

A patch use model to separate effects of foraging costs on giving-up densities: an experiment with white-tailed deer (*Odocoileus virginianus*)

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Abstract The giving-up density of food (GUD), the amount of food remaining in a patch when a forager ceases foraging there, can be used to compare the costs of foraging in different food patches. But, to draw inferences from GUDs, specific effects of foraging costs (predation risk, metabolic and missed opportunities costs) on GUDs have to be identified. As high predation risk, high metabolic costs and abundant food all should produce high GUDs, this does not allow us to infer directly the quality of a habitat. In order to separate the effect of each foraging cost, we developed an optimal foraging model based on food supplementation. We illustrate the use of our model in a study where we assessed the impact of a power line right-of-way in a white-tailed deer (*Odocoileus virginianus*) winter yard by determining whether the negative effects of cover loss outweigh the positive effects of browse regeneration.

Keywords Giving-up densities · Patch use model · Food supplementation · Optimal foraging · White-tailed deer · *Odocoileus virginianus*

Animals must regularly choose between habitats that differ in their overall quality in terms of foraging benefits and predation risk (Lima and Dill 1990). Optimal foraging theory assumes that animals make decisions that maximise their food intake based on expected gains and costs of foraging within a particular food patch (Stephens and Krebs 1986). According to Brown's optimal patch use model (1988), a forager should leave a patch when the benefits, through the harvest rate of food, no longer exceed the costs of foraging in the patch: the sum of predation risk, metabolic and missed opportunities costs. The rate of food consumption at which a forager leaves a patch, defined as the quitting harvest rate (Brown 1988), provides a quantitative measure of the forager's evaluation of costs of remaining in the food patch. The amount of food remaining in a patch when a forager ceases foraging there, defined by Brown (1988) as the giving-up density of food (GUD), is often used to compare the relative costs of foraging in different food patches (Shochat et al. 2004). But, to draw more complete inferences from information provided by GUDs, specific effects of each foraging cost.

In order to separate the effects of predation risk, metabolic and missed opportunity costs, we develop an optimal foraging model based on changes in animals' feeding behaviour, specifically, GUDs, due to food supplementation in different habitats. The challenging aspect resides in the fact that high predation risk, high metabolic costs and abundant food (the latter through missed feeding costs defined as the costs of not feeding elsewhere) all should produce high GUDs (Brown 1992; Murden and Risenhoover 1993; Kotler et al. 1994, 2004; Jacob and Brown 2000). Thus, a high GUD alone does not allow us to infer that a habitat is of high quality because of the high amount of resource available or of low quality because of high predation risk or metabolic costs. A further problem is

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that comparisons within environments may differ from between environments (Olsson and Molokwu 2007) because missed feeding costs are expected to be constant within environments but vary between them. Our model allows us to tease apart the effects of the three critical habitat characteristics in order to make comparisons either within or between environments. Here, we use Olsson and Molokwu's (2007) definition of environment as a habitat or series of habitats used by a given individual. Habitats which are not used by the same individuals are considered in different environments.

The patch use model

We start with Brown's (1992) model for fitness gains while foraging in a patch. The model supposes that an animal gains fitness by foraging but also incurs losses due to metabolic and missed opportunity costs. The animal also risks being the victim of predation while it forages. Brown (1992) suggests that animals which must survive and accumulate resources in order to reproduce at a later date should allocate their time toward feeding in available food patches so as to maximise the quantity $p(F+1)$ subject to the constraint that there is a limited amount of time available for foraging. Here, p is the probability of surviving when using a given foraging strategy (allocation of time among patches) and F is the expected number of descendents given the amount of food which will be consumed using this strategy. Brown (1992) uses the Lagrange function $L = p(F+1) + \Phi(T - \sum t_i)$ to find the optimal allocation of time to a given patch i , where T is the total time available, t_i is the time allocated to food patch i and Φ is the rate at which opportunities are lost while foraging in a given patch. He differentiates this expression with respect to t_i , sets the differential equal to zero, substitutes $\partial p / \partial t_i = -\mu_i p$ and $\partial e / \partial t_i = f_i - c_i$, and solves for f_i , the harvest rate at which the animal should leave patch i . His solution is:

$$f_i = \frac{\mu_i(F+1)}{\partial F / \partial e} + \frac{\Phi}{p \partial F / \partial e} + c_i \quad (1)$$

where $\partial F / \partial e$ is the rate of increase in fitness per unit of food consumed and μ_i is the instantaneous risk of predation while foraging in habitat i .

Here, we propose that the density of food left in a patch when a forager leaves at a quitting harvest rate of f_i is given by $\text{GUD}_i = f_i / a_i$ where a_i is the encounter rate with food at the quitting harvest rate in patch i . Thus, the GUD in patch i will be

$$\text{GUD}_i = \left(\frac{\mu_i(F+1)}{\partial F / \partial e} + \frac{\Phi}{p \partial F / \partial e} + c_i \right) / a_i \quad (2)$$

Now we attempt to separate the effects of predation cost from other costs by adding food to the habitat. Suppose that we add a quantity X of food by adding an additional feeder to a number of food patches in a given habitat. This food supplement will not alter the food intake rate or the predation risk in the food patch which has not received the supplement, but it will increase the missed opportunity costs there by a quantity X/m where m is proportional to the total number of patches in the habitat and inversely proportional to the number of patches which received a supplement and the rate of consumption per unit of food present. It will also decrease the rate of conversion of energy to reproductive success, $\delta F / \delta e$, to a new value of $\delta F^x / \delta e$. We follow the lead of Olsson and Molokwu (2007) among others, in assuming that feeding is the only important missed cost for which our time constraint must account. Now, the GUD for a patch when a supplemental feeder is present will become:

$$\text{GUD}_i^x = f_i / a_i = \left(\frac{\mu_i(F+1)}{\partial F^x / \partial e} + \frac{\Phi + X/m}{p \partial F^x / \partial e} + c_i \right) / a_i \quad (3)$$

From Eqs. 2 and 3, we see that food supplementation increases the GUD by an amount:

$$\begin{aligned} \Delta \text{GUD}_i &= \text{GUD}_i^x - \text{GUD}_i \\ &= \frac{X}{a_i m p \partial F^x / \partial e} + \frac{(\delta F / \delta e - \delta F^x / \delta e)}{a_i \delta F / \delta e \delta F^x / \delta e} \\ &\quad \times \left(\mu_i(F+1) + \frac{\Phi}{p} \right). \end{aligned} \quad (4)$$

Only two factors in Eq. 4 vary among patches within a habitat, μ_i and a_i . If we assume that a_i is constant over the food levels available in our patches, then variation in ΔGUD within habitats should represent only variation in predation risk μ_i ; the greater the predation risk, the higher ΔGUD will be. However, when comparing ΔGUD s between habitats, the situation is not so clear as low survival probabilities (p) and abundant food (high ϕ and low m) will both produce large ΔGUD s.

In this latter case, it is more appropriate to compare the GUD (GUD^S) in the supplemental feeder with the GUD in the initial feeder which was placed beside it. Thus, we have two measures (GUD^S and GUD^X) in the same habitat at the same time. These two GUDs will be subjected to the same predation risk (μ_i) and the same metabolic costs. However, they will differ in their missed feeding costs and in feeding rates. Missed feeding costs will be lower in the supplemental feeder than in the initial one because alternate food in the habitat consists of all natural food sources (and possibly other supplements) plus the initial feeder, which has less food in it than the supplemental feeder. We express this as

$\Phi + bX/m$ where $0 < b < 1$. Feeding rate in the supplemental feeder will be higher than in the original feeder because the former contains more food. In fact, we can express this as $\partial e / \partial f_i = f_i + a_i X - c_i$. Thus, the GUD in the supplemental feeder will be

$$\text{GUD}_i^S = \left(\frac{\mu_i(F+1)}{\partial F^x / \partial e} + a_i X + \frac{\Phi + bX/m}{p \partial F^x / \partial e} + c_i \right) / a_i \quad (5)$$

Taking the difference between Eqs. 5 and 3, we obtain

$$\Gamma \text{GUD}_i = \text{GUD}_i^S - \text{GUD}_i^X = X \left(a_i - \frac{1-b}{mp \partial F^x / \partial e} \right). \quad (6)$$

This measure should not vary within habitats but is appropriate for comparing between habitats. High survival rate (low predation risk) will produce small values of ΓGUD while abundant food (high values of m) will produce high values of ΓGUD .

Now we can use Eqs. 4 and 6 to draw inferences about habitat quality from GUD data. Within habitats, when patch A has a higher GUD than patch B, we can infer that the difference is due to predation risk if habitat A has a higher value of ΔGUD . However, if the patch with the highest GUD does not have the highest ΔGUD , then metabolic costs must be the cause of the higher GUD. Comparing between habitats, if the habitat with the highest GUD also has the highest ΓGUD , then food abundance is the cause of the high GUD. If not, then either predation risk or metabolic cost is responsible, suggesting that the habitat is of low quality.

ΔGUD and ΓGUD can also generate inferences when the initial GUD value does not differ. If ΔGUD is higher in patch A than in patch B within a habitat, we can infer that patch A has higher predation risk than patch B while the latter has higher metabolic costs (missed opportunity costs being equal across patches within habitats). If GUDs are equal between habitats but ΓGUD differs, then we infer that the habitat with the highest ΓGUD has the highest missed opportunity cost (and is thus the best quality) while that with the lowest ΓGUD is of lowest quality because of predation risk. While we expect that risky habitats will often provide more food than safe habitats because foragers will leave more food in risky habitats (Brown 1992), it is useful to develop a technique which can separate the effects of predation risk and food abundance.

Applying the patch use model

We illustrate the use of this approach in a study of white-tailed deer (*Odocoileus virginianus*) winter habitat. Rieucou et al. (2007) recently used white-tailed deer habitat to

develop another approach to estimating habitat quality using animals' foraging behaviour. That study, based on statistical use of a priori contrasts, showed negative impacts of maintaining an opening in a cedar-dominated forest, but it did not identify the causal factor involved. Further, it was unclear whether that approach could evaluate deer's estimate of food abundance over a sufficiently small spatial scale.

On the northern limit of their range, white-tailed deer congregate in habitats, called deer yards, to cope with inclement weather during winter (Dumont et al. 1998; Sabine et al. 2001). Deer often confine their activity to such habitats through much of the winter (Gaston et al. 1990). Generally in deer yards, coniferous species limit the amount of snow which reaches the ground, thus reducing snow depth and facilitating deer escape from predators. However, extensive browsing by deer, winter after winter, often leaves little food available within the yard (Rooney and Waller 2003). Modifications of yard composition by forestry operations can alter the effectiveness of these habitats for deer (Garant 1992). A common cause of the loss of the protective cover is the maintenance of open corridors, called power line right-of-way (ROW), for high voltage powerline network. This network requires an extensive vegetation control programme to maintain clearance between electric conductors and the ground. Felling trees reduces cover and leads to greater snow depth making it harder for deer to move about. On the other hand, browse regeneration within cut areas can increase food availability to deer (Harper 1971).

Here, we use our food supplementation model in a study where we assess the impact of a ROW in a white-tailed deer yard by determining whether the negative effects of loss of cover outweigh the positive effects of browse regeneration. In order to estimate ΔGUD and ΓGUD , we place feeders in both exposed and protected areas and in food rich and food poor areas within the deer yard. GUDs are then measured both in the presence and in the absence of a food supplement.

Rieucou et al. (2007) showed, using planned statistical contrasts, that deer left more food uneaten in feeding troughs in areas exposed to higher predation risk and to higher metabolic costs than they did in sheltered areas. However, the approach using planned contrasts to compare GUDs was unable to distinguish between the effects of predation risk and metabolic costs. Also, the effect of increased food availability in the ROW was difficult to detect. Snow depth and snow support capacity influenced the GUD but their effects on predation risk and metabolic costs were not evaluated. In this paper, we expand this approach by using food supplementation in order to tease apart the effects of deer foraging costs.

Variation among habitats in the estimates derived from food supplementation should permit us to infer which habitats are better for deer and why. Because we use deer

behaviour to draw these inferences, we suggest that we evaluate the deer's assessment of its habitat.

Methods

This study was conducted from January 25th to April 5th 2005 in the Calumet deer yard, Quebec (45° 39.870' N, 74° 39.645' O) near the confluence of the Ottawa and Rouge Rivers 100 km west of Montreal. An 80-m wide 315 kV Hydro-Québec power line right-of-way crosses the deer yard. Vegetation in the ROW was "controlled" (all woody plants were cut down) in 2003 and relatively little browse was available for deer in this open area in winter 2005. At Calumet, neighbours did not offer supplemental food and coyote (*Canis latrans*) tracks were seen frequently; lynx (*Lynx canadensis*) were also present.

In the deer yard, six linear transects were established along deer trails which crossed the ROW perpendicularly. Deer were rarely active in the ROW outside these trails and all trails crossed the ROW in an almost straight line. In each transect, we installed feeders in four specific habitats: the middle of the ROW, the ROW edge, the forest edge and finally in the forest well removed from the ROW. We refer to these four sites as separate habitats although some authors might call them microhabitats. We chose these habitats for comparison with Rieucou et al. (2007). Instead of using the approach of Rieucou et al. (2007) of planned contrasts among the habitats, we used our model to draw inferences from our data.

Even though the population density of deer at the Calumet deer yard was unknown during our experiment, we expect that our feeders were visited by different deer on any given evening and the deer which visited a given feeder probably varied from day to day. We thus avoid the problem of pseudo-replication which would occur if the same deer visited a feeder repeatedly.

Feeders consisted of plastic barrels (46×24×24 cm) in which we placed about 66 g (dry weight) of white cedar (*Thuja occidentalis*), a very attractive food for deer (Rieucou et al. 2007), mixed with a non-edible substrate of 32 PVC plastic tubes (5 cm long×3 cm diameter) weighing about 700 g to ensure that animals had a significant cost of searching for food while foraging.

We achieved food enrichment by placing a supplemental feeder containing about 132 g (dry weight) of white cedar mixed with the same number of plastic tubes next to the initial feeder. Our experimental design involved that every station always had at least an initial feeder. We conducted the habitat enrichment by placing supplemental feeders next to the initial ones at half of the stations at a time. First supplemental feeders were placed on three of the six transects from February 13th to February 28th and from

March 5th to March 23rd for the other three, then moved back to the first three transects from March 31st to April 5th 2005.

We removed leftover food from all feeders each day (feeding occurred mostly at dusk) and feeders were replenished for the next day. Leftover food, collected in plastic bags, was dried at 80°C for 24 h and weighed to a precision of ±0.001 g thus measuring a GUD at each feeder (both initial and, if present, supplemental) each day.

Graduated posts were planted in the ground near each feeder to measure snow accumulation. A graduated copper pipe weighing 1,930 g (approximately the leg pressure of a mature deer; Hepburn 1978) was used to measure snow support capacity. We used portable thermometers to record ambient temperature at each feeding station in the yard every day.

Data analyses

We analysed our data in three different ways. First, following Rieucou et al. (2007), we compared mean GUDs using only the data from the initial feeder and when no supplement was present.

Next, based on Eq. 4, we used a covariance analysis, with the GUD from the initial feeder as the dependent variable, to test for differences in GUD among habitats and between days with and without a supplemental feeder. Transect was included as an additional factor in this analysis and covariates included snow depth, snow support capacity and temperature and their interaction effects with the principal factors. GUD values were log-transformed in order to ensure normality in the residuals of this analysis.

Finally, we used an analysis of variance to compare the difference between the two GUDs at the two feeders within a given patch based on Eq. 6. This analysis tested whether predation risk, as opposed to any other factor in our models, affected GUDs. We compared this difference among habitats and transects with both these factors nested within the day on which the difference was measured. We used a nested analysis to account for daily variation in GUDs and because we expect that variations in temperature, snow depth, and penetrability change a given patch on a daily basis.

Results

Giving-up densities differed among the habitats sampled ($F_{3,393}=28.5$, $p<0.0001$). When no food supplement was present, deer left more food in the two ROW feeders (centre and edge) than in the two forest feeders (Fig. 1) suggesting that either predation risk or metabolic costs influence the GUDs.

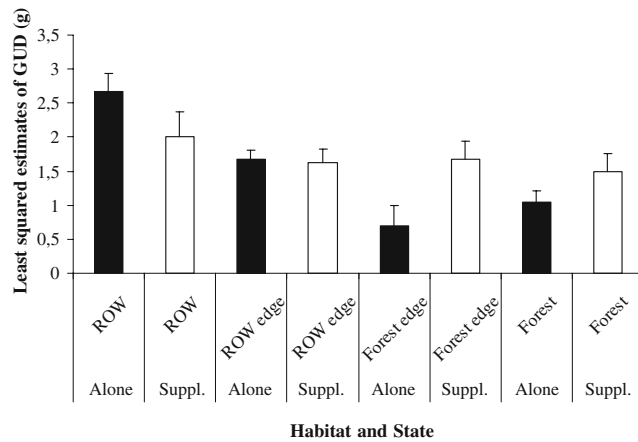


Fig. 1 Least squared estimates of mean giving-up density in the four habitats, with and without supplemental feeders in the Calumet deer yard

Based on Eq. 4 of our model, we tested for the effect of food supplementation through the habitat by food interaction term of the analysis of covariance. The addition of food increased GUDs ($F_{1,393}=5.36$, $p=0.021$) and this effect was similar in the four habitats. Several other factors also influenced GUDs in the deer yard (Table 1). Deer left more food where snow depth were higher ($F_{1,393}=82.84$, $p<0.0001$) and temperatures lower ($F_{1,393}=43.48$, $p<0.0001$). Also, GUDs were higher where deer sunk deepest in the snow ($F_{1,393}=39.25$, $p<0.0001$). Food supplementation produced the greatest increase in GUDs at feeders where a deer's leg would have sunk deepest in the snow ($F_{1,393}=16.19$, $p<0.0001$). There was also a difference in GUDs among transects ($F_{5,393}=5.79$, $p<0.0001$).

Based on Eq. 6 of our model, the nested analysis of variance showed that the difference in GUDs between the initial and the supplemental feeder differed among days ($F_{17,70}=4.53$; $p<0.0001$), and among habitats ($F_{45,70}=2.42$; $p=0.0004$) and transects ($F_{32,70}=3.20$; $p=0.0019$) nested within days. The greatest difference between the two GUDs (Δ GUD) occurred in the middle of the right-of-way (Fig. 2).

Table 1 Analysis of variance table for tests of hypotheses on the GUD in the initial feeder over four habitats (ROW, ROW edge, forest edge and forest) in two states (without supplementary food and with supplementary food) at the Calumet deer yard (probabilities less than 0.05 in bold)

Source of variation	DF	Denominator DF	F value	Probability
Habitat	3	393	10.95	<0.0001
State (enrichment or none)	1	393	5.36	0.02
Transect	5	393	5.79	<0.0001
Habitat \times state	3	393	1.07	0.35
Habitat \times transect	15	393	2.22	0.005
State \times transect	5	393	2.01	0.07
Habitat \times state \times transect	15	393	17.77	0.51
Snow depth (SD)	1	393	82.84	<0.0001
Snow support capacity (SSC)	1	393	39.25	<0.0001
Temperature	1	393	43.48	<0.0001
State \times SSC	1	393	16.19	<0.0001

On average, the GUD in the supplemental feeder (GUD^S) was 9.0 g greater than that in the original feeder beside it.

Discussion

Our patch use model allows us to examine habitat quality using a forager's evaluation of the costs and benefits of remaining in a given food patch. Investigating habitat variation generally requires that one aspect of habitat quality differs among habitats while all other aspects remain constant in order to draw inferences from foraging decisions. Here, we present a method which separates the effects of predation risk, metabolic cost and missed feeding costs on GUDs when all three vary among habitats.

Our results allow us to expand on the findings of a previous study (Rieucan et al. 2007) in another white-tailed deer yard. We confirm the result that deer leave more food in feeders in open habitats (ROW and ROW edge) than they do under protective cover (forest and forest edge). We now see why this happens: high GUDs in open habitats are due to high metabolic costs of feeding. At Calumet, deer left more food in the ROW than in the forest but Δ GUD was lowest in the ROW suggesting that predation risk was not the cause. As deer likely have access to all feeding patches along a given transect, we assume that their missed feeding costs are equal in both ROW and forest (i.e. we are comparing within an environment). Thus, metabolic costs are the only remaining factor which might have caused the difference in GUDs.

The fact that additional food produced higher GUDs in both our analyses shows that deer do react to additional food as has previously been shown in other species (Olsson and Holmgren 1999; Olsson and Molokwu 2007; Stenberg and Persson 2006).

Interestingly, we found that GUDs were higher where deer would have sunk deepest in the snow. Further, when a supplement was added, the habitats at which deer would

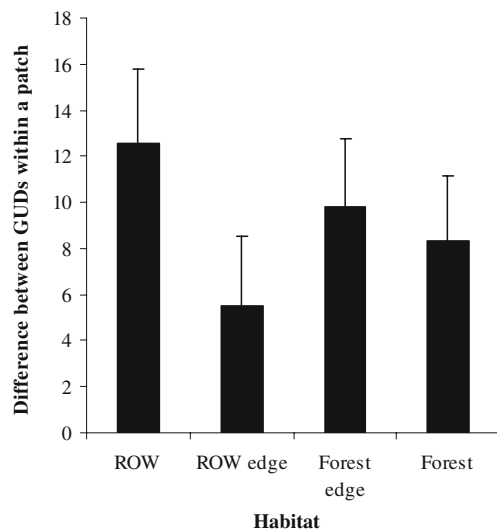


Fig. 2 Mean difference, in grams, between the GUDs at two feeders with different initial food densities within the same habitat patch. The difference is measured as the GUD at the feeder which started with 132 g of food minus the difference at the feeder which started with 66 g

have sunk the deepest had the greatest increase in GUDs. This suggests that deer did react to local differences in predation risk associated with snow support capacity even though we did not detect such an effect with our comparison among habitats. Deer will find it difficult to flee from predators when snow does not support them well and will thus evaluate habitats in which they sink deep into the snow as risky. As a result, they leave higher GUDs. That no difference was found among habitats can be explained by the fact that the support capacity of snow varied strongly between and among habitats. The ROW was not always the habitat where deer sunk the most into the snow and, in some cases, they also experienced poor snow support capacity in the forest. However, we found that snow depth had the opposite effect on GUDs compared to snow support capacity; the deeper the snow, the lower the GUD. This may seem paradoxical because snow depth and penetration were positively correlated. However, we found opposite effects on deer feeding. Deep snow covers many potential food sources. This reduces the alternate food supply for deer when they eat at our feeders. Thus, they will eat more food (and leave lower GUDs) in our artificial food patches when snow is deep. However, if the deep snow does not support deer well the effect will be the opposite.

We found that temperature negatively affected the GUDs. This is likely related to the observation that deer left more food in our feeders located in the ROW where the absence of a protective cover did not provide a natural barrier against wind. Schmitz (1991) showed that the absence of protective cover against wind chill accelerates deer body heat loss and increases energetic expenditures. In

a previous study in grey squirrels (*Sciurus carolinensis*) and in American crows (*Corvus brachyrhynchos*) investigating the effect of thermoregulatory costs on foraging decisions in cold winter conditions (Kilpatrick 2003), GUDs were lower in high ambient temperature habitats (where animals experienced lower energetic costs) compared to habitats where ambient temperatures were lower.

If our comparison had been between rather than within habitats, we could have used Eq. 6 and the nested analysis of variance to compare the difference between feeders placed side-by-side. This would have suggested that deer estimate the highest food availability in the ROW because this is where the greatest Γ GUD occurs. The Γ GUD would imply that deer find the ROW richer in food but the ROW edge riskier as the highest values of Γ GUD occurred in the middle of the ROW while the lowest occurred at the edge. Altendorf et al. (2001) have found that mule deer (*Odocoileus hemionus*), under predation pressure from mountain lions (*Puma concolor*), perceived the edge of a forest of Douglas fir (*Pseudotsuga menziesii*) as a riskier habitat than the interior of the forest or even open areas. We mention this point here as an illustrative example of our approach even though we think it unlikely that different groups of deer forage in the ROW as opposed to the forest, based on trails created by deer across the ROW and through the forest.

Previous studies have showed that high missed opportunity costs lead to an increase of GUDs (Olsson and Holmgren 1999; Olsson and Molokwu 2007; Stenberg and Persson 2006). In these studies, foragers were found to leave the food patches with higher GUDs in rich patches. Moreover, food supplementation is expected to decrease the marginal value of energy and the effects of a decrease in the marginal value of energy on GUDs is more pronounced in habitats with higher resource density (Kotler et al. 1999; Olsson and Molokwu 2007). In a recent theoretical modelling exercise, Olsson and Molokwu (2007) found that the greatest difference in GUDs between habitats (or environments) was mainly triggered by a difference in habitat richness and this effect was mostly due to variation in missed opportunity costs. Also differences in risk of predation between habitats negligibly affected the foragers' quitting harvest rate.

Our model and our empirical results do not suggest that food abundance is the factor producing higher GUDs. This probably results from the fact that our data compare within an environment and not between environments as was the case for the above authors. Our data underline the importance of distinguishing between the two cases because if we had assumed that our study compared between environments, it would have agreed with the above authors that food richness is the factor generating high GUDs. Rather, we find that creating a linear opening in the forest habitat raises the

metabolic cost of feeding. Further, areas where snow offers poor support for deer (their legs will penetrate deep into the snow) generate high predation risk.

We conclude that the creation of ROWs in a deer yard decreases habitat quality because the ROW exposes deer to higher metabolic costs. Further, predation risk will likely increase when loose snow, offering little support capacity, accumulates in the ROW. We cannot exclude the possibility that food produced in the ROW could be beneficial to deer. In the winter of 2005, there was almost no such food available because shrubs in the ROW were eliminated in 2003. A study in a winter when substantial regrowth is available in the ROW would allow us to compare results with the 2005 data (using the between environment model and FGUD) and test whether new vegetation in the ROW is beneficial to deer.

We demonstrate here that GUDs do reflect animals' adjustments to their foraging costs and benefits. The pattern in which these adjustments vary over space and time can be used to draw inferences about the costs and benefits they incur in different habitats, as we have done above. The GUD method has been widely used in ecology (habitat selection—Abramsky et al. 1996, patch assessment—Valone and Brown 1989, coexistence—Kotler and Brown 1999). As a result, such behavioural indicators, like GUDs, can provide reliable tools for conservation/restoration programmes (Whelan and Jedlicka 2007). By using our optimal foraging model in order to separate the effect of each foraging cost, we show that it can be a powerful and promising means to compare habitats and to assess the specific effects of habitat modification.

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