



# Comparing habitat quality within and between environments using giving up densities: an example based on the winter habitat of white-tailed deer *Odocoileus virginianus*

William L. Vickery, Guillaume Rieucou and G. Jean Doucet

W. L. Vickery (*vickery.william@uqam.ca*) and G. Rieucou, *Dépt des sciences biologiques, Univ. du Québec à Montréal, CP 8888, Succ. "Centre-Ville", Montréal, QC, H3C 3P8, Canada. Present address for GR: Laboratoire Évolution et Diversité Biologique (EDB), UMR 5174 Centre National de la Recherche Scientifique (CNRS) – Univ. Paul Sabatier, 118 Route de Narbonne, FR–31062 Toulouse, France. – G. J. Doucet, TransÉnergie. 800 de Maisonneuve E. Montréal, QC, H2L 4M8, Canada.*

We previously developed a model, based on the precepts of optimal patch use, to compare habitat quality both within and between environments. Here we illustrate the use of this model in a study estimating quality of winter habitats (deer yards) of white-tailed deer *Odocoileus virginianus* near the northern limit of their range by following their foraging behaviour. We compare giving up densities (GUDs), the amount of food remaining in a patch when a forager ceases foraging there, with and without the presence of supplemental food in order to draw inferences about the relative quality either of habitats within an environment or of distinct environments. We use our model to evaluate the impact of alterations to the winter habitat of deer at two distinct sites that differed in their level of predation risk and food availability. The first site, the Mont Rigaud deer yard, was surrounded by farm land and gradually-expanding suburbs. Predators were rare and food was available in winter either in farm fields or around private homes but deer browsing in the past had left little food in the forest. At the second site, the Calumet deer yard, deer experienced a higher predation risk and did not have access to supplemental food from farm fields or private homes. However, past browsing by deer had not drastically reduced food in the forest. We offered food to deer in four habitats per site (forest, forest edge, clearing, clearing edge) with four to six replicates per site and measured the GUDs after 24 h. Analysis of these data, interpreted according to our model, suggests that deer are more sensitive to metabolic costs at Mont Rigaud and food availability at Calumet; predation risk does not alter deer behaviour between the two sites. Within habitats, deer at Mont Rigaud reacted to clearings as though they imposed higher metabolic costs than the forest. They also reacted to an interaction in which missed food costs influenced GUD only when metabolic costs were not too high. Thus our model appears to provide a convenient tool for comparing habitat quality both within and between environments.

Despite recent advances in the estimation of habitat quality (Goetz et al. 2010), many authors seem to have forgotten Van Horne's (1983) warning that species abundance is not necessarily a correlate of habitat quality. This is an important issue in conservation biology, wildlife management and studies of biodiversity. We cannot assume that because a species is abundant in a given habitat that the habitat is of high quality. Nor can we assert that vegetation associated with high abundance constitutes quality habitat. Here, we illustrate an approach to evaluating habitat quality based on an animal's behaviour in the habitat.

We (Rieucou et al. 2009) recently developed an optimal patch use model which allows us to infer differences in habitat quality, both within and between environments, based on foraging behaviour. The model compares giving up densities (GUDs), the amount of food which an animal leaves behind when it stops foraging in a food patch, among habitats. GUDs reflect an animal's perception of the cost of predation risk, missed feeding cost (a function of the amount

of food available) and metabolic costs in a habitat (Brown 1988). Our model deals with only one of Brown's (1988) possible missed opportunity costs, the missed feeding cost, because only the latter is manipulated in our field work. We assume that other missed opportunities do not vary as a result of our manipulations.

The costs of predation risk, missed feeding opportunities and metabolism are the major factors determining an animal's foraging success at a given place and time. Our model compares changes in the GUD which result from increasing missed feeding costs by adding food to a habitat. This comparison among habitats both with and without extra food allows us to separate the effects of food availability (and the resultant missed feeding cost) on habitat quality from the effects of metabolic and predation costs. Because abundant food increases the quality of a habitat whereas predation and metabolic foraging costs decrease its quality, it is necessary to separate their effects in order to use GUD data appropriately when comparing habitat quality. Here we follow Van

Horne's (1983) lead in using 'habitat quality' to mean the extent to which the habitat furnishes the resources and conditions which permit survival, growth and reproduction for a given species.

Previously, Olsson and Molokwu (2007) and Olsson et al. (2008) emphasised the difference between comparing GUDs within environments as opposed to comparing between them. The former predicted that predation cost should be the factor which varies most among habitats within an environment because missed feeding costs should be constant within an environment. On the other hand, they predict that missed feeding costs should have the greatest effect when comparing between environments because the cost of predation has inconsistent effects on GUDs. Here we test these predictions in two populations of white-tailed deer using our optimal patch use model (Rieucou et al. 2009).

Our model (Rieucou et al. 2009) is developed from Brown's (1992) prediction of an optimal quitting harvest rate  $f_i = \frac{\mu_i(F+1)}{\partial F/\partial e} + \frac{\Phi}{p \partial F/\partial e} + c_i$  where  $\mu_i$  is the instantaneous

predation risk while foraging in habitat  $i$ ,  $F$  is the expected number of descendants which will be produced given the amount of food consumed by following this strategy,  $\partial F/\partial e$  is the rate of increase in fitness per unit of food consumed,  $c_i$  is the metabolic cost of foraging in patch  $i$  and  $\Phi$  is the rate at which opportunities are lost while foraging in a given patch. We argue that this optimal quitting harvest rate will produce an optimal GUD =  $\left( \frac{\mu_i(F+1)}{\partial F/\partial e} + \frac{\Phi}{p \partial F/\partial e} + c_i \right) / a_i$

where  $a_i$  is the encounter rate with food at the quitting harvest rate in patch  $i$ . From this we show that when we increase missed feeding costs by adding an amount of food  $X$  at a second feeder, beside the first, the optimal GUD in the first feeder should rise by an amount

$$\Delta \text{GUD}_i = \frac{X}{a_i m p \partial F^x/\partial e} + \frac{\left( \frac{\partial F}{\partial e} - \frac{\partial F^x}{\partial e} \right)}{a_i \frac{\partial F}{\partial e} \frac{\partial F^x}{\partial e}} \left( \mu_i(F+1) + \frac{\Phi}{p} \right)$$

where the superscript  $X$  denotes conditions when the supplement is present and  $m$  is related to the animal's perception of food availability elsewhere in the habitat. If we assume that attack rates do not vary over levels of food in our patches we find that the only variable which does vary among patches is predation risk. This allows us to compare patches within an environment because it predicts that GUDs in the first feeder will rise most in patches where predation risk is highest.

To compare between environments we need to compare the GUD in the first feeder with that in the second. We suggest that animals will adjust their estimate of food supply (and thus of missed feeding cost) in the environment based on which feeder they are sampling at a given time. This should

produce a difference of  $\Gamma \text{GUD}_i = X \left( a_i - \frac{1-b}{m p \partial F^x/\partial e} \right)$

between the two feeders where  $b$  (between 0 and 1) expresses the relative importance of the rich feeder compared to the poor. High values of  $\Gamma \text{GUD}_i$  will occur when there is a large

difference in food availability between environments due to the factor  $m$ . If predation or metabolic cost causes differences between environments then we do not expect  $\Gamma \text{GUD}_i$  to vary between these environments.

For comparisons between environments which are sufficiently far apart that no given animal will use both environments within the study period, our model (Rieucou et al. 2009) predicts that when abundant food produces high GUDs then adding a richer food patch will produce a greater difference in GUDs between these adjacent patches than if high GUDs are caused by predation or metabolic costs. Thus, adding a rich food patch to both environments allows us to determine which environment is of higher quality (has high GUDs due to high food availability and not due to predation or metabolic costs).

For comparisons within environments, among habitats which a given animal may exploit during the study period, we compare GUDs at a given feeder in the presence versus the absence of a second feeder. Our model predicts that habitats subject to predation risk will produce the greatest increase in GUDs when food is added (Rieucou et al. 2009).

Rieucou et al. (2009) used data from a white-tailed deer *Odocoileus virginianus* winter habitat, deer yard, to illustrate the use of the model comparing only habitats within the same environment. To survive in northern conditions, deer confine their activity in deer yards offering both shelter (coniferous cover reducing snow accumulation and wind chill) and food (deciduous browse) (Dumont et al. 1998). Here we show how our model can compare habitats in two very different environments (deer yards) that differ in predation risk and food availability. At Mont Rigaud, the deer yard (described by Rieucou et al. 2007) is surrounded by farmland and human habitations. Winter after winter, the excessive exploitation of this site by deer has led to a dramatic decrease in the amount of food available. Indeed, almost every white cedar tree *Thuja occidentalis*, the main vegetative shelter in the deer yard, has been browsed to the maximum height a deer can reach, leaving little food available in the forest. However, when snow does not restrict their movement, deer can forage in neighbouring farm fields or access feeders offered throughout the winter by people living near the deer yard. Also, there is little evidence of predators at Mont Rigaud. The Calumet site (described by Rieucou et al. 2009) is embedded in a larger forest with only a few farms and no supplemental feeding nearby. However, in the Calumet deer yard, cedars have not all been browsed the way they were at Mont Rigaud. Moreover, predator tracks (coyote and lynx) were often sighted in the Calumet deer yard. Both deer yards are crossed by a transmission line right-of-way (ROW) in which vegetation was regularly cut to avoid any interference with the electrical lines resulting, thus, in a loss of the protective cover. The Calumet site contained a 60 m wide cleared 315 kV ROW oriented east-west whereas the Mont Rigaud 120 kV ROW was only 30 m wide and oriented north-south.

The first objective of this study was to use our behavioural model to compare habitat quality between the two sites. If predation risk is higher at Calumet we expected GUDs to be higher in a lone feeder there with little difference between the GUD in a lone feeder and a supplemental feeder beside it. On the other hand, if food availability differs between

Table 1. Synopsis of the predictions to be tested. On each line of the table, the Cause indicates the hypothesis being tested and the two effects are the results which will confirm the hypothesis.

(a) Comparison between environments (Mont Rigaud vs Calumet)		
Cause	Effect on a lone feeder	Effect when a supplement is present
Greater predation risk at Calumet	Higher GUD at Calumet	No detectable change
More food at Mont Rigaud	Higher GUD at Mont Rigaud	Greater increase in GUD at Mont Rigaud
More food at Calumet	Higher GUD at Calumet	Greater increase in GUD at Calumet
(b) Comparison between habitats within Mont Rigaud		
Cause	Effect on a lone feeder	Effect when a supplement is present
Greater predation in the ROW	Higher GUD in the ROW	Greater increase in GUD in the ROW
Greater metabolic costs in the ROW	Higher GUD in the ROW	Same increase in GUD in all habitats

the sites (either more food in the forest at Calumet or more food in surrounding areas at Mont Rigaud) then we expected a higher GUD at the site with the most food and a greater difference between the lone and supplemental feeder at that site.

A second objective was to compare habitats within the Mont Rigaud site in order to test the hypothesis that foraging in the ROW imposes higher predation or metabolic costs on deer than foraging in the forest as found at Calumet by Rieucou et al. (2009). Specifically, we expected GUDs to be higher in the ROW than in the forest and food addition to increase GUDs more in the ROW than in the forest if deer are reacting to predation risk; GUDs would increase by the same amount in both habitats if deer were reacting to metabolic costs. Table 1 provides a synopsis of our predictions.

## Methods

We conducted our study over two winters (2005 at Calumet 45°40'N, 74°40'W; 2006 at Mont Rigaud 45°26'N, 74°20'W) at sites where deer aggregated during the winter. A major river (the Ottawa) and 37 km separate the two sites. Coniferous forest, dominated by white cedar at Mont Rigaud and by cedar and eastern hemlock *Tsuga canadensis* at Calumet, covered both sites. Each site was traversed by a ROW which served as the focal point of our sampling. We established six sampling transects at each site. Each transect had one feeder in the forest habitat, one in the forest at the edge of the ROW, one in the ROW at the edge of the forest and one in the middle of the ROW. This design allowed us to evaluate the effects of the ROW on habitat quality within

each site (Rieucou et al. 2007, 2009). Using the same design at the two sites also allowed us to compare between them.

Each feeder consisted of half a plastic barrel (46 × 24 × 24 cm). Initially, we placed about 66 g (DW) of freshly cut white cedar leaves and 32 PVC plastic tubes (each 5 cm long by 3 cm diameter) weighing about 700 g in each feeder. The cedar is an attractive food for deer (Rieucou et al. 2007). By placing the PVC tubes in each feeder, we insured that deer had a significant cost of searching for food while foraging and almost always left some cedar (a GUD) behind. During a second phase of testing we added a second feeder of the same dimensions as the first at each site on half the transects. This second feeder contained twice as much cedar as the first and the same number of PVC tubes. During a third testing phase the extra feeders were moved to the other half of the transects and so on (see dates for each phase at each site in Table 2).

We filled feeders daily in the afternoon and returned the following afternoon to remove the remaining food from each feeder. The latter was dried at 80°C for 24 h and weighed to a precision of ± 0.001 g. This provided the GUD for a given station on a given day. Even though the population density of deer at each deer yard was unknown during our experiment, we expected that the feeders were visited and exploited by different individuals on a given day and the individual which visited a given feeder probably differed from day to day through the experimental period. We thus avoided the problem of pseudo-replication that could arise if the same individual exploited a feeder repeatedly.

As deer movements are mostly restricted by snow, we measured snow depth (on a graduated post driven into

Table 2. Dates on which the various treatments were implemented at the two sites over two winters.

Location	Phase	Transects receiving only 66 g of cedar	Transects receiving an additional 132 g of cedar	Initial date	Final date
Calumet	1	all	None	25-01-2005	08-02-2005
Calumet	2	4.5.6	1.2.3	13-02-2005	28-02-2005
Calumet	3	1.2.3	4.5.6	05-03-2005	23-03-2005
Calumet	4	4.5.6	1.2.3	31-03-2005	05-04-2005
Rigaud Mountain	1	all	None	24-01-2006	07-02-2006
Rigaud Mountain	2	1.2.6	3.4.5	08-02-2006	22-02-2006
Rigaud Mountain	3	3.4.5	1.2.6	23-02-2006	19-03-2006
Rigaud Mountain	4	all	None	20-03-2006	22-03-2006

the ground) and snow penetrability by dropping a 1930 g graduated copper pipe representing approximately the leg pressure of a mature deer weight from the snow surface (Hepburn 1978). We also measured ambient temperature using a portable thermometer at each feeding site.

We analysed our data in three stages. First we compared GUDs observed when no supplemental food was available using a linear mixed model in which the main factor was the study site (comparing Calumet with Mont Rigaud). In our model, transect and habitat (forest, forest edge, ROW edge and ROW) were nested within site and were treated as random effects because feeders were placed at the same location every day. Temperature, snow depth and penetration were included as fixed effects. GUDs were log transformed in all analyses in order improve the homoscedasticity and normality of the residuals in our analyses. The model which best described the GUD data was chosen using Akaike's information criterion (AIC) (Akaike 1974, Burnhan and Anderson 2002). The second stage of the analysis involved comparisons of the difference between the GUD in the supplemental feeder (offering 132 g of cedar) and the original feeder (offering 66 g) beside it. Categories, nesting, random and fixed effects, and analyses were the same as the first stage. Finally, we compared GUDs among habitats within the Mont Rigaud site. We also used a linear mixed model for comparing the GUD at the original feeder in the presence versus the absence of the supplementary feeder, as proposed by Rieucau et al. (2009), using the same variables and procedure which were used for the between site comparison. All statistical analyses were performed using R software (ver. 2.7.1; R Development Core Team 2006) and the lme4 package for linear mixed models.

## Results

### Between-site results

The GUDs at a lone feeder at Calumet as compared to Mont Rigaud were best described by a model which contained only transect and temperature (Table 3). GUDs varied among transects (nested within sites) (Fig. 1) and GUDs were higher when the temperature was colder. The AIC value of the best adequate model was substantially better than that of any model containing site as a factor, suggesting that GUDs did not differ between Calumet and Mont Rigaud.

When two feeders were present (one with twice as much food as the other), the difference in GUDs between the two feeders was best described by a model containing site and temperature (Table 3). The difference between the two feeders was greater at Calumet than at Mont Rigaud and when temperatures were warmer.

### Within-site results

At Mont Rigaud the best prediction of the GUDs in the initial feeder came from a model which contained all factors except habitat (and their interactions with the presence or absence of a supplementary feeder) (Table 4). A second model, including all the factors in the first plus habitat (but not the habitat interaction term) was almost as good as the

Table 3. Akaike criteria for the linear mixed models which best predict the GUD (log transformed) of a lone feeder and the difference between GUDs (both log transformed) at adjacent feeders. Si = site (Calumet in 2005 vs Mont Rigaud in 2006); H = habitat (a random effect); tr = transect (a random effect); Sn = snow depth; P = snow penetrability; and T = ambient temperature. All other models have larger AIC values (> 620 for the GUD and > 670.85 for the difference between GUDs).

Model	GUD		Difference between GUDs		
	DF	AIC	Model	DF	AIC
tr+T	4	614.57	Si+T	4	667.34
tr+P+T	5	616.55	Si	3	668.92
H+tr+T	5	616.57	T	3	668.93
Si+tr+T	5	616.61	Si+Sn	4	669.18
tr+Sn+P+T	6	618.51	Si+Sn+T	5	669.34
H+tr+Sn+T	6	618.55	tr+T	4	669.82
H+tr+P+T	6	618.55	Sn+T	4	670.30
Si+tr+P+T	6	618.57	Si+P	4	670.67
Si+tr+Sn+T	6	618.61	Si+tr+Sn+P	6	670.67
Si+H+tr+T	6	618.61	P+T	4	670.82

best model (Table 4). Figure 2 shows that GUDs were higher in the ROW than in the forest but this difference did not change when a supplementary feeder was added.

We found that GUDs increased when the supplementary feeder was present (Fig. 2). For each of the interaction terms, the condition which produced the highest GUDs with a lone feeder produced the smallest increase in GUD when the supplementary feeder was added. This is the opposite of what is predicted if predation is causing the difference in GUDs. For instance, GUDs decrease as penetration into the snow increases. However, when the supplementary feeder is present the biggest change in GUD occurs when snow penetration is greatest (where the GUD was smallest without the supplement).

## Discussion

Our results suggest that deer have more food available at Calumet than at Mont Rigaud because the difference in GUDs between adjacent feeders is greater at Calumet. That

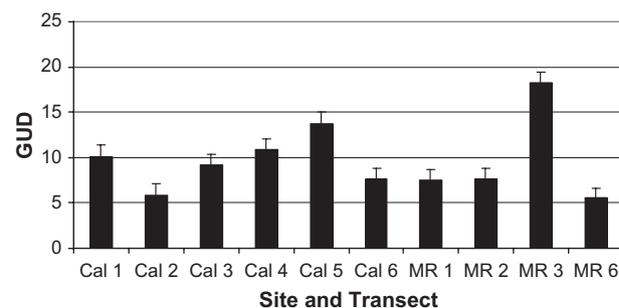


Figure 1. Mean GUD (g) as a function of site and transect based on days when no supplemental food was available. Error bars represent 1 SE. Means were calculated from logged GUDs and then back-transformed. (Cali means the ith transect at Calumet and MRI means the ith transect at Mont Rigaud)

Table 4. Akaike criteria for the best linear mixed models predicting the GUD (log transformed) of a lone feeder with and without an adjacent feeder at Mont Rigaud. Sf = Supplementary food (present or absent); H = habitat (a random effect); tr = transect (a random effect); Sn = snow depth; P = snow penetrability; and T = ambient temperature. (All other models have an AIC value >1050).

Model	DF	AIC
Sf+tr+Sn+P+T+Sf×tr+Sf×Sn+Sf×P+Sf×T	11	1045.1
Sf+H+tr+Sn+P+T+Sf×tr+Sf×Sn+Sf×P+Sf×T	12	1045.4
Sf+H+tr+Sn+P+T+Sf×H+Sf×tr+Sf×Sn+Sf×P+Sf×T	13	1047.4
Sf+H+tr+Sn+P+T	11	1047.4
Sf+H+Sn+P+T+Sf×H+Sf×Sn+Sf×P+Sf×T	11	1048.0
Sf+tr+Sn+P+T+Sf×Sn+Sf×P+Sf×T	11	1048.0
Sf+tr+Sn+P+T+Sf×tr+Sf×Sn+Sf×P	10	1048.4
Sf+H+tr+Sn+P+T+Sf×H+Sf×Sn+Sf×P+Sf×T	12	1048.4
Sf+Sn+P+T+Sf×Sn+Sf×P+Sf×T	11	1049.0
Sf+tr+Sn+P+Sf×tr+Sf×Sn+Sf×P	11	1049.0

we detected this difference but did not detect a difference between the two sites when only one feeder was present suggests that a second factor (either higher predation risk or greater metabolic cost at Mont Rigaud) also affected the GUDs. Predator activity at Calumet was higher than at Mont Rigaud so it is unlikely that higher predation risk at Mont Rigaud balanced out the effect of less food there. It is more likely that metabolic costs differed between the sites and affected deer foraging behaviour. In fact our temperature data show that Mont Rigaud in 2006 was 1.2° colder than Calumet in 2005.

Our analysis shows that deer are sensitive to temperature as this factor was included in the best models for predicting both GUDs between sites and GUDs between adjacent feeders between sites. GUDs were always higher in colder weather as predicted by Brown's (1988) GUD model. However the difference between adjacent feeders was smallest in cold weather (near -10°C in our study); increasing in warmer weather (approaching +20°C). This suggests an interaction

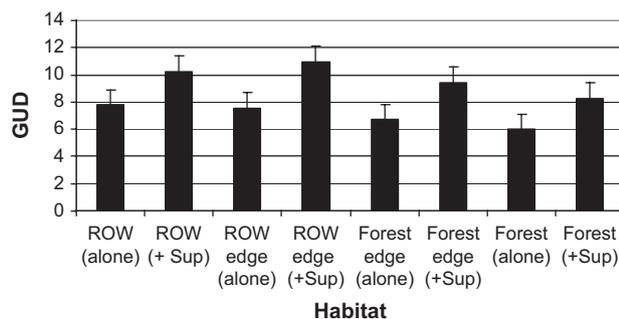


Figure 2. Mean GUD (g) as a function of habitat and the presence or absence of supplementary food. Error bars represent one standard error. Means were calculated from logged GUDs and then back-transformed. (Error bars represent 1 SE). + indicates the presence of a supplementary feeder.

between metabolic costs and missed feeding costs. Deer seem to consider alternate food to be important when the weather is warm but in cold weather they opt to stop foraging regardless of the amount of alternate food available.

The inference that deer estimate that there is more alternate food in Calumet than in Mont Rigaud probably reflects the fact that the latter deer yard has been heavily browsed for many years leaving little to eat in the forest. In Mont Rigaud, deer were often seen feeding in farm fields and near houses. In Calumet deer only browsed vegetation available directly in the forest. It appears that deer consider food in the forest to be of greater importance than supplementary food in surrounding areas.

The difference among transects in the between-site analysis was likely not due to food availability (missed foraging costs) because we found that the difference between GUDs at adjacent feeders did not vary among transects. This supports one of the assumptions of our within-site model (Rieucan et al. 2009) that missed feeding costs do not vary within sites.

In the within-site analysis at Mont Rigaud, there were two candidates of almost equal value for best model. The candidate models differed in that one included habitat (but not its interaction with supplementary food). Otherwise their structures were identical, including all factors and their interactions with supplementary food. We interpret this to mean that GUDs did vary among habitats but the food supplementation had the same effect in all habitats (Fig. 2). This suggests that predation risk was not the cause of the differences among habitats. As we assume that missed feeding cost is uniform within any site (and this is supported by our between-site analysis), we conclude that metabolic costs are higher in the cleared right-of-way than they are within the forest. We previously showed this pattern at Calumet (Rieucan et al. 2009). Exposure to wind in the ROW and not the forest or radiative heat loss to the sky (Schmitz 1991) after sunset (greater in the ROW than the forest) may have produced this effect.

The addition of a second feeder with twice as much food as the first caused GUDs to increase (Fig. 2) in all habitats. This reaction has been described previously by Olsson and Holmgren (1999), Stenberg and Persson (2006), Olsson and Molokwu (2007) and, at Calumet, by Rieucan et al. (2009). That the increase was even across habitats suggests that predation risk does not vary among habitats, contrary to the findings of Altendorf et al. (2001) for mule deer *Odocoileus hemionus* and Hochman and Kotler (2007) for Nubian ibex *Capra ibex*.

At Mont Rigaud, transect, snow depth, snow penetrability and ambient temperature all affected the GUDs and the extent to which supplemental food increased the GUDs. In every case, the condition which produced the highest GUDs also produced the lowest increase in GUD when the supplementary feeder was added. This is exactly the opposite of the prediction we would make if predation cost is affecting the GUDs. Thus, we conclude that deer are not adjusting their foraging decisions among habitats, snow depths, penetration or temperature as a function of predation. This is not surprising as we did not see any sign of predators at this site. We suspect that these interactions involve a tradeoff between metabolic costs and missed feeding costs. These

conditions change through the winter as temperatures rise from late January through March and snow depth decreases in late winter after having increased earlier on. Moreover, we detected a pattern in which additional food has little effect when conditions are difficult (cold weather, deep snow, and the transect with the highest GUD) but has a clear effect when weather is warmer, when snow is not so deep and on transects where the initial GUD is lower.

Analyses of the Mont Rigaud data agree well with Rieucan et al.'s (2009) previous results for the Calumet deer yard. At both sites, deer leave more food at feeders in rights-of-way than in the forest and their reaction to a food supplement implies, under the assumptions of our model, that this difference is mostly due to the higher metabolic cost of foraging in the right-of-way rather than predation costs.

Olsson and Molokwu's (2007) model predicts that missed feeding cost should be the principle difference between two environments. Our analysis also allows us to infer that deer probably react to an interaction between differences in metabolic and missed feeding costs. Within the Mont Rigaud site, we did not find differences due to predation, but rather infer that the metabolic costs imposed by foraging in the open habitat produce higher GUDs. While Brown's (1988) initial description of GUDs does show that they are susceptible to metabolic costs, little attention has been paid to them lately. Our results suggest that this oversight needs to be corrected.

In this study we have used our data from two distinct deer yards to illustrate our method for comparing habitat quality both within and between sites. If we accept the inferences drawn from our model, it is clear that the existence of a ROW through a deer yard has a negative impact on deers' perception of habitat quality. While this study does not test the validity of the model, we argue that most approaches to measuring habitat quality remain untested because they assume that high population density is a sign of good habitat. But this assumption is not necessarily true (Van Horne 1983). Tests of habitat quality estimates will require studies which compare these estimates with measures of fitness (or proxies such as reproductive success – Olsson et al. (1999), Morris and Davidson (2000)) in each habitat. An isodar approach (Morris 1987) might be appropriate. Such studies will be difficult with large animals like deer; smaller organisms with shorter generation time may be more appropriate for such tests. Once tested, behaviour-based estimates such as ours can be used to validate the assumptions of methods based on population abundance or vegetation structure associated with population abundance.

*Acknowledgements* – This study was supported by TransÉnergie, Hydro-Québec and by the Natural Sciences and Engineering Research Council of Canada. GR is also financially supported by a Fyssen Foundation Postdoctoral Fellowship. We thank Serge Gagnon for his enthusiastic field assistance. We thank Auberge des Gallant for giving us access to their land.

## References

- Akaike, H. 1974. A new look at statistical model identification. – IEEE Trans. Automat. Contr. 19: 716–23.
- Altendorf, K. B. et al. 2001. Assessing effects of predation risk on foraging behaviour of mule deer. – J. Mammal. 82: 430–439.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation use and competition. – Behav. Ecol. Sociobiol. 22: 37–47.
- Brown, J. S. 1992. Patch use under predation risk. 1. Models and predictions. – Ann. Zool. Fenn. 29: 301–309.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd ed. – Springer.
- Dumont, A. et al. 1998. Caractéristiques des peuplements forestiers recherchés par le cerf de Virginie en hiver à la limite nord de son aire de répartition. – Can. J. Zool. 76: 1024–1036.
- Goetz, S. J. et al. 2010. Lidar remote sensing variables predict breeding habitat of a Neotropical migrant bird. – Ecology 91: 1569–1576.
- Hepburn, R. L. 1978. A snow penetration gauge for studies of white-tailed deer and other northern mammals. – J. Wildlife Manage. 42: 663–667.
- Hochman, V. and Kotler, B. P. 2007. Patch use, apprehension, and vigilance behaviour of Nubian ibex under perceived predation risk. – Behav. Ecol. 18: 368–374.
- Morris, D. W. 1987. Spatial scale and the cost of density-dependent habitat selection. – Evol. Ecol. 1: 379–388.
- Morris, D. W. and Davidson, D. L. 2000. Optimally foraging mice match patch use with habitat differences in fitness. – Ecology 81: 2061–2066.
- Olsson, O. and Holmgren, N. M. A. 1999. Gaining ecological information about Bayesian foragers through their behaviour. I. Models with predictions. – Oikos 87: 251–263.
- Olsson, O. and Molokwu, M. N. 2007. On the missed opportunity cost, GUD, and estimating environmental quality. – Isr. J. Ecol. Evol. 53: 263–278.
- Olsson, O. et al. 1999. Gaining ecological information about Bayesian foragers through their behaviour. II. A field test with woodpeckers. – Oikos 87: 264–276.
- Olsson, O. et al. 2008. A guide to central place effects in foraging. – J. Popul. Biol. 74: 22–33.
- Rieucan, G. et al. 2007. An innovative use of white-tailed deer (*Odocoileus virginianus*) foraging behaviour in impact studies. – Can. J. Zool. 85: 839–846.
- Rieucan, G. et al. 2009. A patch use model to separate effects of foraging costs on giving-up-densities: an experiment with white-tailed deer (*Odocoileus virginianus*). – Behav. Ecol. Sociobiol. 63: 891–897.
- Schmitz, O. J. 1991. Thermal constraints and optimization of winter feeding and habitat choice in white-tailed deer. – Ecology 72: 104–111.
- Stenberg, M. and Persson, A. 2006. Patch use behaviour in benthic fish depends on their long-term growth prospects. – Oikos 112: 332–341.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. – J. Wildlife Manage. 47: 893–901.