# The efficiency of yarding behaviour by white-tailed deer as an antipredator strategy

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Received December 23, 1983

MESSIER, F., and C. BARRETTE. 1985. The efficiency of yarding behaviour by white-tailed deer as an antipredator strategy. Can. J. Zool. **63**: 785–789.

This study shows that white-tailed deer (*Odocoileus virginianus*) reduce their vulnerability to coyote (*Canis latrans*) predation by congregating in a traditional wintering area (yard). Distribution of deer and coyotes were monitored within a 36-km² yard (≃630 deer) and the surrounding area. Coyote pairs and packs preferentially used areas of low deer density where only 12% of the deer wintered; 18 of 23 deer killed by coyotes were located in these areas. We postulate that the greater number of runways in high deer density areas enhanced escape from coyotes. By congregating in a yard during winter months, deer also benefited from a lower coyote:deer ratio. Territorial behaviour kept the coyotes from concentrating in the yard. We consider yarding behaviour to be an antipredator strategy in addition to an energy-conserving strategy.

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Cette étude montre que la concentration dans des quartiers d'hiver chez le cerf de Virginie (*Odocoileus virginianus*) réduit le risque d'être tué par un coyote (*Canis latrans*). Nous avons quantifié la distribution des cerfs et des coyotes à l'intérieur d'un quartier d'hiver de 36 km² (≃630 cerfs) ainsi que dans la région périphérique. Les coyotes vivant en couples ou en meutes ont fréquenté d'une façon préférentielle les endroits à faible densité de cerfs où seulement 12% des cerfs hivernaient; 18 des 23 cerfs abattus par les coyotes l'ont été dans ces endroits. Une plus grande disponibilité de sentiers dans les milieux à forte densité de cerfs semble avoir permis aux cerfs d'échapper plus facilement aux attaques des coyotes. En se concentrant dans le quartier d'hiver, les cerfs ont bénéficié en plus d'un rapport coyotes:cerfs plus bas. Le comportement territorial des coyotes empêchait ceux-ci de se concentrer dans le quartier d'hiver. Nous considérons la formation de quartiers d'hiver chez le cerf de Virginie comme une stratégie propre à diminuer le risque d'être tué, tout en minimisant les dépenses énergétiques.

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## Introduction

At the northern limits of its range the white-tailed deer shows a clear tendency to concentrate in traditional wintering areas, a phenomenon referred to as yarding behaviour (Verme 1973; Huot 1974; Drolet 1976; Nelson and Mech 1981; Potvin et al. 1981). Common characteristics of deeryards include low elevations, south-facing slopes, and forest types offering shelter and browse (Telfer 1970; Huot 1974; Drolet 1976; Potvin 1978; Potvin and Huot 1983). The most obvious characteristic of a yard is the presence of a network of trails used to forage. In early December deer move up to 40 km to winter with conspecifics in such yards, and usually will return to their summer range in mid-April (Verme 1973; Drolet 1976; Nelson and Mech 1981). Some yards contain over 1000 animals and may exceed 30 km² (Huot 1974).

Commonly, yarding behaviour is considered as an energy-conserving strategy. Cost of locomotion is minimized by use of communal trails, and by the lower snow accumulation typically found in yards (Mattfeld 1974; Parker et al. 1984). Convective heat loss is reduced in coniferous stands and radiative heat gain is enhanced on south-facing slopes (Ozoga 1968; Ozoga and Gysel 1972; Moen 1976).

Messier (1979, p. 118) and Nelson and Mech (1981) argued that yarding behaviour should also be considered as an antipredator strategy. Deer may be able to reduce their vulnerability to predators by clumping more densely within a yard (i.e., density within a patch) and (or) by forming large yards containing many individual animals (i.e., number and dispersion of these patches).

This study examines whether deer reduce their vulnerability to coyote predation by congregating within a given yard. We postulated that as long as the benefit from lower predation outweighs the negative effect of increased food competition, yarding behaviour will have a selective advantage as an antipredator strategy.

## Study area

The research was conducted in a 155-km² forested area in southern Québec (70°25′ W, 46°00′ N; Fig. 1), about 125 km southeast of Québec City. The topography consists of rolling hills characteristic of the Appalachian region. Annual precipitation averages 100 cm, of which 35% is snow. Snow accumulation frequently reaches 60 cm, and the ground is covered with snow from mid-November until late April. The area lies within the Great Lakes – St. Lawrence forest region, Eastern Townships section (Rowe 1972). An important feature of the area is the presence of a 36-km² white-tailed deer yard. Each winter, approximately 630 deer from surrounding areas reside in this yard from early December until April (Pichette 1979). During winter, coyote density was about 1 per 8 km² (Messier 1979), and bobcats (*Lynx rufus*) were less abundant given the few tracks observed (8 vs. 1468 coyote tracks).

## Methods

Fieldwork was conducted from 15 November to 1 April in 1976–1977, and 1977–1978. To evaluate the relationship between individual vulnerability to predation and deer density, we collected information on the distribution of deer, coyotes, and deer kills. Deer distribution within the yard was quantified by means of track counts and pellet group counts. Track counts gave temporal indices of deer distribution along a predetermined network of trails used also to census coyote tracks. The purpose of these track surveys was to correlate coyote space use with deer distribution. Pellet group counts were used to evaluate deer density (integrated over the winter) in the vicinity of each kill. Track counts could not be used here because kills were mostly located outside our network of trails.

Counts of deer tracks were conducted on 28 November, 5 and 24 December 1977, 24 January and 9 February 1978. More counts were made in early winter when deer distribution was more variable. The network of trails (Fig. 1), controlled by gates, followed available logging roads (75.5 km), bush trails (21.1 km), and waterways (14.4 km) widely distributed over the yard and the surrounding area. Deer tracks and runways (four or more tracks) were recorded on an aerial photograph mosaic between 20 and 28 h after a snowfall. Even at the minimum rate of four tracks per day, a runway rapidly becomes a

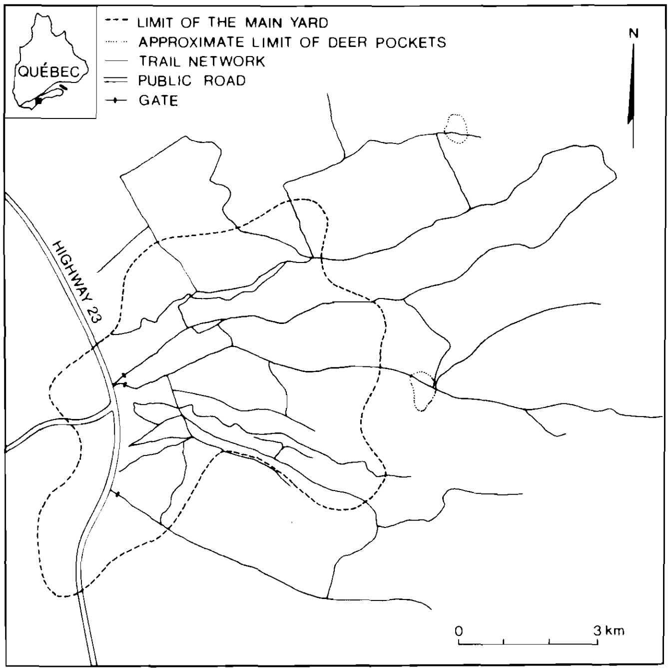


FIG. 1. Location of the study area and map of the trail network used for white-tailed deer and coyote track surveys. The 36-km$^2$ deeryard and two outlying winter deer pockets are also depicted.

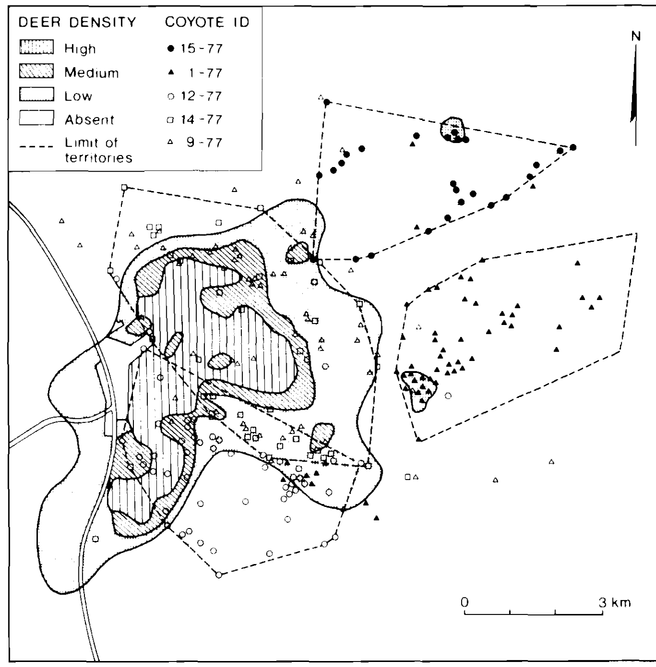


FIG. 2. Track frequencies of coyotes travelling as singles, pairs, and packs in areas outside the yard and in areas of low, medium, and high deer densities within the yard. The 95% confidence intervals and deviations from homogeneous distribution are also presented: +, significantly greater ($P < 0.05$); −, significantly lower ($P < 0.05$) (from Bonferroni Z-test, within each type of coyote grouping). Deer runway counts (stippled) are depicted as relative deer densities.

packed route. Using these observations, the network of trails was arbitrarily partitioned into four classes of deer density; nil or outside the yard, low, medium, and high. A new partitioning was made immediately after each deer track survey and prior to the interim coyote track counts. These partitionings were used for the analysis of coyote track distribution.

Each winter the yard was outlined from an aerial survey. In early summer, pellet group counts were used to estimate the deer population of the previous winter (Pichette 1979). Deer distribution was determined from 352 plots (80 m$^2$) systematically laid along transects (200 m between plots, 500 m between transects). A plot with less than two pellet groups was considered as a low density area, two to five, and over five pellet groups were considered to be medium and high densities, respectively. For comparison, the overall mean number of pellet groups per plot was 3.9. From maps of deer densities we associated a class of deer density with each predator kill. The possibility exists that deer density at time of kill differed from the intergrated deer density estimated from pellet group counts. Considering the breadth of deer density classes, this seems unlikely. Mean number of pellet groups per plot in a given class was taken as an index of deer density. The total number of pellet groups deposited in areas of low, medium, and high deer densities was assumed to reflect the number of deer present (or deer days). Here we assumed a linear relationship between pellet group numbers and deer numbers (i.e., a constant defecation rate between areas).

Coyote distribution was monitored by track surveys using snowmobiles on the trail network (Fig. 1). We conducted surveys each day that weather conditions permitted. During the 5 h needed to cover the network (two observers), we recorded each coyote track on the aerial photograph mosaic, noting the number of coyotes involved in each track record. When it was obvious that the same animal(s) had crossed the circuit more than once within a short distance (<200 m), only one crossing was counted. The tracks of each census were erased by our passage in the snowmobile. The time elapsed between two surveys, or since the last snowfall, was recorded to obtain the activity period covered by each track survey.

Most deer killed (i.e., only those with evidence of pursuit or tooth punctures to the neck region; Messier (1979) by coyotes were found independently (with no apparent bias) from radio tracking of coyotes (Messier and Barrette 1982). All groups of coyotes using the yard in 1977–1978 were located daily. When a kill was made, coyotes tended to stay nearby for many days. When we observed these typical, limited wanderings we followed the coyote tracks to locate the kill. Six kills were located incidentally when patrolling the network. Because our trail network covered the yard in proportions similar to those covered by deer density classes (58, 18, and 24% for yard area compared with 65, 19, and 16% for the trail network), sampling of these kills was likely unbiased with regard to classes of deer density.

In addition to the major deeryard, four outlying deer pockets (i.e., small peripheral yards) were investigated. No defined runways were observed implying that deer density was rather low. We estimated that a maximum of 30 deer inhabited these four pockets.

## Results

### *Deer distribution*

Average numbers of deer tracks in parts of the trail network, classified as low, medium, and high density, were 2.9, 7.4, and 14.5/km, respectively. Corresponding values for runways were 0.4, 3.5, and 7.5, respectively (Fig. 2). Indices of deer density, deer numbers, and deer distribution are presented in Table 1 and Fig. 3.

### *Coyote distribution*

The trail network was patrolled 131 times during the two winters of the fieldwork. We recorded 1468 coyote tracks of which 631 (43%) were single, 501 (34%) in pairs, and 335 (22%) in groups of three to five individuals. Tracks observed along a plowed road ($n = 302$) were discarded in the following analysis because they were either more difficult to observe or partly obliterated by the plow.

As winter progressed, numbers of coyote tracks encountered did not increase along the part of the trail network inside the yard, or along the entire network covering the area surrounding

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TABLE 1. Occurrence of white-tailed deer killed by coyotes or bobcats in relation to winter deer densities and deer numbers

| Deer density | Index of deer density[a] | Approximate no. of deer (%)[b] | No. of coyote kills (bobcat kills) |
|---|---|---|---|
| Low | 0.5 | 80 (12) | 18 (2) |
| Medium | 3.2 | 95 (15) | 3 |
| High | 12.6 | 485 (73) | 2 |

[a]Mean number of pellet groups per plot of 80 $m^2$.
[b]Calculated from the total number of pellet groups deposited (i.e., 13 pellet groups·$day^{-1}$·$deer^{-1}$, 150 wintering days·$deer^{-1}$). Thirty deer were added to low-density areas counting for the four outlying deer pockets.

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the yard (Table 2). Within the yard, significantly ($P < 0.05$) more tracks were observed in December, but this trend did not persist. To avoid bias between months, the comparison was based on track surveys ($n$ = 40) with similar times of track deposition (i.e., within 20–28 h).

Coyote activity was not higher in areas of greater deer densities (Fig. 2). Instead we found that areas of low deer density were more frequently used by coyotes (Bonferroni Z-test, $P < 0.05$). Among classes of deer density, a significant difference was observed between coyotes traveling as singles, pairs, and packs ($\chi^2[6] = 60.0$, $P < 0.05$; Fig. 2). Single coyotes showed no difference in use among the four classes of deer density ($P > 0.05$). Pairs used areas of low deer density significantly more, and areas of high deer density less ($P < 0.05$). Packs also used areas of low deer density significantly more, and areas outside the yard less ($P < 0.05$). These analyses used the Bonferroni Z-test after the $\chi^2$ test had led to the rejection of homogeneity of coyote frequentation between classes of deer density (see Neu et al. 1974).

A similar pattern of coyote space use emerged from the analysis of coyote radio locations compared to track surveys. Single coyotes expressed no difference in use among classes of deer density (Table 3), whereas pairs and packs used areas of low deer density areas significantly more, and areas of high deer density less (Table 3, Fig. 3).

*Kill distribution*

A greater proportion of the kills was observed in areas of low deer density. During the two winters of fieldwork we located 23 deer definitely killed by coyotes (18 in areas of low deer density, 3 in areas of medium deer density, and 2 in areas of high deer density) (Table 1, Fig. 4). This distribution differs markedly from respective distribution of deer; 80, 95, and 485 ($\chi^2[2] = 96.5$, $P < 0.01$; Table 1). Considering also that two deer were killed by bobcat in areas of low deer density, 20 of 25 kills (80%) were located in an area where only about 12% of the deer population wintered (Table 1). Despite our limited sample size of kills, deer were clearly much safer in areas of high density.

## Discussion

*Vulnerability to predation vs. deer density in a yard*

Within a yard, deer density differs markedly according to habitat structure, browse availability, and topography (Huot 1974; Potvin 1978; Potvin and Huot 1983). We would expect coyotes to exhibit specific hunting tactics in a way to maximize their foraging efficiency. In our study area, deer represented ≃80% of winter diet of coyotes (Messier 1979). One tactic indicated by the coyote track surveys and telemetry data was the preferential use of areas of low deer density, a tendency

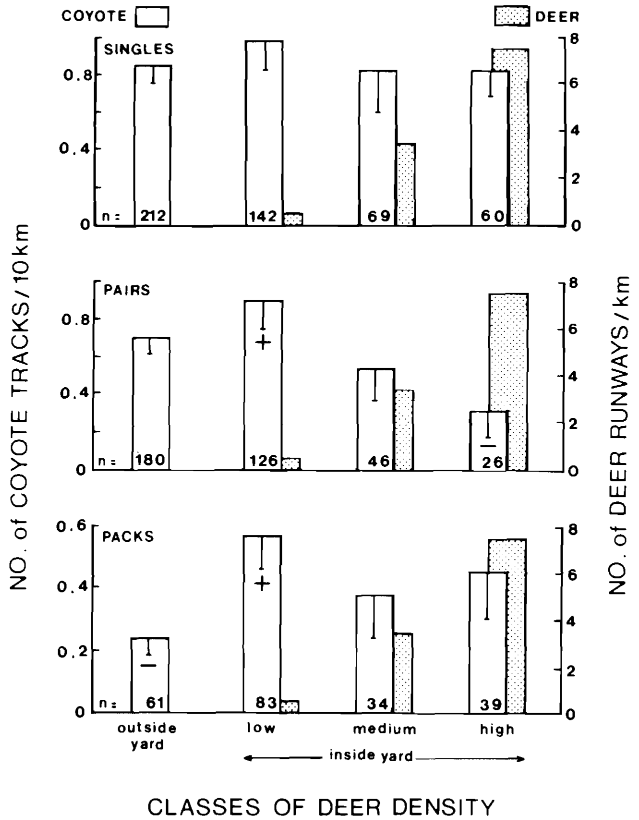


FIG. 3. Radio locations of the five coyotes living as pairs or packs from 1 December 1977 to 31 March 1978 in relation to the 1977–1978 winter deer density. Coyote locations from Messier and Barrette (1982).

significant for pairs and packs. Coyote pairs and packs also made the majority of the kills (17 of 18 known cases; (Messier 1979), most of them in areas of low density. These observations strongly suggest that pairs and packs foraged more effectively in areas of low deer density despite the obvious lower rate of deer encounters. In contrast, solitary coyotes showed no significant foraging tendency relative to deer density. They also had a more diversified winter diet, consisting primarily of scavenged deer carcasses (56%) and snowshoe hare (*Lepus americanus*; 27%) (Messier 1979).

Coyotes likely have a greater chance of killing a deer in areas of low deer density, this being related to the basic structure of a yard, the trail web. Along 438 km of snow-tracking coyotes, we observed 13 deer chases of which 10 successful (9:1:0 for low, medium, and high deer density, respectively), and 3 unsuccessful (1:1:1, respectively). From this tracking, it became clear that deer killing depends primarily on the opportunity to corner the quarry in deep snow where the animal is harassed until exhausted or suffocated by a throat grip (Messier 1979). Deer must rely on a quick escape (e.g., successful chases, 80 ± 23 m, $n$ = 10; failed chases, 150 ± 43 m, $n$ = 3) and we believe that the density of the runways constitutes a critical element of a successful escape. For example, numbers of runways encountered per kilometre along the trail network were 0.4, 3.5, and 7.6 in areas of low, medium, and high deer density, respectively. In areas of low density, deer are therefore relatively further away from an escape route. Indeed, kill distribution indicated that a deer experiences a higher chance of being killed in these areas (Table 1).

Disproportionately heavier predation in wintering areas with

TABLE 2. Indices of coyote frequentation along the entire network, and the portion inside the yard (Fig. 1) during the winter 1976–1977 and 1977–1978. Portion of the network inside the yard, and the entire network were treated separately

| | Entire network | | | Portion of the network in the yard | | |
|---|---|---|---|---|---|---|
| | Distance patrolled (km) | Tracks observed | Tracks/10 km (±95% CL) | Distance patrolled (km) | Tracks observed | Tracks/10 km (±95% CL) |
| Nov. | 165.6 | 53 | 3.20±1.09 | 95.7 | 31 | 3.24±1.41 |
| Dec. | 408.6 | 115 | 2.81±0.60 | 253.2 | 97 | 3.83±0.88* |
| Jan. | 593.3 | 138 | 2.33±0.45 | 328.5 | 95 | 2.89±0.65 |
| Feb. | 1082.3 | 245 | 2.26±0.29 | 560.5 | 139 | 2.48±0.43 |
| Mar. | 158.2 | 50 | 3.16±1.10 | 84.8 | 22 | 2.59±1.41 |

*Significantly higher, $P < 0.05$; Bonferroni Z-test, DF = 4.

TABLE 3. Radio-location distribution of coyotes living as singles, pairs, or packs in relation to relative deer densities within the study area, 1 December 1977 to 31 March 1978

| Deer density | Proportion of deer wintering area | Proportion of coyote locations, singles | Proportion of coyote locations, pairs or packs |
|---|---|---|---|
| Low | 0.50 | 0.47±0.14 (37) | 0.63±0.10 (82)* |
| Medium | 0.21 | 0.20±0.11 (16) | 0.25±0.09 (32) |
| High | 0.29 | 0.32±0.13 (25) | 0.12±0.07 (16)** |

NOTE: Coyote distribution is presented as a proportion of locations within each class of deer density ±95% CL with $n$ in parentheses. Deviations from homogeneous distribution are denoted as follows: *, significantly higher ($P > 0.05$); **, significantly lower ($P < 0.05$) (Bonferroni Z-test). The deer wintering area west of Highway 23 (Fig. 1) was excluded from the analysis since no coyote was radio tracked there. Coyote locations from Messier (1979), and Messier and Barrette (1982): singles = 4-77, 5-77, and 6-77; pairs or packs = 1-77, 9-77, 12-77, 14-77, and 15-77.

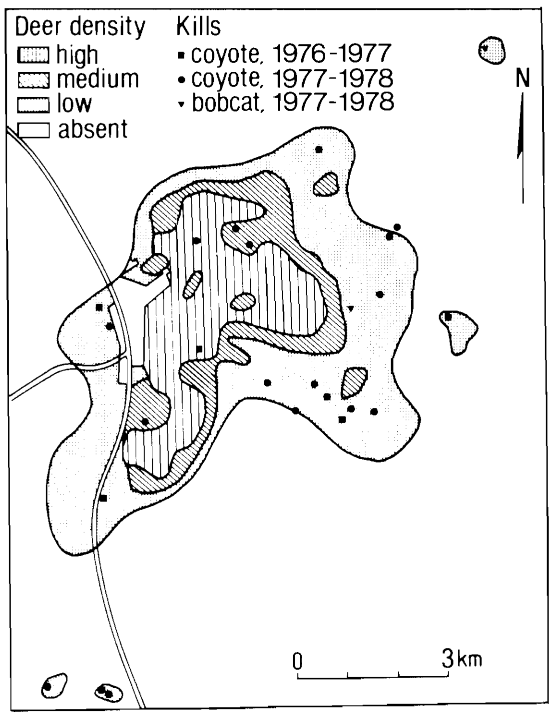


FIG. 4. Locations of 25 deer killed by coyotes or bobcats in relation to winter deer densities. Deer densities are for the winter 1977–1978, the density in vicinity of the four 1976–1977 kills was unchanged.

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low deer density (e.g., edges of main yards, outlying deer pockets) appears to be a typical phenomenon of wolf (*Canis lupus*) – deer systems as well. In Ontario, Kolenosky (1972) reported that wolves preferentially used areas of low deer density where more kills were made. During a major deer decline in the Superior National Forest, Minnesota, small winter yards (with presumably low deer densities) in wolf territories were the first to vanish (Nelson and Mech 1981). In the Beltrami Island State Forest, Minnesota, most deer killed by wolves were observed outside or near the edges of traditional yards (Fritts and Mech 1981).

The exact mechanism involved in the reduction of deer vulnerability to predation with an increase of density was not clearly demonstrated in this study. We believe that the ease of escape along runways is the most influential element. However, we do not rule out other factors such as increased predator detection (Kenward 1978) and greater predator confusion in a pursuit (Jarman 1974), although we consider them as less important. Regardless of the mechanism involved, the lower predation risk gained from being in high density areas should reinforce the tendency for deer to concentrate in wintering areas.

*Vulnerability to predation vs. number of deer in a yard*

In winter, coyotes did not concentrate in the deeryard to benefit from this potential prey (Table 2). This observation is most likely related to a strong territorial behaviour in coyotes which limited the number of coyotes able to use the yard. The existence of territoriality in coyote pairs and packs was evident from their use of space and scent-marking behaviour (Barrette and Messier 1980; Messier and Barrette 1982). Nonterritorial, solitary coyotes could have concentrated in a yard, but our data (Table 2) do not show this occurring.

When predators cannot change their living areas at will, individual yarding deer may benefit from a lower predator–prey ratio, i.e., dilution effect (Hamilton 1971; Foster and Theherne 1981; Nelson and Mech 1981). However, this benefit only occurs when deer aggregate sufficiently to leave some predator territories without access to a traditional yard. That appears to be the situation in the coyote–deer system we investigated since two coyote families had a limited access to the yard (Fig. 3; Messier and Barrette 1982). For predators with much larger territories, such as wolves, the advantage to a yarding deer by lowering the predator–prey ratio is probably much less important because each territory would usually include one or more deeryards (Van Ballenberghe et al. 1975; Fritts and Mech 1981). However, in either case a deer is more secure from being in areas of higher density.

*Management considerations*

Our results suggest that predation might be minimized by promoting large yards with a high deer density. Deer can reduce their vulnerability to predators by clumping more densely, but at the expense of a greater food competition. One way that deer can minimize their exposure to predators is to remain in areas of high density when they are resting, and move to areas of lower density with less food competition, but less security from predators, during foraging periods. In such a context, not only is browse production important, but also its distribution in relation to the stands offering protective cover where deer can concentrate during resting periods (Potvin 1978; Potvin and Huot 1983) in relative safety from predation.

## Acknowledgements

Funding for this study was provided by a grant from the Ministère du Loisir, de la Chasse et de la Pêche, Québec. We are grateful to Domtar Inc. for allowing us to study coyotes on their private land. François Messier wishes to thank the Natural Sciences and Engineering Research Council of Canada for financial support. F. L. Bunnell, M. Crête, T. K. Fuller, J. Huot, D. Seip, and D. M. Shackleton provided useful comments on the manuscript. Finally, we thank C. Pichette for permission to use results of the pellet group counts.

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