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## Snowshoe Hares (*Lepus americanus*) Alter Feeding Behavior in Response to Coyote (*Canis latrans*) and Moose (*Alces alces*) Cues at Diverse Vegetation Densities

Zachary K. Lankist  
*University of Southern Maine, zachlankist@gmail.com*

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**Snowshoe hares (*Lepus americanus*) alter feeding behavior in response to  
coyote (*Canis latrans*) and moose (*Alces alces*) cues at diverse vegetation densities**

by

Zachary K. Lankist

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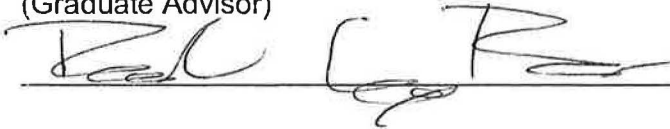
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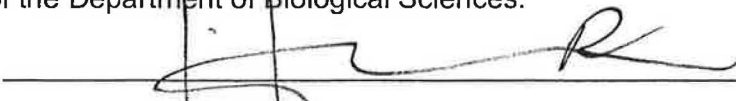


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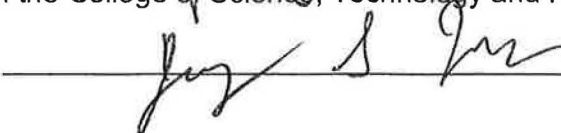
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## Abstract

Prey interpret predator cues as a warning and use them to assess the danger of a given area. Multiple prey species avoid chemical cues from predators at feeding sites because the risk of death outweighs the benefit of food. However, we lack information regarding avoidance of chemical cues from competitors as well as how foraging behavior changes alongside vegetative cover. To test if chemical cues and vegetative cover alter prey vigilance, number of visits, and time spent at feeding sites, I observed snowshoe hares (*Lepus americanus*) in plots containing coyote (*Canis latrans*; predator) and moose (*Alces alces*; competitor) urine across a spectrum of vegetation densities. Snowshoe hares significantly reduced the number of visits to feeding plots when coyote or moose urine was administered. In plots containing coyote urine, number of visits decreased significantly as plots became more densely vegetated. Neither chemical cues nor vegetation density had a large effect on snowshoe hare vigilance or time spent in plots. These results suggest that competition between snowshoe hares and moose has selected for an avoidance response. This study also reinforces the idea that an increase in vegetation density could prove disadvantageous to prey, perhaps because some predators may utilize dense vegetation to their advantage while stalking.

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## Introduction

Interspecific competition can result in a dominant competitor species excluding a subordinate competitor species from a limiting resource (Hersteinsson and Macdonald 1992; Connell 1961). According to Gause's law of competitive exclusion (Gause 1934), such exclusion can result in reduced fitness, or even total extirpation, of 1 or more competitors in an area, and thus interspecific competition can change the community structure of an ecosystem drastically (Capitan et al. 2017; Hairston et al. 1960). This type of competition can manifest itself as an interference interaction, e.g., direct, physical combat occurs between competitors to secure a resource, or an exploitative interaction, e.g., a dominant competitor more efficiently uses a resource, which can lead to cue avoidance by subordinates (Miller, 1967).

Due to the costs of losing a vital resource to a rival competitor, some organisms act aggressively toward heterospecifics, which can increase the ability of the aggressor to take control of a resource (Bach et al. 1976; Murray 1971). For example, when an adult signal crayfish (*Pacifastacus leniusculus*) is placed into a tank containing a heterospecific adult European crayfish (*Astacus astacus*), *P. leniusculus* establishes dominance over *A. astacus* by performing unilateral aggressive attacks, thus securing for itself the contested space inside the tank (Soderback 1991). In their natural environment, this increase in aggressiveness toward heterospecifics could lead to *P. leniusculus* outcompeting other species and monopolizing limiting resources such as food and shelter. Similarly, noisy miner (*Manorina melanocephala*) colonies in Australia interact aggressively with all heterospecifics that attempt to enter their territory (Dow 1977). These aggressive interactions, which may lead to the death of intruding heterospecifics, ensure that noisy miners remain in control of their territories and the food sources within those territories (Dow 1977). Among hermit crabs in the Florida Keys, an

interspecific dominance hierarchy occurs among 3 species, *Clibanarius tricolor*, *C. antillensis*, and *Calcinus tibicen* (Bach et al. 1976). When fighting for new shells, *C. tibicen* becomes dominant over *C. tricolor*, which, in turn, becomes dominant over *C. antillensis*. The aggressive dominance of *C. tibicen* allows it to secure the best shells in its environment, leading to increased brood size and better protection from predators (Bach et al. 1976).

Whereas increasing aggressive behavior proves beneficial to some organisms, it also can be costly (Hack 1997; Riechert 1988). To avoid the potentially high cost:benefit ratio associated with increased aggression, some organisms avoid direct interactions by gathering information from environmental cues. These cues can consist of visual, auditory, and chemical signals that relay information to an organism about places to avoid (Dickman 1991; Durant 2000; Yoshimoto 2009). Even though this latter, more passive, option also can be costly, because organisms switch to suboptimal habitats with fewer resources to avoid negative direct interactions, it reduces the risk of injury and death through aggressive interactions (Vanak et al. 2013).

Reliance on visual cues, whether to interact with other species or to self-orient, is widespread among animals (Dacke et al. 2013; Hankison and Morris 2003; Yoshimoto 2009). Avoidance of an interspecific competitor based on visual cues occurs when the beetle *Rhomborrhina japonica* visually detects a competitor at a food source (Yoshimoto 2009). After being displaced from a feeding patch, *R. japonica* waits near the patch until the competitor leaves, which then prompts *R. japonica* to continue foraging. The visual cue used by the subordinate competitor allows it to both avoid combat and gather food. Similarly, but focusing on a different type of signal, cheetahs (*Acinonyx jubatus*) use auditory cues to avoid competitors while hunting (Durant 2000). Upon hearing the call of a lion (*Panthera leo*) or a spotted hyena (*Crocuta crocuta*), cheetahs are less likely to hunt and more likely to be attentive to their

surroundings. In doing so, cheetahs experience the costs of a lower kill rate, but they benefit by avoiding harmful interactions associated with dominant competitors, including death. Finally, as an example of use of chemical cues, parasitoid wasp *Cotesia marginiventris* females avoid the scent of the rival wasp species *Campoletis sonorensis* when seeking a place to lay eggs (Tamo et al. 2006). To optimize time spent looking for a suitable host, *C. marginiventris* females avoid the dominant competitor because a physical interaction costs both time and energy.

In addition to relaying information about nearby competitors, chemical cues left by predators present valuable information to prey species. The use of predator chemical cues as repellents has been well studied in predator-prey relationships, where early predator detection by prey could mean the difference between life and death (Sullivan et al. 1985). In places that prey commonly visit, e.g., feeding areas, the scent of a predator can act as a natural repellent and significantly reduce prey activities (Apfelbach et al. 2005). For example, mountain beavers (*Aplodontia rufa*) consume significantly less food if the surrounding area contains the scent of predatory minks (*Mustela vison*) or coyotes (*Canis latrans*), and beavers reduce feeding in the area for multiple days (Epple et al. 1993). Similarly, white-tailed deer (*Odocoileus virginianus*) reduce feeding on Japanese yews (*Taxus cuspidata*) if urine of bobcats (*Lynx rufus*) or coyotes is applied topically (Swihart et al. 1991). Chemical cues left by predators work in a similar manner to cues left by dominant competitors, and such odors ward off prey species from resource patches. The act of prey leaving one potentially dangerous patch for another, safer, patch can be explained by the concept of giving-up densities, where an organism leaves a patch once the food source has been reduced to a certain amount (Brown 1988; Bedoya-Perez et al. 2013). The benefits of remaining in dangerous patches (food items to be gained by prey species) do not

outweigh the cost of staying (increased risk of predation), so prey abandon foraging in these areas and move to other patches.

Another species that avoids areas containing predator-associated chemical signals is the snowshoe hare (*Lepus americanus*; Sullivan 1986; Sullivan et al. 1985). With a range extending from the northern treeline of North America to the southern mountains of Tennessee, snowshoe hares prefer areas with dense vegetation and are well adapted for travel through snow (Keith 1990; Keith and Bloomer 1993; Litvaitis et al. 1985; Murray 2003; Murray and Boutin 1991; Orr and Dodds 1982). Because individual home ranges overlap extensively, researchers suspect snowshoe hares are not territorial (Murray 2003). However, snowshoe hares fight conspecifics when densities are high around a limiting resource (Grange 1932; Murray 2003; Quenette et al. 1997).

Snowshoe hare mortality is mostly attributed to mammalian and avian predators (Boutin et al. 1986; Hodges et al. 2001; Keith et al. 1984; Murray 2003; Murray et al. 1997; O'Donoghue 1994; Wirsing et al. 2002). Hares reduce feeding in areas containing feces, anal gland secretions, or urine of predators, including bobcats, short tailed weasels (*Mustela erminea*), and wolverines (*Gulo gulo*). Furthermore, given favorable environmental conditions such as time periods without rain, this suppression can last for several days (Sullivan et al. 1985). Because predator urine suppresses hare activity, researchers suggest using it as a defense against snowshoe hare herbivory (Sullivan et al. 1985).

Whereas snowshoe hares avoid predator chemical cues, we have less understanding about how they react to cues associated with a competitor. The majority of research associated with avoidance of competitor chemical cues focuses on similar organisms within a genus or family. However, there is a gap in the literature pertaining to avoidance of competitor urine of different

organisms across orders. Although competition between disparate mammals occurs, such as the competitive relationship between roe deer (*Capreolus capreolus*) and mountain hares (*Lepus timidus*), this aspect of competitive interactions is generally overlooked, with almost no focus on anti-competitor behavior (Holbert and Anderson 2001). Therefore, my study focused on how snowshoe hares react to the urine of a potential competitor, the moose (*Alces alces*; Belovsky 1984; Dodd 1960; Telfer 1972). Moose are the largest living species in the family Cervidae, and the range of the moose stretches from coast to coast in Canada and the northern United States, with spruce (*Picea* spp.), fir (*Abies* spp.), and pine (*Pinus* spp.) forests being the preferred habitat (Bowyer et al. 2003; Karns 1998; Telfer 1984). Home range size of a moose varies from 3.6 km<sup>2</sup> to 92 km<sup>2</sup>, and individuals establish this range when they are 2–3 years old (Addison et al. 1980; Bowyer et al. 2003; Houston 1968; Hundertmark 1998).

Snowshoe hares and moose show similarities in resource consumption as well as habitat distribution, with overlap occurring in multiple states and provinces in the U.S. and Canada, respectively (Bowyer et al. 2003; Dodd 1960; Murray 2003). Both species prefer herbaceous plant material in summer and switch to a woody diet in winter (Dodd 1960). During winter in Newfoundland, snowshoe hares and moose feed on at least 27 of the same species of woody plants and prefer plants less than 2 m high (Dodd 1960). In particular, species such as white birch (*Betula papyrifera*) and balsam fir (*Abies balsamea*) are especially sought after by both moose and snowshoe hares (Dodd 1960).

Due to these similarities in foraging preference, researchers suspect that, despite their vast size differences, with moose weighing upwards of 770 kg versus the average snowshoe hare weight of 1.3 kg, interspecific competition occurs between moose and snowshoe hares, with the former acting as the dominant competitor (Belovsky 1984; Dodd 1960; Grange 1932; Rowan and

Keith 1959; Schwartz et al. 1987; Telfer 1972). In general, areas with high moose density have low snowshoe hare density and vice versa, and interspecific competition is the likely explanation (Dodd 1960). When moose heavily browse and trample plants, they reduce the amount of food available to hares and also remove overhead vegetation under which snowshoe hares hide (Belovsky 1984; Dodd 1960). This reduction in vegetation could lead to greater predation risk and may cause hares to spend less time feeding and more time vigilant (Altendorf et al. 2001).

Based on data that snowshoe hares avoid certain chemical cues and prefer areas containing dense vegetation, and the hypothesis that a competitive relationship could exist between moose and snowshoe hares, my objectives were to determine 1) if chemical cues, in the form of urine from a moose (a potential competitor) and a coyote (a predator), alter snowshoe hare foraging behavior in a natural setting and 2) if vegetation density alters snowshoe hare foraging behavior (Dodd 1960; Litvaitis et al. 1985, Sullivan et al. 1985). Because moose may outcompete snowshoe hares, I predicted that snowshoe hares visit areas marked with moose urine less often than unmarked locations (Belovsky 1984; Dodd 1960). Furthermore, because coyotes are a major predator of snowshoe hares, I predicted that hares visit areas marked with coyote urine less often than unmarked locations (O'Donoghue et al. 1997; Patterson et al. 1998). Because humans do not regularly prey on snowshoe hares, I predicted that hares would not visit areas marked with human urine any less often than unmarked locations.

Moose may browse or trample plants, reducing the amount of cover under which snowshoe hares hide. Thus, the competitor also may increase predation risk indirectly (Belovsky 1984; Litvaitis et al. 1985). I predicted that snowshoe hares would be more apt to avoid (no appearance within a plot during the week of testing), decrease total number of visits, and spend

less time in open plots compared to dense plots because hares were less concealed from predators in more open areas.

Both indirect chemical cues and removal of overhead vegetation may lead to changes in activity levels of prey (Altendorf et al. 2001; Belovsky 1984; Sullivan et al. 1985). I predicted that snowshoe hares spend more time vigilant in plots containing coyote urine than in other plots because of the perceived predator threat (Sullivan et al. 1985). In plots surrounded by dense vegetation, I predicted that hares spend less time vigilant and more time feeding than in more exposed plots because they are concealed from predators.

## MATERIALS AND METHODS

*Study sites.*—I conducted this study at 2 sites in Maine: Lily Bay State Park (374 ha; 45°34'N, 69°32'W) and Seboomook Public Reserved Land (20,821 ha; 45°55'N, 69°51'W) from early June to early October 2018. Each location borders Moosehead Lake, a 30,534 ha body of water located in Piscataquis County, Maine, and contains important plants found in moose and snowshoe hare diets (including *Abies balsamea*, *Betula papyrifera*, and *Acer spicatum*; Dodd 1960). Both moose and snowshoe hares commonly occur in these areas throughout the year (Bowyer et al. 2003; Murray 2003).

*Creating food bags.*—In this experiment, I used food to bait snowshoe hares into the study areas. I mixed 1 banana and 2 apples with 100 g of both Timothy hay (*Phleum pratense*) and rabbit feed (Small World Complete Rabbit Feed, Manna Pro Products, Chesterfield, Missouri). I placed the mixture in a plastic bag for transportation to and from the study sites. At the plots, I distributed the food mixture across a 50 cm × 50 cm piece of black mesh to keep the food contained in 1 location for the duration of the trial.

*Setting up plots.*—At each study site I established a set of plots containing 3 treatment plots and 1 control plot. In each set, the 4 plots measured 2 m × 2 m and I placed them in random order along a transect, each separated by 100 m. At the center of each plot I placed a food bag and drove a metal stake (0.5 m) into the ground, to which I fastened a plastic vial. In 3 treatment plots, the vials contained 10 ml of Pete Rickard's Moose in Heat moose urine (Pete Rickard's Co., Galeton, Pennsylvania), Pete Rickard's coyote urine, or human urine. For the control plot, the vial contained 10 ml of distilled water. Finally, I attached a game camera (Browning Dark Ops model BTC-6 or Browning Dark Ops Extreme model BTC-6HDX) to a nearby tree and programmed it to take a snapshot of activity every 5 s once an animal came into frame. Each game camera was situated 0.5-1 m above ground and was camouflaged to avoid disrupting passing animals. After 7 days, I collected data and moved the sets to a new area within the chosen location to begin a new trial.

*Data collection.*— I inspected images from the game cameras to determine the number of times snowshoe hares visited each plot per week, duration of each visit, and whether or not the hares avoided the plot for the entire week. I also noted whether other species visited the plots. I counted any hare located inside a plot as a visitor, and if that hare left the frame and subsequently returned after a 10-min interval, I counted it as a separate visitor because I could not differentiate individual hares. I utilized time stamps on each picture taken to determine duration of snowshoe hare visits. These stamps displayed time to the nearest minute, so any visit that lasted less than 1 min was counted as a 30 s visit. For input into the model, I calculated the mean amount of time snowshoe hares spent at each treatment per week.

To test the prediction that hares prefer feeding in areas surrounded by dense vegetation, I employed the method used by Wolff (1980) to measure vegetation density. I constructed a



placard containing 64 squares (8 x 8), with each square measuring 5 cm<sup>2</sup>. I placed the placard at the center of each plot and observed it from 3 m away, counting every square not covered by vegetation, to determine horizontal vegetation density. I made these observations while looking from the north, south, east, and west. Afterwards, I used a 4 m piece of wood, stabilized by dual 1 m metal supports, to raise the placard 4 m above the center of the plot and made another observation to determine vertical vegetation density. I then divided the number of squares that were covered by 512 to determine density percentages for each plot. I gathered all vegetation density data after each 7-day urine trial, so that my scent did not further disturb the plots.

To test whether snowshoe hares are more or less vigilant depending on vegetation density and treatment, I inspected game cameras and classified all pictures of hares in each plot as vigilant (head up, scanning), feeding, vigilant-feeding (food in mouth while scanning), investigating (nose in close proximity to the urine vial), moving, or grooming. I divided the number of pictures in each behavioral category by the total number of pictures per plot to determine the percentage of time that snowshoe hares participated in each activity. For input into the model, I calculated the mean percent vigilance of snowshoe hares per week at each treatment.

*Statistical analysis.*— I used the program R (R Core Team 2017) to perform all statistical analysis. Due to habitat differences between the study sites, with Lily Bay State Park having less diverse microenvironments and greater human presence than Seboomook Public Reserved Land (Z. Lankist, pers. obs.), I analyzed them separately in every statistical test. I used generalized linear mixed effect models (glmm) with Poisson distributions (link = log;  $p < 0.05$ ) to compare number of snowshoe hare visits among plot types and vegetation densities. The response variable, number of visits, was dependent upon treatment and vegetation density, the fixed

variables. Transects within study sites were included as random effect variables because their locations changed every week.

I used linear mixed effect models (lmm) with Gaussian distributions (link = identity;  $p < 0.05$ ) to compare snowshoe hare avoidance and the amount of time spent in a plot across plot types and vegetation densities. The response variables, avoidance and time spent in plot, were dependent on treatment and vegetation density (fixed variables).

I used linear mixed effect models with Gaussian distributions (link = identity;  $p < 0.05$ ) to compare percentage of time that snowshoe hares spent vigilant across plot types and vegetation densities. Vigilance (response variable) depended on treatment and vegetation density (fixed variables).

## RESULTS

*Number of visits.*—Chemical cues, in the form of urine, played a role in altering the number of snowshoe hare visits at both study sites. At Lily Bay State Park, the mean number of visits per week to coyote plots decreased by 21%, and the mean number of visits to moose plots declined by 49% compared to control plots treated with water (Fig. 1a; Table 1). Visits to plots treated with human urine did not differ notably from plots treated with water, with a 3% increase in mean number of visits per week. Plots at Seboomook Public Reserved Land had similar results to those at Lily Bay (Fig. 1b; Table 1). Mean number of visits to both coyote and moose plots each week decreased by 40% compared to control plots treated with water. Plots treated with human urine differed only slightly from control plots treated with water, exhibiting 1% decrease in mean number of weekly visits.

Effects of vegetation density on number of hare visits depended on treatment. At both sites, number of visits to plots treated with water, human urine, and moose urine increased

slightly as vegetation density increased (Fig. 2; Table 2). Conversely, number of visits to coyote plots decreased as vegetation density increased at both Lily Bay State Park (Fig. 2a; Table 2) and Seboomook Public Reserved Land (Fig. 2b; Table 2).

*Avoidance and time in plot.*—Neither type of urine nor vegetation density played a significant role in whether or not snowshoe hares avoided plots (Table 3). At both Lily Bay State Park and Seboomook Public Reserved Land, the probability for snowshoes hares to avoid water-treated control plots did not exceed 40% (Figs. 3, 4). Likewise, avoidance of experimental plots at either location did not differ from the trend seen in their respective controls (Table 3).

Chemical cues did not significantly alter the amount of time that snowshoe hares stayed in plots (Table 4). Mean amount of time spent in coyote and moose plots at Lily Bay State Park increased by 14% and decreased by 18%, respectively, compared to plots treated with water (Fig. 5a; Table 4). Mean amount of time spent in plots treated with human urine increased by 52% compared to water-treated plots. At Seboomook Public Reserved Land, mean amount of time spent in coyote plots decreased by 38% compared to water-treated plots, and mean amount of time spent in moose plots decreased by 8% (Fig. 5b; Table 4). Plots treated with human urine exhibited a 7% increase in time spent in plot.

The effect of vegetation density on amount of time spent in a plot did not differ across plot types. At Lily Bay State Park, time in plot decreased slightly as vegetation density increased in the water-treated control plot, and the trend in the experimental plots did not differ from this treatment (Fig. 6a; Table 5). Likewise, at Seboomook Public Reserved Land, the amount of time spent in control plots showed a slight increase as density increased, with no differences compared to experimental plots (Fig. 6b; Table 5).

*Percent vigilance.*—Similar to time spent in plots, chemical cues did not alter vigilance levels of snowshoe hares (Table 6). At Lily Bay State Park, mean percent time spent vigilant in coyote plots decreased by 4% and increased at moose plots by 4% compared to control plots treated with water (Fig. 7a; Table 6). At plots treated with human urine, mean percent time spent vigilant per week increased by 27% compared to water-treated control plots. At Seboomook Public Reserved Land, mean percent vigilance per week decreased by 8% in coyote plots and increased by 17% at moose plots compared to water-treated control plots (Fig. 7b; Table 6). Mean percent vigilance per week at human plots decreased by 17% compared to water-treated plots.

Percent vigilance was not notably affected by vegetation density. At Lily Bay State Park, percent vigilance in the water-treated control plot showed a slight increase as vegetation density increased, and the experimental plots displayed similar results (Fig. 8a; Table 7). Snowshoe hares at Seboomook Public Reserved Land did not positively or negatively alter their vigilance levels in the water-treated control plot as vegetation density changed; experimental plots did not differ significantly from this treatment (Fig. 8b; Table 7).

## DISCUSSION

Predator urine can limit activity, suppress nondefensive behaviors, and cause habitat shifts of prey species in an area (Apfelbach et al. 2005). In my study, I looked at how chemical cues from a coyote affected snowshoe hare visits to feeding areas. Plots treated with urine from this predator had a mean number of snowshoe hare visits that was 21%–40% lower than visits to water-treated control plots. This result is consistent with my prediction and with previous work that found snowshoe hares avoid areas marked with urine of a major predator (Sullivan et al. 1985). A generalized meat-eater cue may exist in the urine of predators, due, in part, to high

sulfur content that acts as a warning to prey species (Nolte et al. 1994). In the red fox (*Vulpes vulpes*), the sulfide in particular is 3-methyl-3-butenyl methyl sulfide, a constituent that induces a fear response in snowshoe hares (Sullivan and Crump 1986). Considering the dietary overlap between red foxes and coyotes in North America, 3-methyl-3-butenyl methyl sulfide also could be the main fear-inducing factor found in coyote urine that wards snowshoe hares away from food sources (Green and Flinders 1981; Lapierre 1985).

Similarly to how prey avoid chemical cues of predators, some organisms avoid chemical cues from heterospecific competitors (Baudoin et al. 2012; De Jonge 1980). Moose and snowshoe hares show similarities in geographical distribution and dietary preferences; thus, the 2 species may compete for resources (Bowyer et al. 2003; Dodd 1960; Murray 2003). Feeding plots treated with moose urine were visited 40%–49% less, on average, compared to water-treated control plots. This result is consistent with my prediction that snowshoe hares avoid areas marked with moose urine. My findings thus support the hypothesis that these 2 vastly different species compete for food. Just as snowshoe hares avoid specific compounds in the urine of predators, snowshoe hares may have evolved to avoid a certain factor in moose urine to reduce competition. Because snowshoe hares did not show a significant change in number of visits to plots treated with human urine, it is unlikely that they avoided moose plots due to a general component in urine. Moose, like many other ungulates, utilize specific compounds in their urine for scent advertisement (Bowyer et al. 2003, McCullough 1969). Future work could isolate and identify the compound in moose urine that is offensive to snowshoe hares.

Predatory success can decline as density of vegetation increases, which could explain why many prey species prefer to be in, or near, areas with dense vegetation (Conroy et al. 1979; Lee et al. 1999; Litvaitis et al. 1985; Savino and Stein 1982). Thus, I measured how number of

visits, avoidance, and time spent in plots changed for snowshoe hares over a spectrum of vegetation densities. Snowshoe hares increased the number of visits to water treated plots as vegetation densities increased, and visits to moose and human plots did not differ significantly from this trend. Feeding in an area surrounded by dense vegetation offers multiple benefits to snowshoe hares. High vegetation density not only conceals prey from a scanning predator but also decreases the likelihood that a predator will initiate an attack if detection occurs (Bongi et al. 2008; Ortiz et al. 2011; Rainho et al. 2010). In cases where attacks occur, the obstacles and general clutter associated with areas of dense vegetation can reduce the catch rate of a predator significantly (Rainho et al. 2010).

Despite these obvious benefits that vegetation density provides, snowshoe hare visitation to coyote plots showed a decline as vegetation density increased, which was unexpected. Coyotes are a main mammalian predator of snowshoe hares (Murray 2003), so I predicted that snowshoe hares would increase visits to coyote scented plots only at high vegetation densities due to the antipredator obstacles that this environment provides. However, predators use different hunting tactics. Raptors mainly sit on a perch and scan surroundings for prey; a strategy that is hindered by high vegetation densities (O'Rourke et al. 2010; Toland 1987). However, predators that stalk prey, such as coyotes, can use the concealing properties of dense vegetation to their advantage (Bekoff and Gese 2003; Moreno et al. 1996). Considering that coyotes may utilize dense vegetation, snowshoe hares may avoid densely vegetated areas containing coyote urine because the dual effects of coyote scent plus inability to scan surroundings indicate a dangerous feeding area.

I predicted that snowshoe hares would avoid and spend less time in plots that were not densely vegetated, and that prediction was not supported. Complete avoidance of predator cues is

not necessarily beneficial in natural settings. Despite the risks, predator inspection by prey can deter predation, provide information about resource location, and allow individuals to warn conspecifics (Garvey et al. 2016; Godin and Davis 1995; Pitcher et al. 1986). Similarly, visitation to patches with lesser vegetation density can offer benefits such as increased caloric intake if the organism can rely on escape behavior (Spencer et al. 2014). Snowshoe hares that completely avoid a seemingly unsafe area would miss out on these benefits.

Neither vegetation density nor chemical cues had a significant effect on time spent in plots. Movement between patches increases rate of predation because transient prey are more recognizable by a sit-and-wait predator than stationary prey (Kislalioglu and Gibson 1976; Sakai and Noon 1997; Sih 1984). Therefore, snowshoe hares that have made it into risky patches might not necessarily benefit by reducing their foraging time, because low-movement foraging can be less dangerous than high-movement relocation.

Some prey species alter vigilance levels depending on characteristics of surrounding predators and the environment (Altendorf et al. 2001; Liley and Creel 2008; Metcalfe 1984; Periquet et al. 2012). However, snowshoe hares did not vary in time spent vigilant based on type of urine present. While these results were expected for hares in moose and human urine plots (nonpredator/occasional predator), I had predicted that hares would spend more time vigilant in plots containing coyote urine because of the perceived predator threat. Similarly, the differences between vigilance levels in densely covered plots versus less covered plots were minimal, a result that I did not expect because snowshoe hares are more hidden from predators when the surrounding vegetation is thick. One explanation for these results is my simplistic method of scoring vigilance in snowshoe hares, i.e., erect head with ears pointed forward. This approach ignores valuable detection behaviors, such as head movement, and assumes by default that the

organism is ignorant to fear-inducing stimuli while performing other behaviors (Jones et al. 2007; Scannell et al. 2001). Although detection ability may increase when prey devote all their energy to vigilance, they still can be aware of their surroundings while performing other behaviors (Lima and Bednekoff 1999). Lagomorphs rely on hearing for predator detection as much as they rely on sight, which could allow snowshoe hares to simultaneously feed and be alert (Arias-Del Razo et al. 2012; Flinders and Chapman 2003). Thus, in experimental plots with a seemingly greater risk of predation (coyote urine/less dense), snowshoe hares are likely to be more attuned to their surroundings even if this behavior is undetectable to a human observer.

In conclusion, I provide evidence that snowshoe hares alter their feeding behavior in response to both vegetation density and cues from antagonistic species, with the response to moose, a potential competitor, being similar to that of coyote, a major predator. Vegetative cover and cues from heterospecifics play a significant role in patch choice by prey that both maximizes energy intake and minimizes risk of direct contact with an adversary. Thus, as a snowshoe hare approaches a patch, the volatile constituents of moose urine likely signal that a certain patch has the potential for low energetic intake (a decrease in patch benefits resulting from being outcompeted), whereas coyote urine constituents signal that the chance of death is high (an increase in patch risk resulting from predation). These chemical cues coalesce with visual cues that snowshoe hares receive, pertaining to the surrounding vegetation density, and ultimately affect snowshoe hare foraging behavior. This research complements the work of others in regard to prey attentiveness to predator cues and the ability to stay hidden in a patch, while offering additional insight on competition between unrelated species of disparate sizes.



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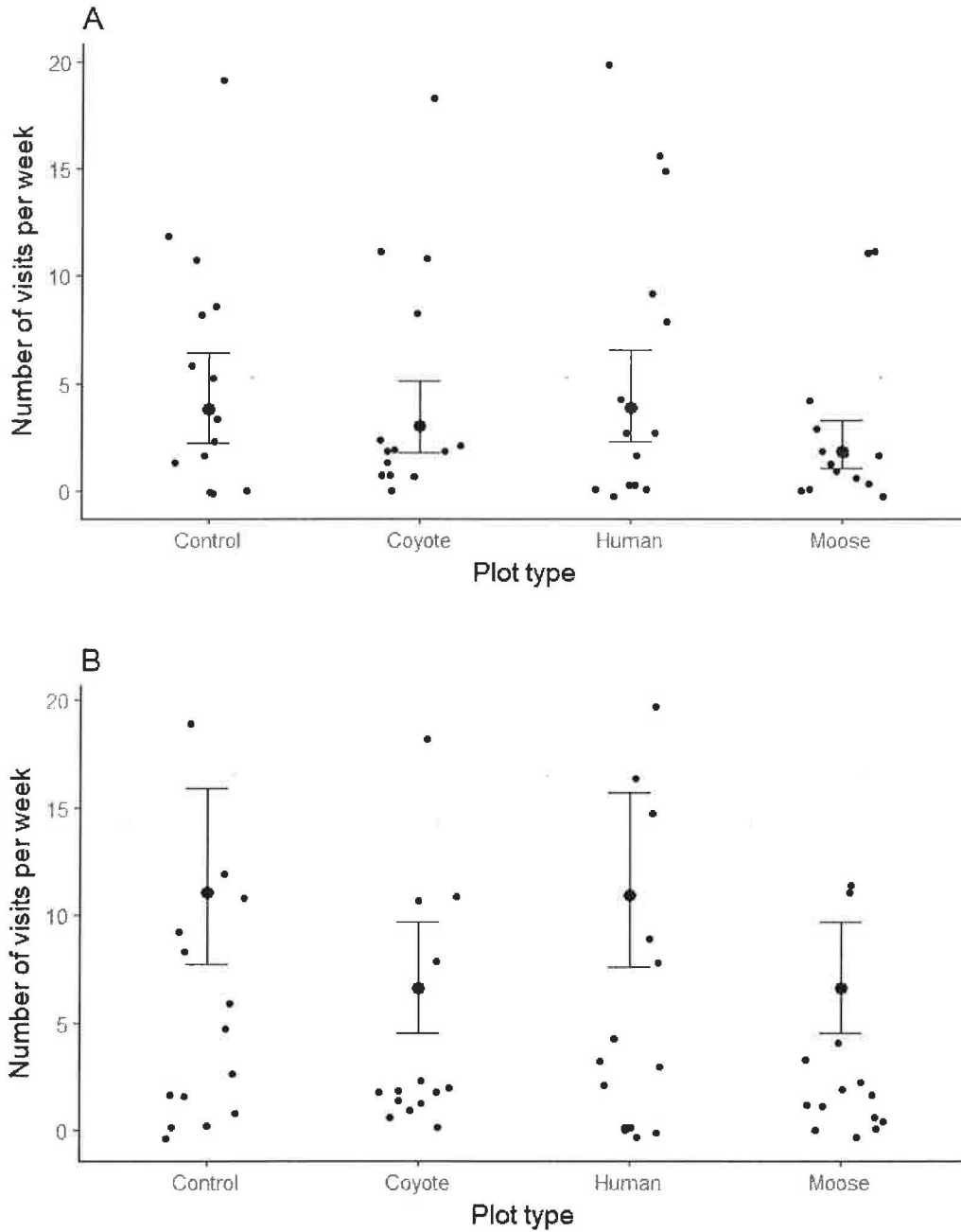
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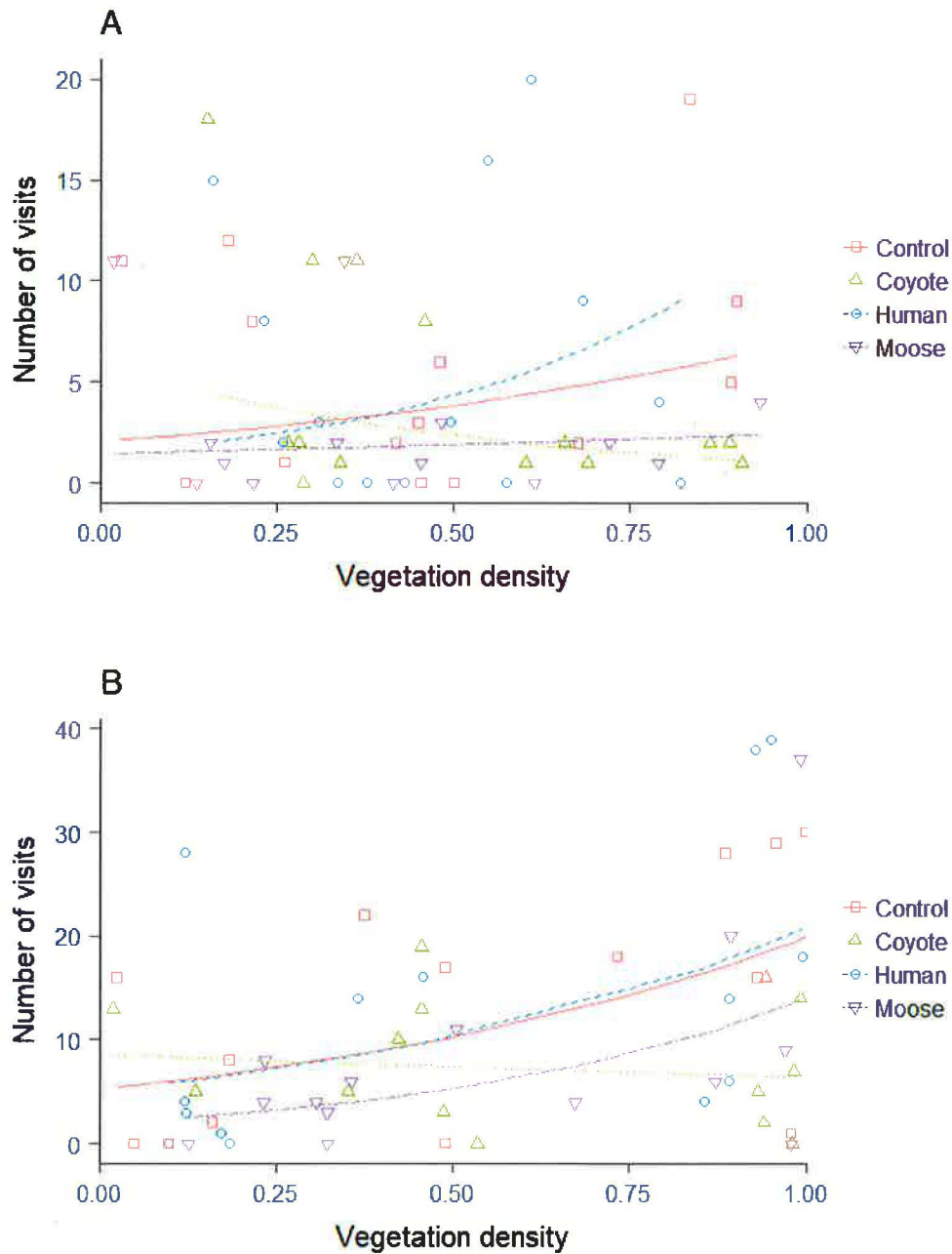
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**Fig. 1.**—Mean ( $\pm$  CI) number of snowshoe hare visits to plots treated with 4 scents from June to October, 2018 at A) Lily Bay State Park in Beaver Cove, Maine and B) Seboomook Public Reserved Land in Somerset and Piscataquis Counties, Maine. Each black point represents the number of visits for that treatment for 1 week. Note the scale.

**Table 1.**—Results of the generalized linear mixed effect model describing number of snowshoe hare plot visits for each treatment at 2 sites in northern Maine from June to October, 2018.

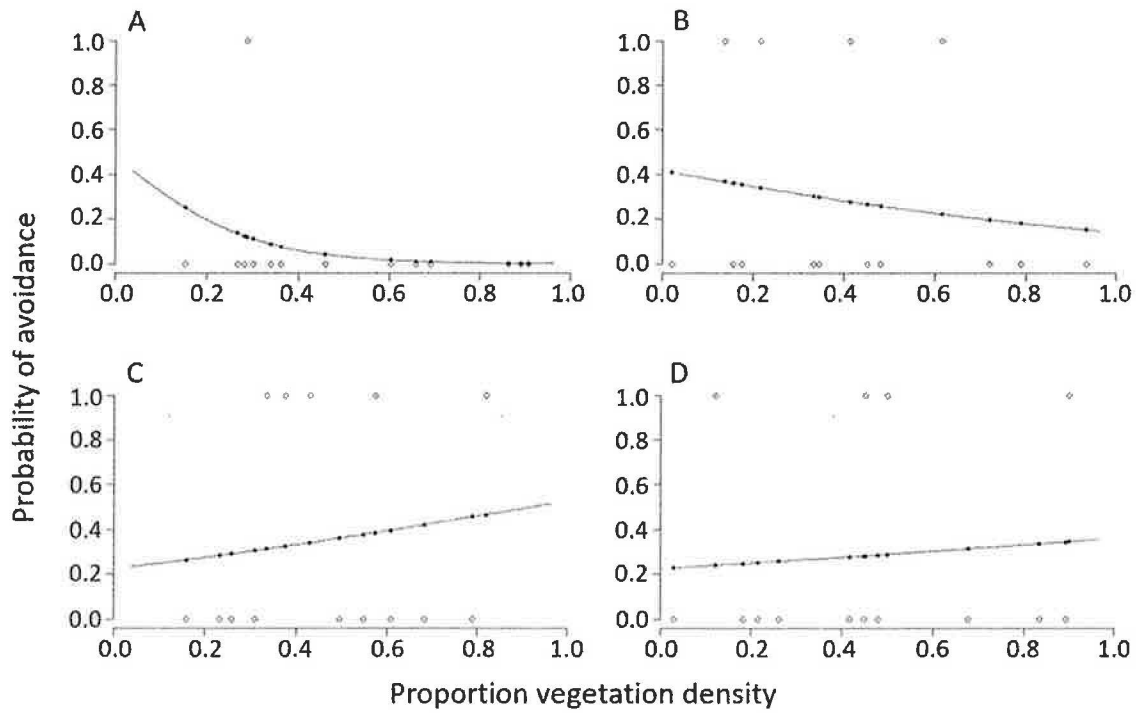
Location	Model	Treatment	Z—Value	P—Value	N (weeks)
Lily Bay State Park	glmm	Coyote	-1.36	0.173	14
		Moose	-3.67	<0.001	14
		Human	0.161	0.872	14
		Control	N/A	N/A	14
Seboomook Public Reserved Land	glmm	Coyote	-4.31	<0.001	14
		Moose	-4.31	<0.001	14
		Human	-0.104	0.917	14
		Control	N/A	N/A	14



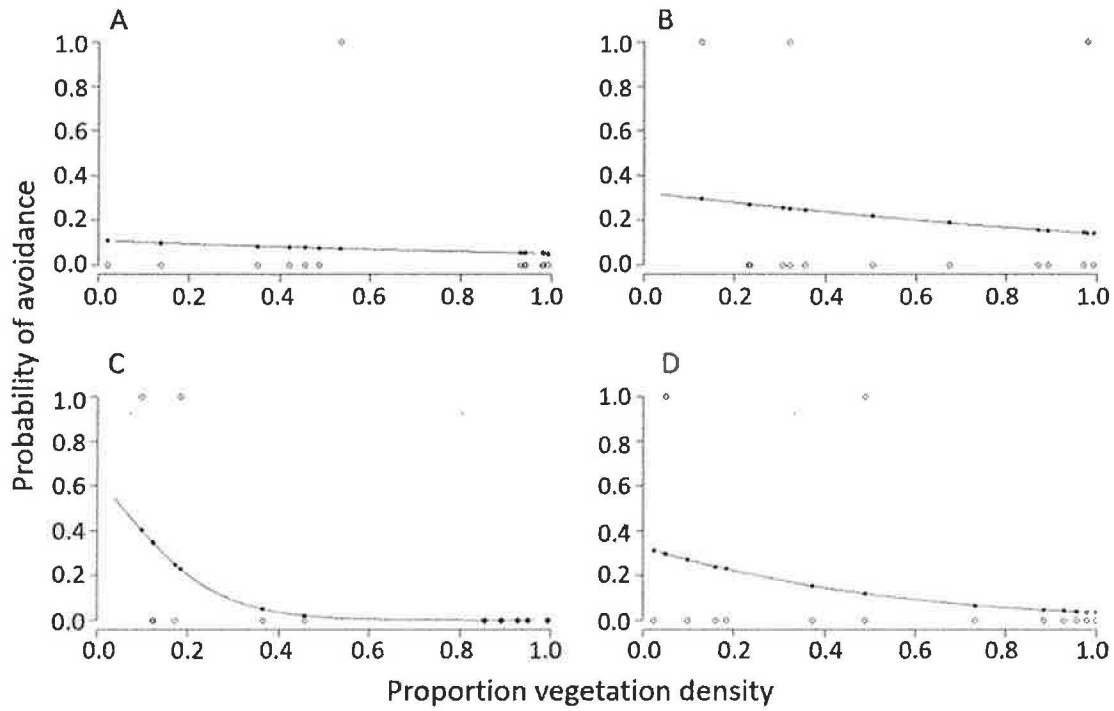
**Fig. 2.**—Mean number of weekly visits by snowshoe hares as a function of vegetation density for plots treated with 4 scents from June to October, 2018 at a) Lily Bay State Park in Beaver Cove, Maine and b) Seboomook Public Reserved Land in Somerset and Piscataquis Counties, Maine. Each point represents the mean number of visits for 1 week. Note the scale.

**Table 2.**— Results of the generalized linear mixed effect model describing number of plot visits by snowshoe hares for each treatment at varying vegetation densities. Testing occurred at 2 sites in northern Maine from June to October, 2018.

Location	Model	Treatment	Z—Value	P—Value	N (weeks)
Lily Bay State Park	glmm	Coyote	-3.67	<0.001	14
		Moose	-1.01	0.313	14
		Human	1.36	0.173	14
		Control	N/A	N/A	14
Seboomook Public Reserved Land	glmm	Coyote	-4.40	<0.001	14
		Moose	1.55	0.120	14
		Human	0.234	0.815	14
		Control	N/A	N/A	14



**Fig. 3**—Avoidance of plots by snowshoe hares for each week as a function of vegetation density for plots treated with a) coyote urine, b) moose urine, c) human urine, and d) water from June to October, 2018 at Lily Bay State Park in Beaver Cove, Maine. Open circles represent measured avoidance, whereas closed circles represent predicted avoidance.

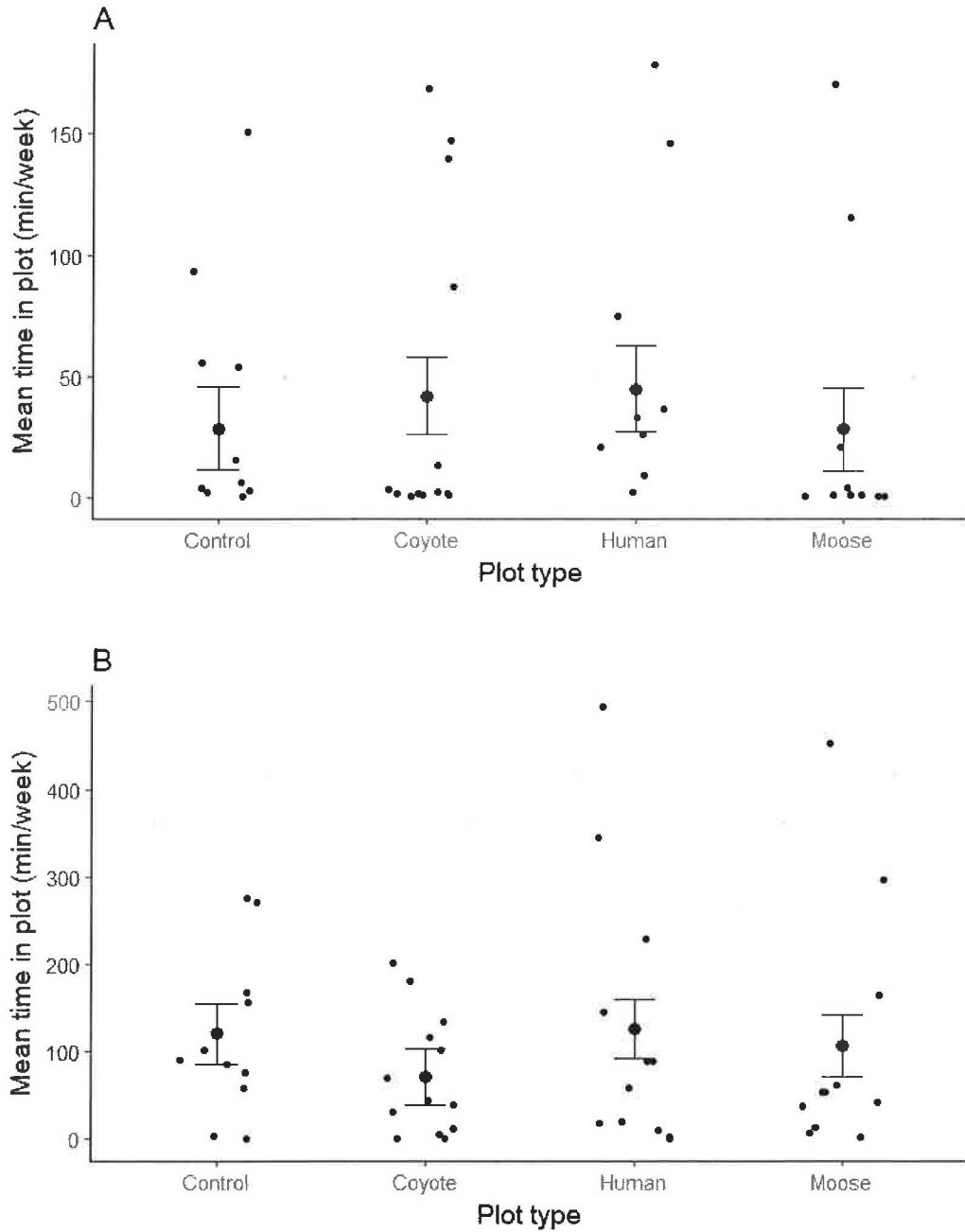


**Fig. 4.**— Avoidance of plots by snowshoe hares each week as a function of vegetation density for plots treated with a) coyote urine, b) moose urine, c) human urine, and d) water from June to October, 2018 at Seboomook Public Reserved Land in Somerset and Piscataquis Counties, Maine. Open circles represent measured avoidance, whereas closed circles represent predicted avoidance.



**Table 3.**—Results of the generalized linear mixed effect model describing avoidance for each treatment at varying vegetation densities. Testing occurred at 2 sites in northern Maine from June to October, 2018.

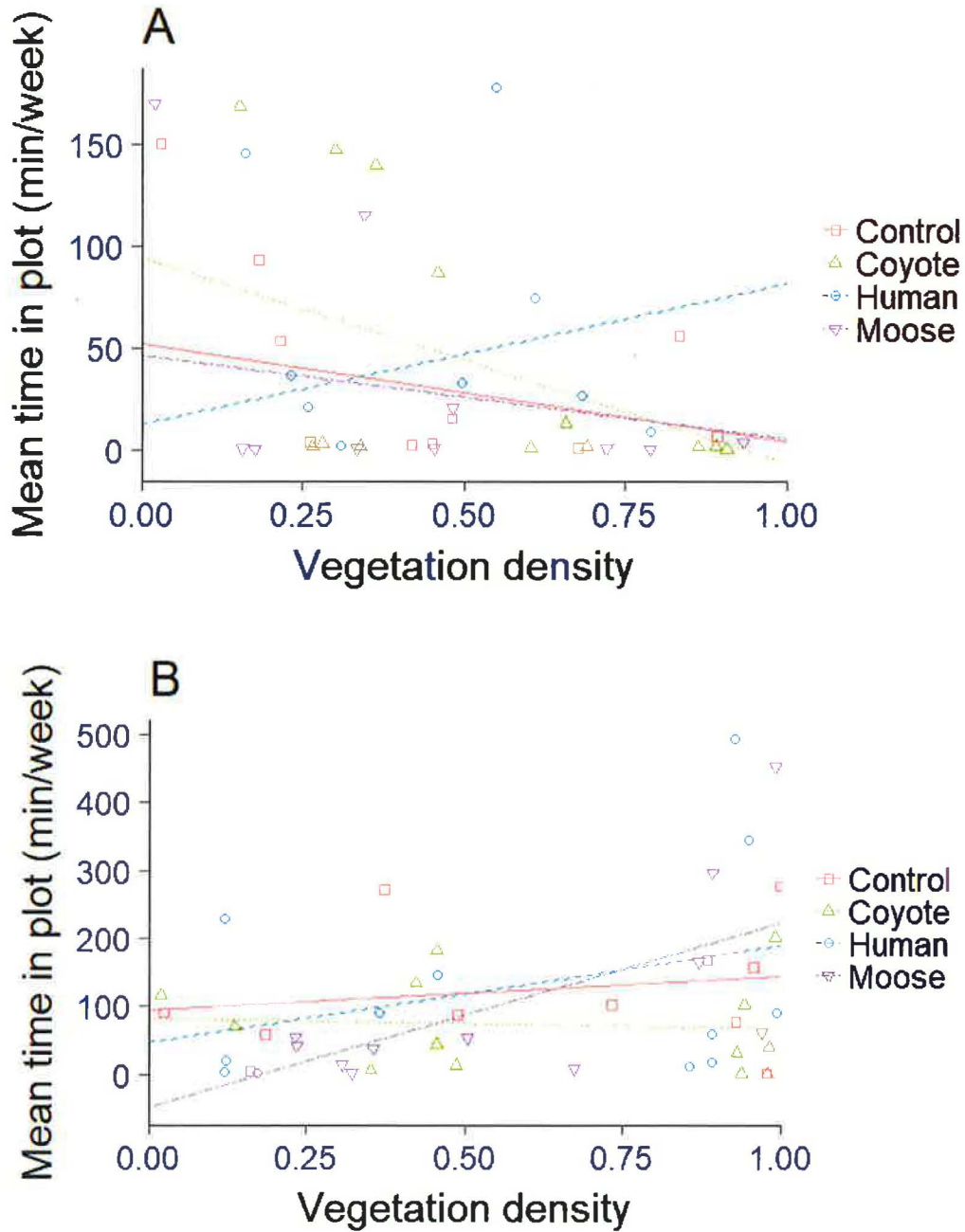
Location	Model	Treatment	Z—Value	P—Value	N (weeks)
Lily Bay State Park	glmm	Coyote	0.800	0.424	14
		Moose	0.658	0.510	14
		Human	-0.192	0.847	14
		Control	N/A	N/A	14
Seboomook Public Reserved Land	glmm	Coyote	-0.430	0.667	14
		Moose	0.438	0.661	14
		Human	0.554	0.580	14
		Control	N/A	N/A	14



**Fig. 5.**—Mean ( $\pm$  model SE) amount of time that snowshoe hares spent in plots treated with 4 scents from June to October, 2018 at a) Lily Bay State Park in Beaver Cove, Maine and b) Seboomook Public Reserved Land in Somerset and Piscataquis Counties, Maine. Each black point represents the mean amount of time snowshoe hares spent in the plot for 1 week. Note the scale.

**Table 4.**—Results of the linear mixed effect model describing mean time snowshoe hares spent in plot for each treatment. Testing occurred at 2 sites in northern Maine from June to October, 2018.

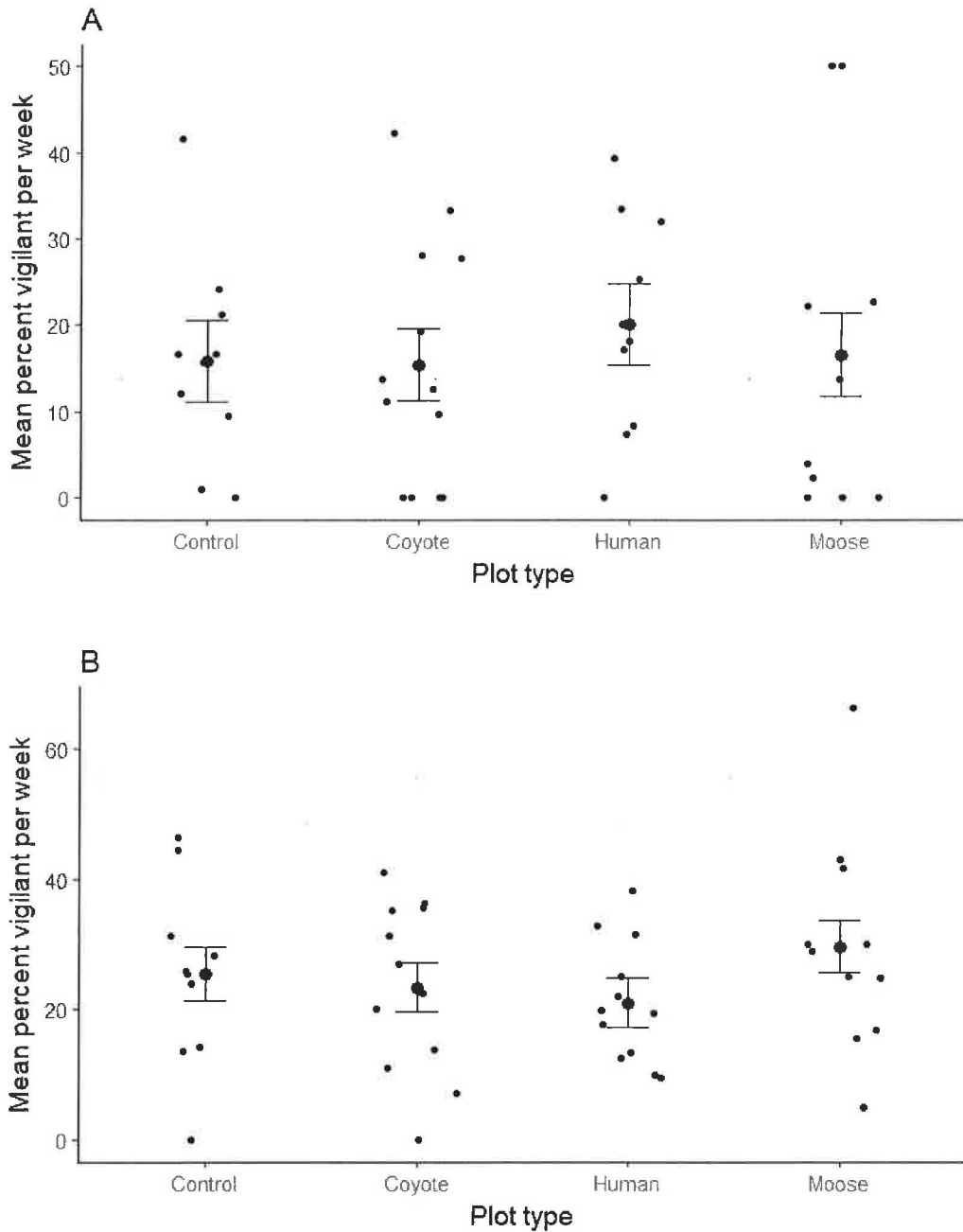
Location	Model	Treatment	T—Value	P—Value	N (weeks)
Lily Bay State Park	Imm	Coyote	0.871	0.391	13
		Moose	-0.023	0.982	10
		Human	0.946	0.353	9
		Control	N/A	N/A	10
Seboomook Public Reserved Land	Imm	Coyote	-1.24	0.224	13
		Moose	-0.324	0.748	11
		Human	0.146	0.885	12
		Control	N/A	N/A	11



**Fig. 6.**— Time spent in plots by snowshoe hares as a function of vegetation density for plots treated with 4 scents from June to October, 2018 at a) Lily Bay State Park in Beaver Cove, Maine and b) Seboomook Public Reserved Land in Somerset and Piscataquis counties, Maine. Each point represents the mean amount of time snowshoe hares spent in the plot over 1 week. Note the scale.

**Table 5.**—Results of the linear mixed effect model describing mean time snowshoe hares spent in plot for each treatment at varying vegetation densities. Testing occurred at 2 sites in northern Maine from June to October, 2018.

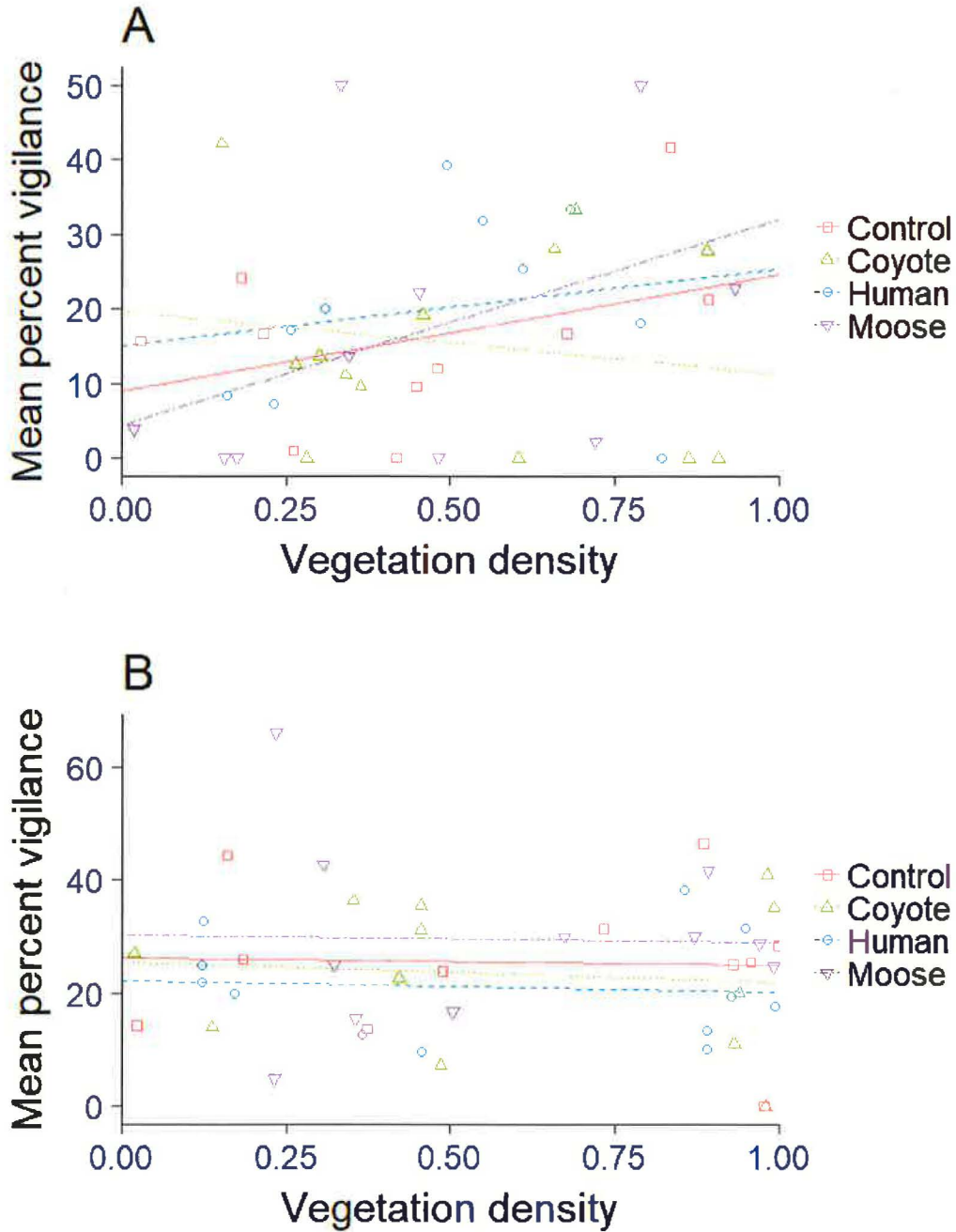
Location	Model	Treatment	T—Value	P—Value	N (weeks)
Lily Bay State Park	Imm	Coyote	-0.857	0.400	13
		Moose	0.116	0.909	10
		Human	1.61	0.120	9
		Control	N/A	N/A	10
Seboomook Public Reserved Land	Imm	Coyote	-0.582	0.565	13
		Moose	1.71	0.0983	11
		Human	0.831	0.413	12
		Control	N/A	N/A	11



**Fig. 7.**—Mean ( $\pm$  model SE) percent time that snowshoe hares spent vigilant in plots treated with 4 scents from June to October, 2018 at a) Lily Bay State Park in Beaver Cove, Maine and b) Seboomook Public Reserved Land in Somerset and Piscataquis counties, Maine. Each black point represents mean vigilance for 1 week. Note the scale.

**Table 6.**—Results of the linear mixed effect model describing mean percent vigilance by snowshoe hares for each treatment. Testing occurred at 2 sites in northern Maine from June to October, 2018.

Location	Model	Treatment	T—Value	P—Value	N (weeks)
Lily Bay State Park	Imm	Coyote	-0.086	0.916	13
		Moose	0.104	0.925	10
		Human	0.657	0.527	10
		Control	N/A	N/A	10
Seboomook Public Reserved Land	Imm	Coyote	-0.382	0.726	12
		Moose	0.752	0.435	11
		Human	-0.819	0.447	12
		Control	N/A	N/A	11



**Fig. 8.**—Mean percent vigilance by snowshoe hares as a function of vegetation density for plots treated with 4 scents from June to October, 2018 at a) Lily Bay State Park in Beaver Cove, Maine and b) Seboomook Public Reserved Land in Somerset and Piscataquis counties, Maine. Each point represents mean vigilance for 1 week. Note the scale.



**Table 7.**—Results of the linear mixed effect model describing mean percent vigilance by snowshoe hares for each treatment at varying vegetation densities. Testing occurred at 2 sites in northern Maine from June to October, 2018.

Location	Model	Treatment	T—Value	P—Value	N (weeks)
Lily Bay State Park	Imm	Coyote	-1.03	0.312	13
		Moose	0.503	0.618	10
		Human	-0.197	0.845	10
		Control	N/A	N/A	10
Seboomook Public Reserved Land	Imm	Coyote	-0.115	0.909	12
		Moose	0.011	0.991	11
		Human	-0.049	0.961	12
		Control	N/A	N/A	11