

# Predator size and distance to edge: is bigger better?

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**Abstract:** I investigated the use of edge by soil arthropods by testing whether mesoarthropod predators were closer to edge than expected and whether large predators were closer to edge than small predators. The experimental design consisted of 120 boxes, each covering 200 cm<sup>2</sup> of soil, that were randomly distributed within a 0.13-km<sup>2</sup> aspen stand located in the Canadian prairie region. Each 2-kg box depressed the leaf litter, creating a microhabitat island for soil arthropods consisting of 61 cm of edge. During 20 weekly surveys from May to September in 1997 and 1998, numbers and distribution of arthropods located immediately beneath the boxes were recorded. Mesoarthropod predators were found closer to edge than expected. Centipedes, beetle larvae, and predatory mites (Acari) were found at intermediate distances to edge, whereas beetles, ants, adult flies, bugs, and spiders were distributed adjacent to edge. Generally, larger mesoarthropod predators were found closer to edge than smaller individuals, within each taxonomic group. Collembola, the major mesofauna prey, were distributed randomly with respect to edge during wet periods of high density. During the subsequent dry periods, reduced densities of Collembola occurred and distribution became skewed, with greater numbers in interior areas and reduced densities near edges. Temperature and moisture under the boxes did not vary with distance to edge, although the microclimate was cooler and more humid under the experimental boxes relative to beyond the boxes. These results support the hypotheses that mesoarthropod predators forage along box edges (i.e., linear corridors) and that larger individuals may gain access to edge owing to their larger size, although alternative explanations are possible, depending on the particular taxonomic group.

**Résumé :** J'ai étudié l'utilisation des bordures chez des arthropodes du sol en essayant de déterminer si les mésoarthropodes prédateurs sont plus près des bordures que prévu et si les gros prédateurs se tiennent plus près des bordures que les petits prédateurs. Le protocole expérimental consistait à répartir au hasard 120 boîtes recouvrant chacune 200 cm<sup>2</sup> de sol dans un boisé de trembles de 0,13 km<sup>2</sup> dans la Prairie canadienne. Chaque boîte de 2 kg écrasait la litière de feuilles, créant un îlot de microhabitat constitué de 61 cm de bordure. Au cours de 20 relevés hebdomadaires, de mai à septembre en 1997 et 1998, le nombre et la répartition des arthropodes se trouvant immédiatement sous les boîtes ont été enregistrés. Les mésoarthropodes prédateurs se trouvaient plus près des bordures que prévu. Les mille-pattes, les larves de coléoptères et les acariens prédateurs ont été trouvés à des distances intermédiaires des bordures, alors que les coléoptères, les fourmis, les mouches adultes, les punaises et les araignées occupaient des positions adjacentes aux bordures. De façon générale, les gros mésoarthropodes prédateurs dans chacun des groupes taxonomiques se tenaient plus près des bordures que les prédateurs plus petits. Les collemboles, principales proies de la mésofaune, étaient répartis au hasard par rapport aux bordures durant les périodes humides de haute densité. Durant les périodes sèches subséquentes, la densité des collemboles était réduite et leur répartition suivait une tendance définie, c'est-à-dire qu'ils étaient plus nombreux dans les zones intérieures et leur densité était moindre le long des bordures. La température et l'humidité sous les boîtes n'ont pas varié en fonction de la distance des bordures, bien que le microclimat se soit avéré plus frais et plus humide sous les boîtes que dans les espaces entre les boîtes. Ces résultats supportent les hypothèses suivantes : les mésoarthropodes prédateurs cherchent leur nourriture le long des bordures des boîtes (i.e. dans des corridors linéaires) et les prédateurs les plus gros peuvent avoir accès aux bordures à cause de leur taille; cependant, d'autres explications sont possibles selon le groupe taxonomique.

[Traduit par la Rédaction]

## Introduction

One area of interest in studying the relationship between the environmental landscape and patterns in the distribution

and abundance of organisms (Urban et al. 1987; Wiens and Milne 1989; Gunnarsson 1990; Crist et al. 1992; Hamazaki 1996) is the effect of edge on trophic relations. For example, predator-prey interactions are influenced by landscape patterns (Wiens 1976; Turchin 1991). The distribution of prey influences the movement of predators across landscapes (Smith 1974; O'Neill et al. 1988; Kotliar and Wiens 1990; Kolasa and Rollo 1991) and the spatial configuration of prey consumed by predators has important consequences for the dynamics of nutrient and energy fluxes in ecosystems (Oksanen et al. 1981; Wiens et al. 1985; Schaefer 1995). One prediction of edge theory is that greater densities of predators occur within edge habitat and greater predation occurs close to edge (Kareiva 1987). For example, bird egg

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mortality rates are considerably greater near edges than in the interior (Paton 1994; Andr n 1995; Major and Kendal 1996; Hartley and Hunter 1998).

Edge features provide an opportunity to study habitat discontinuities that can affect the structure of animal communities at different scales (Huston 1994; Matheson and Larson 1998; Lidicker 1999). The experimental design used here to study trophic-level edge effects consisted of boxes distributed within a stand of undisturbed aspen (*Populus tremuloides*). The mass of the boxes depressed the litter layer in a manner similar to a rock on the forest floor. Microclimate differences under the box included increased humidity and decreased temperature, which offered a home to a diverse soil fauna community. The side of the box created a linear discontinuity (i.e., edge) between the undersurface of the box and the microclimate of the leaf litter. Previous research found microarthropods at higher densities in box patterns with less edge (S.H. Ferguson).<sup>2</sup> One explanation for this pattern is that the greater amount of edge favoured predation (e.g., Murcia 1995; Oehler and Litvaitis 1996) and, thus, microarthropods occurred in decreased numbers owing to greater predation by mesoarthropods along edges. Here, I test two hypotheses: (i) mesoarthropod predators are located closer to edge than microarthropods and (ii) large predators are closer to edge than small predators.

## Methods

The study area consisted of a 0.13-km<sup>2</sup> stand of undisturbed trembling aspen (*P. tremuloides*) located within 1.5 km of the city of Saskatoon in the prairie region of south-central Saskatchewan, Canada (52°10'N, 106°41'W). Grassland prairies include small patches of forest, such as the study site, with the canopy dominated by >40-year-old aspen, serviceberry (*Amelanchier* spp.) as the dominant understory, and a 4- to 6-cm organic soil horizon. Precipitation on dry-climate prairies is highly variable both within and between years (Sala and Lauenroth 1982). Monthly mean daily temperature (1961–1990 normal temperatures) varied from 3°C in April to 18.6°C in July (annual mean = 2.0°C) and precipitation varied from 19.7 mm in April to 63.4 mm in June (annual mean = 28.9 mm) (Environment Canada; www.cmc.ec.gc.ca/climate/normals). There is no evidence or known history of heavy grazing or other agriculture use of the site.

I randomly placed 24 groups of five boxes (total = 120 boxes, each weighing approximately 2 kg) within a 0.13-km<sup>2</sup> stand of aspen. Each box consisted of two 2-L milk cartons fitted together to create a 21 × 9.5 × 9.5 cm box (998 cm<sup>3</sup>) half filled with sand and weighing about 2 kg. Boxes depressed the soil an average of 1.3 cm (range 0.2–2.9 cm). The amount of edge for each box was equal to the perimeter of the box (61 cm). Milk cartons had a plastic coating and were red and white.

To view the arthropod community, I overturned boxes and recorded numbers, size, and distance to edge of the box for all mesoarthropods and some microarthropods. A total of 20 weekly surveys were conducted from 17 May to 4 October 1997 and another 20 weekly surveys were conducted from 4 April to 5 September 1998. Surveys were conducted between 11:00 and 17:00. Leaf litter was not moved and only arthropods directly under the box were recorded. For mesoarthropods, I placed a toothpick at the site of the first observation before distribution shifted as a response to the movement of the box. I measured the distance in millimetres from the centre of individual arthropods to the closest box edge.

An average of 0.6 mesoarthropods (range 0–7) were observed under each box. For ants (Formicidae), I only measured distance to edge if less than 3 ants were under an individual box, as large numbers of ants were associated with colonies. For the more numerous microarthropods (Collembola and Acari), I randomly selected two boxes every survey and recorded locations on a box-sized sheet of paper for later measurement of distance to edge. To obtain available distances to edge, I randomly generated and calculated the distance to edge for 100 location points (including edge, distance = 0.0 cm) within the digitized perimeter of a box, using SPANS<sup>TM</sup> geographic information system (SPANS<sup>TM</sup> GIS, Intera Tydac Technologies Inc., Nepean, Ont. 1993).

Arthropods observed under boxes were grouped into “taxonomic group” by visual inspection, which was judged sufficiently accurate for the purpose of this study (see Fraser and Grime 1999). For example, predatory Acari were placed in one taxonomic group, as most are nonspecific predators (e.g., Berg et al. 1998). The Araneae species were grouped together, as food specialization does not occur among the spiders encountered in Saskatchewan (M. Braun, Agriculture Canada, personal communication). All Collembola were placed in one taxonomic group, as most species consume fungi (Hopkin 1997). Any cryptic biological species that might have been grouped together because they have the same external features are likely to have the same predator–prey relationships (Basset and Arthington 1992; Paquin and Coderre 1997). In the analyses, I used nine taxonomic categories and, owing to low numbers, I excluded adult Diplura (and larvae), phytophagous Acari, Homoptera, Pseudoscorpiones, Lepidoptera (and larvae), Anopla, Gastropoda, and Isopoda. Springtails (Collembola; Badejo et al. 1998; Brand and Dunn 1998) and predatory mites (family Gamasides; Krough 1995) that feed mainly on springtails were the most abundant microarthropods. Predatory mesoarthropods eat prey of about their own size or, more usually, smaller than themselves (Enders 1975; Nentwig and Wissel 1986; Sabelis 1992). Many mesoarthropod groups preyed on springtails and mites (personal observations). Beetles (order Coleoptera) were subdivided into larvae (families Carabidae and Staphylinidae) and adults (mostly epedaphic ground beetles of the family Carabidae). Most Carabidae and Staphylinidae are polyphagous predators that eat anything they encounter (e.g., dipteran adults and larvae, isopods, other beetles and beetle larvae, and spiders), although springtails and mites are likely too small for the majority of the species (Hengeveld 1980). Other mesoarthropod taxonomic groups included bugs (order Hemiptera, which feed mostly on plant juices), spiders (Arachnida, order Aranea, some of which (e.g., Linyphiidae) will feed on springtails), ants (order Hymenoptera, family Formicidae, which feed on insects in the vegetation, larger arthropods on the soil surface, and ant larvae from colonies), adult Diptera (families Empididae and Phoridae), and centipedes (subclass Chilopoda, which feed on earthworms, dipteran larvae, isopods, and beetles).

For each taxonomic category, I measured the body length of a random sample of 20 arthropods (4 for each of five size classes) that had been preserved in 70% isopropyl alcohol. I used callipers (for specimens longer than 5 mm) or an ocular micrometer on a dissecting binocular microscope (for specimens shorter than 5 mm) to measure (to the nearest 0.1 mm) from the most anterior part of the head to the anus, excluding appendages. For each taxonomic group, I used five categories to estimate body size in the field (categories 1–5: tiny, small, medium, large, and extra large). Subsequently, I used mean values from each of these size categories to calculate biomass from published power function regressions between body length and dry mass biomass (Ganihar 1997). Thus, individuals were separated into size classes, and the mass corresponding to the length of a given size class was calculated. Total dry mass biomass of a taxonomic group was calculated as

<sup>2</sup>S.H. Ferguson. Edge, fractal dimension, and trophic abundance. Submitted for publication.

**Table 1.** Distance to box edge for nine arthropod groups.

Taxonomic group	Multiple comparison*	Mean (cm)	SD	Sample size	Median	Mode
Springtails	<i>ab</i>	2.35	1.14	204	2.0	1.4
Mites	<i>ab</i>	1.76	0.97	139	1.4	1.2
Beetle larvae	<i>bc</i>	1.69	1.16	114	1.7	2.0
Centipedes	<i>bc</i>	1.67	1.29	106	1.7	0.0
Beetles	<i>cd</i>	1.35	1.17	179	1	0
Ants	<i>cd</i>	1.2	1.17	302	0.8	0.0
Adult flies	<i>de</i>	1.20	1.33	121	0.6	0.0
Bugs	<i>e</i>	1.01	1.07	121	0.6	0.0
Spiders	<i>e</i>	0.80	0.94	174	0.5	0
Random points <sup>†</sup>	<i>a</i>	2.43	1.09	100	2.5	1.5

\*Groups with the same letter did not differ using Tukey's multiple comparison test ( $\alpha = 0.05$ ).

<sup>†</sup> One hundred points were randomly generated using SPANS™ GIS software (see Methods).

**Table 2.** Results of a repeated-measures analysis of variance of ranked data to determine the effects of arthropod groups and distance to edge (categories: 0.0–0.5, 0.5–1.0, 1–2, 2–3, 3–4, and 4–5 cm) on density of individuals and the total biomass of individuals, with time (weekly surveys) as the repeated measure.

Source of variation	Density (no./m <sup>2</sup> )			Biomass (mg/m <sup>2</sup> )		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Taxonomic group	8	6.9	0.001	8	7.3	0.001
Distance	5	38.7	0.001	5	37.4	0.001
Time	19	26.1	0.001	19	24.3	0.001
Error	955			955		

size-class-dependent dry mass multiplied by the abundance of the corresponding size class summed over all size classes of all species belonging to that taxonomic group.

An abiotic explanation for changes in arthropod distribution is microclimatic variation under boxes relative to distance to edge. To test for spatial differences in microclimate, I measured temperature (°C) and moisture (relative humidity, Dewpoint °C), using a probe inserted 1 cm into the leaf-litter layer along 17-cm transects aligned perpendicular to the boxes. Measurements were recorded at 1-cm intervals ( $n = 17$ ) for five randomly chosen boxes during four surveys in 1998. Transect lines extended 3.75 cm on each side of a box and 9.5 cm across the width of a box, allowing for nine sample locations under a box and four sample locations on each side.

Statistical analysis was constrained by the nonparametric abundance data that did not conform to a normal distribution after logarithmic transformation. Consequently, I used parametric analysis of ranked data (Conover and Iman 1981). I tested for differences among the taxonomic groups and size classes with regard to distance to edge, using analysis of variance of ranked data (i.e., nonparametric test). I also tested for significant effects of classes of distance to edge (0.0–0.5, 0.5–1.0, 1–2, 2–3, 3–4, and 4–5 cm) and taxonomic group on density of individuals and total biomass per square metre, using repeated-measures analysis of variance of ranked data, with time (weekly surveys) as the repeated measure. I tested only for differences among the main-treatment effects, because interaction terms in multifactorial analyses are uninterpretable when using ranked data (Seaman et al. 1994). I used two-way analysis of variance to test for differences in litter temperature and litter moisture between locations under boxes and locations beyond boxes. Spearman's rank correlations were used to test for differences in distance to edge with litter temperature and litter moisture. Analyses were done using SAS (SAS Institute Inc., Cary, N.C. 1987) statistical software for microcomputers.

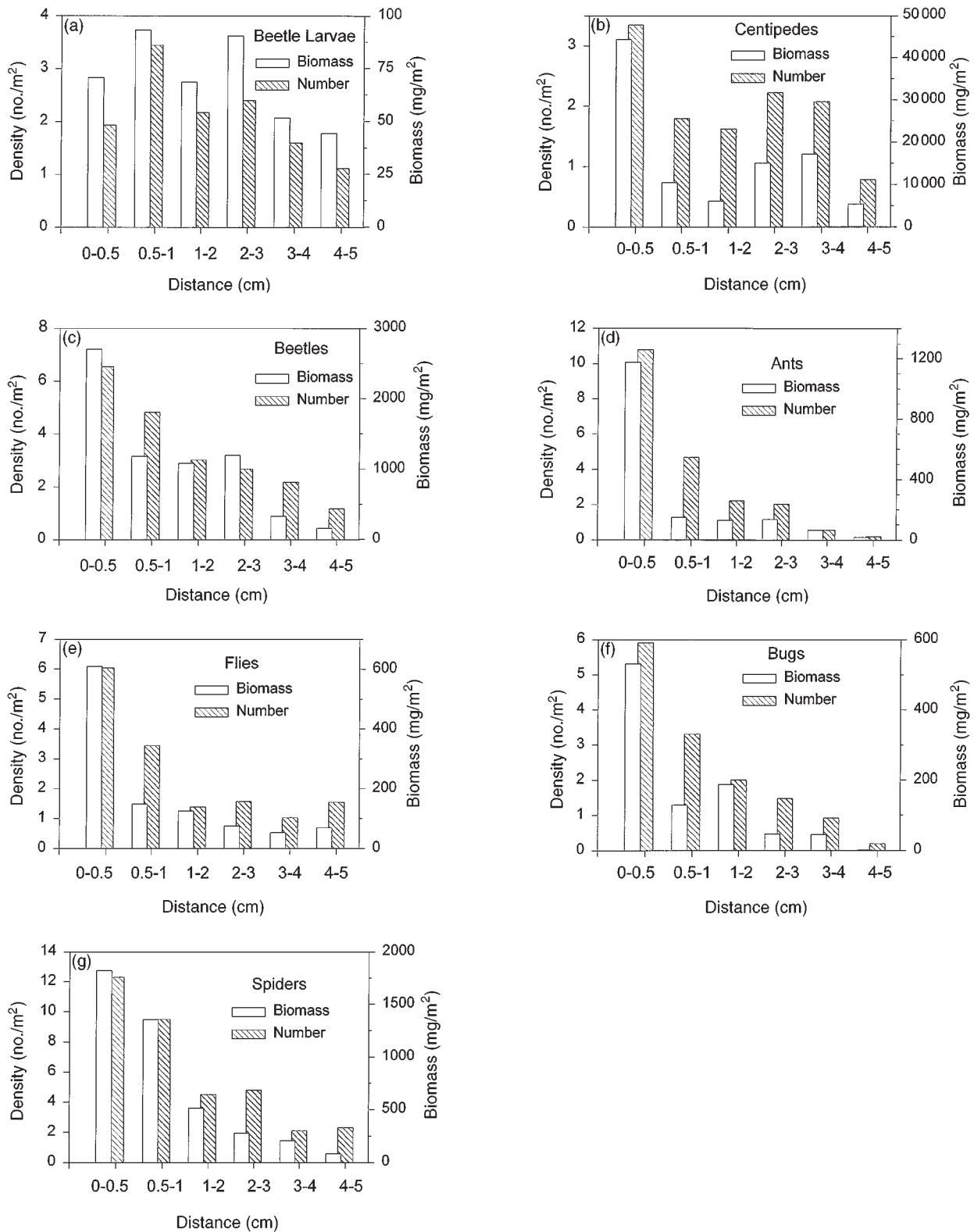
## Results

I analyzed a total of 1460 measures of distance to edge among two microarthropod and seven mesoarthropod taxonomic groups and five size classes. No significant year effect was found ( $P = 0.33$ ), so data from the 2 years were combined for subsequent analyses. Distance to edge differed with taxonomic group ( $F_{[9,1460]} = 8.86$ ,  $P < 0.001$ ) and size of individual ( $F_{[5,1460]} = 6.65$ ,  $P < 0.001$ ). For the two microarthropod groups (springtails and mites), I found no difference in distance to edge relative to random distances (Table 1). Centipedes and beetle larvae were found at greater distances from edge (mean 1.67 and 1.69 cm respectively) relative to random distances, although distances did not differ from those for the two microarthropod groups. Beetles, ants, and adult flies grouped close to edge (mean = 1.35, 1.21, and 1.20 cm, respectively), whereas bugs and spiders were found at mean distances of 1.0 and 0.8 cm from edge, respectively. Thus, most mesoarthropod groups (five of seven) were closer to edge than microarthropod groups.

### Mesoarthropod distribution

Density and biomass differed among taxonomic groups of predators (Table 2). In addition, density and biomass were negatively related to distance to edge. Owing to the likely interaction effect of taxonomic group and distance, I analyzed each group separately and found that most mesoarthropod groups were not distributed similarly with respect to distance (Fig. 1). Beetle larvae density ( $F_{[5,114]} = 1.69$ ,  $P = 0.14$ ) and biomass ( $F_{5,114} = 2.04$ ,  $P = 0.08$ ) distribution

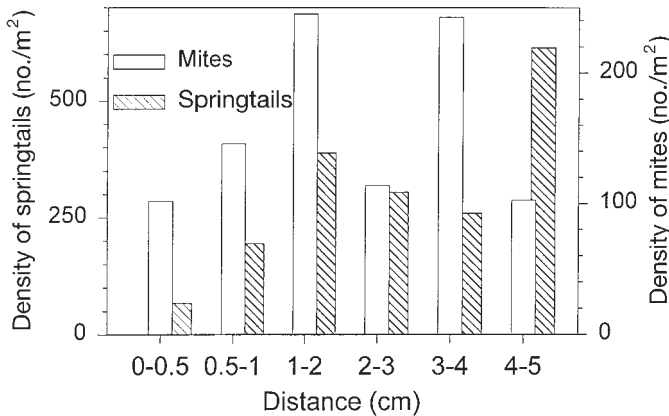
**Fig. 1.** (a–g) Distance from edge versus density (total number/m<sup>2</sup>) and biomass (mg/m<sup>2</sup>) for seven mesoarthropod predator groups found under boxes (998 cm<sup>2</sup>).



did not differ from the random distribution (Fig. 1a). However, density and biomass were negatively related to distance to edge for the remaining six mesoarthropod groups (Figs. 1b–1g). For these six groups, not only were more individuals

close to edge but, within each taxonomic group, larger individuals were closer to edge relative to smaller individuals. Thus, larger predators were closer to edge than smaller predators. No differences in distribution of mesoarthropod groups

**Fig. 2.** Relationship between distance from edge and density (number/m<sup>2</sup>) for microarthropod groups (springtails and mites) found under boxes (998 cm<sup>2</sup>).



**Table 3.** Results of a two-way analysis of variance on the effects of weather (surveys during dry period and surveys following rainfall events) and cover (under boxes versus beyond boxes) on temperature and moisture.

Source of variation	Temperature (°C)			Moisture (Dewpoint °C)		
	df	F	P	df	F	P
Weather	1	359.9	0.001	1	393.6	0.001
Cover	1	119	0	1	26.9	0
Error	334			334		

with respect to edge habitat occurred between wet and dry periods ( $\chi^2 = 9.6$ ,  $df = 5$ ,  $P = 0.27$ ).

**Microarthropod distribution**

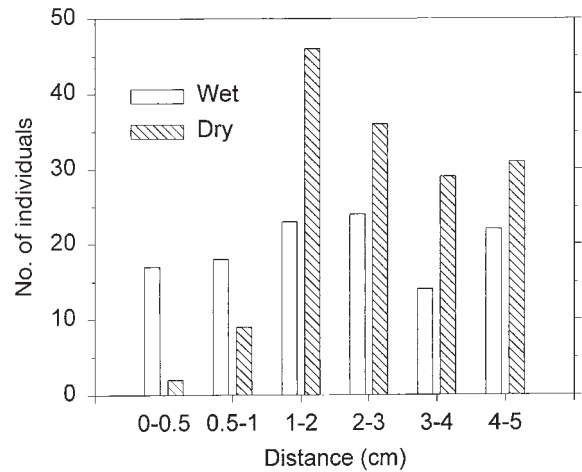
The microarthropod groups were found farthest from edge (Fig. 2) and their distances were not significantly different from random distances (Table 1). For mites ( $F_{[5,139]} = 1.49$ ,  $P = 0.30$ ) and springtails ( $F_{[5,204]} = 1.53$ ,  $P = 0.21$ ), no difference was found in number of individuals relative to distance classes.

The density of springtails varied with humidity; density was higher following rainy periods and lower during dry periods. By dividing the springtail data into dry and wet periods, I found significant differences in their distribution with respect to edge habitat ( $\chi^2 = 17.7$ ,  $df = 5$ ,  $P = 0.003$ ). These results provide evidence that springtail distribution becomes skewed away from edge habitat over time. There were no differences in springtail distribution during wet periods of initial abundance ( $F_{[5,86]} = 0.53$ ,  $P = 0.61$ ), whereas springtails were distributed farther from edge during the subsequent dry periods ( $F_{[5,118]} = 3.53$ ,  $P = 0.02$ ; Fig. 3). No differences were found for mites with respect to distribution during wet and dry periods ( $\chi^2 = 8.53$ ,  $df = 5$ ,  $P = 0.13$ ).

**Temperature and moisture**

Temperature and moisture varied between surveys both before and after rainfall events and between measurements taken under boxes or beyond boxes (Table 3). Temperature was greater beyond boxes than under boxes for all surveys

**Fig. 3.** Effect of wet and dry periods on the distribution of springtails. Note the more even distribution of springtails during periods of high abundance (wet) compared with the uneven distribution during periods of low abundance (dry).



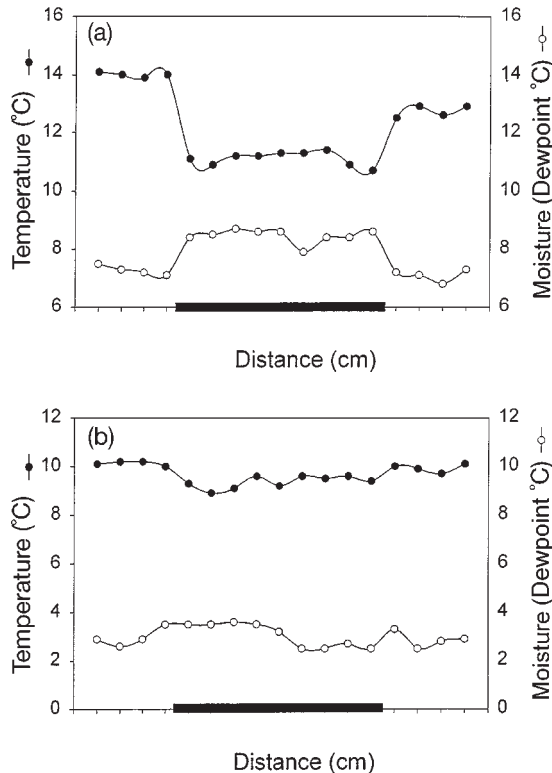
( $F_{[1,16]} > 13.4$ ,  $P < 0.003$ ,  $n = 4$  surveys; Fig. 4). Moisture was greater under boxes relative to beyond boxes only for surveys following significant rainfall events ( $F_{[1,16]} > 13.4$ ,  $P < 0.002$ ,  $n = 2$  surveys; Fig. 4). No significant relationship was found for temperature or moisture with distance to box edge ( $r_s < 0.20$ ,  $P > 0.21$ ,  $n = 85$ ).

**Discussion**

I found more mesoarthropod predators and larger individuals close to edge habitat, and springtail distribution became skewed away from edge over time. Why are mesoarthropod predators closer to edge? Researchers have emphasized the ecology of edges themselves (i.e., abiotic factors; Fagan et al. 1999) as a possible explanation for changes in distribution and abundance. Following this tradition, one possible explanation is that edges offer a comfortable microclimate due to a temperature and humidity gradient related to changes in vegetation structure (Harris 1988; Saunders et al. 1991; Stevens and Husband 1998). Edge habitats are characterized by a greater variety of vegetation and a high degree of spatial heterogeneity that, together, increase wildlife diversity (Leopold 1933; Roth 1976; Morgan and Gates 1982; Harris 1988; Yahner 1988; Matheson and Larson 1998). Temperature and moisture changed abruptly along box edges in this experiment, and arthropod distribution is strongly influenced by local vegetational and structural features (Roth 1976; With and Crist 1995). However, microhabitat characteristics did not vary with distance to edge at the scale of this study, whereas springtail density decreased near edges over time. Also, mesoarthropod predators were less abundant towards the centre of boxes, despite a uniform microclimate under the boxes. These findings are consistent with the hypothesis that the distribution of predators affected the distribution of springtails as prey. Still, many mesoarthropods do not feed on springtails and alternative explanations for the distribution pattern relative to edge are necessary for particular taxonomic groups.

More recent studies have emphasized biotic edge effects that link abiotic changes with population and trophic inter-

**Fig. 4.** Effect of box edge on temperature and moisture following a rainfall event (a) and during a dry period (b). The box (width 9.5 cm) position is indicated by the solid bar.



actions (e.g., Kareiva 1987; Saunders et al. 1991; Roland 1993; Fagan et al. 1999). One biotic explanation for why predators are close to edge is that more prey are available there. Evidence contrary to this explanation was the finding of fewer microarthropod prey in areas with a greater amount of edge (S.H. Ferguson, see footnote 2). Also, springtail densities decreased near edge during dry periods. Another biotic explanation for the greater use of edges is that mesoarthropods are themselves prey for larger predators and they may benefit from using edges as refuges (Lima and Dill 1990). This hypothesis, that cross-edge movement entails increased mortality rates, requires further testing. Edge-mediated mortality may occur in an unbalanced fashion among predators and prey, leading to effects that are mechanistically similar to competitive systems (Connell 1978).

A final biotic hypothesis to explain why predators are close to edge is that edges form linear corridors, providing ease of travel and navigation for predators. Edges may act as physical or behavioural barriers, causing foraging predators to travel parallel to them and resulting in a disproportionate increase in forager activity near edges, leading to increased predation (Bider 1968; Gates and Gysel 1972; Bergerud et al. 1984; Small and Hunter 1988; Oehler and Litvaitis 1996). Predators may use area-restricted search behaviour (Hassell 1976; Shimoda et al. 1997) that may create the patchiness observed in prey distributions (Kareiva and Odell 1987). The finding of decreased springtail density along edge habitat over time supports the predation hypothesis, but does not support this hypothesis exclusively.

Why are larger mesoarthropods found closer to edge than their smaller counterparts? One hypothesis is that the prey

available near edges may differ and provide better food for larger mesoarthropods. This hypothesis is supported by the greater numbers of individuals and size classes found in edge habitat. The requirements of larger mesoarthropods differ from those of their smaller counterparts, in that relative body size influences prey-capture success, the range of prey sizes taken, survival, dispersal capacity, and competitive ability (Sabelis 1992). Larger arthropods may require specific range requirements that include edge habitat as diurnal refuges, whereas active nocturnal foraging may occur among the leaf litter located away from boxes. The box edge is long and narrow from the perspective of an arthropod and may be perceived as a single patch in an individual's territory. If this is the case, arthropods will incorporate the edge sites within their territory when selecting resources from the available habitat heterogeneity. As well, larger arthropods (e.g., ants, which are not vertically depressed) may find locomotion under boxes difficult and, therefore, may be less likely to be found farther from edges.

A final explanation for why larger predators are found close to edge is that they may competitively exclude smaller conspecifics from preferred edge habitat. The effect of interference may also be the avoidance of competitive habitats by less aggressive and correspondingly less well-armoured species (Sabelis 1992). Cannibalistic attacks (Polis and McCormick 1987) and intraguild predation are thought to be size related and this, therefore, could explain competitive exclusion (Yao and Chant 1982; Polis and Strong 1996).

What information do these findings provide concerning conservation? I recommend caution in applying small-scale patterns directly to large-scale systems, as the assumption of scale invariance has not been adequately tested. Still, as with modelling, this approach will add to our understanding of management assumptions and provide direction for future research. For example, the results are consistent with the view that predators compete, or show the effects of historical competition, for habitats that include travel corridors and edge habitat. As well, the findings of this study support the prediction that fragmentation and an increased amount of edge results in an increase in the abundance of a range of medium-sized omnivores (Andr n et al. 1985; Oehler and Litvaitis 1996; Gardner 1998; Crooks and Soul  1999). Research is required into the spatial dynamics of cross-edge dispersal of competitors, mutualists, and natural enemies, as determinants of the outcomes of species interactions in habitat patches. Understanding the importance of among-species differences in overall edge responses for trophic dynamics may help us to better mitigate the effects of human fragmentation of landscape structure.

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## References

- Andrén, H. 1995. Effects of landscape composition on predation rates at habitat edges. *In* Mosaic landscapes and ecological processes. Edited by L. Hansson, L. Fahrig, and G. Merriam. Chapman and Hall, London. pp. 225–255.
- Andrén, H., Angelstam, P., Lindstrom, E., and Widen, P. 1985. Differences in predation pressure in relation to habitat fragmentation: an experiment. *Oikos*, **45**: 273–277.
- Badejo, M.A., Nathaniel, T.I., and Tian, G. 1998. Abundance of springtails (Collembola) under four agroforestry tree species with contrasting litter quality. *Biol. Fertil. Soils*, **27**: 15–20.
- Basset, Y., and Arthington, A.H. 1992. The arthropod community of an Australian rain forest tree: abundance of component taxa, species richness and guild structure. *Aust. J. Ecol.* **17**: 89–98.
- Berg, M.P., Kniese, J.P., Bedaux, J.J.M., and Verhoef, H.A. 1998. Dynamics and stratification of functional groups of micro- and mesoarthropods in the organic layer of a Scots pine forest. *Biol. Fertil. Soils*, **26**: 268–284.
- Bergerud, A.T., Jakimchuk, R.D., and Carruthers, D.R. 1984. The buffalo of the north: caribou (*Rangifer tarandus*) and human development. *Arctic*, **37**: 7–22.
- Bider, J.R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. *Ecol. Monogr.* **38**: 269–308.
- Brand, R.H., and Dunn, C.P. 1998. Diversity and abundance of springtails (Insecta: Collembola) in native and restored tallgrass prairies. *Am. Midl. Nat.* **139**: 235–242.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science (Washington, D.C.)*, **199**: 1302–1310.
- Conover, W.J., and Iman, R.L. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Stat.* **35**: 124–129.
- Crist, T.O., Guertin, D.S., Wiens, J.A., and Milne, B.T. 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Funct. Ecol.* **6**: 536–544.
- Crooks, K.R., and Soulé, M.E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature (Lond.)*, **400**: 563–566.
- Enders, F. 1975. The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae and Salticidae). *Am. Nat.* **109**: 737–763.
- Fagan, W.F., Cantrell, R.S., and Cosner, C. 1999. How habitat edges change species interactions. *Am. Nat.* **153**: 165–182.
- Fraser, L.H., and Grime, J.P. 1999. Experimental tests of trophic dynamics: towards a more penetrating approach. *Oecologia*, **119**: 281–284.
- Ganihar, S.R. 1997. Biomass estimates of terrestrial arthropods based on body length. *J. Biosci. (Bangalore)*, **22**: 219–224.
- Gardner, J.L. 1998. Experimental evidence for edge-related predation in a fragmented agricultural landscape. *Aust. J. Ecol.* **23**: 311–321.
- Gates, J.E., and Gysel, L.W. 1972. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology*, **59**: 871–883.
- Gunnarsson, B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. *Anim. Ecol.* **59**: 743–752.
- Hamazaki, T. 1996. Effects of patch shape on the number of organisms. *Landscape Ecol.* **11**: 299–306.
- Harris, L.D. 1988. Edge effects and conservation of biotic diversity. *Conserv. Biol.* **2**: 330–332.
- Hartley, M.J., and Hunter, M.L., Jr. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. *Conserv. Biol.* **12**: 465–469.
- Hassell, M.P. 1976. The dynamics of arthropod predator–prey systems. Princeton University Press, Princeton, N.J.
- Hengeveld, R. 1980. Polyphagy, oligophagy and food specialisation in ground beetles (Coleoptera, Carabidae). *Neth. J. Zool.* **30**: 564–584.
- Hopkin, S.P. 1997. The biology of springtails (Insecta: Collembola). Oxford University Press, New York.
- Huston, M.E. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, New York.
- Intera Tydac Technologies Inc. 1993. SPANS™ GIS, spatial analysis tool. Ver. 5.3 for OS/2. Nepean, Ont.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predator–prey interactions. *Nature (Lond.)*, **326**: 388–390.
- Kareiva, P., and Odell, G. 1987. Swarms of predators exhibit ‘preytaxis’ if individual predators use area-restricted search. *Am. Nat.* **130**: 233–270.
- Kolasa, J., and Rollo, K. 1991. Introduction: the heterogeneity of heterogeneity: a glossary. *In* Ecological heterogeneity. Edited by J. Kolasa and S.T.A. Pickett. Springer-Verlag, New York. pp. 1–16.
- Kotliar, N.B., and Wiens, J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, **59**: 253–260.
- Krough, P.H. 1995. Effects of pesticides on the reproduction of *Hypoaspis aculeifer* (Gamasida: Laelapidae) in the laboratory. *Acta Zool. Fenn.* **196**: 333–337.
- Leopold, A. 1933. Game management. Charles Scribner’s Sons, New York.
- Lidicker, W.Z., Jr. 1999. Responses of mammals to habitat edges: an overview. *Landscape Ecol.* **14**: 333–343.
- Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.
- Major, R.E., and Kendal, C.E. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis*, **138**: 298–307.
- Matheson, J.D., and Larson, D.W. 1998. Influence of cliffs on bird community diversity. *Can. J. Zool.* **76**: 278–287.
- Morgan, K.A., and Gates, J.E. 1982. Bird population patterns in forest edge and strip vegetation at Remington Farms, Maryland. *J. Wildl. Manage.* **46**: 933–944.
- Murcia, C. 1995. Edge effects in fragmented forests: implications of conservation. *Trends Ecol. Evol.* **10**: 58–62.
- Nentwig, W., and Wissel, C. 1986. A comparison of prey lengths among spiders. *Oecologia*, **68**: 595–600.
- Oehler, J.D., and Litvaitis, J.A. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Can. J. Zool.* **74**: 2070–2079.
- Oksanen, L., Fretwell, S.D., Arruda, J., and Niemala, P. 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* **118**: 240–261.
- O’Neill, R.V., Milne, B.T., Turner, M.G., and Gardner, R.H. 1988. Resource utilization scales and landscape pattern. *Landscape Ecol.* **2**: 63–69.
- Paquin, P., and Coderre, D. 1997. Changes in soil macroarthropod communities in relation to forest maturation through three successional stages in the Canadian boreal forest. *Oecologia*, **112**: 104–111.
- Paton, P.W. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conserv. Biol.* **8**: 17–26.
- Polis, G.A., and McCormick, S.J. 1987. Intraguild predation and competition among desert scorpions. *Ecology*, **68**: 332–343.
- Polis, G.A., and Strong, D.R. 1996. Food web complexity and community dynamics. *Am. Nat.* **147**: 813–846.

- Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia*, **93**: 25–30.
- Roth, R.R. 1976. Spatial heterogeneity and bird species diversity. *Ecology*, **57**: 773–782.
- Sabelis, M.W. 1992. Predatory arthropods. In *Natural enemies: the population biology of predators, parasites and diseases*. Edited by M.J. Crawley. Blackwell Scientific Publications, London. pp. 225–264.
- Sala, O.E., and Lauenroth, W.K. 1982. Small rainfall events: an ecological role in semiarid regions. *Oecologia*, **53**: 301–304.
- SAS Institute, Inc. 1990. SAS/STAT Guide. Ver. 6, 4th ed. Vol. 2. Cary, N.C.
- Saunders, D.A., Hobbs, R.J., and Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* **5**: 18–32.
- Schaefer, M. 1995. Interspecific interactions in the soil community. *Acta Zool. Fenn.* **196**: 101–106.
- Seaman, J.W., Jr., Walls, S.C., Wise, S.E., and Jaeger, R.G. 1994. Caveat emptor: rank transform methods and interaction. *Trends Ecol. Evol.* **9**: 261–263.
- Shimoda, T., Shinkaji, N., and Amano, H. 1997. Prey stage preference and feeding behaviour of *Oligota kashmirica benefica* (Coleoptera: Staphylinidae), an insect predator of the spider mite *Tetranychus urticae* (Acari: Tetranychidae). *Exp. Appl. Acarol.* **21**: 665–675.
- Small, M.F., and Hunter, M.L. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia*, **76**: 62–64.
- Smith, J.N.M. 1974. The food searching behaviour of two European thrushes. II: the adaptiveness of the search patterns. *Behaviour*, **49**: 1–61.
- Stevens, S.M., and Husband, T.P. 1998. The influence of edge on small mammals: evidence from Brazilian Atlantic forest fragments. *Biol. Conserv.* **85**: 1–8.
- Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology*, **72**: 1253–1266.
- Urban, D.L., O'Neill, R.V., and Shugart, H.H. 1987. Landscape ecology. *BioScience*, **37**: 119–127.
- Wiens, J.A. 1976. Population responses to patchy environments. *Annu. Rev. Ecol. Syst.* **7**: 81–120.
- Wiens, J.A., and Milne, B.T. 1989. Scaling of “landscapes” in landscape ecology, or, landscape ecology from a beetle’s perspective. *Landscape Ecol.* **3**: 87–96.
- Wiens, J.A., Crawford, C.S., and Gosz, J.R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos*, **45**: 421–427.
- With, K.A., and Crist, T.O. 1995. Critical thresholds in species’ responses to landscape structure. *Ecology*, **76**: 2446–2459.
- Yahner, R.H. 1988. Changes in wildlife communities near edges. *Conserv. Biol.* **2**: 333–339.
- Yao, D.S., and Chant, D.A. 1982. Population growth and predation interference between two species of predatory phytoseiid mites (Acarina: Phytoseiidae) in interactive systems. *Oecologia*, **80**: 183–197.