Agricultural land use alters trophic status and population density of deer mice (*Peromyscus maniculatus*) on the North American Great Plains

A.J. White, R.G. Poulin, B. Wissel, J.L. Doucette, and C.M. Somers

Abstract: Habitat conversion is among the most important causes of environmental change worldwide, yet relatively little is known about its potential influence on trophic interactions. We investigated the effects of agricultural land use on carbon and nitrogen stable isotope values, trophic status, population density, and body condition of deer mice (*Peromyscus maniculatus* (Wagner, 1845)) in a grassland ecosystem. Muscle δ^{15}N (cropland = 7.6‰ ± 1.3‰; hay fields = 7.9‰ ± 1.3‰; native prairie = 7.2‰ ± 2.1‰) from deer mice did not vary with land use despite baseline soil and vegetation δ^{15}N differences. Enrichment of deer mice over vegetation ($\Delta\delta^{15}$N) was, on average, a full trophic level (~2.5‰) higher on native prairie (6.4‰ ± 1.6‰) than on cropland (3.9‰ ± 2.3‰), and intermediate in hay fields (5.9‰ ± 2.0‰). Relative density of deer mice was more than twofold higher in crop and hay fields compared with native prairie, but body condition did not vary with land use. Our results suggest that agricultural activity caused a shift in the trophic level and relative abundance of a generalist grassland omnivore. Soil and vegetation δ^{15}N reflected anthropogenic N inputs to agricultural fields but were not useful as general markers of habitat use in this study.

Key words: small mammals, grassland, fertilizer, stable isotopes, trophic ecology, deer mouse, *Peromyscus maniculatus*.

Résumé : Si la transformation d’habitats est l’une des plus importantes causes de modification de l’environnement à l’échelle mondiale, les connaissances sur son influence potentielle sur les interactions trophiques sont assez limitées. Nous avons étudié les effets de l’utilisation agricole du sol sur les valeurs d’isotopes stables du carbone et de l’azote, l’état trophique, la densité de population et l’état corporel de souris sylvestres (*Peromyscus maniculatus* (Wagner, 1845)) dans un écosystème de prairie. Les valeurs de δ^{15}N de muscles de souris sylvestres (terre cultivée = 7,6 ‰ ± 1,3 ‰; prairie de fauche = 7,9 ‰ ± 1,3 ‰; prairie naturelle = 7,2 ‰ ± 2,1 ‰) ne montraient aucune variation en fonction de l’utilisation du sol et ce, malgré des différences dans les valeurs de référence de δ^{15}N des sols et de la végétation. L’enrichissement des souris sylvestres par rapport à la végétation ($\Delta\delta^{15}$N) était en moyenne un niveau trophique complet (~2,5 ‰) plus élevé dans les prairies naturelles (6,4 ‰ ± 1,6 ‰) que dans les terres cultivées (3,9 ‰ ± 2,3 ‰), et intermédiaire dans les prairies de fauche (5,9 ‰ ± 2,0 ‰). La densité relative des souris sylvestres était plus de deux fois plus élevée dans les terres cultivées et les prairies de fauche que dans les prairies naturelles, bien que l’état corporel ne montrait aucune variation selon l’utilisation du sol. Nos résultats suggèrent que l’agriculture a entraîné la modification du niveau trophique et de l’abondance relative d’un omnivore de prairie généraliste. Les valeurs de δ^{15}N des sols et de la végétation reflétaient des apports anthropiques de N dans les champs agricoles, mais ne se sont pas avérées utiles en tant qu’indicateurs généraux de l’utilisation d’habitat dans le cadre de l’étude.

Mots-clés : petits mammifères, prairie, engrais, isotopes stables, écologie trophique, souris sylvestre, *Peromyscus maniculatus*.

[Traduit par la Rédaction]

Introduction

Worldwide, conversion of grasslands for agricultural land use has created areas where vegetation communities, disturbance regimes, and food webs are distinct from those of native habitats. In North America, more than 70% of native grasslands on the Great Plains have been lost since European settlement, primarily owing to agricultural activities (Samson et al. 2004). The distribution and abundance of various taxa in the mosaic of cropland and remnant native patches have been profoundly affected, and grasslands are now among the most threatened habitats on the continent (Herkert 1995; Clark et al. 1998; Murphy 2003). Consequently, research on the effects of agricultural land use on animal ecology in grasslands

Received 2 March 2012. Accepted 2 May 2012. Published at www.nrcresearchpress.com/cjz on 22 June 2012.

A.J. White, B. Wissel, J.L. Doucette, and C.M. Somers. Department of Biology, University of Regina, 3737 Wascana Parkway, Regina, SK S4S 0A2, Canada.
R.G. Poulin. Life Sciences, Royal Saskatchewan Museum, 2340 Albert Street, Regina, SK S4P 2V7, Canada.

Corresponding author: C.M. Somers (e-mail: chris.somers@uregina.ca).

doi:10.1139/Z2012-055

has focused primarily on understanding negative impacts to species of conservation concern (e.g., Clayton and Schmutz 1999; Kamler et al. 2003; Laliberte and Ripple 2004; Wilson et al. 2005; Askins et al. 2007). The majority of these species are carnivorous birds or mammals, so it is of principal interest to understand the quality of agricultural land as habitat for prey species.

Small mammals (mice, voles, and shrews) are abundant and widespread on the Great Plains and are an important prey base for many predators. Habitat quality for small mammals is directly associated with amounts of vegetative cover and food availability (Lin et al. 2006), and landscape heterogeneity has been shown to alter key aspects of small-mammal ecology (Adler 1985; Kaufman and Kaufman 1990; Stapp and Van Horne 1997; Corbalán et al. 2006; Wauters et al. 2007). Deer mice (*Peromyscus maniculatus* (Wagner, 1845)), generalist omnivores on the Great Plains, show increased population density in agricultural fields (e.g., Kaufman and Kaufman 1989; Sullivan et al. 1998), but the mechanism for this increase is not well understood. The ability of deer mice to exploit a wide range of habitats and to subsequently reach high densities in crop fields may be related to the dietary flexibility of this species, which is capable of consuming green vegetation, seeds, and arthropods, and may shift diet composition based on habitat and food availability (Jameson 1952; Whitaker 1966; Morris 1997; Ortega et al. 2004). However, most diet studies of deer mice to date have been based on stomach-content analysis, which represents only short-term diet and may also be affected by important detection and analytical biases (Hansson 1970). Thus, we lack a more general understanding of the trophic ecology of deer mice and potential changes to diet of deer mice caused by human alterations to habitat. In addition, to enhance our perspective on predator habitat use, e.g., from food caches of deer mice as in Poulin et al. (2001), there is a current need to develop simple markers of agricultural provenance for abundant small mammals like deer mice.

Changes to biogeochemical processes associated with anthropogenic N inputs to cropland may alter carbon and nitrogen stable isotope ratios, thereby creating a useful means by which animal diet and habitat use can be examined. Fertilizer application and other forms of management in agricultural systems have been found to cause enrichment of soil ^{15}N in relation to atmospheric nitrogen (δ^{15}N), and changes to carbon cycling have also been reported (reviewed in Makarov 2008; Stevenson et al. 2010). Inorganic fertilizers generally have δ^{15}N values near 0‰ (e.g., nitrate $\delta^{15}\mathrm{N} = 2.26$‰, ammonia $\delta^{15}\mathrm{N} = 0.51$‰; Shearer et al. 1974), so higher soil δ^{15}N values likely stem from enhanced isotopic fractionation owing to nitrate leaching, denitrification, and ammonia volatilization (Stevenson et al. 2010). Any such change to soil δ^{15}N values is likely to be reflected in the δ^{15}N of vegetation, which is at least in part determined by the isotope ratios of nitrogen compounds in the soil (although other factors may also play a role; reviewed in Makarov 2008). As a result, agricultural activity may act to create a chemical marker in the tissues of consumers, which reflect dietary δ^{15}N values. The potential for animal δ^{15}N values to vary in fertilized agricultural areas has previously been demonstrated (e.g., big brown bats, *Eptesicus fuscus* (Beauvois, 1796); Sullivan et al. 2006). However, to our knowledge the influence of land use on stable isotopes values in a flexible dietary generalist has not been examined in a grassland ecosystem.

Stable isotopes of nitrogen are generally used to investigate food-web structure, as the tissues of consumers in terrestrial systems become enriched in heavy nitrogen (^{15}N) by, on average, +2.3‰ to +3.4‰ with each trophic level (DeNiro and Epstein 1981; McCutchan et al. 2003). Animal δ^{15}N values can as a result be used to determine diet and to estimate trophic relationships within a food web. More recently, patterns of ^{15}N enrichment have also been compared between habitats to assess changes in feeding ecology that may be associated with human disturbance (Nakagawa et al. 2007; Gibb and Cunningham 2011). Different δ^{15}N values for individuals of the same species occupying different habitats may be used to infer a shift in diet, with greater ^{15}N enrichment indicating a possible increase in consumer trophic level. Agricultural land use may cause significant changes to resource availability, and food-web structure is known to have important consequences for the functioning of ecosystems (Thébault and Loreau 2003). Thus, dietary shifts and trophic position may influence the population size, density, and quality of individuals that a given habitat can support.

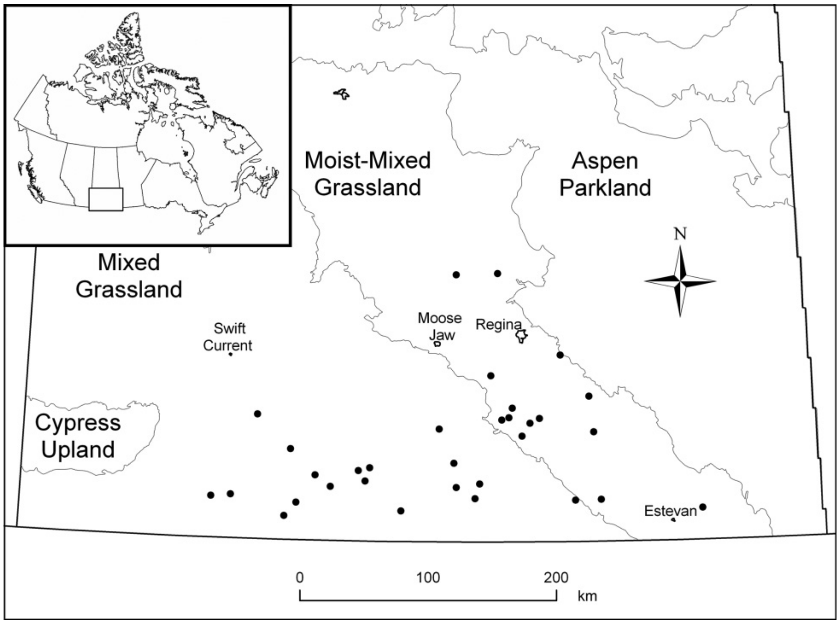
Here we assess how agricultural land use affects variation in nitrogen and carbon stable isotope ratios, trophic level, relative density, and body condition of deer mice on the northern Great Plains. Our study had three primary objectives: (1) to evaluate whether stable isotopes of nitrogen and carbon can be used to distinguish among small mammals captured within cropland, tame grass, and native prairie; (2) to determine whether agricultural land use causes systematic changes in trophic ecology of deer mice; and (3) to quantify changes in population density and body condition in agricultural habitats, which are important features of adaptation to different environments (Millar 1981). At the landscape level, we predicted that δ^{15}N values would be higher for soil, vegetation, and deer mice on cropland compared with native prairie owing to use of anthropogenic fertilizer. We did not make specific predictions regarding the direction or magnitude of variation in trophic level among habitats, but generally we expected trophic level to reflect potential differences in the relative availability of primary food resources (i.e., arthropods vs. vegetation). Similarly, we predicted that body condition would reflect potential variation in the overall availability of food resources. Finally, we predicted that deer mice would have increased population density in areas of cropland compared with native prairie, as this effect has been demonstrated in other study areas (e.g., Kaufman and Kaufman 1990).

Materials and methods

Study area and sample collection

Our study was conducted within a large region of the northern Great Plains in southern Saskatchewan, Canada, from June to August 2009 (Fig. 1). Much of the mixed and moist-mixed native grassland in this area has been converted to cropland, used largely for production of wheat, canola, flax, peas, lentils, and oats. A small proportion of the land has been seeded to non-native grasses (tame grass) for the production of hay or for use as livestock pasture. The majority of native-prairie pastures are grazed by cattle. We sampled

Fig. 1. Map of study site showing the locations sampled (●) and the major ecoregions in southern Saskatchewan, Canada.



soil, dominant vegetation (all of which were C_3 plants), and deer mice from habitat triads consisting of crop, tame grass, and native prairie at each of 23 locations (Fig. 1). Sites within triads were 2–10 km apart so that they would be independent but geographically similar. Using a landcover map, sites of native grass and tame grass were chosen to be comparable in size within a triad, and a crop site was chosen at random within the area of each triad. Crop type was not considered in our analysis (only “crop” as a land-use category), but we sampled a variety of crop plants over our large study area, including wheat, canola, flax, peas, oats, and lentils. At each location, samples of soil from 0 to 50 mm below the surface and dominant aboveground vegetation were collected from a randomly selected point. To sample deer mice, 1–3 transects of snap traps were set per habitat type for three nights. Transects consisted of 50 snap-traps set 10 m apart and were located at least 100 m from field edges. Traps were baited with a mixture of peanut butter, rolled oats, and bird seed and checked daily. Mass was used to assign mice to juvenile (<14 g) or adult (>17 g) age classes as in Fairbairn (1977). We also recorded sex using external anatomical features (McCravy and Rose 1992). Mice were stored in a freezer until laboratory processing. Mice were captured and handled according to procedures approved by the University of Regina President’s Committee on Animal Care.

Stable isotopes analysis

To examine variation in nitrogen and carbon stable isotopes ratios among land-use types (i.e., crop, tame grass, native prairie), we analyzed soil and vegetation samples corresponding to sites from which mice were selected for analysis (see below). For soil, whole samples were dried at 55 °C for 72 h and ground with a mortar and pestle. A subsample was more finely ground with an amalgamator and 10–15 mg weighed into tin capsules to be analyzed. For vegetation, a portion of the aboveground plant (leaves and stem) was rinsed with deionized water and dried. Dried samples were ground with an amalgamator and 3–5 mg weighted into tin capsules. We selected one representative adult deer mouse from each of 20 crop-field, 19 tame-grass, and 17 native-prairie sites. When possible, deer mice from sites within complete triads were chosen for analysis; in some instances this was not possible because of low capture rates. Muscle tissue, which can be used to determine diet in the 1–2 months prior to trapping (N half-life of muscle from deer mice = 24.8 days; Miller et al. 2008), was removed from both hind limbs of individual mice and frozen for storage. Tissue was later thawed, rinsed with deionized water, and dried at 55 °C for 72 h. Dried samples were ground to a fine powder with an amalgamator and 0.5–1.0 mg of each sample weighed into tin capsules.

All samples of soil, vegetation, and muscle from deer mice were analyzed with an isotope ratio mass spectrometer (Finnigan Delta Plus; Environmental Quality Analysis Laboratory, University of Regina, Regina, Saskatchewan, Canada). We did not perform lipid extractions on mouse tissues, as this has been deemed unnecessary for deer mice (Smith et al. 2010) and, in general, for terrestrial mammals with low (<10%) lipid content (Post et al. 2007). Stable isotope ratios are expressed using delta notation (δ),

$$\delta = (R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1) \times 1000$$

where R is the ratio of the fractional abundance of heavy to light isotopes ($^{15}N/^{14}N$ or $^{13}C/^{12}C$), which is measured against atmospheric nitrogen or Vienna–PeeDee Belemnite standards for nitrogen and carbon, respectively. The analytical precision of the mass spectrometer is 0.2‰; replicate runs of the same samples generally did not deviate by more than this value.

Capture rates and body-condition analysis

Relative density of deer mice was compared among habitat types based on the number of captures per 100 trap-nights. To determine body condition, we measured the combined head and body length (nose to anus) of all mice to the nearest millimetre and weighed mice to the nearest 0.1 g. Mice that were partly decomposed or otherwise not intact were excluded from analysis. We used a total of 440 adult males and nonreproductive adult females to compare condition among the three land-cover types; of these, 208 were captured from crop fields, 188 from tame-grass plots, and 44 from native-prairie sites. Data for males and females were pooled, as there was no significant difference in variance ($F_{[47,369]}$ = 1.09, $p = 0.341$), slope ($F_{[1,436]}$ = 0.80, $p = 0.373$), or intercept ($F_{[1,437]}$ = 0.39, $p = 0.533$) between male and female length–mass regressions. Both mass and length measurements were log-transformed prior to regression analysis.

Statistical analyses

Nitrogen and carbon stable isotope ratios for soil, vegetation, and muscle tissue were compared separately among the three land-cover types using an analysis of variance (ANOVA). Variances by habitat for soil δ^{15}N and vegetation δ^{13}C were found to be unequal (Levene's statistic) and were therefore checked for robustness using Games–Howell post hoc testing. All other post hoc comparisons were done using Tukey's test. Trophic shifts ($\Delta\delta^{15}$N) from vegetation to muscle tissue were calculated for each site by subtracting δ^{15}N of vegetation from that of muscle from deer mice from the same site and compared among habitat types using ANOVA. The relationship between soil and muscle δ^{15}N, as well as vegetation and muscle δ^{15}N, was examined with ordinary least-squares (OLS) regression. Capture rates of deer mice and vegetation carbon-to-nitrogen (C:N) ratios were compared among land-use types using a single-factor ANOVA. To analyze body condition, we generated residuals from OLS linear regression of log-transformed mass on log-transformed body length. Tests of assumptions for heteroscedasticity and linearity of residuals were performed as in Schulte-Hostedde et al. (2005). We used residual values as an index of condition and a single-factor ANOVA to compare the index among land-cover types. All data sets met assumptions for normal distributions unless otherwise reported. Tests for significance employed an α value of 0.05 and were performed using Statistix version 9 (Analytical Software) and PASWStatistics version 18.0 (SPSS Inc., Chicago, Illinois, USA).

Results

Stable isotopes analysis

Nitrogen stable isotope ratios for soil and vegetation varied significantly among the three habitat types (Table 1; ANOVA; soil: $F_{[2,52]}$ = 12.8, $p < 0.001$; vegetation: $F_{[2,51]}$ = 5.3, $p = 0.008$). Post hoc comparisons showed that soil δ^{15}N values in crop and tame-grass fields were 2.3‰–2.4‰ higher, on average, compared with those in native prairie (Table 1). The mean δ^{15}N value for vegetation in crop fields was significantly enriched relative to native prairie (+2.8‰), but mean δ^{15}N values for vegetation on tame-grass fields and native prairie were not significantly different. All three habitat types followed the same general pattern of having relatively low δ^{15}N values for vegetation (depleted by 4‰–5‰) compared with soil sampled from the same fields. C:N ratios of vegetation were also found to vary significantly among the three land-use types ($F_{[2,50]}$ = 23.3, $p < 0.001$). Post hoc comparisons revealed that the C:N ratios of vegetation on native prairie (33.1 ± 9.3, mean ± SD) and tame grass (29.5 ± 8.8) were approximately twofold higher than that of vegetation sampled from cropland (15.7 ± 5.8).

Soil δ^{13}C varied significantly among the three habitat types (Table 1; $F_{[2,52]}$ = 6.019, $p = 0.004$). Post hoc comparisons showed that soil from native prairie was significantly depleted in ^{13}C compared with crop and tame grass by, on average, –3.1‰ to –3.2‰. Vegetation δ^{13}C, however, did not differ significantly with land use (Table 1; $F_{[2,51]}$ = 2.1, p = 0.135), varying by only 0.8‰–1.8‰, on average. All three land-use types followed the same general pattern of soil being depleted in ^{13}C (1‰–6‰) relative to vegetation sampled from the same sites. Crop fields tended to have the largest difference between soil and vegetation δ^{13}C values, as well as the highest variance among sites (Table 1).

In contrast to results for soil and vegetation, and despite a significant relationship between soil and muscle δ^{15}N (r = 0.550, $p < 0.001$; data not shown) and vegetation and muscle δ^{15}N ($r = 0.619$, $p < 0.001$; data not shown), δ^{15}N values for muscle from deer mice did not vary by habitat type (Table 1; $F_{[2,53]}$ = 0.8, p = 0.461). However, trophic enrichment ($\Delta\delta^{15}$N) of muscle from deer mice did vary significantly with land use (Table 1; $F_{[2,51]}$ = 7.7, p = 0.001). Post hoc comparisons showed that trophic enrichment of deer mice relative to vegetation was greater for native prairie (6.4‰ ± 1.6‰, mean ± SD) and tame grass (5.9‰ ± 2.0‰) than for cropland (3.9‰ ± 2.3‰). Specifically, deer mice were enriched in ^{15}N by 2.5‰ more, on average, in native prairie compared with crop fields, but only by 0.5‰ more compared with those in tame grass. Muscle δ^{13}C from deer mice did not vary with land use (Table 1; $F_{[2,53]}$ = 1.524, p = 0.227), and there was also no significant variation in trophic enrichment of carbon ($\Delta\delta^{13}$C; data not shown; $F_{[2,51]}$ = 2.012, p = 0.144).

Capture rates and body-condition analysis

Deer mouse captures per 100 trap-nights varied among the three land uses (Fig. 2; $F_{[2,66]}$ = 5.1, $p < 0.01$). Post hoc comparisons indicated that the more than twofold higher capture rates on crop-field plots (7.4 ± 5.3, mean ± SD) and tame-grass plots (6.8 ± 5.6) were significantly greater than that for the native-prairie plots (3.1 ± 3.2). A significant proportion of variation in the body mass of adult deer mice for all captures was explained by head and body length (r^2 = 0.306, $p < 0.0001$). Mean residual values (body-condition index) were very similar and near 0 for mice caught on all three land-use types (crop = 0.004 ± 0.05, mean ± SD; tame grass = –0.004 ± 0.04, native = 0.000 ± 0.04; $F_{[1,438]}$ = 1.3, p = 0.277), indicating that mass was generally as expected based on the regression; i.e., mice were in similar body condition on all habitats. Likewise, body mass (g) itself also did not vary with habitat type (crop = 21.1 ± 2.8; tame grass = 20.9 ± 2.6; native prairie = 21.4 ± 2.9; ANOVA: $F_{[2,438]}$ = 0.60, p = 0.547).

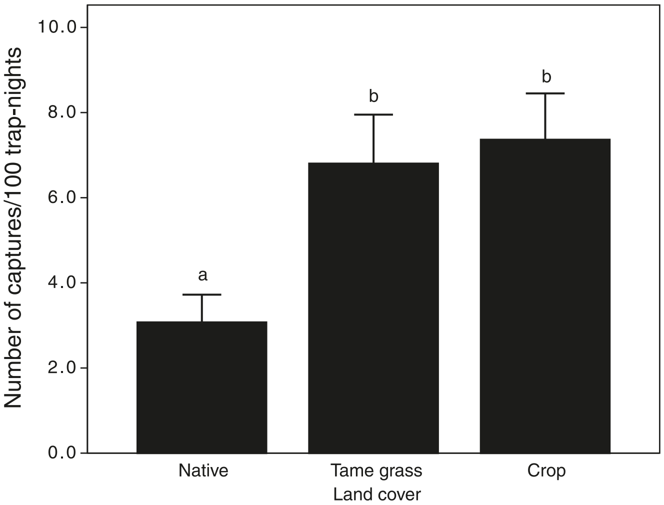
Discussion

Agricultural land use altered the δ^{15}N values of soil and vegetation in our Great Plains study area as predicted based on findings in other locations and habitats. Soil δ^{15}N values

Table 1. Nitrogen and carbon stable isotope values of various sample types and levels of trophic enrichment (mean ± SD) for deer mice (*Peromyscus maniculatus*), sampled from each of three land-cover types on the northern Great Plains.

	Soil			Vegetation			Muscle			
	δ^{15}N	δ^{13}C	*n*	δ^{15}N	δ^{13}C	*n*	δ^{15}N	δ^{13}C	*n*	$\Delta\delta^{15}$N
Native	4.8±2.1	–27.5±2.8	17	0.9±2.6	–26.5±3.2	17	7.2±2.1	–24.3±0.8	17	6.4±1.6
Tame	7.1±1.3	–30.6±3.8	19	2.0±2.1	–27.3±1.0	18	7.9±1.3	–23.7±1.7	19	5.9±2.0
Crop	7.2±1.4	–30.7±2.6	19	3.7±3.1	–23.7±1.7	19	7.6±1.3	–23.9±0.6	20	3.9±2.3

Fig. 2. Number (mean + 1 SE) of captures per 100 trap-nights for deer mice (*Peromyscus maniculatus*) on each land-cover type. Mean values for categories with the same letter are not significantly different from one another ($p < 0.05$).



were, on average, 2.4‰ higher on cropland than on native prairie, a level of enrichment similar to what has been found in other anthropogenically altered systems. For example, Stevenson et al. (2010) also demonstrated variation in soil δ^{15}N values according to the intensity of human land use, with the lowest values found for indigenous forest (2.1‰) and the highest for cropland (6.2‰). They suggested that because all major N inputs to their system were near 0‰ (e.g., the mean value for urea was –1.1‰), enrichment in soil δ^{15}N was likely a result of fractionation during N losses. Although the type and rate of fertilizer application are not known specifically for our study sites, most fertilizer nitrogen compounds have δ^{15}N values near 0‰ (Shearer et al. 1974; Vitòria et al. 2004), suggesting that the enrichment documented here was also caused by the fractionating loss of light nitrogen. For each land-use type, vegetation δ^{15}N values were depleted relative to soil, which is a generally observed pattern of enrichment (Amundson et al. 2003). Although there was substantial variance within land-use types, nitrogen stable isotopes appear to provide a marker of anthropogenic inputs for vegetation and soil in our study area.

In contrast, δ^{15}N of deer mice did not vary in absolute value among habitats, likely owing to variation in the levels of trophic enrichment ($\Delta\delta^{15}$N). This finding suggests that while nitrogen isotopes were not useful as markers of habitat use in our study area, δ^{15}N values did reveal changes in the diet of deer mice in the different habitats sampled. Trophic enrichment for deer mice captured within native prairie ($\Delta\delta^{15}$N = 6.4‰) was, on average, 2.5‰ higher than for mice in cropland ($\Delta\delta^{15}$N = 3.9‰) and 2.0‰ greater than for mice in hay fields ($\Delta\delta^{15}$N = 5.9‰). As mean $\Delta\delta^{15}$N can vary from +2.3‰ to +3.4‰ (DeNiro and Epstein 1981; McCutchan et al. 2003), the variation found here reflects a shift in diet of approximately one full trophic level. Mice living in crop fields appear to have a predominantly plant-based diet, whereas arthropods may be a more important dietary source for mice in native prairie and hay fields. Anthropogenic changes to crop fields therefore appear to have caused a marked shift in the trophic ecology of this small-mammal species.

The principal factors responsible for the altered trophic status of deer mice in these different land-use types are not completely understood. Deer mice are clearly flexible in their diet, and although arthropods are likely a preferred food resource because of their low C:N ratio (i.e., higher nutritional quality; Shaner and Macko 2011), varying proportions of arthropods and vegetation can be incorporated based on availability (e.g., Pearson et al. 2000). A possible explanation for our results is that seeds and vegetation were highly abundant on cropland, resulting in a shift in diet towards the producer trophic level for deer mice inhabiting these sites. The greater density of deer mice found for cropland and tame grass compared with native prairie helps to support this conclusion, as a similar pattern of variation in population density among agricultural land-use types has previously been linked to a higher abundance of seeds in crop fields (Kaufman and Kaufman 1990). In addition, our finding that crop plants had a mean C:N ratio that was approximately twofold lower than that of vegetation from native-prairie and tame-grass sites further suggests that food on cropland may have not only been present at higher quantities (e.g., Kaufman and Kaufman 1990), but that the vegetation may have been of higher quality as well.

It should be noted that our results are based on δ^{15}N values for leaves and stems only and values for seeds and arthropods were not separately examined. However, consistent variation in δ^{15}N values among aboveground plant parts (i.e., leaves and stems vs. seeds) has not generally been observed (Codron et al. 2005), and δ^{15}N values for seeds are therefore likely to have been similar to those obtained via our sampling. In addition, vegetation δ^{15}N values provide a baseline for each habitat, which together with known levels of trophic enrichment from the literature (+2.3‰ to +3.4‰) allows us to re-construct approximate trophic interactions without having δ^{15}N values for arthropods specifically. The magnitude of variation in $\Delta\delta^{15}$N for deer mice found here (+2.0‰ to +2.5‰ for native prairie compared with tame grass and crop, respectively) represents approximately one full trophic level, and we can therefore conclude that there was a shift in diet for mice inhabiting the different land-use types.

Deer mice were in similar body condition in all habitats despite differences in their relative density and trophic status. Thus, the best metric to indicate habitat quality for deer mice is likely relative density; i.e., all habitats support deer mice in good condition, but crop and tame-grass fields support more than twice as many animals as native prairie. An alternative explanation is that the residual index of body condition based on the length–mass regression used here did not detect differences by habitat because of the low body fat percentage of our study species. For example, Schulte-Hostedde et al. (2001) suggested that fat content (approximately 5%) of the body of deer mouse may be too low for variation to be reflected in overall body mass. The same authors, however, concluded that this index of condition likely remains useful for determining other differences in body composition that may relate to fitness, such as variation in lean dry mass. For this study, we conclude that there was no evidence of systematic variance in body condition by habitat type, and therefore no important consequences of relative density and trophic status for this component of fitness.

Stable carbon isotope (δ^{13}C) ratios were relatively uninformative for determining land use in our study system. Although mean soil values for δ^{13}C were significantly depleted in anthropogenic habitats (3.1‰–3.2‰ for crop and hay fields), plant carbon is derived from atmospheric CO_2, and the δ^{13}C value of vegetation therefore determined by the photosynthetic pathway used (Peterson and Fry 1987). As most plant species in southern Saskatchewan including the major crop varieties have C_3 pathways (Wang et al. 2006), our finding of a lack of variation in δ^{13}C by location or land use is not unexpected (DeNiro and Epstein 1978). Despite the potential use of animal δ^{13}C values to distinguish between agricultural habitats (e.g., invertebrates in hay and hedgerows vs. corn and soybean fields; Girard et al. 2011), the usefulness of this marker is clearly restricted to systems in which the major land types differ in C_3 and C_4 plant varieties.

In conclusion, results from this study suggest that the feeding ecology and population density of deer mice are significantly influenced by the habitat variation associated with agricultural activity. Human land use may therefore have substantial effects on small-mammal ecology, but certain species such as deer mice may also be highly adaptable as indicated by the lack of response in body condition. The extent to which the results of this study can be applied to other small-mammal communities is currently unknown, as the response of individual species of small mammals to human activity is often highly species-specific (Clark et al. 1998). Nitrogen and carbon stable isotopes revealed several interesting properties of grassland ecosystems dominated by agriculture, including a dramatic trophic shift in a generalist omnivore but were not useful as general markers of habitat use in our study area.

Acknowledgements

The research was funded though Saskatchewan Environment's Fish and Wildlife Development Fund, Environment Canada's Habitat Stewardship Program, the Innovation and Science Fund of the province of Saskatchewan, the Natural Sciences and Engineering Research Council of Canada, and the Canada Research Chairs program. We thank the Royal Saskatchewan Museum and the Friends of the Royal Saskatchewan Museum for logistic support, as well as E. Jenkins, for providing assistance with rodent dissections. We also thank H. Hennin, B. Hennin, and K. Neudorf for assistance in the field. Two anonymous reviewers provided helpful feedback on a previous version of this work.

References

Adler, G.H. 1985. Habitat selection and species interactions: an experimental analysis with small mammal populations. Oikos, **45**(3): 380–390. doi:10.2307/3565574.

Amundson, R., Austin, A.T., Schuur, E.A.G., Yoo, K., Matzek, V., Kendall, C., Uebersax, A., Brenner, D., and Baisden, W.T. 2003. Global patterns of the isotopic composition of soil and plant nitrogen. Global Biogeochem. Cycles, **17**(1): 1031–1041. doi:10.1029/2002GB001903.

Askins, R.A., Chávez-Ramírez, F., Dale, B.C., Haas, C.A., Herkert, J.R., Knopf, F.L., and Vickery, P.D. 2007. Conservation of grassland birds in North America: understanding ecological processes in different regions. Report of the AOU Committee on Conservation. Ornithol. Monogr. **64**: 1–46.

Clark, B.K., Clark, B.S., Homerding, R., and Munsterman, W.E. 1998. Communities of small mammals in six grass-dominated habitats of southeastern Oklahoma. Am. Midl. Nat. **139**(2): 262–268. doi:10.1674/0003-0031(1998)139[0262:COSMIS]2.0.CO;2.

Clayton, K.M., and Schmutz, J.K. 1999. Is the decline of Burrowing Owls *Speotyto cunicularia* in prairie Canada linked to *Speotyto cunicularia* changes in Great Plains ecosystems? Bird Conserv. Int. **9**(2): 163–185. doi:10.1017/S0959270900002288.

Codron, J., Codron, D., Lee-Thorp, J.A., Sponheimer, M., Bond, W.J., de Ruiter, D., and Grant, R. 2005. Taxonomic, anatomical, and spatio-temporal variations in the stable carbon and nitrogen isotopic compositions of plants from an African savanna. J. Archaeol. Sci. **32**(12): 1757–1772. doi:10.1016/j.jas.2005.06.006.

Corbalán, V., Tabeni, S., and Ojeda, R.A. 2006. Assessment of habitat quality for four small mammal species of the Monte Desert, Argentina. Mamm. Biol. **71**(4): 227–237. doi:10.1016/j.mambio.2006.02.002.

DeNiro, M.J., and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta, **42**(5): 495–506. doi:10.1016/0016-7037(78)90199-0.

DeNiro, M.J., and Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta, **45**(3): 341–351. doi:10.1016/0016-7037(81)90244-1.

Fairbairn, D.J. 1977. The spring decline in deer mice: death or dispersal? Can. J. Zool. **55**(1): 84–92. doi:10.1139/z77-009.

Gibb, H., and Cunningham, S.A. 2011. Habitat contrasts reveal a shift in the trophic position of ant assemblages. J. Anim. Ecol. **80**(1): 119–127. doi:10.1111/j.1365-2656.2010.01747.x. PMID: 20831728.

Girard, J., Baril, A., Mineau, P., and Fahrig, L. 2011. Carbon and nitrogen stable isotope ratios differ among invertebrates from field crops, forage crops, and non-cropped land uses. Écoscience, **18**(2): 98–109. doi:10.2980/18-2-3390.

Hansson, L. 1970. Methods of morphological diet micro-analysis in rodents. Oikos, **21**(2): 255–266. doi:10.2307/3543682.

Herkert, J.R. 1995. Analysis of Midwestern breeding bird population trends: 1966- 1993. Am. Midl. Nat. **134**(1): 41–50. doi:10.2307/2426481.

Jameson, E.W., Jr. 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boylei*, in the northern Sierra Nevada, California. J. Mammal. **33**(1): 50–60. doi:10.2307/1375640.

Kamler, J.F., Ballard, W.B., Fish, E.B., Lemons, P.R., Mote, K., and

Perchellet, C.C. 2003. Habitat use, home ranges, and survival of swift foxes in a fragmented landscape: conservation implications. J. Mammal. **84**(3): 989–995. doi:10.1644/BJK-033.

Kaufman, D.W., and Kaufman, G.A. 1989. Nongame wildlife management in Central Kansas: implications of small mammal use of fencerows, fields, and prairie. Trans. Kans. Acad. Sci. **92**(3–4): 198–205. doi:10.2307/3628453.

Kaufman, D.W., and Kaufman, G.A. 1990. Small mammals of wheat fields and fallow wheat fields in north-central Kansas. Trans. Kans. Acad. Sci. **93**(1–2): 28–37. doi:10.2307/3628126.

Laliberte, A.S., and Ripple, W.J. 2004. Range contractions of North American carnivores and ungulates. Bioscience, **54**(2): 123–138. doi:10.1641/0006-3568(2004)054[0123:RCONAC]2.0.CO;2.

Lin, Y.K., Keane, B., Isenhour, A., and Solomon, N.G. 2006. Effects of patch quality on dispersal and social organization of prairie voles: an experimental approach. J. Mammal. **87**(3): 446–453. doi:10.1644/05-MAMM-A-201R1.1.

Makarov, M.I. 2008. The nitrogen isotopic composition in soils and plants: its use in environmental studies. Eur. J. Soil Sci. **42**: 1335–1347.

McCravy, K.W., and Rose, R.K. 1992. An analysis of external features as predictors of reproductive status in small mammals. J. Mammal. **73**(1): 151–159. doi:10.2307/1381877.

McCutchan, J.H., Jr., Lewis, W.M., Jr., Kendall, C., and McGrath, C.C. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen and sulfur. Oikos, **102**(2): 378–390. doi:10.1034/j.1600-0706.2003.12098.x.

Millar, J.S. 1981. Body composition and energy reserves of northern *Peromyscus leucopus*. J. Mammal. **62**(4): 786–794. doi:10.2307/1380599.

Miller, J.F., Millar, J.S., and Longstaffe, F.J. 2008. Carbon- and nitrogen-isotope tissue–diet discrimination and turnover rates in deer mice, *Peromyscus maniculatus*. Can. J. Zool. **86**(7): 685–691. doi:10.1139/Z08-042.

Morris, D.W. 1997. Optimally foraging deer mice in prairie mosaics: a test of habitat theory and absence of landscape effects. Oikos, **80**(1): 31–42. doi:10.2307/3546513.

Murphy, M.T. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. Auk, **120**(1): 20–34. doi:10.1642/0004-8038(2003)120[0020:APTWTE]2.0.CO;2.

Nakagawa, M., Hyodo, F., and Nakashizuka, T. 2007. Effect of forest use on trophic levels of small mammals: an analysis using stable isotopes. Can. J. Zool. **85**(4): 472–478. doi:10.1139/Z07-026.

Ortega, Y.K., Pearson, D.E., and McKelvey, K.S. 2004. Effects of biological control agents and exotic plant invasion on deer mouse populations. Ecol. Appl. **14**(1): 241–253. doi:10.1890/02-5276.

Pearson, D.E., McKelvey, K.S., and Ruggiero, L.F. 2000. Non-target effects of an introduced biological control agent on deer mouse ecology. Oecologia (Berl.), **122**(1): 121–128. doi:10.1007/PL00008828.

Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**(1): 293–320. doi:10.1146/annurev.ecolsys.18.1.293.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montana, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia (Berl.), **152**(1): 179–189. doi:10.1007/s00442-006-0630-x. PMID:17225157.

Poulin, R.G., Wellicome, T.I., and Todd, L.D. 2001. Synchronous and delayed numerical responses of a predatory bird community to a vole outbreak on the Canadian prairies. J. Raptor Res. **35**: 288–295.

Samson, F.B., Knopf, F.L., and Ostlie, W.R. 2004. Great plains ecosystems: past, present, and future. Wildl. Soc. Bull. **32**(1): 6–15. doi:10.2193/0091-7648(2004)32[6:GPEPPA]2.0.CO;2.

Schulte-Hostedde, A.I., Millar, J.S., and Hickling, G.J. 2001. Evaluating body condition in small mammals. Can. J. Zool. **79**(6): 1021–1029. doi:10.1139/z01-073.

Schulte-Hostedde, A.I., Zinner, B., Millar, J.S., and Hickling, G.J. 2005. Restitution of mass–size residuals: validating body condition indices. Ecology, **86**(1): 155–163. doi:10.1890/04-0232.

Shaner, P.-J.L., and Macko, S.A. 2011. Trophic shifts of a generalist consumer in response to resource pulses. PLoS ONE, **6**(3): e17970. doi:10.1371/journal.pone.0017970. PMID:21437248.

Shearer, G.B., Kohl, D.H., and Commoner, B. 1974. The precision of determinations of the natural abundance of nitrogen-15 in soils, fertilizers, and shelf chemicals. Soil Sci. **118**(5): 308–316. doi:10.1097/00010694-197411000-00005.

Smith, J.J., Millar, J.S., Longstaffe, F.J., and Boonstra, R. 2010. The effect of metabolic rate on stable carbon and nitrogen isotope compositions in deer mice, *Peromyscus maniculatus*. Can. J. Zool. **88**(1): 36–42. doi:10.1139/Z09-116.

Stapp, P., and Van Horne, B. 1997. Response of deer mice (*Peromyscus maniculatus*) to shrubs in shortgrass prairie: linking small-scale movements and the spatial distribution of individuals. Funct. Evol. **11**(5): 644–651. doi:10.1046/j.1365-2435.1997.00133.x.

Stevenson, B.A., Parfitt, R.L., Schipper, L.A., Baisden, W.T., and Mudge, P. 2010. Relationship between soil δ^{15}N, C/N and N losses across land uses in New Zealand. Agric. Ecosyst. Environ. **139**(4): 736–741. doi:10.1016/j.agee.2010.10.020.

Sullivan, T.P., Sullivan, D.S., Hogue, E.J., Lautenschlager, R.A., and Wagner, R.G. 1998. Population dynamics of small mammals in relation to vegetation management in orchard agroecosystems: compensatory responses in abundance and biomass. Crop Prot. **17**(1): 1–11. doi:10.1016/S0261-2194(98)80006-9.

Sullivan, J.C., Buscetta, K.J., Michener, R.H., Whitaker, J.O., Jr., Finnerty, J.R., and Kunz, T.H. 2006. Models developed from δ^{13}C and δ^{15}N of skin tissue indicate non-specific habitat use by the big brown bat (*Eptesicus fuscus*). Écoscience, **13**(1): 11–22. doi:10.2980/1195-6860(2006)13[11:MDFCAN]2.0.CO;2.

Thébault, E., and Loreau, M. 2003. Food-web constraints on biodiversity–ecosystem functioning relationships. Proc. Natl. Acad. Sci. U.S.A. **100**(25): 14949–14954. doi:10.1073/pnas.2434847100. PMID:14638942.

Vitòria, L., Otero, N., Soler, A., and Canals, A. 2004. Fertilizer characterization: isotopic data (N, S, O, C, and Sr). Environ. Sci. Technol. **38**(12): 3254–3262. doi:10.1021/es0348187. PMID:15260321.

Wang, R.Z., Liu, X.Q., and Bai, Y. 2006. Photosynthetic and morphological functional types for native species from mixed prairie in southern Saskatchewan, Canada. Photosynthetica, **44**(1): 17–25. doi:10.1007/s11099-005-0153-4.

Wauters, L.A., Vermeulen, M., Van Dongen, S., Bertolino, S., Molinari, A., Tosi, G., and Matthysen, E. 2007. Effects of spatio-temporal variation in food supply on red squirrel *Sciurus vulgaris* body size and body mass and its consequences for some fitness components. Ecography, **30**: 51–65.

Whitaker, J.O. 1966. Food of *Mus musculus*, *Peromyscus maniculatus bairdi*, and *Peromyscus leucopus* in Vigo County, Indiana. J. Mammal. **47**(3): 473–479. doi:10.2307/1377688.

Wilson, J.D., Whittingham, M.J., and Bradbury, R.B. 2005. The management of crop structure: a general approach to reversing the impacts of agricultural intensification on birds? Ibis, **147**(3): 453–463. doi:10.1111/j.1474-919x.2005.00440.x.