Deer mice mediate red-backed vole behaviour and abundance along a gradient of habitat alteration

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ABSTRACT

Hypotheses: (1) Intra- and inter-specific competition should increase with anthropogenic disturbances that reduce habitat quality. (2) In forested ecosystems, predation risk for small consumers should increase with the intensity of disturbance. (3) For the same level of disturbance, foragers living in higher-quality habitats should protect their assets by investing more in anti-predatory behaviours than those living in low-quality habitats.

Organisms: Red-backed voles (*Myodes gapperi*) living in sympatry with deer mice (*Peromyscus maniculatus*).

Place and time: Twenty-nine pairs of natural and logged habitats sampled during 2006 in managed boreal forest, Province of Québec, Canada.

Methods: We identified a gradient of habitat disturbance along principal components summarizing 12 habitat variables. We estimated competition by measuring the giving-up density of rodents along the gradient of habitat disturbance. We assessed predation risk by measuring the giving-up density of rodents foraging in safe and risky patches. We tested for differences with multi-level statistical modelling.

Conclusions: Competition and predation risk increased with habitat disturbance in the boreal forest studied. Foragers living in higher-quality habitats experienced higher predation costs than foragers living in low-quality habitats. Intra- and inter-specific competition, rather than predation, was the main mechanism responsible for the decline of red-backed vole populations associated with forest harvesting.

Keywords: adaptive foraging behaviour, asset-protection principle, behavioural indicator, competition, giving-up density, habitat alteration, habitat selection, *Myodes gapperi*, *Peromyscus maniculatus*, predation risk, quitting-harvest rate.

INTRODUCTION

Conservation of biodiversity depends on our ability to understand the impacts of habitat alteration on natural populations (Clemmons and Buchholz, 1997; Gosling and Sutherland, 2000; Festa-Bianchet

and Apollonio, 2003). A major effect of habitat changes on population dynamics arises from the modification of adaptive mechanisms of habitat selection (Kotler *et al.*, 2007; Morris *et al.*, 2009). For example, competition may be affected directly by changes in food resource availability or indirectly by the colonization of competitor species, while predation may vary through the alteration of anti-predatory cover or predator abundance (Caro, 2007).

Foraging behaviour has been shown to reflect the impact that natural and anthropogenic disturbances can have on habitat quality, and more specifically on how these disturbances influence competition and predation costs (e.g. Reed *et al.*, 2005; Morris and Davidson, 2000; Morris and Mukherjee, 2007; Andruskiw *et al.*, 2008). Foragers should exploit a given resource patch until the profit gained from using the patch equals the foraging costs accumulated in that patch (Brown, 1988). Accordingly, the quitting-harvest rate of a patch (H) is expected to equal the sum of the metabolic (C), predation (P), and missed opportunity costs (MOC) of foraging, i.e. $H = C + P + MOC$ (Brown, 1988; Brown *et al.*, 1992). Quitting-harvest rate can be estimated by measuring the giving-up density (GUD) in a patch for which the initial amount of food is known (Brown, 1988; Brown *et al.*, 1992). With the appropriate design, one can assess local differences in metabolic, predation or missed opportunity costs based on differences in giving-up densities. For example, giving-up densities can be measured in pairs of experimental resource patches that are similar except that one patch is placed in the open (risky) while the other is under protective cover (Brown *et al.*, 1992). Differences in giving-up densities should then be proportional to differences in predation costs (Morris and Davidson, 2000; Schmidt *et al.*, 2005; Andruskiw *et al.*, 2008).

Adaptive foraging behaviour may reflect relative habitat quality because natural selection should favour specific decisions, the nature of which varies in a predictive manner depending on the foraging context. According to foraging theory, the higher the quitting-harvest rate (i.e. mean GUD) in a habitat, the higher the profit in the habitat for the forager (Brown, 1988; Brown *et al.*, 1992). In other words, mean GUD is expected to be lower in poor than in rich habitats. Foraging theory also predicts that predation risk should increase with the reduction of anti-predator cover for risk-sensitive foragers living in a low-quality habitat (Verdolin, 2006; While and McArthur, 2006; Eccard *et al.*, 2008). The asset-protection principle of Clark (1994; empirical support provided by Reed *et al.*, 2005; Ydenberg *et al.*, 1995) states that foragers living in a high-quality habitat should invest more in anti-predatory behaviours because they experience greater fitness (or asset) costs by being injured or killed than if they were living in a poor-quality habitat. We therefore predict that predation costs should decrease following the disturbance of high-quality (high fitness) habitats, whereas costs should increase following the disturbance of low-quality habitats. The biggest difference in giving-up densities between habitats is most likely caused by differences in food availability rather than in predation risk (Olsson and Holmgren, 1999; Olsson and Molokwu, 2007).

In this study, we use observations on abundance and foraging behaviour of red-backed voles (*Myodes gapperi*) in a forest ecosystem also occupied by sympatric deer mice (*Peromyscus maniculatus*) to determine how forest harvesting influences intra- and inter-specific competition as well as predation costs. The red-backed vole is an omnivorous species feeding largely on hypogeous fungi (Orrock and Pagels, 2002), which are most abundant in mature and old-growth forests (Johnson, 1996). The main competitor of the red-backed vole, the omnivorous deer mouse (Morris, 1996), is an efficient forager in disturbed forests (Suzuki and Hayes, 2003; Fuller *et al.*, 2004). Quitting-harvest rates (mean GUD) should therefore decrease following forest harvesting for red-backed voles because logging should reduce the abundance of their main food resources and increase competition with deer mice.

The numerical response of the red-backed vole to habitat alteration has been studied intensively, in part because it is the dominant species of the small-mammal community in North American boreal forests (Pearce and Venier, 2005; Lemaître *et al.*, 2009). Conclusions about the impact of forest harvesting on red-backed vole populations are inconsistent. Several studies have documented declines in abundance following logging (e.g. Mills, 1995; Sullivan *et al.*, 1999; Darveau *et al.*, 2001; Moses and Boutin, 2001), while others reported the opposite relationship (e.g. Hayward *et al.*, 1999; Suzuki and Hayes, 2003; Homyack *et al.*, 2005). Behavioural indicators provided by foraging experiments should help us to resolve these conflicting results because they specifically address the biological mechanisms of habitat quality, density, predation, and competition that underlie habitat use.

METHODS AND MATERIALS

Study area and experimental design

The study was conducted in the boreal forest of northeastern Quebec, Canada (51°02′12″ N, 69°11′41″ W; Fig. 1). Annual precipitation ranges from 1000 to 1400 mm, and annual mean temperature varies from −2.5 to 0.0°C (Boucher *et al.*, 2006). Forest stands are dominated by black spruce (*Picea mariana*) or a combination of black spruce, balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*) (Boucher *et al.*, 2006). The study area is character-ized by a long fire cycle (mean cycle length = 400 years), which produces uneven forest
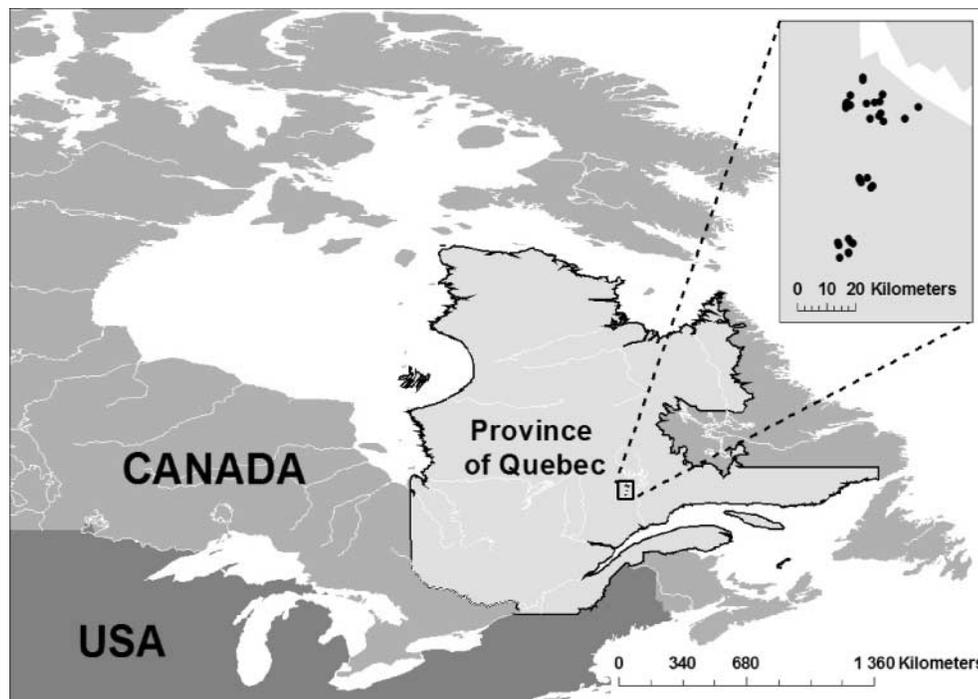
Fig. 1. Location of the study area in the Côte-Nord region of Quebec, Canada. Black dots in the top-right panel indicate habitat pair location (*n* = 29 pairs).

stands shaped by blowdown and senescence (Bouchard *et al.*, 2008). The main harvest regime is clearcutting, although two partial-harvest regimes are also applied in the study area: cut with protection of high regeneration and soils (CPHRS), which protects regeneration up to 2 m; and cut with protection of small merchantable stems (CPPTM), which protects stems <15 cm diameter at breast height.

We surveyed 29 paired habitats during summer 2006. Each pair included a harvested stand adjacent to an uncut one. Stands were harvested with different intensity, which resulted in a tree basal area ranging from 0 to 6 m² per hectare. Tree basal area ranged from 5.5 to 46.5 m² per hectare in uncut stands. Each habitat (cut or uncut stand) covered an area of at least 200×300 m, and pairs shared a boundary of at least 300 m. We pre-selected pairs of habitats using ArcGIS 9.1 (ESRI, 2006) according to three criteria: (1) the stand structure and composition within the forest habitat was relatively uniform; (2) there were no streams and roads in either habitat; and (3) stand structure and composition of the harvested habitat prior to harvesting were similar to the natural habitat. These criteria yielded a total of 116 possible habitat pairs in the study area, of which we selected 29 at random.

Giving-up densities

Each pair of habitats was randomly assigned to one of four sampling sessions (4–6 July, 11–13 July, 29–31 July, and 5–7 August). A session included a 'GUD experiment' followed by live trapping of small mammals. We established two 100-m parallel transects, positioned 100 m apart in each habitat. Transects ran perpendicular from the edge between the two habitats towards their interior. We positioned two feeding stations per transect, one at 60 m and the other at 90 m from the edge between the two habitats (i.e. four feeding stations per habitat). Each feeding station comprised two food patches: one was covered with 4 m² of freshly cut conifer branches to represent a safe microhabitat, while the other was 2 m away and was not covered by branches. This second food patch thus offered a riskier foraging site for small mammals (Morris and Davidson, 2000). By using similar food patches at such close proximity, individuals foraging in either patch should have identical metabolic and missed opportunity costs (Brown, 1988; Brown *et al.*, 1992). Predation costs would thus be responsible for the difference in giving-up density between pairs of patches (Brown *et al.*, 1992; Schmidt *et al.*, 2005).

We estimated quitting-harvest rates of red-backed voles by measuring giving-up density in the artificial food patches. Each identical food patch consisted of a plastic tray ($23 \times 23 \times 18$ cm) to which we added 3 litres of sifted dry sand and 50 unshelled sunflower seeds mixed thoroughly into the sand (Kasparian and Millar, 2004). A 2.5 cm entrance hole prevented access to larger animals such as red squirrels (*Tamiasciurus hudsonicus*). Food patches were baited for 9 days before conducting the 3-day foraging experiment. We sieved the trays each day to collect the uneaten seeds and recharged them with 50 new seeds. The number of uneaten seeds was taken to be the giving-up density of the food patch (Reed *et al.*, 2005).

Small mammal abundance

We placed 20 Sherman collapsible live traps ($7.7 \times 8.8 \times 23.0$ cm; Sherman Traps, Tallahassee, FL) in each habitat to estimate the abundance of small mammals. Traps were located every 10 m along the two 100-m parallel transects running into each habitat. Live

trapping lasted 3 days at each habitat pair, and was conducted immediately after the GUD experiments. Traps were set and inspected at dawn. Captured small mammals were identified to species and marked with a unique ear tag (style 1005-1 from National Band & Tag, Newport, KY) before being released. Red-backed vole abundance was corrected for the number of night-traps at a given site [i.e. corrected for sampling effort, which corresponded to the sum of the traps occupied by unmarked red-backed voles plus traps where no individual was captured (Beauvais and Buskirk, 1999)]. We counted sprung empty traps as one-half of a trap-night (Beauvais and Buskirk, 1999). Traps occupied by recaptured individuals or by species other than the red-backed vole were not included because those traps were not available to capture an unmarked red-backed vole (Beauvais and Buskirk, 1999).

Habitat variables

We characterized vole habitat using 12 variables that represented anti-predator cover (Ucitel *et al.*, 2003; Pearce and Venier, 2005) or reflected food availability for red-backed voles (Orrock and Pagels, 2002; Boonstra and Krebs, 2006). Of the 12 variables, five also provided a quantitative measure of habitat alteration [basal area of black spruce trees, ground cover of moss, bare ground cover, ground cover of fungi, ground cover of fruits available for red-backed voles (i.e. fruits of *Vaccinum* spp. and *Cornus canadensis*)], while the other seven variables provided a quantitative measure of habitat productivity based on indicators of soil fertility [basal area of balsam fir trees, basal area of balsam fir saplings, coarse woody debris volume, ground cover of lichens (epigeous and fallen arboricol), ground cover of *Rhododendron groenlandicum*, ground cover of *Kalmia angustifolia*, ground cover of *Vaccinum* spp.] (Yamasaki *et al.*, 2002).

We measured tree basal area at each feeding station using a 2× prism (Grosenbaugh, 1952). Basal area of saplings (m^2 per hectare) was estimated from the diameter of breast height (dbh) of saplings (i.e. ≤9 cm dbh and ≥1.30 m height) in ten 2 × 2 m quadrats, at each feeding station. Quadrats were located every 2 m along a randomly oriented transect that was centred on the feeding station. We visually estimated the percent-cover of bare ground, mosses, lichens, fruits, epigeous fungi, and ericaceous species within two 1 × 1 m quadrats randomly located within 4 m of the feeding stations. Coarse woody debris (CWD) volume was estimated for each habitat using line intercept sampling (Stahl, 1997) along 100-m transect lines running between the two feeding stations at 60 m and the two feeding stations at 90 m. The diameter of each piece of coarse woody debris (i.e. length ≥2 m and diameter at both ends >9 cm) was recorded at the intersection with the line transect. Coarse woody debris volume per habitat (m^3 per hectare) was calculated using the following equation (De Vries, 1973): CWD volume $= \pi^2/8L \times \Sigma(d^2)$, where $L =$ transect length and $d =$ diameter of the coarse woody debris.

Statistical analyses

We used principal components analysis (PCA) to reduce the 12 habitat variables to fewer independent components. Habitat variables were normalized before analysis with Box-Cox transformations (Box and Cox, 1964) and the significance of loading was assessed by boot-strapping (Peres-Neto *et al.*, 2003). Principal components identified a gradient of habitat alteration, together with a soil fertility gradient (see Results). Using a gradient rather than a bivariate comparison between harvested and natural stands allowed us to account for the

broad habitat productivity that characterized natural stands in this irregular boreal forest (Bouchard *et al.*, 2008) as well as that created by logging with various levels of tree retention.

We tested predictions linking competition and predation costs to habitat disturbance while accounting for the soil fertility gradient obtained with the PCA, and for the presence of deer mice in habitat pairs (i.e. a dummy variable coded '0' when deer mice were absent and '1' when they were present in at least one habitat of the pair). The relationship between mean GUD and the three independent variables [i.e. logging intensity (PC2), soil fertility (PC1), and presence of a deer mouse] was evaluated with a Poisson distribution, using giving-up density per tray per day as the dependent variable, because mean giving-up density (unit = number of seeds) was a discrete variable following a Poisson distribution. The difference between the giving-up density of the open food patch and the giving-up density of the covered food patch within a feeding station per day (ΔGUD) followed a Gaussian distribution, and the relationship between ΔGUD and the three independent variables was thus evaluated with a Gaussian distribution. We accounted for the spatial design of the study using multi-level models (Faraway, 2006). Each pair of food patches (open and covered) was nested in a feeding station, the feeding station was nested in a habitat (harvested or natural), and the habitat was part of a pair ($n = 2$ food patches $\times 4$ feeding stations $\times 2$ habitats $\times 29$ pairs = 464 food patches). We took into account the three days of the experiment using multi-level models with repeated measures (Faraway, 2006). Only pairs for which red-backed voles occupied both habitats were included in the GUD analyses. We evaluated the relationship between the number of red-backed voles and habitat principal components with generalized linear mixed-effect models (GLMM) with a Poisson distribution, using the pair as a random effect to take into account the fact that each harvested stand was compared with its adjacent natural forest stand. We used the Poisson distribution because the number of red-backed voles was a discrete variable following this distribution, while accounting for the local sampling effort (log transformed) through an offset.

We built the global model for each of the three dependent variables (i.e. mean GUD, ΔGUD, and red-backed vole abundance). We then determined whether the least significant variable or interaction in the global model was necessary to the overall model fit using the log-likelihood ratio test ($\alpha = 0.05$) between the global model (n variables) and the model with $n - 1$ variables (Hosmer and Lemeshow, 2000). We continued this backward procedure until we found a significant difference ($P < 0.05$) between models with n and $n - 1$ variables. The model with n variables at this last step was our final model (Hosmer and Lemeshow, 2000). We determined model fit of our GLMM using the pseudo-R^2, i.e. the square of the correlation between fitted and observed values (Zar, 1999). Analyses were conducted with the R software, version 2.4.1 (R Development Core Team, 2006).

RESULTS

Habitat principal components

Tree basal area averaged 2.7 ± 1.1 m² per hectare (mean ± s.d.) in harvested stands and 27.6 ± 14.4 m² per hectare in natural stands. Proportions of black spruce, balsam fir, and white birch in the canopy layer averaged, respectively, 0.47 ± 0.40, 0.18 ± 0.27, and 0.34 ± 0.40 in harvested stands and 0.69 ± 0.27, 0.25 ± 0.22, and 0.07 ± 0.08 in natural forests. The first two PCA axes together explained 54% of the variance within the habitat

Table 1. Loadings and proportion of explained variance of the PCA conducted on 12 habitat variables measured in 29 pairs of adjacent harvested and natural habitats ($n = 58$ habitats) in the boreal forest of eastern Quebec

Variable	PC1	PC2
Variables closely associated with habitat alteration		
Basal area of black spruce trees	−0.09	−0.48 **
Ground cover of fungi	0.04	−0.34 **
Ground cover of mosses	0.13	−0.48 **
Bare ground cover	−0.04	0.33 *
Ground cover of fruits	0.08	0.37 **
Variables closely associated with soil fertility		
Basal area of balsam fir trees	0.37 ***	−0.25 *
Basal area of balsam fir saplings	0.40 ***	−0.18
Volume of coarse woody debris	0.38 ***	0.09
Ground cover of lichens	−0.36 ***	−0.08
Ground cover of *Rhododendron groenlandicum*	−0.42 ***	−0.03
Ground cover of *Kalmia angustifolia*	−0.35 ***	−0.09
Ground cover of *Vaccinum* spp.	−0.30 ***	−0.24 *
Proportion of explained variance	0.31	0.23

Note: Asterisks indicate the significance of each loading according to a bootstrap validation: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

data set (Table 1). The first axis, PC1, mainly represented a soil fertility gradient, from low-fertility habitats (i.e. poor sites, where the ground was largely covered by lichens and ericaceous species; namely, *Rhododendron groenlandicum*, *Kalmia angustifolia*, and *Vaccinum* spp.) to highly fertile habitats (i.e. rich sites, with high basal areas of balsam fir trees and saplings, and a high volume of coarse woody debris) (Fig. 2).

The second PCA axis, PC2, represented a gradient of habitat alteration (Fig. 2). Basal area of black spruce trees, which was highly correlated with basal area of all tree species (Spearman's rank correlation: $r_s = 0.91$, $P < 0.001$), was negatively associated with PC2 (Table 1). Ground cover of fungi, an indicator of mature and old-growth forests (Johnson, 1996), was negatively associated with PC2 (Table 1). Ground cover of mosses, which are primarily found in mature, closed-canopy forests (Fenton and Bergeron, 2007), was also negatively associated with PC2 (Table 1). Conversely, bare ground cover increased with PC2 (Table 1); bare ground was an indicator of habitat alteration because soil in natural stands was covered by a rich floral carpet. Ground cover of fruit-bearing shrubs, which are more abundant in disturbed, open-canopy habitats, increased with PC2 (Table 1).

Mean GUD and ΔGUD

Red-backed voles were present in both the harvested and the uncut forest habitats in 17 of the 29 pairs; they occupied only the forest in eight pairs and only the harvested stand in the remaining four pairs. Deer mice were present in 12 of the 29 pairs: four pairs where they were captured in both habitats and eight pairs where they were found exclusively in the
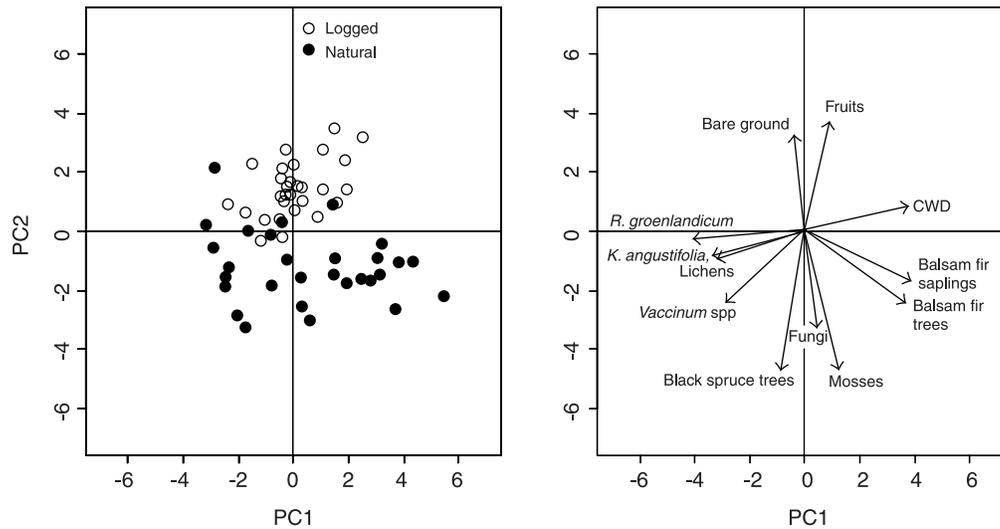
Fig. 2. Principal components analysis conducted on 12 habitat variables in 29 pairs of adjacent harvested and natural forests ($n = 58$ habitats). Habitats are represented in the PCA space on the left-hand panel: black dots represent natural habitats and white dots represent harvested habitats. The right-hand panel presents loadings of the PCA with the arrows' direction and length representing the strength of the correlation between each habitat variable and principal components. PC1 represents a soil fertility gradient, from sites with low to high soil fertility, and PC2 represents a habitat alteration gradient, from natural stands to stands harvested with high intensity.

harvested habitat. We pooled data from all four sampling sessions because the inclusion of temporal changes over the summer never improved model fit ($P > 0.57$) of mean GUD, ΔGUD or red-backed vole abundance.

Three of the 17 pairs where red-backed voles were present in both habitats had at least one habitat with 75–100% of unused feeding stations, which provided little information about spatial patterns in foraging effort. Therefore, we excluded these pairs from the analysis, and conducted the analysis on six habitat pairs without deer mice and eight habitat pairs with deer mice, for a total of 224 feedings stations. Mean GUD decreased with PC2, the gradient of habitat alteration (Fig. 3a), indicating that habitat alteration decreased overall habitat quality. Mean GUD declined more steeply in sites with than without deer mice (significant PC2 × deer mouse interaction; Table 2), suggesting that inter-specific competition of red-backed voles and deer mice contributed to the decrease of habitat quality along the habitat alteration gradient. And mean GUD declined more in sites with low soil fertility (low PC1) than with high soil fertility (high PC1; significant PC1 × PC2 interaction; Table 2). This result supports the hypothesis that high soil fertility is associated with foragers' perception of high-quality habitat. Mean GUD did not vary with PC2 in sites with high soil fertility lacking deer mice (Fig. 3a), suggesting that alteration of habitats with high soil fertility and absence of deer mice was the least inauspicious to red-backed voles.

Giving-up density was 34 ± 11 seeds (mean ± s.d.) in open food patches and 30 ± 11 seeds in covered food patches. As predicted, ΔGUD increased with PC2 in sites with low soil fertility, whereas it decreased with PC2 in sites with high soil fertility (significant PC1 × PC2 interaction; Fig. 3b). ΔGUD was higher in low-fertility than in high-fertility habitats with
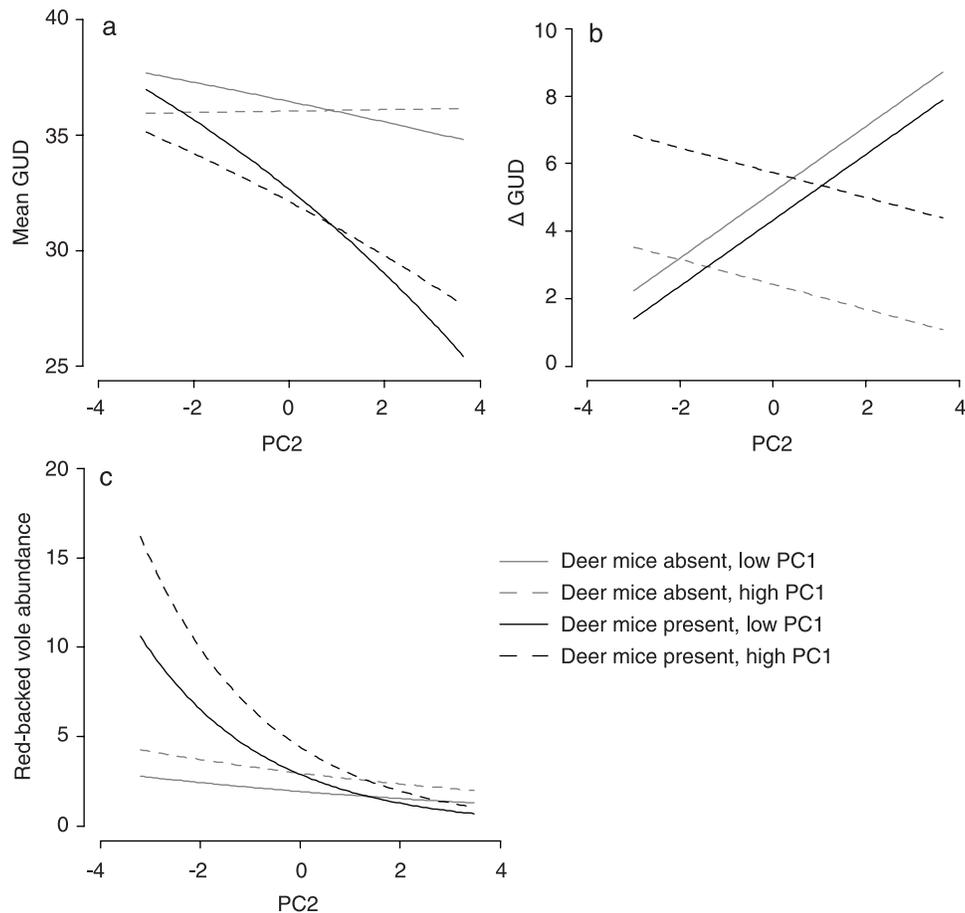
Fig. 3. Interactions between red-backed voles and deer mice as a function of habitat alteration (PC2) and soil fertility (PC1): (a) mean giving-up density (GUD); (b) ΔGUD (i.e. GUD in open minus GUD in the paired covered food patch); and (c) red-backed vole abundance. Lines represent model fits (see Table 1 for estimates and *P*-values). Low PC1 (i.e. sites with low soil fertility) refers to the 1st quartile of PC1, while high PC1 (i.e. sites with high soil fertility) refers to the 3rd quartile of PC1.

deer mice (significant PC1 × deer mouse interaction; Table 2), whereas GUD was lower in low-fertility than in high-fertility habitats without deer mice (Fig. 3b).

Small-mammal abundance

We captured a total of 278 different small mammals over 3480 night-traps. The red-backed vole was the most abundant rodent species (61% of all individuals, *n* = 169) followed by the deer mouse (13%, *n* = 35). We also captured 10 red squirrels, eight rock voles (*Microtus chrotorrhinus*), three heather voles (*Phenacomys intermedius*), and 53 shrews (*Sorex* spp.). Shrews are insectivorous foragers that did not forage in our food patches. Also, the 2.5 cm hole at the entrance of food patches prevented access by red squirrels. Red-backed voles and

Table 2. Multivariable GLMM of mean GUD, ΔGUD (i.e. GUD in open minus GUD in covered food patch), and red-backed vole abundance as a function of habitat alteration (PC2), soil fertility (PC1), and the presence of deer mice in pairs, a dummy variable having no deer mouse as the reference value

Variable	Mean GUD			ΔGUD			Vole abundance		
	β	s.d.	P	β	s.d.	P	β	s.d.	P
Intercept	−2.61	0.13	<0.001	4.10	0.72	<0.001	−3.18	0.13	<0.001
PC1	−0.01	0.01	0.36	−1.15	0.44	0.04	0.18	0.05	<0.001
PC2	−0.02	0.02	0.40	0.48	0.42	0.23	−0.11	0.07	0.10
Deer mouse	−0.25	0.18	0.17	0.74	1.09	0.35	0.40	0.22	0.07
PC1 × PC2	0.01	0.01	0.03	−0.59	0.26	0.04			
PC1 × deer mouse				1.65	0.72	0.06			
PC2 × deer mouse	−0.06	0.03	0.05				−0.29	0.11	0.01

Note: Pseudo-R^2 was 0.58 for mean GUD, 0.08 for ΔGUD, and 0.56 for vole abundance.

deer mice thus represented 95% (204/215) of the individuals that were able to forage in our food patches.

Red-backed vole abundance increased with PC1, implying that voles were more abundant in sites with high soil fertility than sites with low soil fertility (Table 2). Red-backed vole abundance also decreased with the level of habitat alteration (Fig. 3c), an influence that varied with the presence of deer mice (significant PC2 × deer mouse interaction; Table 2). At the undisturbed end of the gradient of habitat alteration (PC2), red-backed voles were three times as abundant in sites with deer mice (10–16 red-backed voles captured per habitat) than in sites without deer mice (3–4 red-backed voles captured per habitat). In contrast, red-backed vole abundance was similar in sites with and without deer mice at the upper end of PC2, with only 2–3 red-backed voles being captured per habitat (Fig. 3c).

DISCUSSION

Our observations are consistent with previous studies reporting a lower abundance of red-backed voles in harvested than natural forest stands (e.g. Mills, 1995; Sullivan *et al.*, 1999; Darveau *et al.*, 2001; Moses and Boutin, 2001). Unlike these other studies, we considered the response of red-backed voles to a broad gradient of habitat alteration made up of clear cuts, high-intensity partial cuts (CPHRS), and low-intensity partial cuts (CPPTM). Also, we analysed the influence of forest harvesting on vole abundance while directly accounting for the presence or absence of deer mice, the red-backed vole's major competitor. We found that the effect of forest harvesting on vole populations did depend on the presence of deer mice. The abundance of voles was three times higher in uncut stands with than without deer mice, suggesting that the presence of this competitor (together with high soil fertility) provides an indication that uncut stands are of an especially high quality for both small mammal species. In addition, we detected a weak decrease in red-backed vole abundance with increasing forest harvesting intensity among sites without deer mice, but found an exponential decrease among sites with deer mice.

Competition

The quitting-harvest rate (mean GUD) decreased with logging intensity (i.e. from low to high PC2 scores), indicating a decline in habitat quality with forest harvest. The presence of deer mice exacerbated this effect, as reported for other rodent species (Ziv and Kotler, 2003; Eccard and Ylonen, 2007). Mean GUD was lower in the presence of deer mice, for which there are two potential causes. First, deer mice might have tended to be the last foragers to visit patches and could possess a lower giving-up density than voles. Second, deer mice might simply have reduced resource abundance in the habitat as a whole. We cannot be certain which effect was most pronounced in our study because we could not differentiate vole and mouse foraging, although mice represented only 17% of the foragers. Regardless, it is apparent that giving-up density was reduced in the presence of deer mice, suggesting that mice are more efficient foragers than voles, and especially so in altered habitats (Suzuki and Hayes, 2003; Fuller *et al.*, 2004). This result follows the $R*$ rule that states that the winner between two exploitative competitor species is the one that can depress mean resource abundance in the habitat to the lowest level while ensuring its survival (Tilman, 1990; Holt *et al.*, 1994). Although red-backed vole abundance was higher in sites with deer mice, mean GUD was similar between uncut forest stands with and without deer mice. This result indicates either that uncut stands could support more red-backed voles where deer mice were present than absent or that deer mice occupy only the best, undisturbed sites.

Predation costs

Red-backed voles also appeared to be risk-sensitive foragers. Red-backed voles should have more to lose by foraging in the risky patches of high soil fertility habitats because overall quality was higher in these sites than in low soil fertility sites. According to the asset-protection principle (*sensu* Clark, 1994), voles should display the weakest anti-predatory behaviour in habitats with high soil fertility (Ekman and Ulliendahl, 1993; Ydenberg *et al.*, 1995; Olsson and Molokwu, 2007). Moreover, forest harvesting generally reduces anti-predator cover (Ucitel *et al.*, 2003; Fuller *et al.*, 2004), which increases predation risk for small mammals (Morris and Davidson, 2000; Verdolin, 2006; Eccard *et al.*, 2008). On the basis of changes in habitat quality and availability of anti-predator cover, we predicted that predation costs (i.e. ΔGUD between risky and safe food patches) would increase with logging intensity in sites with low soil fertility (Ucitel *et al.*, 2003; Fuller *et al.*, 2004), but would be affected less and could even decrease with logging intensity in sites with high soil fertility (Clark, 1994; Olsson and Molokwu, 2007). Our results are consistent with these expectations. ΔGUD indicated that predation costs increased with logging in sites with low soil fertility, but decreased in sites with high soil fertility.

Model fit was lower for ΔGUD than for mean GUD, indicating that the effect of greatest difference in GUDs between environments was generated by a difference in food availability rather than predation costs (Olsson and Holmgren, 1999; Davidson and Morris, 2001; Olsson and Molokwu, 2007). This conclusion is also consistent with Boonstra and Krebs's (2006) contention that competition, rather than predation, is the main mechanism controlling habitat selection by red-backed voles. Red-backed vole populations thus appear to be primarily driven by competition (bottom-up regulation) rather than by predation (top-down regulation).

Finally, the identification of intra- and inter-specific competition as the main mechanism responsible for the decline of red-backed vole populations with forest harvesting is an important cue for conservation and management. One cannot simply use the abundance of

indicator species to assess their habitat quality. Rather, studies must incorporate, explicitly, the effects of habitat variation, habitat selection, and competing species on adaptive (e.g. foraging) behaviour. Our results suggest that expanding the use of behavioural indicators should benefit population ecology and conservation biology by providing insight on the adaptive mechanisms affected by habitat alteration.

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