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Hunting behaviour of a sympatric felid and canid in relation to vegetative cover

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Abstract. Carnivore foraging behaviour is suited for hunting in specific vegetative cover types and therefore is largely stereotypical within taxonomic families. Felids typically employ dense cover to stalk or ambush prey, whereas canids do not make use of vegetation when hunting. Sympatric lynx, *Lynx canadensis*, and coyotes, *Canis latrans*, were tracked in snow for three winters and hunting behaviour in relation to vegetative cover was examined. The major prey of both species was snowshoe hare, *Lepus americanus*. Lynx chased hares more frequently in sparse spruce, *Picea glauca,* canopy than coyotes, whereas coyotes chased hares more often in dense spruce than lynx. Lynx initiated chases by stalking in sparse spruce and by ambushing from beds in dense spruce. Vegetative cover did not affect lynx hunting success, but lynx did have higher success when ambushing versus stalking hares. Coyotes chased hares from closer proximity than lynx and employed a pouncing hunting behaviour. Coyote chases were shorter and more successful in dense versus sparse forest. It is concluded that lynx hunting behaviour is variable according to cover, whereas that of coyotes is fixed. However, coyotes appeared to use vegetation as concealment when approaching hares: the possible influence of snow on hunting tactics of each predator species is discussed.

The behaviour patterns by which carnivores seek, approach, capture and eat prey vary among taxonomic families (Kruuk 1986), because of both morphological differences between groups (Bakker 1983; Taylor 1989) and behavioural specialization to particular vegetation types (Kleiman & Eisenberg 1973). For example, felids typically remain concealed while hunting and initiate their approach to prey from dense vegetative cover (Elliot et al. 1977). Concealment allows felids to hunt either by ambushing prey from beds (sensu Curio 1976) or by stalking and then chasing prey for short distances (Kruuk 1986; Sunquist & Sunquist 1989; Caro & Fitzgibbon 1992). In contrast to felids, canids either pounce on small prey at close range (Henry 1986) or exhaust larger prey by chasing them over longer distances (Kruuk & Turner 1967; Kleiman & Eisenberg 1973). Canids typically do not use vegetation as concealment, and in fact may achieve their greatest hunting success in habitats lacking vegetative cover (Wells & Bekoff 1982).

Differences in hunting behaviour between canids and felids imply that even when species rely on the same prey, the two groups should hunt in areas with different types of cover. Studies that have examined habitat use and diet of sympatric populations of canids and felids have noted considerable overlap, however (Witmer & DeCalesta 1986; Major & Sherburne 1987; Litvaitis & Harrison 1989; Koehler & Hornocker 1991), suggesting that both canids and felids hunt in similar habitats. We have shown that sympatric lynx, *Lynx canadensis*, and coyotes, *Canis latrans*, travel and hunt in a variety of habitat types during winter (Murray et al. 1994). Nevertheless, it remains unclear whether the hunting behaviour of canids and felids is stereotypical with respect

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to taxonomic group or plastic according to vegetative cover. The objective of this study was to compare the hunting behaviour and success of one felid and one canid species living in sympatry, to evaluate the influence of behaviour as a function of vegetative cover.

METHODS

Study Area

The study area was a 175 km^2 valley in southwestern Yukon (61°N, 138°W), with white spruce, *Picea glauca*, as the dominant tree species (Douglas 1974). Spruce forests covered most of the area, and other vegetation types were deciduous forests, *Populus* spp., shrub (*Salix* spp.), and open areas that consisted of meadows, steep slopes and frozen water. The primary species in the diet of lynx and coyotes was the snowshoe hare, *Lepus americanus*; other prey species included red squirrel, *Tamiasciurus hudsonicus*, other small mammals, *Peromyscus maniculatus*, *Clethryonomys rutilus* and *Sorex cinereus*, and grouse, *Bonasa umbellus*, *Lagopus lagopus* and *Dendragapus canadensis* (Murray 1991). We estimated from radio-collared individuals and associated tracks that lynx and coyote numbers ranged from 10 to 50 and eight to 20 individuals, respectively, between 1987–1988 and 1989–1990 (S. Boutin, unpublished data).

Tracking in Snow

We tracked predators in snow during December–March 1987–1988 and November–March 1988–1989 and 1989–1990. We followed lynx and coyote travel routes that crossed a network of snowmobile trails, and attempted to randomize our sampling of the area by not concentrating tracking in one section for more than 3 consecutive days. We undertook tracking after snowfall and continued until fresh tracks were indistinguishable from older trails (4–10 days). We estimated distances tracked by counting paces with a hand counter (Parker 1981).

We noted major vegetative cover types encountered while tracking and classified canopy according to percentage of overstory cover. Spruce forests included very closed spruce (76–100% canopy cover), closed spruce (51–75%), open spruce (26–50%) and very open spruce (6–25%). We combined spruce forests into dense (very closed spruce plus closed spruce) and sparse (open spruce plus very open spruce) cover in some analyses. We estimated that on average, we could detect snowshoe hares closer than 15 m and 35 m in dense and sparse spruce, respectively. We classified understory cover as absent (cover <6%), moderate (5%<cover<76%), or abundant (cover>75%).

We interpreted a chase as a sequence of distinct bounding tracks by a lynx or coyote directed towards tracks of a prey species. The number of bounds in the chase and its outcome (unsuccessful attempt or kill) were noted. In some instances, however, bounds associated with a chase were not counted because the snow had been disturbed by the predator's activities after the chase. We identified beds as depressions in the snow where a predator had clearly lain, and those found less than 30 m before a chase were defined as ambush beds. Other hunting techniques used by lynx included stalking, which was evidenced by a shorter gait pattern or body marks in the snow preceding the chase. Coyotes typically pounced on prey, which involved a short sequence of bounds that left no body marks in the snow. Although we measured hunting success by the percentage of chases that resulted in a kill, we could only assess success when signs of a chase were observable. Thus, encounters that did not result in a chase were not noted. Both lynx and coyotes also scavenged during our study, but the frequency of visits and volume of food available at carcasses suggest that scavenging was not an important source of food for either species (Murray et al. 1994).

We indexed the length of time that each bed was used by noting whether the snow in the depression was ice-encrusted (long bed), hard-packed (short bed) or loosely packed (crouch; Parker 1981).

Statistical Procedures

We used *G*-tests (with Williams' correction; Sokal & Rohlf 1981) and log-linear models to compare the distribution of chases by lynx and coyotes to that expected from their use of cover. We calculated expected values from habitat traversed as determined from snow tracking (Murray et al. 1994), and pooled data across years. We did not find hares in areas completely lacking cover, and did not include open areas when calculating expected values. We tested for selection or avoidance of specific cover types by establishing 95% confidence intervals via a Bonferroni z-statistic (Neu et al. 1974; Alldredge & Ratti 1986, 1992). Confidence intervals for hunting success were approximated from the normal distribution (Krebs 1989). The number of bounds in a chase was log transformed and analysesd via two-factor ANOVA. We considered probability values between 0·05 and 0·10 marginally significant.

RESULTS

Prey Choice

Lynx and coyotes were tracked for a total of 559 km and 432 km, respectively, and snowshoe hare was the main prey chased by both (lynx: 94% of 337 chases; coyotes: 80% of 151 chases). We encountered 95 kills of hare by lynx and 46 by coyote. Other species killed included grouse (lynx: N=4; coyote: N=1) and red squirrels (lynx: N=3; coyote: N=3). Lynx and coyotes also hunted and killed rodents, but usually no prey remains were distinguishable. As a result, it was often difficult to discern whether the hunt had resulted in a kill or an unsuccessful attempt. Lynx chased three and killed at least two small mammals, whereas coyotes chased 15 and killed at least three. Given the overall importance of snowshoe hare to lynx and coyote diets, we focused our analysis of hunting behaviour on chases directed at that prey species.

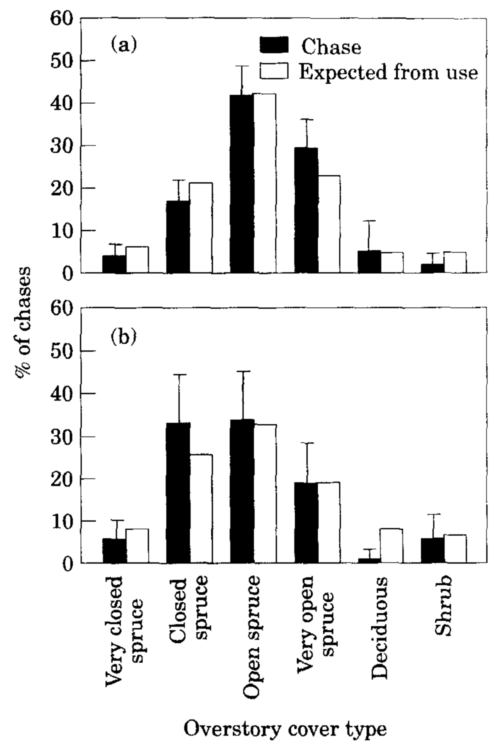

Figure 1. Per cent of chases of snowshoe hare by (a) lynx and (b) coyotes in relation to use of overstory by each species. Expected values were calculated from canopy types used for travel during three winters of tracking in snow. Bonferroni z-statistics were used to establish 95% CI. N=316 and 121 chases for lynx and coyotes, respectively.

Distribution of Hunting Activities

Lynx (N=316) and coyotes (N=121) chased (unsuccessful attempts and kills pooled) hares in significantly different types of overstory cover (G=23·42, df=6, P=0·001), with lynx chasing more hares in very open spruce (Fig. 1). Lynx and coyotes also chased hares in different understory cover types (G=5·47, df=2, P=0·065), with lynx chasing fewer hares than did coyotes where understory cover was absent (Fig. 2).

Lynx chased hares in different cover types than that expected by their use for travel, for both overstory (G=16·95, df=5, P=0·005) and understory (G=8·00, df=2, P=0·018). They chased hares more often in very open spruce (Fig. 1a) and less frequently where understory was absent than expected (Fig. 2a). In contrast, coyotes chased hares relative to their frequency of use of both overstory (G=7·47, df=5, P=0·118; Fig. 1b) and understory cover (G=1·05, df=2, P=0·592; Fig. 2b).

Hunting Success

We evaluated hunting success by comparing the frequencies of kills to unsuccessful attempts in various situations. Hunting success did not differ between lynx and coyotes among overstory (G=8·47, df=5, P=0·123; Fig. 3a) and understory (G=0·34, df=2, P=0·842; Fig. 3b) cover types, but it did differ marginally between dense (closed and very closed spruce) and sparse (open and very open spruce) cover (G=3·14, df=1, P=0·076). Therefore we analysed each species separately for dense versus sparse cover.

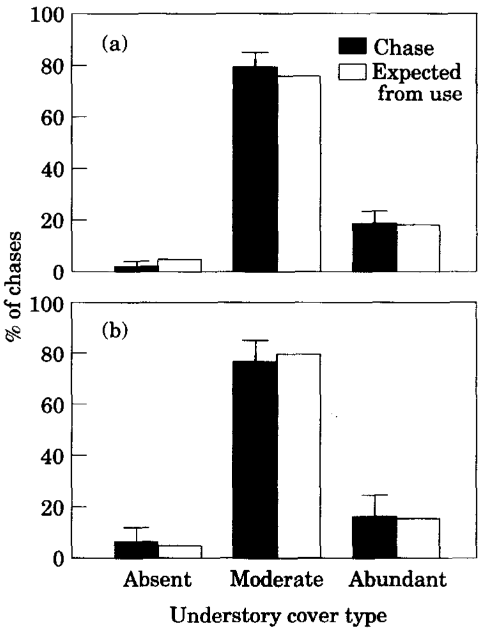

Figure 2. Per cent of chases of snowshoe hare by (a) lynx and (b) coyotes in relation to use of understory by each species. Expected values were calculated from cover types used for travel during three winters of tracking in snow. Bonferroni *z*-statistics were used to establish 95% CI. N=316 and 121 chases for lynx and coyotes, respectively.

Lynx showed similar hunting success in both dense and sparse spruce (G=0·10, df=1, P=0·752), killing 30 ± 5% (±95% CI) of the hares chased. Conversely, coyotes were more successful in dense cover (G=6·06, df=1, P=0·014), killing 51 ± 17% and 28 ± 13% in dense and sparse spruce, respectively.

When species were pooled, hunting success also differed marginally among the three understory cover types (G=4·97, df=2, P=0·083) and even more between the two understory cover types with vegetation present (G=4·24, df=1, P=0·040). This difference was reflected in a 30 ± 5% (N=343) success where understory was moderate, and 43 ± 11% (N=79) success where abundant.

Bounds in the Chase

The distance covered by lynx and coyote bounds was similar (1·0–1·4 m per bound). We were able to count bounds for 96% and 93% of the chases of hare made by lynx and coyotes, respectively. Lynx made more bounds in chases than coyotes ($F_{1,421}$=19·2, P<0·001); lynx kills averaged two bounds more than those by coyotes, whereas unsuccessful chases had similar numbers of bounds (Table I). Fewer bounds were recorded in kills than unsuccessful attempts by both species ($F_{1,421}$=227·25, P<0·001), and a significant interaction was found between species and the number of bounds in kills and unsuccessful attempts ($F_{1,421}$=6·44, P=0·012). Lynx kills tended to become shorter as forest cover became more sparse, whereas both kills and unsuccessful attempts by coyotes were longer in sparse spruce.

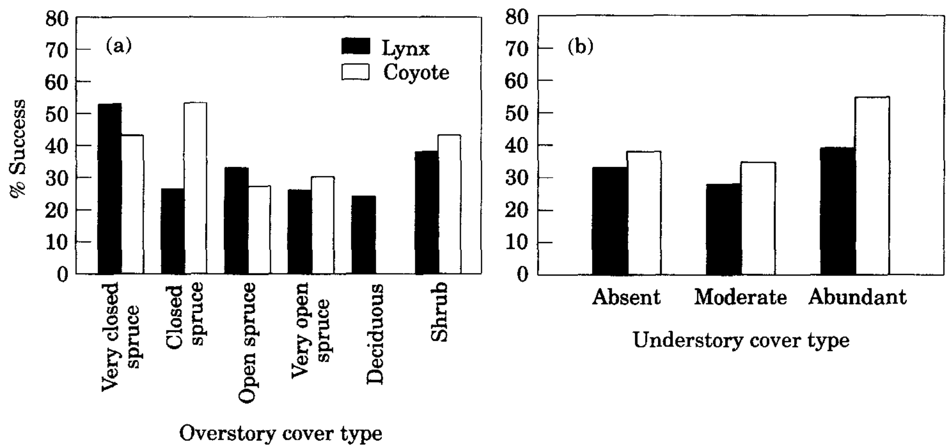

Figure 3. Per cent hunting success of lynx and coyotes in relation to (a) overstory and (b) understory cover. Hunting success in cover types with fewer than five chases was not included.

Table I. Mean (± SD) number of bounds in kills and unsuccessful attempts by lynx and coyotes on snowshoe hare

Overstory cover type	Lynx Kill $\bar{X}$ ± SD	Lynx Unsuccessful attempt $\bar{X}$ ± SD	Coyote Kill $\bar{X}$ ± SD	Coyote Unsuccessful attempt $\bar{X}$ ± SD
Very closed spruce	4·4 ± 7·1 (7)	6·2 ± 2·7 (6)	0·5 ± 0·7 (2)	3·5 ± 2·1 (4)
Closed spruce	4·1 ± 6·1 (14)	6·2 ± 4·5 (39)	0·7 ± 0·9 (17)	4·1 ± 3·9 (19)
Open spruce	2·5 ± 3·8 (42)	6·7 ± 4·9 (89)	1·1 ± 2·1 (10)	5·8 ± 4·7 (30)
Very open spruce	2·4 ± 2·6 (22)	6·6 ± 4·1 (62)	1·0 ± 1·5 (6)	9·1 ± 7·5 (16)
Deciduous	1·0 ± 1·4 (4)	6·8 ± 4·7 (11)	—	—
Shrub	1·0 — (1)	7·3 ± 2·6 (6)	0·3 ± 0·6 (3)	8·0 ± 4·6 (4)
Open	—	—	—	7·0 — (1)
Total	2·8 ± 4·2 (90)	6·6 ± 4·5 (213)	0·8 ± 1·4 (38)	6·1 ± 5·4 (74)

Chases where not all bounds were counted are not included. Sample sizes are given in parentheses.

We performed two-factor ANOVA on chase outcome versus cover type for each species. For lynx, the interaction between chase outcome and overstory cover was not significant ($F_{5,301}$=1·16, P=0·330), and number of bounds did not differ relative to overstory type ($F_{5,301}$=0·70, P=0·622). Kills typically consisted of two to five fewer bounds than unsuccessful attempts in the same canopy type ($F_{1,301}$=54·53, P<0·001; Table I). Unsuccessful attempts consisted of similar numbers of bounds in all cover types.

For coyotes, the interaction between chase outcome and overstory cover was also not significant ($F_{4,101}$=1·101, P=0·408) and the number of bounds was similar among overstory types ($F_{4,101}$=1·19, P=0·321; Table I). On average, coyotes killed hares after three to eight fewer bounds than unsuccessful attempts in the same canopy type ($F_{1,101}$=69·42, P<0·001). However, coyotes chased hares for marginally shorter distances in dense than in sparse spruce ($F_{1,100}$=3·76, P=0·055). The mean (± SD) number of bounds for kills in dense versus sparse spruce was 0·6 ± 0·9 (N=19) and 1·1 ± 1·8 (N=16) bounds, respectively, whereas unsuccessful attempts consisted of 4·0 ± 3·6 (N=23) and 6·9 ± 6·0 (N=46) bounds, respectively.

The number of bounds in chases by both lynx ($F_{2,307}$=1·11, P=0·330) and coyotes ($F_{2,106}$=0·27, P=0·768) were similar between understory types.

Ambushing of Prey

We considered 11% of lynx beds (N=603) as having been used in ambush. We found 77% of ambush beds (N=69) closer than 10 m from the starting point of a chase and only 16 of 69 (23%) between 10 and 30 m from the chase (Fig. 4). Overall, 19% (N=316) of chases and 33% (N=95) of kills made by lynx were the result of ambushing. In contrast, we detected no evidence that coyotes had used beds to ambush hares. Only seven coyote beds preceded chases that were nearer than 100 m, representing 4% (N=160) of all beds. Three per cent of coyote beds preceded chases that were nearer than 30 m, representing 2% (N=46) and 3% (N=75) of kills and unsuccessful attempts, respectively.

Overall, we encountered lynx beds at a rate of 1·1 per km (N=603 beds), whereas we encountered coyote beds at a rate of 0·4 per km (N=160).

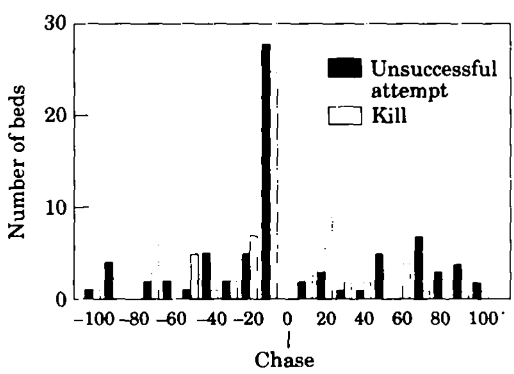

Figure 4. The distance of hunting beds by lynx from the site of a chase of snowshoe hare. Negative values on the abscissa indicate beds made before a chase; positive values represent beds made after the chase. Beds were pooled into 10-m increments, and only beds made less than 30 m before a chase were considered to be used in ambush.

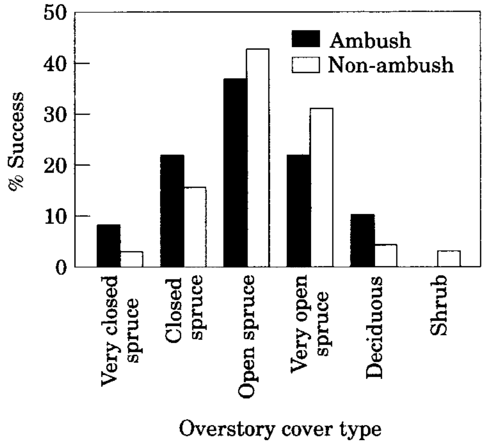

Figure 5. Per cent of lynx chases in which snowshoe hares were ambushed versus those where hares were not ambushed (stalked). Sample sizes were 69 and 247 kills by ambush and non-ambush, respectively.

The snow consistency of lynx beds was softer than that of coyotes (G=67·7, df=2, P<0·001); 42% and 23% of lynx beds consisted of loosely packed and ice-encrusted snow, respectively. In contrast, coyote beds consisted of 11% and 46% of loosely packed and ice-encrusted snow, respectively, suggesting that coyotes used beds for longer periods than lynx.

Cover type appeared to play an important role in the hunting technique used by lynx, because no ambushes occurred where overstory was lacking and only two were noted in the absence of understory. Lynx ambushed hares more frequently in dense spruce and deciduous canopy, whereas more non-ambushes (most of which consisted of stalks) were found in sparse spruce (G=13·92, df=4, P=0·008; Fig. 5). The distrubution of chases by ambush versus those not by ambush, however, did not differ significantly between understory cover types (G=0·636, df=2, P= 0·728). Hunting success was significantly higher for ambushes than for non-ambushes (ambush: 46 ± 13%, N=69; non-ambush: 27 ± 6%, N=247; G=4·25, df=1, P=0·039). Ambushing success did not differ between dense and sparse canopy cover types (G=0·662, df=1, P=0·416), but success was 47% higher where understory cover was abundant than where it was only moderate (G=5·37, df=1, P=0·020).

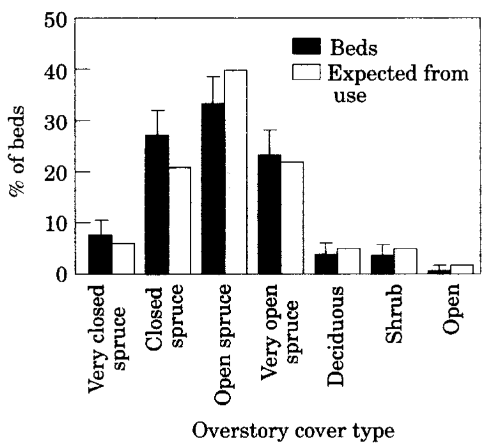

Figure 6. The per cent distribution of lynx beds in relation to use of overstory by the species. Expected values were calculated from habitats used for travel during three winters of tracking in snow. Bonferroni z-statistics were used to establish 95% CI. N=603 beds.

Location of Beds

We examined the distribution of lynx beds relative to use of vegetative cover by the species (areas lacking overstory and understory included), and found that beds were not distributed as expected according to overstory use (G=28·09, df=6, P<0·001). Instead, more beds were found in closed spruce cover (Fig. 6). Similarly, more beds were located where understory was abundant than expected (G=7·90, df=2, P=0·019). In contrast, coyote beds were distributed similarly to that expected by their use of both overstory (G=7·581, df=6, P=0·270) and understory (G=3·0, df=2, P=0·223), which implies that coyotes did not select bed sites on the basis of cover.

DISCUSSION

We found that two carnivores living in sympatry did not use similar cover types when hunting; lynx chased more hares in sparse overstory, whereas coyotes chased more hares in dense overstory. Lynx hunting technique was sensitive to vegetation; lynx captured hares by stalking when in sparse cover and by ambushing from beds in dense canopy. Conversely, coyotes pounced on hares from close range in all cover types but were more successful when hunting in dense spruce. Although our study is limited to winter when snow is on the ground (November–March), and by the fact that our data consist of indirect measures of predator hunting behaviour (tracks in the snow), we believe that our results still illustrate that carnivore hunting behaviour may differ from the familial stereotype.

Differences in cover use between species occurred at different points in the predation sequence. Lynx chased more hares per distance of trail travelled in sparse than in dense cover. Hare densities were not greater in sparse cover (Murray et al. 1994), so the difference must be due to predator behaviour. We cannot tell, however, whether lynx detected more hares, or if once detected, they chose to chase more hares in sparser habitats. In contrast, coyotes used cover for predation in two ways. First, coyotes selected denser habitats than lynx (Murray et al. 1994); then, once hares were chased, coyotes were more successful in killing them therein.

Typically, felid hunting behaviour is sensitive to vegetation (Kruuk 1986; Sunquist & Sunquist 1989); in our study lynx showed this by ambushing prey in dense canopy versus stalking them in sparse cover. Flexibility in hunting technique is likely to be a common response to variable predation sequences (Kruuk 1964; Taylor 1984), and ambushing is usually effective only when the predator is adequately concealed from prey (Curio 1976). Adequate concealment of lynx may have been rare, however, given the limited availability of dense canopy in our area (Murray et al. 1994). Indeed, only 2% and 16% of the area consisted of very closed and closed spruce, respectively. This limitation could have forced lynx to stalk hares in most predatory encounters, even though hunting success was higher when hares were ambushed from dense cover. The high frequency and soft snow consistency of lynx beds relative to coyote beds suggests that lynx invested considerable effort into ambushing, even though only 19% of unsuccessful attempts and 33% of chases occurred via that hunting technique.

In contrast, coyotes usually approached hares to within a short distance (ca 1 m) before making a pounce. Canids typically pounce on small rodents, however (Henry 1986; Halpin & Bissonette 1988), rather than on cursorial species such as snowshoe hares. The fact that coyotes were more successful and had shorter chases in dense cover, however, suggests that vegetation allowed coyotes to approach hares to within killing distance. In contrast to lynx we did not note that coyotes had approached hares by stalking; rather, their gait remained the same up to the point where the chase was initiated. Although the use of concealment while hunting is more typical of felids than canids (Kleiman & Eisenberg 1973), the technique is often used when the sustained speed of a predator does not permit a successful capture (Curio 1976). In our study this condition was probably caused by the large differential in foot-load (ratio of body mass to foot surface area) between coyotes and hares, and the adverse effects of snow on coyote hunting (Murray & Boutin 1991). Conversely, the lower foot-load of lynx was likely to enable them to capture hares effectively after more bounds in the snow, and to initiate successful chases when hares were at greater distance.

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