured in August 2024. Rates are divided into unengaged (observations of individuals more than one body length from the cache; blue) and engaged (observations of individuals within one body length of the cache; orange) categories. The shaded areas around the engaged and unengaged trendlines represent a 95% confidence interval.

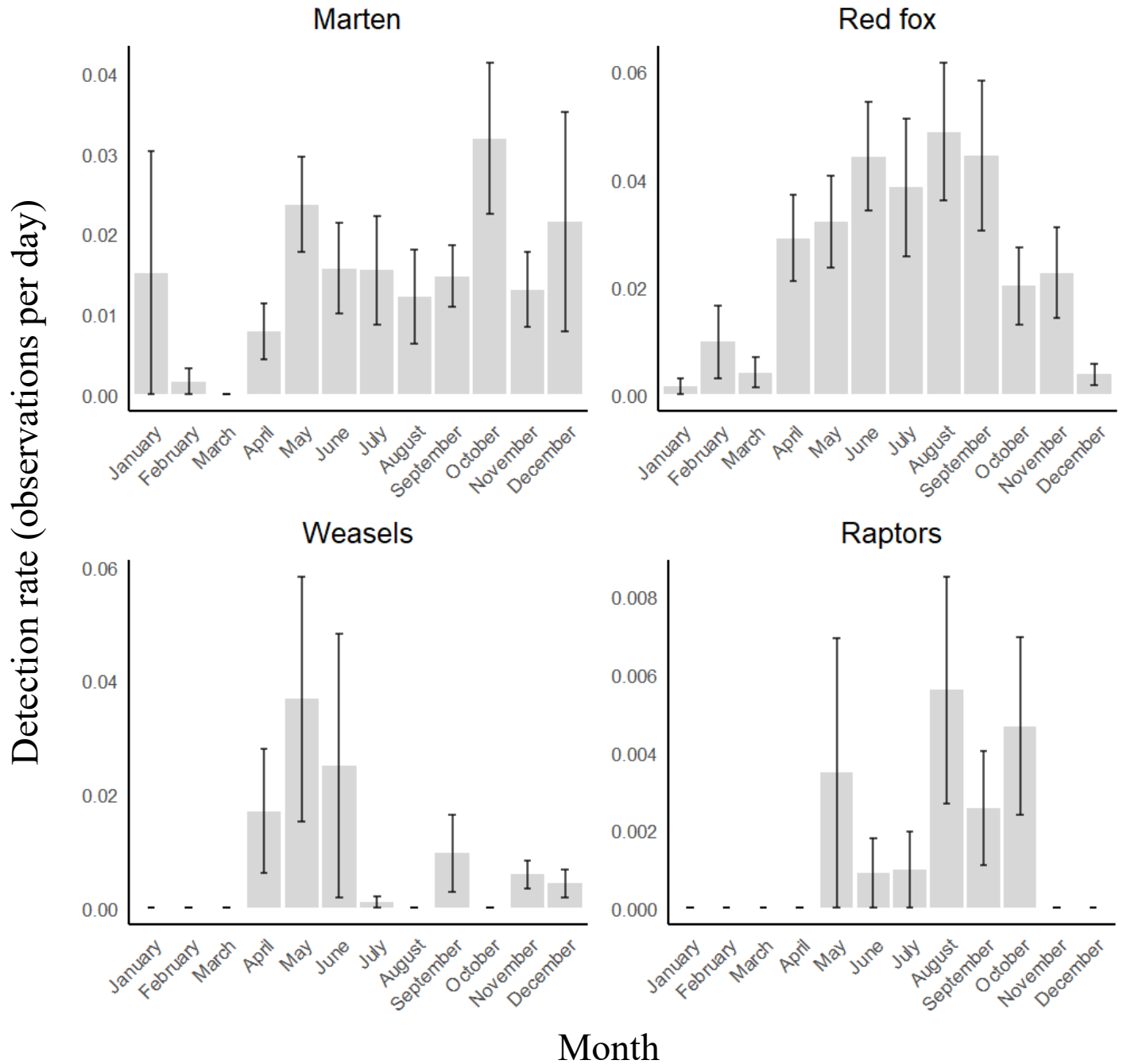


Figure 7: Monthly detections rates (observations per functioning camera day; mean $\pm$ SE) of predator taxa at red squirrel caches, assessed through trail camera imagery near Churchill, MB, from August 2020 to September 2025 (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025).

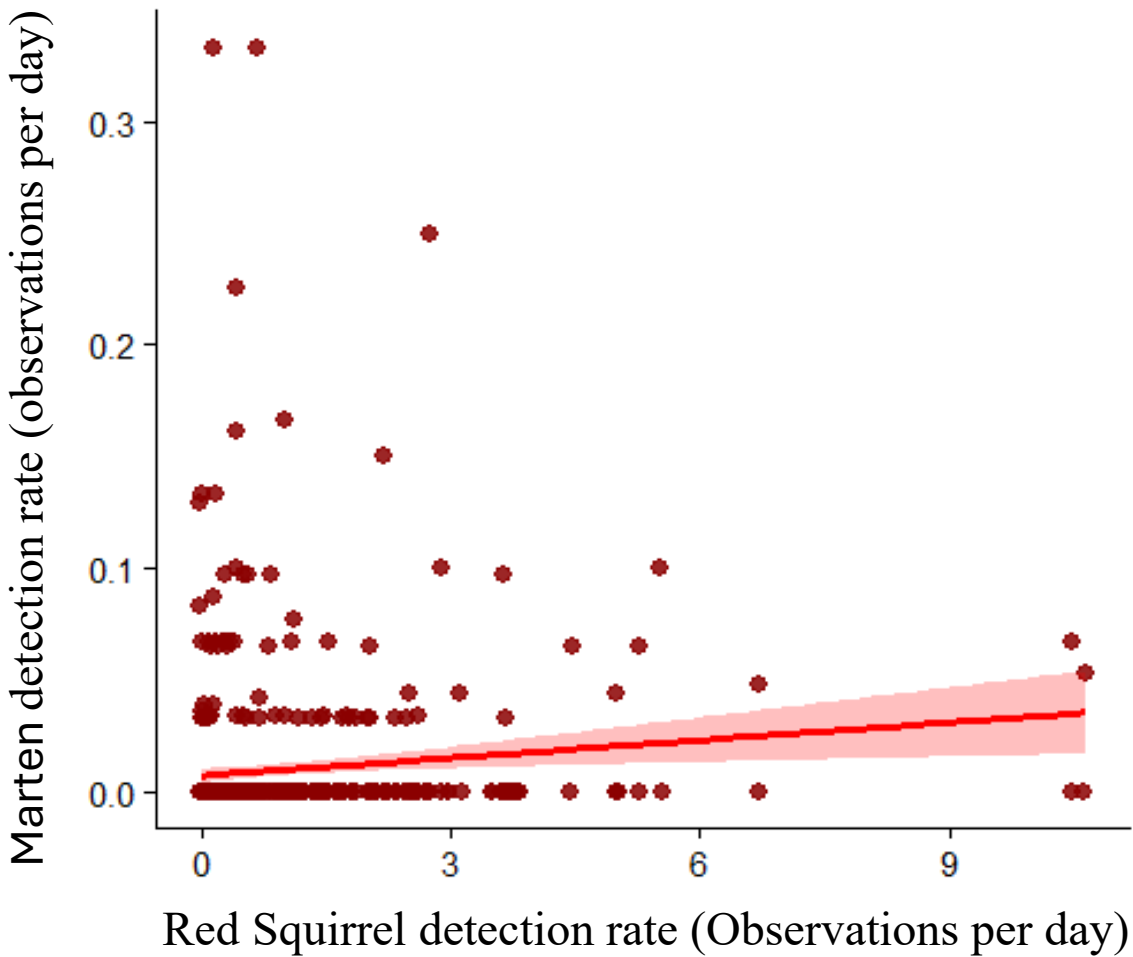


Figure 8: Relationship between the detection rates (detections per day per month) of American martens (*Martes americana*) and engaged (observations of individuals within one body length of a red squirrel cache) red squirrels (*Tamiasciurus hudsonicus*), captured on remote camera trap images in treeline habitat near Churchill, MB, from August 2020 to September 2025 (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025). The shaded areas around the engaged and unengaged trendlines represent a 95% confidence interval.

Appendix

Table A1: Full model summaries for paired-design wildlife GLMMs examining the effects of cache presence and month on vertebrate detections near Churchill, Manitoba, May–September 2025 (7 paired sites in May, 10 from June to August, and 9 in September). Engagement level was treated as a categorical variable with engaged detections as the reference level.

Species	Predictor	χ^2	<i>df</i>	<i>p</i>	β	<i>SE</i>
Snowshoe hare	Type	0.61	1	0.44	0.43	0.97
	Month	9.14	1	0.0025	-0.33	0.16
	Type $\times$ Month	0.02	1	0.88	-0.03	0.22
Red-backed vole	Type	9.23	1	0.0024	2.47	2.60
	Month	8.61	1	0.0033	0.77	0.47
	Type $\times$ Month	0.10	1	0.75	-0.16	0.52
American robin	Type	0.24	1	0.62	0.75	1.45
	Month	14.04	1	<0.001	0.72	0.22
	Type $\times$ Month	0.48	1	0.49	-0.22	0.31
Insectivorous birds	Type	0.82	1	0.36	-1.6	1.25
	Month	10.29	1	0.0013	0.22	0.18
	Type $\times$ Month	2.50	1	0.11	0.41	0.26
Granivorous birds	Type	0.00	1	0.98	-2.86	1.53
	Month	8.06	1	0.0045	0.19	0.19
	Type $\times$ Month	3.77	1	0.052	0.59	0.31
Canada goose	Type	0.26	1	0.61	-2.84	7.58
	Month	0.00	1	0.95	-0.28	1.24
	Type $\times$ Month	0.07	1	0.80	0.46	1.78
Willow ptarmigan	Type	0.50	1	0.48	1.62	2.09
	Month	2.59	1	0.11	-0.34	0.44
	Type $\times$ Month	0.33	1	0.57	-0.31	0.54
Canada jay	Type	0.58	1	0.44	-1.47	1.35
	Month	1.64	1	0.20	-0.36	0.23
	Type $\times$ Month	0.8	1	0.37	0.30	0.33
American marten	Type	1.18	1	0.28	4.68	1.63
	Month	1.58	1	0.21	0.46	0.3
	Type $\times$ Month	7.09	1	0.0077	-0.97	0.36

Red fox	Type	0.80	1	0.37	2.62	1.23
	Month	0.03	1	0.86	0.32	0.22
	Type $\times$ Month	3.81	1	0.051	-0.54	0.28

Table A2: Full model summaries for long-term wildlife GLMMs examining the effects of seasonality, cache area, engagement level, and habitat variables on vertebrate detections near Churchill, Manitoba, August 2020–September 2025 (maximum of 7 cameras in 2020, 10 in 2021, 17 in 2022–2023, 15 in 2024, and 12 in 2025). Engagement level was treated as a categorical variable with engaged detections as the reference level.

Taxon	Predictor	χ^2	<i>df</i>	<i>p</i>	<i>B</i>	<i>SE</i>
Snowshoe hare	Cache area	2.66	1	0.10	0.48	0.25
	Engagement	10.72	1	0.0011	-0.31	0.10
	Month ²	8.24	2	0.016	3.17	1.80
	Tree density	3.96	1	0.047	0.42	0.21
	Cache area × Engagement	6.28	1	0.012	-0.21	0.08
	Engagement × Month ²	4.55	2	0.10	-5.28	2.64
American robin	Cache area	2.01	1	0.156	0.47	0.29
	Engagement	2.44	1	0.118	-0.33	0.22
	Month	10.92	1	<0.001	0.41	0.18
	Tree density	1.39	1	0.24	0.31	0.26
	Cache × Engagement	0.77	1	0.38	-0.18	0.21
	Engagement × Month	0.01	1	0.93	0.020	0.25
Granivorous Passerines	Cache area	3.14	1	0.076	0.73	0.42
	Engagement	0.01	1	0.93	0.08	0.33
	Month	19.44	1	<0.001	1.12	0.32
	Tree density	1.28	1	0.26	0.46	0.41
	Cache area × Engagement	0.04	1	0.84	-0.05	0.26
	Engagement × Month	0.22	1	0.64	-0.20	0.42
Insectivorous Passerines	Cache area	0.51	1	0.48	0.40	0.29
	Engagement	0.13	1	0.72	-0.09	0.24
	Month	17.9	1	<0.001	0.84	0.27
	Tree density	1.93	1	0.17	0.35	0.25
	Cache area × Engagement	4.07	1	0.044	-0.47	0.23
	Engagement × Month	0.00	1	0.99	0.01	0.36
Red-backed vole	Cache area	0.72	1	0.39	0.39	0.64
	Engagement level	5.57	1	0.018	-0.19	0.47
	Month ²	25.23	2	<0.001	-55.08	13.43
	Tree density	1.36	1	0.24	0.74	0.63
	Cache area × Engagement level	0.88	1	0.35	0.29	0.31
	Engagement level × Month ²	4.01	2	0.13	30.13	16.21

Willow ptarmigan	Cache area	0.09	1	0.76	0.13	0.27
	Engagement level	10.65	1	0.0011	-0.82	0.30
	Month ²	17.38	2	<0.001	-9.68	4.82
	Tree density	1.08	1	0.30	-0.23	0.22
	Cache area × Engagement level	0.98	1	0.32	-0.32	0.32
	Engagement level × Month ²	0.96	2	0.62	7.37	7.54
Spruce grouse	Cache area	7.56	1	0.0060	0.60	0.21
	Engagement level	0.00	1	0.97	0.05	1.58
	Month ²	3.41	2	0.18	-62.88	30.01
	Tree density	0.81	1	0.37	0.25	0.28
	Cache area × Engagement level	1.77	1	0.18	-3.65	2.74
	Engagement level × Month ²	2.33	2	0.31	46.20	33.3
Canada jay	Cache area	0.57	1	0.45	0.20	0.22
	Engagement level	0.96	1	0.33	1.00	0.50
	Month ²	35.12	2	<0.001	-64.96	14.51
	Tree density	2.96	1	0.085	0.33	0.19
	Cache area × Engagement level	0.29	1	0.59	-0.10	0.19
	Engagement level × Month ²	5.58	2	0.061	28.23	16.48
Canada goose	Cache area	6.40	1	0.011	-9.96	5.39
	Engagement	0.49	1	0.48	1.20	2.70
	Month	0.08	1	0.77	-0.21	0.80
	Tree density	8.53	1	0.0030	2.16	0.74
	Cache × Engagement	0.07	1	0.79	1.62	6.09
	Engagement × Month	0.01	1	0.92	0.10	0.96
Red fox	Tree density	2.87	1	0.09	0.27	0.16
	Vole rate	0.10	1	0.75	-0.02	0.08
	Hare rate	1.96	1	0.16	0.12	0.09
	Goose rate	0.82	1	0.36	0.05	0.05
	Squirrel rate	2.65	1	0.10	0.13	0.08
	Month ²	23.88	2	<0.001	-20.46	4.19

American marten	Tree density	2.69	1	0.10	0.26	0.16
	Vole rate	1.72	1	0.19	0.16	0.12
	Hare rate	1.19	1	0.28	0.14	0.13
	Squirrel rate	6.47	1	0.011	0.32	0.13
	Month ²	1.09	2	0.58	-1.39	4.42
Weasels	Tree density	0.17	1	0.68	0.11	0.28
	Vole rate	0.02	1	0.89	0.03	0.23
	Month ²	1.26	2	0.53	-7.22	7.03
Raptors	Vole rate	0.52	1	0.47	0.13	0.18
	Hare rate	0.06	1	0.81	-0.08	0.33
	Grouse rate	0.03	1	0.86	-0.18	0.97
	Squirrel rate	1.55	1	0.21	0.25	0.20
	Month	1.92	1	0.17	0.46	0.33

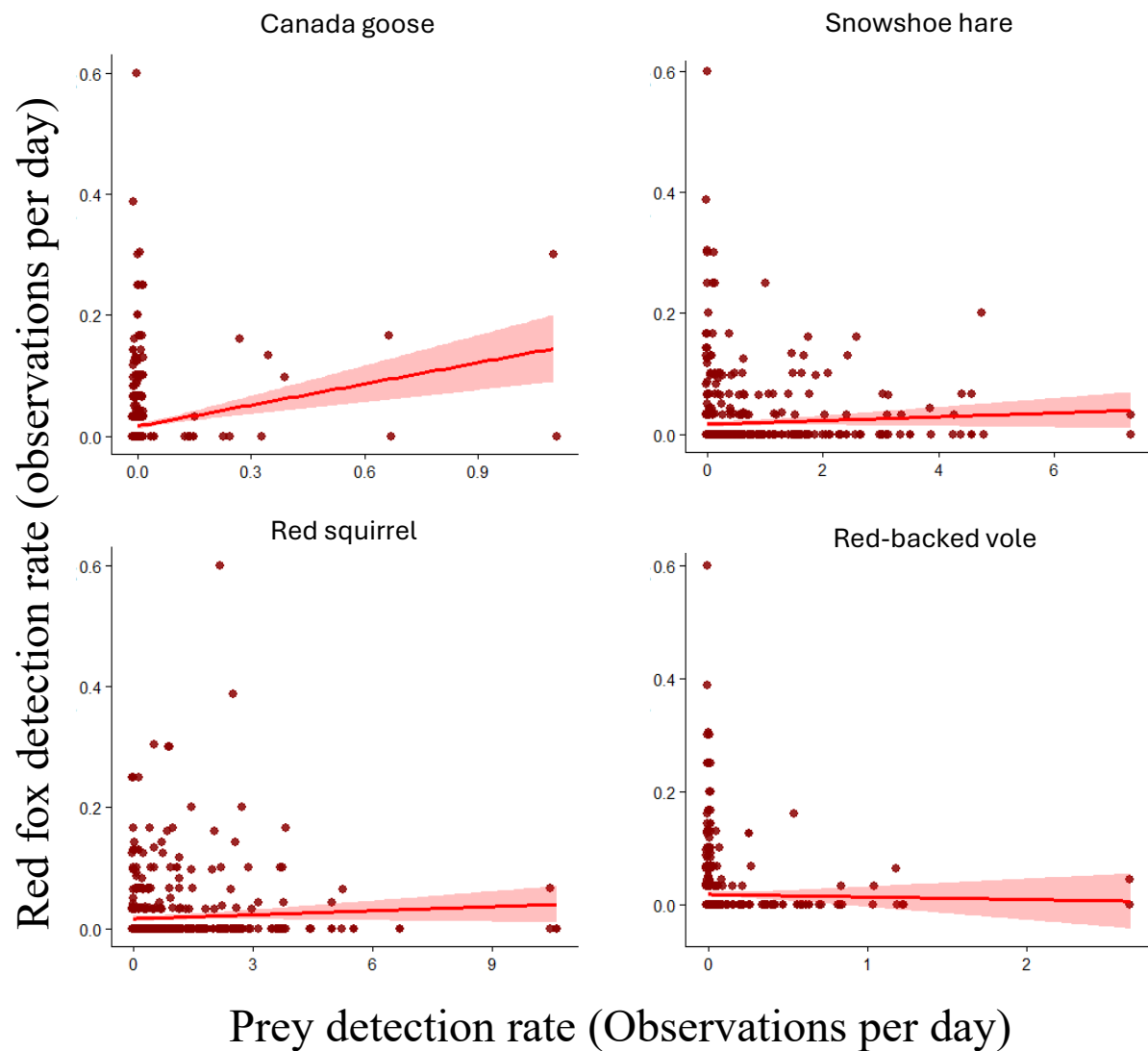


Figure A1: Relationship between the detection rates (detections per day per month) of red foxes (*Vulpes vulpes*) and engaged (observations of individuals within one body length of a red squirrel cache) prey items, captured on remote camera trap images in treeline habitat near Churchill, MB, from August 2020 to September 2025 (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025). The shaded areas around the engaged and unengaged trendlines represent a 95% confidence interval.

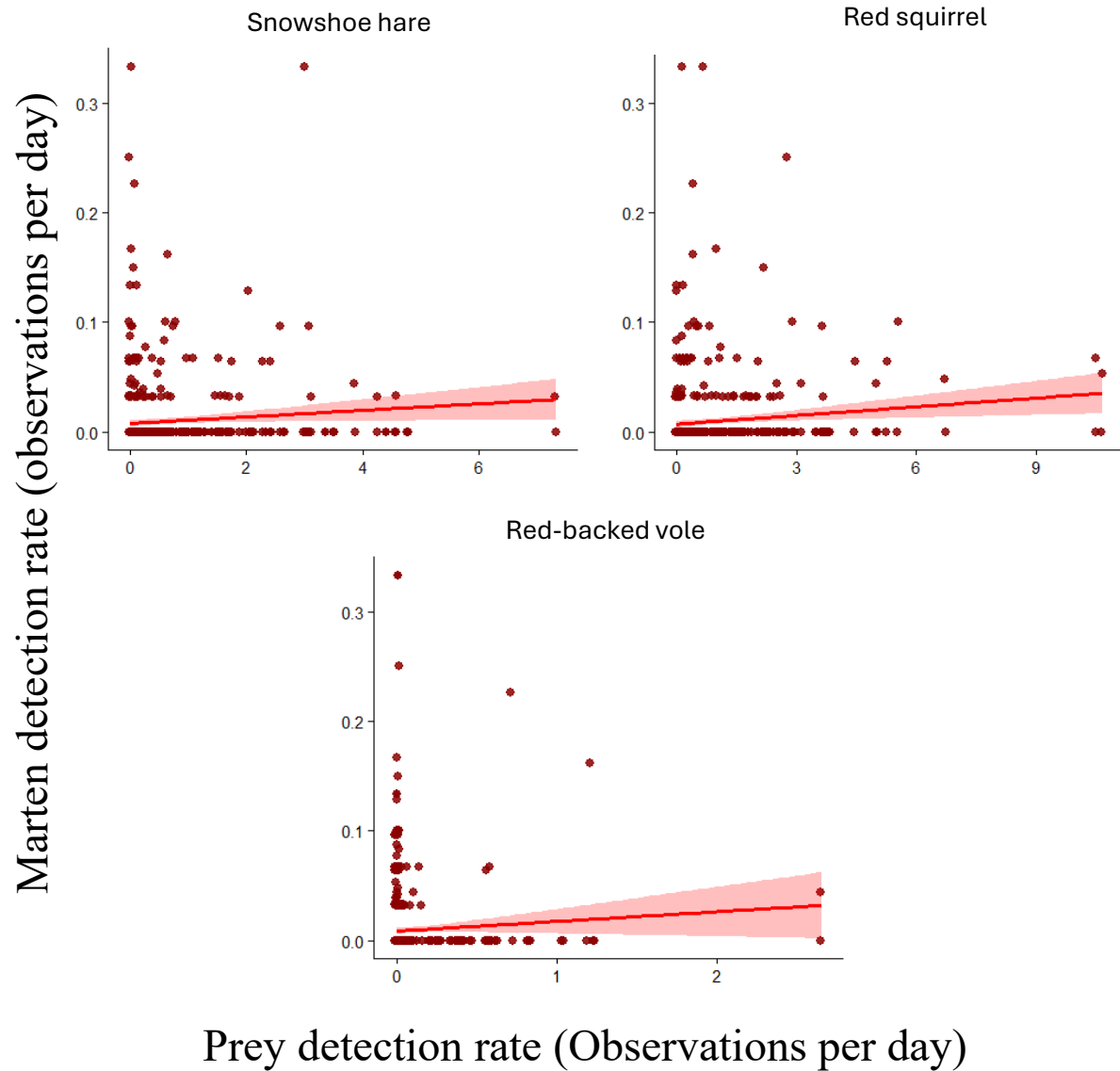


Figure A2: Relationship between the detection rates (detections per day per month) of American marten (*Martes americana*) and engaged (observations of individuals within one body length of a red squirrel cache) prey items. captured on remote camera trap images in treeline habitat near Churchill, MB, from August 2020 to September 2025 (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025). The shaded areas around the engaged and unengaged trendlines represent a 95% confidence interval.

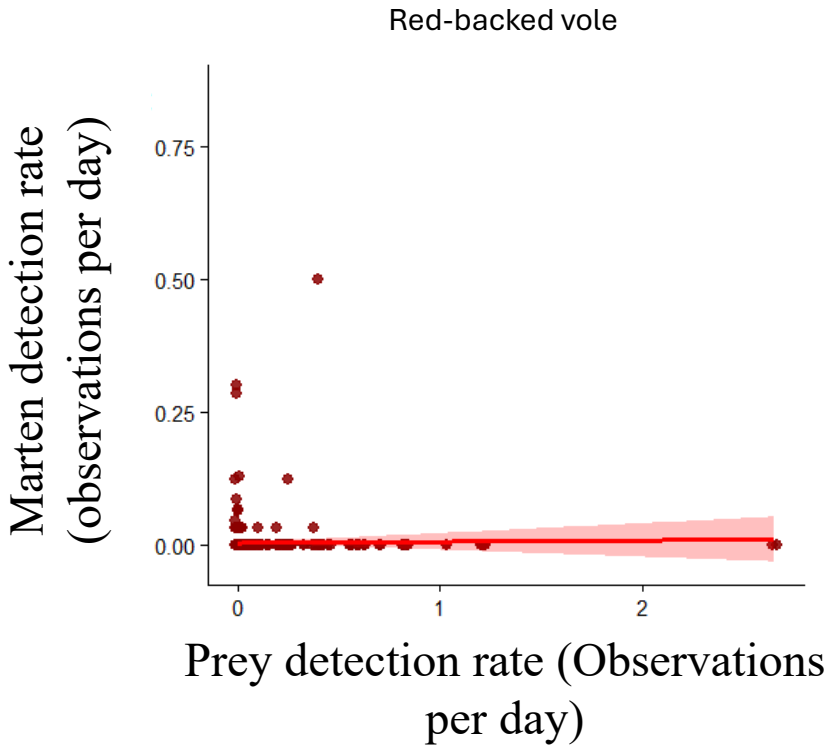


Figure A3: Relationship between the detection rates (detections per day per month) of northern treeline-dwelling weasels (*Mustela* spp.) and engaged (observations of individuals within one body length of a red squirrel cache) boreal red-backed voles (*Clethrionomys gapperi*) captured on remote camera trap images in treeline habitat near Churchill, MB, from August 2020 to September 2025 (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025). The shaded areas around the engaged and unengaged trendlines represent a 95% confidence interval.

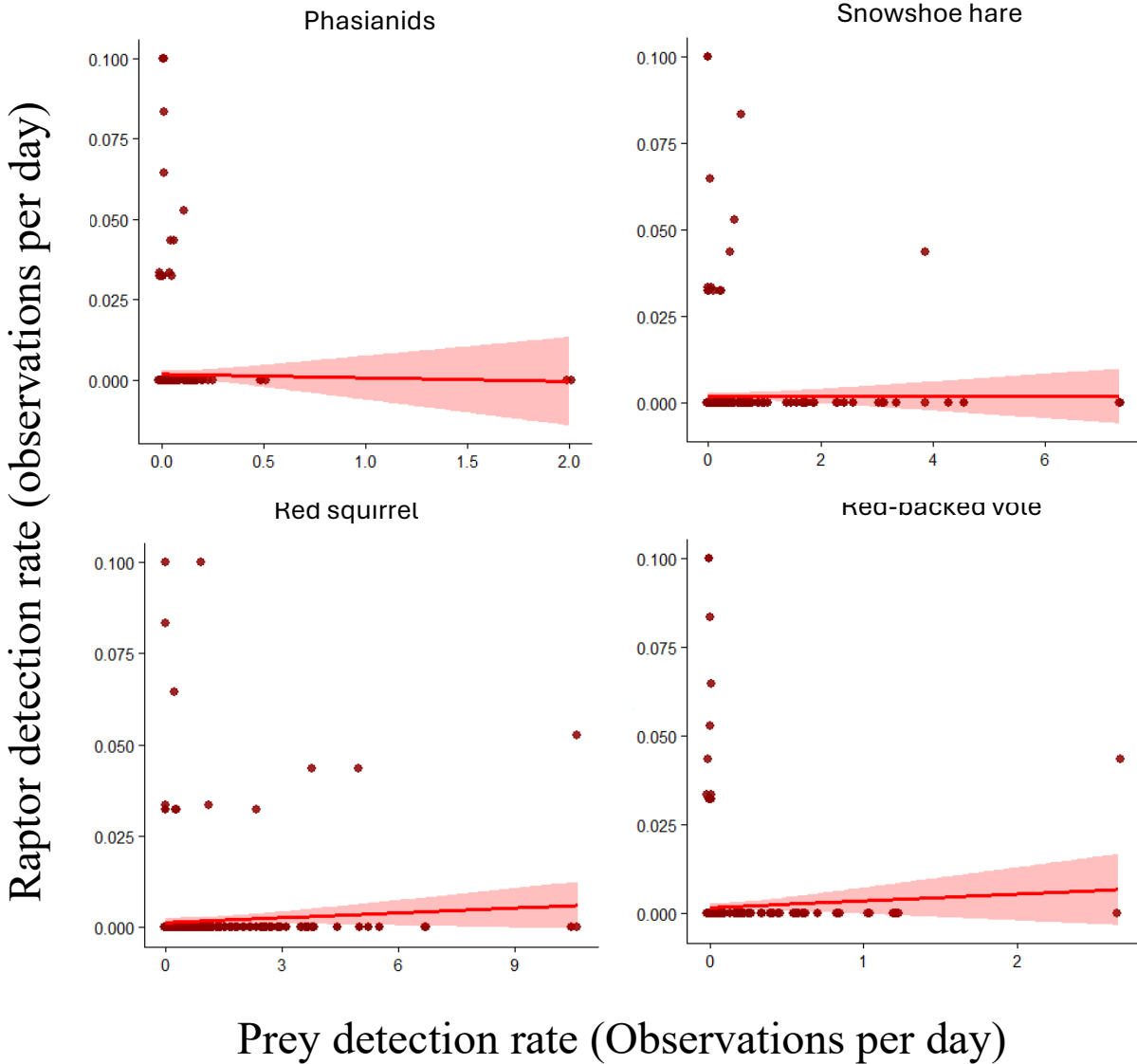


Figure A4: Relationship between the detection rates (detections per day per month) of treeline-inhabiting raptors (Accipitriformes) and engaged (observations of individuals within one body length of a red squirrel cache) prey items. captured on remote camera trap images in treeline habitat near Churchill, MB, from August 2020 to September 2025 (7 cameras in 2020, 10 in 2021, 17 between 2022 and 2023, 15 in 2024 and 12 in 2025). The shaded areas around the engaged and unengaged trendlines represent a 95% confidence interval.