

# Avoiding and escaping predators: Movement tortuosity of snowshoe hares in risky habitats <sup>1</sup>

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**Abstract:** Prey animals use different strategies to avoid detection by predators and to flee once detected. Key issues are what aspects of movement prey change in response to predation risk and how differences in habitat affect escape movements. We answer these questions for snowshoe hares (*Lepus americanus*) in Montana, using an experimental manipulation and habitats for which annual mortality rates varied more than fourfold. We examine a) whether the mortality risk of a habitat affects movement tortuosity and speed of foraging snowshoe hares and b) whether tortuosity and speed of hares fleeing from a predator (a leashed dog, *Canis familiaris*) differ among these forest stands. Snowshoe hares did not differ in tortuosity or speed while foraging in these stands, suggesting that other anti-predator behaviours were used. Hares fleeing from the leashed dog showed much faster and straighter movements than foraging hares, but escape trajectories were similar in all forest stands, suggesting a relatively inflexible response while fleeing. Varying tortuosity and speed are clearly part of the snowshoe hare's behavioural repertoire for escaping predation, but these attributes of movement were insensitive to the annual mortality rates in each forest stand.

**Keywords:** escape trajectory, foraging, *Lepus americanus*, movements, predation risk, tortuosity.

**Résumé:** Les proies animales utilisent différentes stratégies afin d'éviter d'être détectées par des prédateurs et pour s'enfuir une fois détectées. Les questions clés sont : quels aspects des déplacements des proies changent en réponse au risque de prédation et comment les différences d'habitats influencent les mouvements de fuite. Nous répondons à ces questions pour des lièvres d'Amérique (*Lepus americanus*) au Montana en utilisant une manipulation expérimentale et des habitats dans lesquels les taux annuels de mortalité varient de plus du quadruple. Nous examinons a) si le risque de mortalité associé à un habitat a un effet sur la tortuosité et la vitesse des déplacements de lièvres d'Amérique en quête alimentaire et b) si la tortuosité et la vitesse des déplacements de lièvres s'enfuyant d'un prédateur (un chien en laisse, *Canis familiaris*) diffèrent entre ces habitats (des peuplements forestiers). Il n'y avait pas de différences dans la tortuosité ou la vitesse des déplacements des lièvres d'Amérique en quête alimentaire dans ces peuplements, suggérant que d'autres comportements anti-prédation étaient utilisés. Les lièvres qui s'enfuyaient du chien se déplaçaient beaucoup plus rapidement et plus en ligne droite que les lièvres en quête alimentaire, mais les trajectoires de fuite étaient semblables dans tous les peuplements forestiers, suggérant que la réponse de fuite est relativement stable. Les changements dans la tortuosité et la vitesse des déplacements font manifestement parties du répertoire comportemental du lièvre d'Amérique pour fuir les prédateurs, mais ces caractéristiques des déplacements étaient insensibles aux taux annuels de mortalité associés aux différents peuplements forestiers.

**Mots-clés:** déplacements, *Lepus americanus*, quête alimentaire, risque de prédation, tortuosité, trajectoire de fuite.

**Nomenclature:** Banfield, 1974; Kershaw, Mackinnon & Pojar, 1998.

## Introduction

Movement behaviours are under strong selection for prey species. Prey movement patterns and habitat choices affect the likelihood of encountering a predator (Lima & Dill, 1990; Stankowich & Blumstein, 2005), and once a predator is encountered the prey must decide whether to freeze; when, how fast, and in what direction to flee; whether to flee in a straight line or zigzag; and when to stop fleeing, especially if the prey animal does not have an absolute refuge

available (Ydenberg & Dill, 1986; Cooper, 2003; Domenici, Blagburn & Bacon, 2011a,b). Wrong choices can lead to death; alternatively, costs of evading predators include high energetic expenditures and lost foraging opportunities.

Studies of foraging animals often measure path tortuosity, with increased tortuosity predicted in habitats rich in resources (Nams & Bourgeois, 2004; Newbury & Nelson, 2007; Fuller & Harrison, 2010). To date, the majority of studies examining tortuosity of movements have focused on how tortuosity changes with resource distribution, individual characteristics (e.g., sex, age, reproductive condition, mass), or habitat type (McIntyre & Wiens, 1999; de Knegt *et al.*, 2007; Cameron & Spencer, 2008; Webb *et al.*, 2009; Valeix *et al.*, 2010) rather than on how tortuosity changes with actual mortality rates within a given habitat. If animals can reliably detect and attempt to minimize risk, movement tortuosities should decrease as risk increases, as low tortuosities would reduce the time the animal spent in unsafe habitats.

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When fleeing from a predator, pathway tortuosity depends in part on the physical capabilities of predator and prey. Specifically, models show that for prey that can simply out-run their predators, relatively straight-line escapes headed away from the predator are the best option (Domenici, Blagburn & Bacon, 2011a), although variation in the flight angles can help prey to escape because predators will not know which direction the fleeing animal will take (Weihs & Webb, 1984; Furuichi, 2002). If the predator can run faster than the prey, escaping becomes a matter of the prey staying ahead for long enough that the predator halts the chase. In this case, sharp turning angles when the predator and prey are close together can enable a more manoeuvrable prey animal to escape its predator because the sudden sideways movement can extend the lead of the prey animal, thus increasing the odds the predator will stop the chase before making a kill (Furuichi, 2002). Manoeuvrability is affected by body size (Ilany & Eilam, 2008) and biomechanics, *i.e.*, being able to withstand the forces of a sudden turn at high speed without sustaining an injury (Howland, 1974; Farina, Blanco & Christiansen, 2005; Angilletta *et al.*, 2008), with smaller animals typically more manoeuvrable than larger ones.

The role of habitat along escape pathways is poorly understood as yet, because most studies on escaping prey derive from laboratory studies, aquatic animals, or mathematical models, rather than from terrestrial animals in complex habitats (Domenici, Blagburn & Bacon, 2011a,b; but see Stankowich & Coss, 2007). Habitat has little impact on escaping African ungulates (Caro, 1994; Caro *et al.*, 2004), but these animals were hunted in open grassland habitats rather than in complex forests. Tree or shrub density in forests might affect escape pathways, because larger animals presumably would find it harder to navigate dense forest than would smaller animals.

Here, we examine how forest habitats that differed in annual mortality rates affect movement tortuosity of foraging and fleeing snowshoe hares (*Lepus americanus*). Because hares are active in winter, high-quality tracks in the snow enable quantification of their movements. Snowshoe hares are approximately 1.4-kg forest herbivores that elude predators through colour camouflage, using cover, and evasion, as they do not have absolute refuges. Predation is by far the dominant cause of mortality for snowshoe hares, with predator-induced deaths typically ranging from 85 to 100% of mortality in different regions and throughout their 10-y population cycle (Hodges, 2000a,b). Snowshoe hares strongly differ in movement distances, microhabitat selection, and foraging behaviour in forest stands that vary in structure (Hodges 1999; 2000a,b; Hodges & Sinclair, 2005), in areas with different abundances of mammalian predators (Hik, 1995; Hodges, 1999), and in relation to snow cover and moonlight (Griffin *et al.*, 2005). They are thus a good species to use for analysis of movements because predation is common and hares are known to vary movements and other behaviours in relation to risk.

We examined pathways of snowshoe hares in 4 coniferous forest stands in western Montana that differed in their actual predation risk, as measured by known-fate survival and habitat-use analysis of 163 radio-collared

hares (Griffin & Mills, 2009; risk was assigned on the basis of number of relocations of individual hares in the different stand types). Closed-canopy mature stands had by far the lowest annual mortality rates (58%), compared to 75% for closed-canopy young forests and 91% for open-canopy stands (Griffin & Mills, 2009). Hares experience high mortality rates year-round. We used direct exposure to a predator (a large leashed dog, *Canis familiaris*) to induce fleeing behaviour, but we did not allow a chase; this design simulated the case of a prey animal fleeing away from a predator with a reasonable distance between them, rather than the short predator-prey distances that are predicted to induce zigzagging. Hares do not have absolute refuges; thus, we can rule out the idea hares attempt to take the shortest possible route to a specific shelter.

This study system, with habitats of known risk and predators that stopped chasing hares after the initial startling, enabled us to test 2 key hypotheses about how prey change movements in response to predators and predation risk in forest:

- 1) the riskiness of the habitat affects pathway tortuosity and speed of foraging hares; and
- 2) fleeing hares flee similarly regardless of habitat type.

These hypotheses offer a sharp contrast in the effects of habitat on movement, because foraging hares are responding to habitat cues and perceived risk, whereas fleeing hares are responding to an actual predator. In our system, we predict a) that foraging hares use the most tortuous movements and lowest speeds in low-risk habitats, *i.e.*, in closed-canopy mature forest, intermediate movements and speeds in closed-canopy young forest, and the least tortuous and fastest movements in open forests and b) that fleeing hares move straight and fast, without a clear impact of habitat type on movements. We further expect fleeing hares to move faster and straighter, with less variability, than foraging hares. To test for the role of vegetation in influencing movement, we quantified cover along pathways to evaluate if foraging hares are closer to cover as they seek shelter or food along a pathway and to test whether fleeing hares selected or avoided cover.

## Methods

We conducted this work near Seeley Lake, Montana, in 4 forest stands that were 9 ha each and adjacent to each other; hares could and did move among the stands (Griffin *et al.*, 2005; Griffin & Mills, 2009). Forests were composed of lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), Englemann's spruce (*Picea engelmannii*), and western larch (*Larix occidentalis*). The 4 stands varied in stand age and canopy density, ranging from open mature forest to open young forest, closed-canopy young forest, and closed-canopy mature forest. Closed mature stands were dominated by trees >150 y old with >30-cm diameters and >40% overhead canopy closure; the closed young stands were stands regenerating post-harvest with >5600 saplings·ha<sup>-1</sup>. Open mature stands had big, old trees but <30% canopy closure; open young stands had <3360 saplings·ha<sup>-1</sup> (Griffin & Mills, 2004). Winter (13 December – 2 April) survival of

snowshoe hares was lowest and equal in the 2 open-canopy forest stands (65.2%), intermediate in the closed-canopy young forest (74.8%), and highest in the closed-canopy mature forest (80.4%; Griffin, 2004; a similar pattern occurred throughout the year, Griffin & Mills, 2009). We therefore collapsed the open young and open mature forest into the single category of open forest for this study because the predation risk to hares was the key gradient we were interested in examining.

#### SNOWSHOE HARE PATHWAYS

We tracked radio-collared snowshoe hares during December 1999 – March 2001 and January – March 2003 (details of trapping and collaring are provided in Griffin & Mills, 2009) to obtain 2 kinds of pathways: pathways from foraging hares and pathways from hares escaping from a predator. A few pathways were obtained from non-radioed animals whose tracks we crossed or a couple of instances where the dog flushed an animal we were not radio-tracking at the time. All analyses are based on the entire pathway; we obtained 39 foraging pathways and 17 predator-trial pathways.

Along each pathway, we measured 5-m lengths and marked the segment end points with pin flags. At each pin flag, we visually estimated to the nearest 5% the amount of undergrowth (1 m above snow level) in a 1-m-radius circle. To measure turning angles of each hare pathway, we used a sighting compass to determine bearings between flags. We quantified hare speed as the number of tracks per 5-m path segment (fewer tracks indicate higher speed). This index assesses the travel velocity along each pathway, but does not account for time a hare spends feeding.

We obtained foraging pathways by locating a hare, then backtracking it for up to 70 m. We analyzed pathways of 30 m or more, as snow conditions sometimes prevented us from obtaining a full 70-m track, especially if a hare used a hare runway, which prevented us from determining which hare we were following when tracks subsequently diverged. We saw evidence of browsing (tracks adjacent to twigs with the characteristic 45° angle of browse) or deposition of faecal pellets along all foraging pathways (hares defecate while foraging; Hodges, 1999). In a few cases, we were not able to obtain a count of the number of tracks per 5-m pathway segment because foraging hares frequently step on their own tracks as they browse multiple twigs from a given shrub or tree. In these cases, we assigned a value of 12 to the number of tracks because very few of the actual counts were 12 or larger (the maximum recorded was 16), indicating we could consistently resolve track counts below 12. We also tested speeds of pathways omitting these counts or using 15 as a track count instead of 12; all results were qualitatively similar, so we present results using 12 for these cases.

Pathways of escaping hares were obtained by using telemetry to locate a snowshoe hare, then approaching the hare with a leashed dog until the hare flushed (trapping, radio-collaring, and this dog protocol were all approved by the University of Montana Institutional Animal Care and Use Committee). We used different dogs in 2001 and 2003; both were large dogs of mixed ancestry and were thus good

proxies in mass and size for the main mammalian predators of hares in this area (Canada lynx, *Lynx canadensis*, and coyote, *Canis latrans*). We detected no difference in the behaviour of the 2 dogs with respect to their interest in and ability to flush snowshoe hares. After a hare flushed, we removed the dog from the vicinity, then forward-tracked each hare for 20 to 70 m; many snowshoe hares returned to cover at a shorter distance than 70 m.

#### CALCULATING TORTUOSITY OF MOVEMENT PATHWAYS

We used fixed-step increments to support analysis via a correlated random walk model (Bovet & Benhamou, 1988). Given  $\alpha_i$  as the consecutive turning angles in the path, this model describes an  $N$ -step path with  $\Phi$ , its mean vector, where  $\Phi = \arctan(\sum \sin \alpha_i / \sum \cos \alpha_i)$ . The correlation to this vector describes the directional bias of the path:  $[(\sum \cos \alpha_i)^2 + (\sum \sin \alpha_i)^2]^{0.5} / (N - 1)$ , where  $N$  is the number of points in the path. As  $r$  lies between 0 (random) and 1 (perfect correlation to a line and therefore zero tortuosity), tortuosity ( $t$ ) is simply  $1 - r$ . We calculated tortuosities in Excel (Microsoft Inc., Redmond, Washington, USA), and used Minitab (v. 15 2011, State College, Pennsylvania, USA) for statistics. We performed two-way ANOVAs to test whether treatment (foraging or fleeing), forest stand type (open, closed mature, and closed young), or their interaction affected movements of snowshoe hares. We used regression to relate pathway tortuosity and speed, as well as to test whether tortuosity varied in relation to understory cover.

## Results

We obtained 39 foraging pathways: 21 were in open forest, 9 in closed young forest, and 9 in closed mature forest. We had 17 pathways where the dog startled the hare, with 6 each in open forest and closed young forest and 5 in closed mature forest. A few radio-collared hares were tracked up to 3 times each and we had some tracks from unknown animals; at minimum, we obtained pathways from 28 distinct hares foraging and 13 hares fleeing, and we suspect our actual numbers of distinct animals were higher. For foraging pathways, the average distance tracked was the same in all forest types, 56.5 m (or 12.3 end-points of 5-m segments, and hence turning angles). Overall, 64% of foraging pathways had 12–15 end-points. Pathways of fleeing hares were shorter: in closed old forest, they averaged 8.2 end-points (36 m); in open forest, 9.7 end-points (43.5 m); and in closed young forest, 10.2 end-points (46 m). Only 3 of 17 escape pathways reached the 70 m (15 end-points) at which we stopped tracking; 19 of 37 foraging pathways were this long (*i.e.*, the snow conditions permitted us to track for that distance).

There were no statistically detectable effects of forest type on tortuosities of foraging hares (Figure 1a;  $F_{2, 48} = 2.00$ ,  $P = 0.15$ ; interaction  $F_{2, 48} = 0.13$ ,  $P = 0.88$ ), speed (Figure 1b;  $F_{2, 50} = 1.50$ ,  $P = 0.23$ ; interaction  $F_{2, 50} = 0.53$ ,  $P = 0.59$ ), or variance in speed (Figure 1c;  $F_{2, 50} = 0.57$ ,  $P = 0.57$ ; interaction  $F_{2, 50} = 0.75$ ,  $P = 0.48$ ). The average tortuosity was 50% higher and the average foraging speeds were 15% slower in closed mature forest, where known mortality rates were lowest, but both variables had high variance, and means were not significantly different.



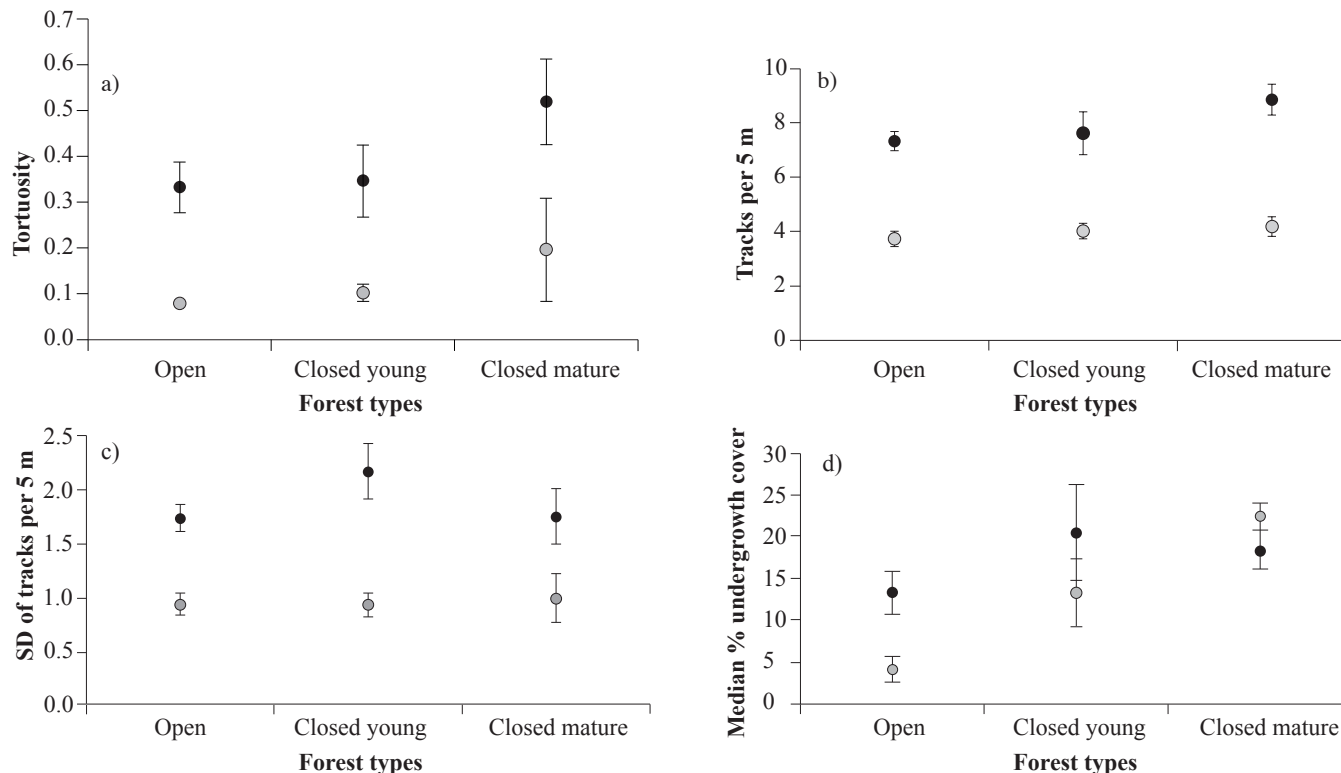


FIGURE 1. Movements of snowshoe hares in 3 forest types that differ in risk. Open forests had the highest risk of predation and closed mature forests the least risk. We obtained 39 foraging pathways (black circles) and 17 predator trial pathways (grey circles). a) Movement tortuosity. Tortuosities near 0 are close to a straight line and higher values indicate more tortuous pathways. The SE for open forest predator trials is obscured by the data point. b) Movement speed. Our index is tracks per 5 m, with more tracks indicating slower movement speeds. c) Variation in movement speed. d) Undergrowth along snowshoe hare pathways. Every 5 m along each pathway, we assessed the percentage of vegetative cover in a 1-m-radius circle at 1 m height; for each pathway, we calculated the median percentage cover. The figure shows the means ( $\pm 1$  SE) of these medians across the forest types.

Escaping hares had sharply different tortuosities than foraging hares (Figure 1a), with hares moving far straighter when fleeing from a predator ( $F_{1,48} = 17.63$ ,  $P < 0.001$ ). Fleeing hares exposed to the dog on a leash also moved much faster than foraging hares (Figure 1b), taking about half as many steps per 5 m ( $4.0 \pm 0.15$ , mean  $\pm$  SE) as did foraging hares ( $7.8 \pm 0.3$ ;  $F_{1,50} = 69.63$ ,  $P < 0.001$ ). Also, hares startled by the dog had standard deviations (SD) of speed about half those of the foraging hares (Figure 1c;  $0.94 \pm 0.08$  escaping,  $1.8 \pm 0.11$  foraging;  $F_{1,50} = 28.22$ ,  $P < 0.001$ ).

The median percentage of undergrowth along hare pathways was significantly related to forest stand type (Figure 1d;  $F_{2,48} = 4.8$ ,  $P = 0.013$ ) but was not significantly different for foraging *versus* escaping hares ( $F_{1,48} = 1.58$ ,  $P = 0.21$ ; interaction  $F_{2,48} = 1.50$ ,  $P = 0.24$ ). Pathway tortuosity and speed were unrelated (Figure 2) both for foraging pathways ( $r^2 = 0.007$ ,  $P = 0.64$ ) and for predator trial pathways ( $r^2 = 0.014$ ,  $P = 0.65$ ). Tortuosity was unrelated to median undergrowth along pathways both for foraging pathways (Figure 3;  $r^2 = 0.03$ ,  $P = 0.29$ ) and for predator trial pathways ( $r^2 = 0.003$ ,  $P = 0.83$ ).

## Discussion

We did not find significant differences in mean tortuosity of foraging pathways or movement speed of snowshoe hares among stands that differed substantively in annual

mortality rates. However, the variance in tortuosities was much higher in mature forest than in the other stands; thus, the lower risk in this stand type appears to increase tortuosity and decrease foraging speed of at least some foraging hares, even though differences in mean rates were not significant.

By contrast, our second hypothesis was supported: fleeing hares moved similarly in all stand types. Furthermore, there was neither clear avoidance of nor an affinity for dense cover along fleeing pathways. These results suggest that fleeing is a much more constrained behaviour than is foraging. Fleeing hares moved faster and straighter than foraging hares, with less variation in movement speed. The relative straightness of the escape paths is in accord with models showing that prey well ahead of their predators should move in a relatively straight line, whereas zigzags are more effective when the distance between prey and predator is short (Caro *et al.*, 2004).

We saw no relationship between tortuosity and speed. For foraging hares, this lack of relationship makes sense: a hare foraging in heavy browse will take more steps than one moving between locations in which to forage, so spatial variation in browse availability is expected to lead to high variance in movement speed. For fleeing hares, the trade-off between speed and manoeuvrability observed in other species (Higham, Davenport & Jayne, 2001; Farina, Blanco & Christiansen, 2005) is primarily related to turning at sharp

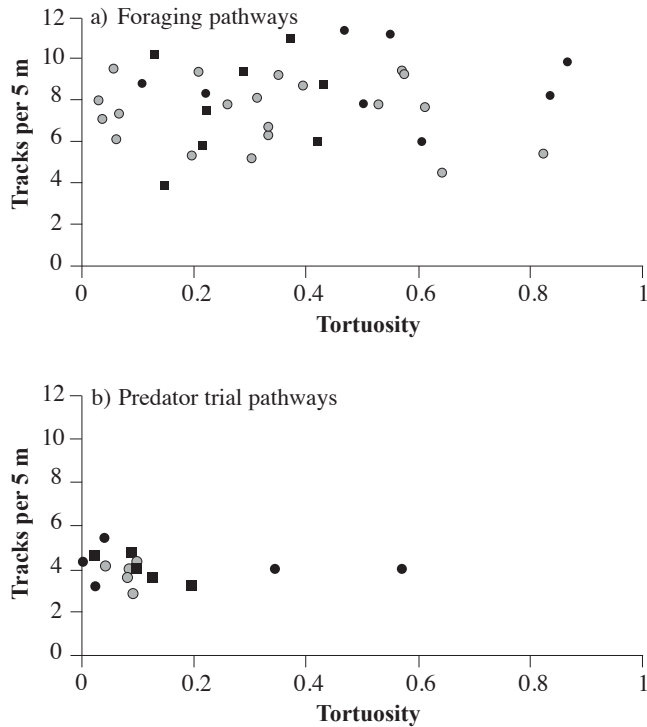


FIGURE 2. Movement speed in relation to pathway tortuosity for snowshoe hares that were a) foraging or b) startled by the predator in open forests (grey circles), closed young forests (black squares), and closed mature forests (black circles). Our movement speed index is tracks per 5 m, with more tracks indicating slower movement speeds.

angles at high speeds. Our leashed dogs were not allowed to chase the hares, so the distance between the hare and the dog was large enough that sharp turns were not likely to be elicited. Our data showing relatively straight-line escapes thus provide a nice confirmation of this prediction about escape behaviour by a forest vertebrate navigating in a complex environment.

These results collectively suggest that snowshoe hares mitigate risk by multiple mechanisms beyond foraging movements. Hares manage time in different habitat types (Hik, 1995), with time allocation additionally affected by choices of how much to eat and where to rest when not foraging (Hodges & Sinclair, 2003). For example, we almost never observed radio-collared hares resting in the open stands, but resting hares were common in the closed stands. Characteristics of foraging pathways are probably driven by details of the available forage and the internal state of the hare (*e.g.*, degree of satiation, body mass). Snowshoe hares are highly selective of forage species and the size of browse (Hodges & Sinclair, 2003), and the amount they browse per plant is affected by the surrounding cover (Hodges & Sinclair, 2005). We suspect the high variability in pathway tortuosity and speed of foraging hares reflects variations in the location of desirable browse.

Fleeing hares and foraging hares had similar vegetation along the pathways, with the amount of vegetation affected by habitat type, as open habitats had less cover. The lack of difference between foraging and fleeing hares in the pathway vegetation suggests fleeing hares were not

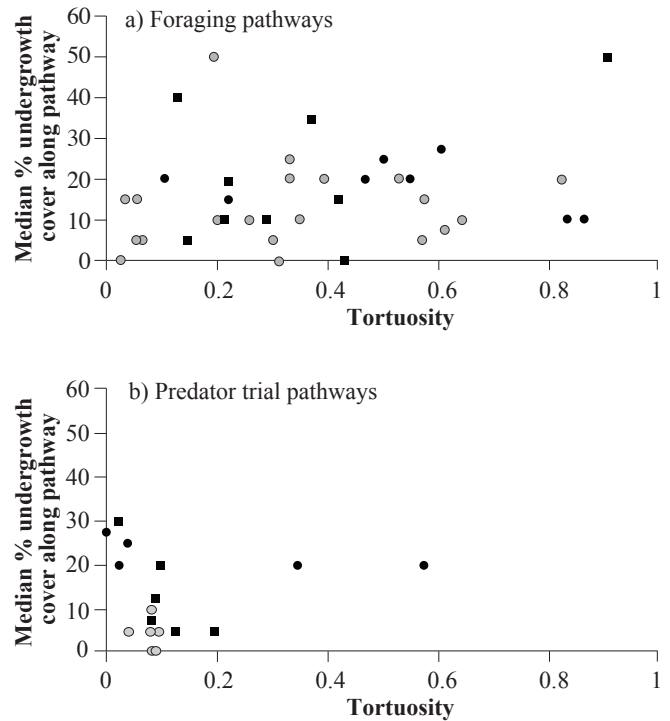


FIGURE 3. Vegetation cover in relation to pathway tortuosity for snowshoe hares. Every 5 m along each pathway, we assessed the percentage of vegetative cover in a 1-m-radius circle at 1 m height; for each pathway, we calculated the median percentage cover. The figure shows pathway medians in relation to pathway tortuosity for a) foraging hares and b) hares startled by the predator in open forests (grey circles), closed young forests (black squares), and closed mature forests (black circles).

actively seeking nor avoiding dense cover as they escaped. Interestingly, this result is consistent with analyses of hares whose seasonal coat colour camouflage was in varying states of mismatch with snow or bare ground (Mills *et al.*, 2013); hares did not exhibit behavioural plasticity in micro-habitat choice or flight distances (Zimova *et al.*, 2014). Although it might seem intuitive that hares might avoid cover because it slows movement, or prefer cover as a means to decrease predator hunting success because hares are able to move through cover more readily than their large-bodied predators, our results did not support either of these options. This result is likely sensitive to the type of chase; in our case, hares were startled but not pursued. In an actual chase, hares might make more use of sharp turns as well as vegetative cover to try to impede larger and less manoeuvrable terrestrial predators. Observing escape pathways of hares chased by natural predators (*e.g.*, lynx, coyotes) and comparing the availability of vegetation to its use by fleeing hares would be useful ways to test this idea.

We chose a 5-m fixed step-length as a reasonable distance for our analyses. Fleeing hares can cover 5 m with 2–3 leaps, so if the fixed step-length were much shorter (approximately 3 m or less), we could end up with cases where no hare tracks occurred in that span. In addition to obscuring some finer-scale tortuosity, a step-length larger than 5 m would be more difficult to measure in the field. Our target of 15 steps was designed to give us reasonable

ability to estimate tortuosity while also being biologically obtainable; hares make use of runways periodically, so it is difficult to obtain longer pathways that can be assigned to a single hare. Based on many hours spent tracking hares on these and other study sites, we are confident the pathways we observed are typical of hares and hence that the estimates of tortuosity are reliable even for pathways less than our target 15 steps. We therefore think the high variability in foraging tortuosities we observed reflects genuine biology rather than sampling issues.

The hare escape pathways were typically shorter than 70 m; only 3 of 17 pathways reached the 70-m point at which we stopped tracking. Although lynx and coyotes pursue hares for longer when hare densities are low, even then unsuccessful chases (*i.e.*, the hare escapes) are typically under 25 m; the majority of unsuccessful coyote and lynx chases on snow are under 10 m (O'Donoghue *et al.*, 1998a). These distances are well below the median escape pathway of 40 m we observed, and in our case the leashed dog stopped at the beginning of the chase rather than being allowed to follow the hare. It would be interesting to see how long hare escape paths are when fleeing from a predator that gives up after a chase.

Taken altogether, these results show a sharp difference in behaviour for hares responding directly to a predator *versus* responding to riskiness of the habitat. One possible explanation for this pattern is that hares are unable to detect differences in the riskiness of habitats and thus behave similarly everywhere. We do not believe this explanation is correct, because hare densities were lowest in the riskiest habitats and individual radio-collared hares spent more time in the less risky closed-canopy forests (Griffin & Mills, 2009). Further, in the high-risk environment of full moons on snow, hares move significantly less (Griffin *et al.*, 2005). These time and density observations are consistent with the majority of hare-habitat studies, which also find that open-canopy forest stands support fewer hares than closed-canopy forest (Hodges, 2000a,b). Instead, we think hares first make a choice about where to be, allocating time preferentially to safer habitats, with movement tortuosity and speed only weakly affected by the inherent riskiness of the habitat. Hares differ markedly in what they eat (Hodges & Sinclair, 2003) and the cover in which they forage (Hodges & Sinclair, 2005; Zimova *et al.*, 2014), so there may be anti-predator behaviours while foraging that differed with habitat type that our metrics did not describe, and that contribute to the high variance we found in the among-habitat measurements of foraging speed and tortuosity.

These results differ slightly from those of Hodson, Fortin, and Bélanger (2010), who compared hare movements in canopy gaps and in the surrounding mature forest in southern Quebec. They found hares avoided canopy gaps (similar to our system, where hares avoided open-canopy forest), but that hares moved faster in the canopy gaps (unlike our lack of difference in movement speed). The spatial scales of the habitats in our 2 studies were quite different, as were the forage species available; more work is needed to determine how the spatial scale of the habitat interspersed affects hare movements.

Even though some habitats are clearly higher risk for snowshoe hares than others, predators make use of a wide

range of forest types (O'Donoghue *et al.*, 1998b; Fuller & Harrison, 2010). Although predators often focus on the habitats with highest prey densities, in some cases they accept areas with medium prey densities but in which the probability of successful chases is high (Fuller, Harrison & Vashon, 2007; Fuller & Harrison, 2010). Risk is also ephemeral, due to the movements of predators (Lima & Bednekoff, 1999; Griffin *et al.*, 2005). Habitat structure therefore may not be a particularly strong cue for herbivores to use when assessing predation risk.

Movement tortuosities and speeds were clearly and strongly different between foraging and escaping snowshoe hares. We suspect it is common that fleeing animals have less tortuous paths than foraging animals; the literature on prey escaping from predators suggests sharp turns are used primarily when predator and prey are very close and the prey must either out-manoeuvre the predator or be caught (Howland, 1974; Weihs & Webb, 1984; Domenici, Blagburn & Bacon, 2011a,b). Movement tortuosity while foraging may alter in response to habitat risk, but tortuosity also integrates fine-scale reactions to food plants and potentially other factors as well as risk.

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