

An innovative use of white-tailed deer (*Odocoileus virginianus*) foraging behaviour in impact studies

G. Rieucou, W.L. Vickery, G.J. Doucet, and B. Laquerre

Abstract: We developed an innovative method for estimating human impacts on animal species by measuring changes in feeding behaviour. We illustrate our approach with a study of the effect of vegetation control in a power-line right-of-way (ROW) passing through essential winter habitat of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) at the northern limit of their range. We used giving-up density (GUD; i.e., the amount of food left behind when an animal stops foraging in a patch) to evaluate, in one deer yard, if the loss of forest shelter caused by the power-line installation had a greater effect on deer than the gain of food regenerated in the cleared area. We used GUDs to compare deer estimate of habitat quality in the ROW and in the forest. Our results suggest that the ROW had a negative impact on deer. GUDs were lower in the forest compared with the ROW. Either increased metabolic costs or increased predation risk in the ROW, apparently the latter, lead deer to abandon more food in the ROW than elsewhere. Higher GUDs were strongly correlated with greater snow depth in the ROW. Deer preferred habitats at the edge of the ROW where food and cover were both available.

Résumé : Nous avons mis au point une méthode innovatrice pour estimer les impacts des humains sur les espèces animales d'après les changements des comportements alimentaires de ces animaux. Nous illustrons notre méthodologie par une étude des effets du contrôle de la végétation dans une emprise électrique (ROW) qui traverse un ravage de cerfs de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)) à la limite boréale de leur répartition géographique. Nous utilisons la densité de nourriture abandonnée (GUD, « giving-up density »; c'est-à-dire la quantité de nourriture qui reste lorsqu'un animal arrête de se nourrir dans une parcelle alimentaire) pour déterminer si, dans un ravage de cerfs, la perte de refuges forestiers due à la présence de la ligne électrique a plus d'effets sur les cerfs que le gain de nourriture causé par la régénération dans l'emprise. Nous utilisons les valeurs de GUD pour comparer l'estimation de la qualité de l'habitat par les cerfs dans le ROW et la forêt. Nos résultats indiquent que le ROW a un impact négatif sur les cerfs. Les GUD sont plus bas dans la forêt que dans le ROW. Les coûts métaboliques accrus et le risque plus élevé de prédation dans le ROW, apparemment surtout ce dernier facteur, amènent les cerfs à délaisser plus de nourriture dans le ROW qu'ailleurs. Il y a une forte corrélation entre les valeurs élevées de GUD et l'épaisseur plus importante de neige dans le ROW. Les cerfs préfèrent les habitats en bordure du ROW où il y a à la fois de la nourriture et une couverture végétale.

[Traduit par la Rédaction]

Introduction

Studies of human impacts on wildlife are often based on changes in population density. This can be costly and time-consuming. Furthermore, it may not reflect real impacts because density does not necessarily reflect habitat quality (Van Horne 1983). In this paper we develop an alternate approach to evaluating human impacts on habitat quality based on animals' feeding behaviour. This new approach attempts to detect small-scale effects that would only be detectable at the population level if they were repeated over a larger scale. Evaluating effects at the smaller scale may be more cost effective than at the larger scale because the latter will require more time and probably greater negative impacts on the population being studied to detect significant effects. We illustrate our approach using a study of small-scale removal of winter-cover habitat for white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)).

We propose that an animal's foraging behaviour reveals information about the animal's perception of the place (its habitat) which it currently occupies (Brown 1988; Kotler et al. 1994). Thus measures of foraging behaviour will allow us to infer how animals evaluate variations in their habitat. These inferences can be drawn at the habitat scale at which animals change their behaviour. We focused on foraging behaviour to draw inferences about habitat quality because of the close relationship of food with growth, survival, and reproduction. Moreover, animals often expose themselves to predation risk while they are foraging. So, we expect their foraging behaviour to reveal whether they consider a habitat to be of high quality (providing both food and protection from predators) or low quality (lacking one or both of these elements).

We define a food patch as a place where animals find food: perhaps a single shrub, a clump of shrubs, or even an

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entire field or grove. Optimal foraging theory predicts that an animal should adjust its foraging behaviour to maximize its fitness by engaging in feeding activities only as long as the expected benefits outweigh the foraging costs (Charnov 1976). Brown (1988) argues that animals leave food patches when the benefits they provide (through the harvest rate of food) are equal to the costs (the sum of metabolic cost, predation risk, and missed-opportunity cost) of foraging there. Brown's "quitting harvest rate" (the rate of food consumption at which deer leave a food patch) provides a quantitative measure of the animal's assessment of costs of remaining in the food patch. The amount of food remaining in a specific food patch when an animal ceases foraging there is defined as the giving-up density (GUD; Brown 1988). Thus GUDs are related to important characteristics of the habitat: predation risk, food availability, and metabolic costs of foraging. Therefore GUDs can be used to compare the relative costs of foraging in different food patches (Shochat et al. 2004). But, to use GUDs to compare deer's assessment of the quality of different habitats, we have to identify how each foraging cost affects the amount of food left by deer. As missed-feeding cost rises (we assume that feeding is the only opportunity which varies among habitats), GUDs will also rise, reflecting abundant food in the surrounding area (Brown 1992; Murden and Risenhoover 1993). However, as predation risk or metabolic costs rise, GUDs will also rise (Kotler et al. 1994) because foragers will balance these foraging costs by leaving the food patch at a higher harvest rate (Brown et al. 1988). Thus, high GUD values can indicate either abundant food (high-quality habitat) or elevated costs (poor-quality habitat). Therefore, to use GUDs to estimate habitat quality, we must separate the effects of missed-feeding costs on the one hand and predation risk and metabolic costs on the other.

In this paper, we study the effects of maintaining a power-line right-of-way (ROW) in the winter habitat of white-tailed deer. The ROW can have several effects. Reduced cover in the ROW can increase predation risk (deer are more visible to predators and less able to escape in deeper snow) and metabolic costs (owing to increased exposure to wind chill). On the other hand, plant regrowth in the ROW can supply additional food for deer. We separate these effects using GUDs despite the fact that both should cause GUDs to rise. Planned statistical contrasts are used to compare GUDs in places where one of the above effects is held constant.

To survive in northern conditions, most deer confine their activity to wintering areas called yards (Morrison et al. 2002). These yards represent a small fraction of their annual range (Rongstad and Tester 1969), about 3% in Quebec (Pichette 1980). High-quality habitat offers deer both shelter (coniferous cover) and food (deciduous browse) (Dumont et al. 1998). Deer migration into yards is generally induced by an increase in snow depth and a decrease in ambient temperatures (Sabine et al. 2002).

In Quebec, about fifty yards are crossed by transmission power-line ROWs in which woody vegetation is cut regularly to avoid interference with the electrical lines. These "control" or "maintenance" cuts result in a loss of protective cover against predation and wind, which can be detrimental to deer (Hershey and Legee 1976), and an increase

in browse availability (Garant 1992) through regeneration within the ROW, which may be helpful to deer.

Coniferous cover reduces snow depth and limits wind chill (Verme 1968). White-tailed deer movements are restricted by snow depth (Parker et al. 1984) and snow cover (Kie 1999) owing to winter rainfalls and low temperatures (Aanes et al. 2000; Solberg et al. 2001), which increase the energetic cost of locomotion. At depths >50 cm (length of a deer's leg), walking is impractical for a 60 kg animal (Moen 1976), and jumping also becomes difficult and energetically costly. Furthermore, the risk of predation increases with snow accumulation and breakable crust because deer have more difficulty walking than their predators (gray wolves (*Canis lupus* L., 1758), coyotes (*Canis latrans* Say, 1823), or dogs) (Telfer and Kelsall 1984; Nelson and Mech 1991).

If coniferous cover is removed, as in the case of a ROW, deer will likely face higher metabolic costs and greater predation risk. But these costs may be compensated by the addition of new food sources as deciduous plants regenerate in the ROW. Excessive annual exploitation of yards by deer leads to a decrease in food availability and prevents regeneration of new plants to an extent that can severely reduce the long-term quality of the yard (Rooney and Waller 2003). Deciduous regeneration in the ROW may produce a food source to compensate, at least partly, for such food shortages. The benefit may be similar to that of supplemental feeding by humans (Ozoga and Verme 1982).

Browsing the terminal parts of deciduous woody species provides the major part of deer's winter diet because forage is not accessible (Martika 1968). When browse is insufficient to supply energy requirements, deer have to use their fat reserves (Ozoga and Gysel 1972). In winter, forage availability depends on snow depth (Martika 1968) and ice crust (Clutton-Brock and Albon 1982; Solberg et al. 2001); deep snow restricts food accessibility and increases the cost of finding food (Nudds 1980). Thus, increases in food availability do not translate to an improvement in habitat quality. The loss of cover and corresponding increase in snow depth can offset these gains.

In this study we show how deer GUDs can be used to evaluate the effect of maintaining a power-line ROW in a deer yard. We use the GUDs to test two hypotheses — that ROW maintenance either (1) causes deer to increase their estimate of predation risk and (or) metabolic costs and (2) allows deer to increase their estimate of food available to them. The first hypothesis predicts that deer will leave higher GUDs where they are exposed to higher predation risk and metabolic costs (in the ROW). The second hypothesis predicts that higher GUDs will be found in habitats where food is more abundant and in years when regenerated vegetation is abundant in the ROW.

Study area

We studied the deer yard on Rigaud mountain, approximately 100 km west of Montréal, Quebec (45°26'N, 74°20'W), where browse rates on young plant growth are high (Brown and Doucet 1991; Doucet and Thompson 2002). The yard, about 25 km², had an estimated 285 animals in 1978 (Parent 1978). No recent population surveys have been conducted, but when snow conditions are severe deer often aggregate in eastern white cedar (*Thuja occiden-*

talis L.) stands. The forest habitat near the ROW is dominated by white cedar and includes deciduous and mixed stands interspersed with small islands of eastern hemlock (*Tsuga canadensis* (L.) Carr.) and balsam fir (*Abies balsamea* (L.) P. Mill.). Other species include hawthorn (genus *Crataegus* L.), staghorn sumac (*Rhus hirta* (L.) Sudworth), redosier dogwood (*Cornus sericea* subsp. *sericea*), quaking aspen (*Populus tremuloides* Michx.), eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.), balsam poplar (*Populus balsamifera* L.), American elm (*Ulmus americana* L.), ashes (genus *Fraxinus* L.), chokecherry (*Prunus virginiana* L.), black cherry (*Prunus serotina* Ehrh.), sugar maple (*Acer saccharum* L.), red maple (*Acer rubrum* L.), and willows (genus *Salix* L.). Deer are more active in white cedar stands, which provide excellent winter cover in the northeast, than other stands. We studied 1 km of a 30 m wide ROW through cedar stands on a gentle, south-facing slope in the southwest part of the yard.

There is little evidence of predation in the study area. Only two carcasses were seen during fieldwork; the cause of death is unknown. Tracks of wild dogs were seen in the yard, and previous studies mentioned the presence of coyotes, but none were seen during this study.

Methods

We measured GUDs in artificial depletable food patches in which food was mixed with nonedible substrate using a technique similar to that developed by Kotler et al. (1994) for ungulates. Kotler et al. (1994) argued that the relevance of measuring GUD in artificial food patches did not depend on the resemblance with natural food patches, but rather on how foragers respond to diminishing returns, and thus changes in the ratio of costs to benefits, as they exploit the artificial patch. While it is possible that several deer visited a given feeder on any given day, we suggest, following Brown (1988) and Kotler et al. (1994), that the resultant GUD represents the decision, based on the amount of food remaining, made by an average individual in the population (in fact, the last deer to visit the feeder).

In our experiments, artificial food patches consisted of plastic feeding boxes placed at sites in both the ROW and the adjacent cedar forest so as to separate the beneficial effects of browse regeneration from the detrimental effects of predation risk and metabolic costs. In each feeder, we placed fresh cedar collected in the yard (66 g dry mass measured in a graduated metal box), an attractive and very palatable food for deer in Rigaud (Laquerre 1997). To minimize our impact on deer energy budgets in this period of food shortage, we offered small quantities of food, approximately 8% of the daily requirement (Lamontagne and Potvin 1994). We built feeding boxes from plastic barrels (46 cm × 24 cm × 24 cm) cut in half. Cedar was mixed with nonedible substrate (5 cm long × 3 cm diameter PVC tubes) to increase foraging cost. Each afternoon leftover food was removed from feeders that deer had exploited (feeding occurred mostly at dusk) and feeders were replenished for the next day. Food left in the feeder was collected in plastic bags then dried (80 °C for 24 h) and weighed (± 0.001 g) as our measure of the GUD, expressed as grams/feeder, as feeders are of standard size and contain a standard quantity

of nonedible material (PVC tubes). We attributed the GUD of a feeder to the last individual that had visited the artificial food patch.

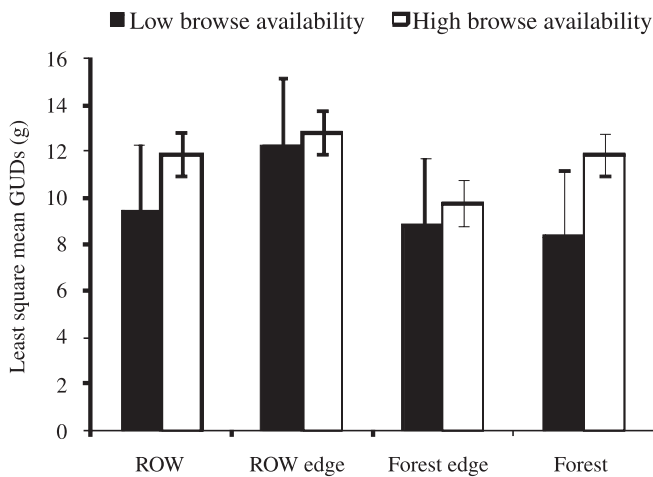
We used each of five perpendicular, replicate transects. Transects were distanced 30–60 m one from the other. This distance and the absence of trails between two adjacent transects in the ROW suggest that the five replicates are independent. We placed on each transect one feeder in the centre of the ROW, one at the edge of the ROW (within 1 m of cedar cover), one at the forest edge (within 1 m of the ROW), and one at least 15 m inside the forest so as to be at least as far from the forest edge as the feeder in the centre of the ROW. The forest feeder was always placed in a cedar grove often >15 m into the forest. We did not place the forest feeder >30 m from the forest edge, because at such distances it would have been ≤ 30 m from other habitat discontinuities (clearings or roads).

Data were collected in the winters of 1995 to 2003, generally from January to March when winter conditions were harshest for deer. No data were obtained in 1998 following an ice storm that resulted in the collapse and rebuilding of the 120 kV power line.

We compared deer foraging behaviour for years with and without regeneration within the ROW. The placement of our feeders allowed us to use planned contrasts to estimate the effects of increased browse and those of predation risk (and metabolic cost) independently. When there was no regeneration available in the ROW owing to maintenance cuts (1996, 1999, and 2003), costs (predation and metabolic combined) were estimated by comparing GUDs in the ROW (centre and edge) with those in the forest (edge and deeper). We assumed, based on estimates of browse available (see Appendix Table A1), that missed-feeding cost was the same (almost nil) in the forest and in the ROW and that it was also the same for the two edge habitats (because they were within 3 m of each other). Thus GUD differences between the ROW and the forest should be attributable to predation risk or metabolic costs but not to missed-feeding costs. This assumption also allowed us to estimate missed-feeding cost by comparing the two edge habitats (high missed-feeding cost) with the forest and the ROW (low missed-feeding cost).

When browse was available in the ROW (1995, 1997, 2000, 2001, 2002, and more than a year after maintenance cut), we had to use different contrasts because the assumptions above were no longer valid. We assessed the effect of predation risk and metabolic costs by comparing GUDs at the forest edge with those at the edge of the ROW (assuming missed-feeding costs are constant because the two feeders are within 3 m). We estimated missed-feeding costs by comparing GUDs in the forest with those at the forest edge (assuming equal predation risk and metabolic costs within the confines of the forest). We attempted to assure that the latter assumption was valid by placing all our forest feeders (edge and interior) in clumps of cedar, which protected deer from wind and from being seen by predators. In addition to these planned contrasts, we also tested the prediction that GUDs would be higher in years when regenerated vegetation was available in the ROW (1995, 1997, 2000, 2001, and 2002) than when it was not (1996, 1999, and 2003) because this increase in browse availability would increase missed-feeding costs at our feeders.

Fig. 1. Mean (\pm SE) giving-up density (GUD) of white-tailed deer (*Odocoileus virginianus*) exposed to low and high browse availability in the four habitat types studied in the Rigaud deer yard.



According to Brown's (1988) model, metabolic costs of foraging depend on climatic conditions such as snow depth, snow support capacity, and temperature. All these climatic variables were measured each day at every feeder. We measured snow accumulation using a graduated post sunk in the ground near each feeder. We dropped a graduated copper pipe weighing 1930 g (approximately the leg pressure on snow of a mature white-tailed deer; Hepburn 1978) from 20 cm above the snow to measure penetration. We used portable thermometers to record ambient temperatures at each feeder.

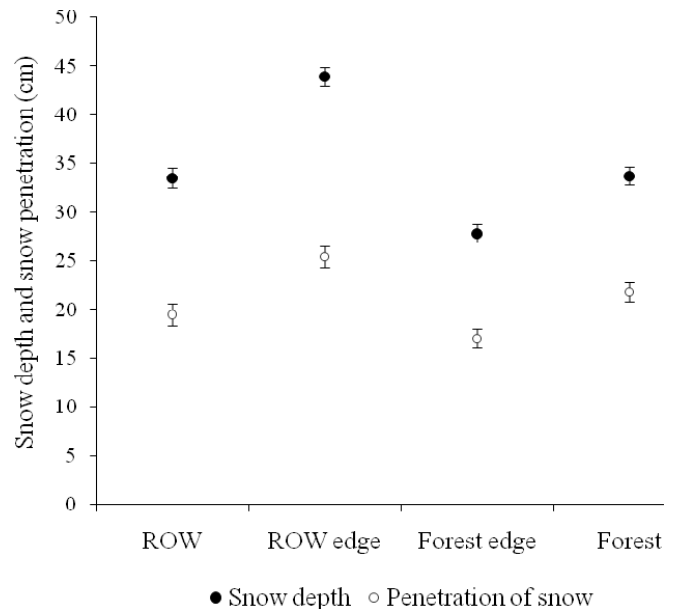
We estimated browse availability at each feeder during the winter of 2003 after snowmelt. All woody stems between 50 and 200 cm above ground level resulting from the previous summer's growth were counted in an area of 4 m \times 10 m along deer trails, with the artificial feeder as centre. This provided a measure of the deer missed-opportunity cost close to feeders in each habitat and also served to describe the four different habitat types under study. We counted all mature trees within 5 m of each feeder to provide a general description of the habitat.

We evaluated the effect of the ROW and factors that influenced GUDs using an analysis of covariance with separate slopes (from JMP[®] version 5; SAS Institute Inc. 2002) and planned contrasts separating predation and missed-opportunity costs. GUD values were considered the dependant variable, while stations (ROW, ROW edge, forest edge, and forest) and type of year (either just after a cut or more than a year later) were the independent variables and climatic conditions were covariates (snow depth, snow penetration, temperature). We compared browse availability among habitats using one-way analysis of variance followed by Tukey's tests. To compare the frequency of visits to feeders, we used χ^2 tests (Sherrer 1984).

Results

During the eight winters studied, deer visited our feeders a total of 1021 times, showing a significant preference ($\chi^2_{[3]} = 14.8$, $p = 0.002$) for feeders in sheltered habitats (on average, feeders were visited 28.4% of the days that they

Fig. 2. Snow depth (mean \pm SE) and penetration of snow (mean \pm SE) by white-tailed deer in the four habitats of the Rigaud deer yard.



were available at the forest edge and 26.4% of the days that they were available in the forest) over those in the open (ROW: 21.0%; ROW edge: 24.2%). Overall, GUDs differed ($F_{[3,992]} = 4.14$, $p = 0.006$, $n = 1010$) among the habitats sampled (Fig. 1). Differences in sample size occurred between the two tests because of some missing snow-penetration data in the first year of the study. We can relate this preference to differences in foraging costs and benefits by comparing GUDs among habitats using our planned contrasts. GUDs were greater in the ROW (middle and edge) than in the forest (edge and away from edge) in years when regeneration was absent ($F_{[1,446]} = 4.98$, $p = 0.02$) and greater at the ROW than at the forest edge when it was present ($F_{[1,539]} = 6.05$, $p = 0.01$). This suggests that the loss of shelter increased metabolic costs or predation risk (or both) and was detrimental for white-tailed deer foraging in the ROW in winter.

On the other hand, planned contrasts testing missed-opportunity (food-availability) costs showed no significant effect either when regenerated browse was available ($F_{[1,539]} = 3.64$, $p = 0.056$) (comparing forest edge with forest habitat) or when it was not ($F_{[1,446]} = 2.40$, $p = 0.12$) (comparing the two edge habitats with the ROW and the forest). Furthermore, mean GUD did not differ significantly between years with and without regeneration ($F_{[1,1010]} = 2.08$, $p = 0.14$) (Fig. 1).

In addition to these main effects, we also estimated the effect on deer feeding behaviour (GUDs) of other parameters (temperature and snow depth) that could vary among the four habitats. GUDs left by deer were higher when and where snow was deeper ($F_{[1,992]} = 75.05$, $p < 0.0001$, $n = 1010$). On average, snow depth was significantly ($F_{[3,5222]} = 156.5$, $p < 0.0001$, $n = 5226$) greater at the edge of the ROW (Fig. 2), which is where the highest GUDs were found (Fig. 1). During the study, snow depth rarely exceeded 50 cm in any year in the yard (Table 1). GUDs were higher ($F_{[1,992]} = 14.9$, $p < 0.0001$, $n = 1010$) when and where deer

Table 1. Mean snow depth in the right-of-way (ROW) and number of days with ≥ 50 cm depth during each winter studied.

	1996	1997	1999	2000	2001	2002	2003
Mean snow depth in the ROW (cm)	20.31	43.29	17.83	18.93	53.46	23.75	33.17
Number of days with snow depth ≥ 50 cm	0	25	0	5	73	0	9

would most likely have sunk deepest into the snow as measured by dropping the graduated copper pipe. Penetration was greatest ($F_{[3,4945]} = 47.5$, $p < 0.0001$, $n = 5226$) at the ROW edge and lowest at the forest edge. Temperature did not vary among habitats ($F_{[3,5141]} = 0.86$, $p = 0.46$, $n = 5141$) and did not affect GUDs ($F_{[1,992]} = 0.72$, $p = 0.38$, $n = 1010$).

Our measures of browse availability (new growth of the previous summer) support our premise that the forest produces less food than the edge habitats (see Appendix Table A1). The edge of the ROW and the edge of the forest provided large amounts of food both in 2000 and in 2003. Other studies show that winter browse in the ROW grew from 35 196 twigs/ha in 2000 (Doucet and Thompson 2000) to 41 601 twigs/ha in 2001 and 88 537 twigs/ha in 2002 (Doucet and Thompson 2002). Few twigs were available during winter 2003 in the ROW because of the maintenance cut in October 2002. These food levels suggest that missed-feeding costs were high in the two edge habitats and low in the forest and the ROW up to 2 years after being cut.

At the forest edge, deer browsed most of the twigs available ($>75\%$ for most species) compared with $<66\%$ for most species at the edge of the ROW. This suggests an important use and preference for forest-edge habitat close to protective cover during winter.

Discussion

The GUD technique provides useful information on free-ranging white-tailed deer foraging behaviour, which can be used to assess the effect of a power-line ROW in a deer yard. The use of GUDs allowed us to distinguish between the detrimental effects of predation risk and metabolic costs from the potential benefits of increased browse availability in a deer yard affected by a power-line ROW. Our analysis based on planned contrasts suggests that the ROW had a negative effect on winter deer foraging by increasing predation and (or) metabolic costs. We found no evidence that deer detected the increase in browse available in the ROW. Our approach does not allow us to clearly separate effects of predation risk and metabolic costs on deer foraging behaviour.

Through most of our study snow depth rarely exceeded 50 cm, the snow depth at which deer locomotion becomes significantly restricted (Parker et al. 1984), even in the ROW. Furthermore, deer established a series of trails across the ROW so that deer movement was not severely restricted most of the time. Nonetheless, deer left higher GUDs in the ROW where snow was deepest. This, plus the high correlation between GUDs and snow depth, suggests that predation risk could influence foraging behaviour. Where snow was deepest, escape from predators became more difficult and so deer would perceive a higher predation risk. It is interesting that deer established trails crossing the ROW, usually perpendicular to the forest edge. They rarely used the ROW

for long-distance movements. This suggests that deer estimate costs associated with the ROW not only while they forage but also during displacements. Several studies have shown a strong effect of escape-substrate composition on the predation costs of foraging (reducing manoeuvrability and (or) the speed of fleeing) for other species (Brown et al. 1992; Thorson et al. 1998). Among ungulates, Kotler et al. (1994) found that feeding-patch use by free-ranging Nubian ibex (*Capra ibex* L., 1758) is directly affected by predation risk. Ibex had greater GUDs at the riskier open sites than at the safer habitats even in the absence of mortality from predators.

We detected no effect of missed-feeding costs in our study. There was no evidence that food regeneration in the ROW increased habitat quality. Such effects were absent both in years when regeneration was available in the ROW and in years when it was absent. Planned contrasts failed to detect such an effect, with one nearly significant difference going in the opposite direction of that hypothesized. Furthermore, in years when regeneration was present, GUDs tended to be lower rather than higher (although the trend was not quite significant); the latter being the predicted result if additional food in the ROW had increased habitat quality.

A possible explanation is that regeneration in the ROW was of insufficient quantity or quality to affect deer foraging behaviour. Potential positive effects of browse production in the ROW are likely dampened because browse availability is kept low owing to two factors: a short vegetation control cycle and excessive browsing by deer (about 80%; Doucet and Thompson 2002). The former allows little time for plants to regenerate and the latter consumes most of the growth that does occur. Together they kept browse in the ROW well below levels recommended for deer-yard management (Germain et al. 1986).

Alternatively, deer may have estimated missed opportunity in the ROW on a larger scale so that the impact of browse regenerated in the ROW was felt equally in all habitats studied. Also, supplemental feeding by humans about 500 m from our study site may have influenced the missed-opportunity effect. However, our results showed no difference in GUDs between years with low and high browse availability. This suggests that regeneration in the ROW had no effect on the deer's estimate of available browse at whatever scale they were using for their estimate.

Our results show that deer feed differently at the forest edge than they do in the forest and in the ROW. They use feeders at the centre of the ROW less often than elsewhere. Preferential feeding at the forest edge has been noted elsewhere by Hershey and Legee (1976) and by Thomas et al. (1979). In our study, deer also leave more food (almost 25% more) in feeders at the edge of the ROW than they do just inside the forest <3 m away. This clearly shows that deer exploit the ROW resources less than those in the forest.

We argue that significant differences in feeding behaviour between habitats reflected differences in the deer's perception of habitat quality. Deer left more food in our artificial feeders at the edge of the ROW where snow was deep and protective cover was absent, suggesting that deer perceived greater feeding costs there. Feeding costs were least at the forest edge, likely owing to an effective vegetative cover that limited snow depth and visibility to predators. Deer visited fewer feeders located in the open area than those in the undisturbed forest and left more food in the ROW, suggesting that the latter is a lower quality habitat.

Management implications

The GUD approach provides valuable information on the impact of habitat modification by making inferences based on the foraging behaviour of free-ranging herbivores. The main results indicate that the ROW had a detrimental effect on deer by increasing perception of predation risk and (or) metabolic costs. We cannot quantify the impact this may have on deer abundance, but we can suggest that the impact will likely be negative. This may occur either because predation risk is higher in the ROW (or because deer must forgo eating a portion of the food available to them to avoid this risk) or because of the absence of protective cover against wind chill accelerating body heat loss (Schmitz 1991). In either case, detection of this effect on a small scale suggests that strategies should be developed to reduce foraging costs and to enhance food availability in the power-line ROW to minimize effects on population abundance.

We do not suggest that clearings in winter habitat always have a negative effect on deer. Our results show that edges created by ROWs are important (see also Hershey and Legee 1976; Thomas et al. 1979) because they create zones of plant regeneration near cover. Several studies have considered the potential of small openings to increase food availability (Drolet 1978; Lyon and Jensen 1980) when snow depth and ice crust did not restrict access.

In winter, if white-tailed deer are confined in deer yards for long periods, they can severely damage the quality of the yards unless they find an adequate source of food (Rooney and Waller 2003). Managers can use the GUD technique to evaluate animals' assessment of habitat quality and to infer their likely effect on plant communities (both food and shelter). Such studies can be used to search for management strategies that increase food availability without increasing predation risk or metabolic costs. This can be done at a small scale without having an appreciable effect on deer densities.

The planned contrasts approach is dependant on assumptions of equality of costs in different habitats. It requires that one aspect of the habitat quality (say food availability) differs among habitats, while all other aspects do not. Important issues for future work could be the development of a modelling tool to separate predation and metabolic costs from missed-feeding costs to avoid the assumptions above and the evaluation of missed-feeding costs at larger scales. Such studies could involve a site where humans do not offer supplemental food and where browse is allowed to regenerate longer in the ROW.

In conclusion, we believe that our illustration of the use of the GUD approach in habitat-alteration assessment in a

white-tailed deer yard underlines the effectiveness of such a tool. The GUD technique allowed us to evaluate the effects of a habitat disturbance without having to assess free-ranging animal abundance or capture animals, thus avoiding increased stress and possibly alteration of deer's perception of risk in their own environment.

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Appendix A (continued on next page)

Table A1. Browse availability and browse intensity of white-tailed deer (*Odocoileus virginianus*) in the Rigaud deer yard during winter 2003.

Location	Species	No. of stems available/5 transects of 4 m × 10 m	No. of browsed twigs/5 transects of 4 m × 10 m	No. of unbrowsed twigs/5 transects of 4 m × 10 m	Browse intensity (%)
ROW	<i>Salix discolor</i> Muhl.	4	5	3	62.5
	<i>Fraxinus americana</i> L.	3	8	2	80
	<i>Ulmus americanus</i>	3	5	5	50
	<i>Betula alleghaniensis</i> Britt.	1	1	0	100
	<i>Cornus sericea sericea</i>	1	2	12	14
ROW edge	<i>Fraxinus americana</i>	73	197	103	65.6
	<i>Betula alleghaniensis</i>	28	103	73	58.5
	<i>Acer saccharum</i>	19	45	29	60.8
	<i>Ulmus rubra</i> Muhl.	10	37	13	74
	<i>Rhamnus cathartica</i> L.	5	15	59	20
	<i>Tilia americana</i> L.	5	12	7	63.2
	<i>Populus tremuloides</i>	5	26	6	81.3
	<i>Salix discolor</i>	4	5	1	83.3
	<i>Prunus virginiana</i>	2	5	0	100
	<i>Crataegus</i> spp.	1	5	13	27.8
	Forest edge	<i>Fraxinus americana</i>	50	121	27
<i>Betula alleghaniensis</i>		26	148	40	78.7
<i>Populus tremuloides</i>		12	30	7	81
<i>Acer saccharum</i>		6	19	9	67.9
<i>Ulmus rubra</i>		4	9	12	42.9
<i>Juglans cinerea</i> L.		3	12	0	100
<i>Prunus virginiana</i>		2	2	0	100
<i>Rhamnus cathartica</i>		1	2	0	100
Forest	<i>Fraxinus americana</i>	11	29	6	82.9
	<i>Prunus virginiana</i>	5	26	7	78.9
	<i>Ulmus rubra</i>	1	1	4	20
	<i>Acer saccharum</i>	1	7	0	100
	<i>Crataegus</i> spp.	1	5	0	100
	<i>Carya cordiformis</i> (Wangenh.) K. Koch	1	2	0	100