

Edge effects of three anthropogenic disturbances on spider communities in Alberta's boreal forest

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Abstract Increasing fragmentation of forests worldwide by timber and industrial development makes it important to understand the edge effects of common anthropogenic disturbances on forest fauna. We collected ground-active spiders along transects across the edge of logging clearcuts, gravel roads and gas pipelines in the boreal forest of Alberta, sampling on the disturbance (10 m from forest edge), and 10, 45, and 200 m into the forest. We asked whether the three disturbances were associated with edge effects on spider communities, and whether the extent of their associated edge effects were equivalent. The spider community at the edges of clearcuts was distinct from interior and on-disturbance communities 10 m into the forest from the clearcut edge, showing an edge effect of between 10 and 45 m from clearcut edges, while no edge effects were apparent at road and pipeline edges. Edge effects therefore differ at linear and non-linear openings in the boreal forest, which suggests that small linear openings may be associated with minimal edge effects compared to large polygonal forest openings. This result has important consequences for forest management, where clearcuts and other non-linear openings are likely to cause edge effects on spider communities that are between 10 and 45 m in their extent. The small size of clearcuts as practiced in the public forests of Canada, and their dense and broad application across the landscape, makes this edge effect of broad spatial significance in protecting biodiversity in managed landscapes.

Keywords Araneae · Boreal forest · Edge effects · Linear disturbance · Spider community

Introduction

The study of animal distributions across habitat edges has been a persistent topic of concern in ecology since the introduction of the idea by Leopold (1933), who recommended that edges be used as a tool for land managers to increase concentrations of game animals. Over the past several decades, evidence has accumulated that edge effects may be detrimental to forest species that require interior habitat to thrive (Laurance et al. 2007; Murcia 1995). For some of these species, sensitivity to the forest edge may be strong enough to void some smaller forest patches completely of interior habitat conditions, rendering them non-habitat and unable to support viable populations of interior species (Ewers and Didham 2008; Woodroffe and Ginsberg 1998). Although edge effects can vary widely in their direction and magnitude in a species-specific fashion (Ries et al. 2004), understanding the depth of edge influence (Harper and Macdonald 2002) for particular taxa can aid land managers in making management decisions that maintain sufficient forest interior habitat for those taxa. As forests worldwide become increasingly fragmented by logging, deforestation and other industrial development (Hansen et al. 2010), the necessity to understand the magnitude of edge effects associated with common anthropogenic disturbances in these habitats becomes ever more pressing (Harper et al. 2005; Harrison and Bruna 1999; Laurance and Curran 2008).

Although there is a rich literature of edge effect studies on vegetation, vertebrates, and insects (Duelli et al. 2002; Gates and Gysel 1978; Heliola et al. 2001; Laurance et al.

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1997, 2002; Magura et al. 2001; Mullen et al. 2003; Ries and Sisk 2008; Taboada et al. 2004; Tylianakis et al. 2005), very little has been documented for edge effects on spiders (c.f. Larrivee et al. 2008; Pearce et al. 2005). Spiders (Arachnida: Araneae) are an abundant and diverse taxon in northern forests (Buddle et al. 2000) and are dominant generalist predators of arthropods of all forest strata (Clarke and Grant 1968; Turnbull 1973). Spiders represent a large portion of forest arthropod communities in their abundance and total biomass, making them important elements of the community as a significant source of food for their arthropod, avian and mammalian predators (Jansson and von Bromssen 1981; Pearce and Venier 2006).

Spiders can be expected to respond strongly to edge effects from forest disturbance. Their activity and habitat selection is strongly constrained by microclimatic conditions such as soil moisture and temperature (e.g., Vlijm and Kessler-Geschiere 1967; Ziesche and Roth 2008), which are greatly influenced in forests by proximity to anthropogenic edges (Chen et al. 1999). Spiders are also highly dependent on habitat structure (Langellotto and Denno 2004; Turnbull 1973). Web-building spiders require suitable surrounding structure for points of web attachment (Robinson 1981), and most hunting spiders sense their environment and their prey predominantly through mechanoreception, which is mediated through structural features in the environment (Uetz 1991).

Habitat structure and microclimate are altered within forest edge zones by both primary and secondary responses (sensu Harper et al. 2005) of the forest edge to the contrasting environments of forest interior and open disturbance. Primary responses include increased tree mortality (Lopez et al. 2006) and additional coarse woody debris deposited on the forest floor in the edge zone (Chen et al. 1992; Harper and Macdonald 2002). Increased wind and solar radiation at exposed forest edges cause higher fluxes in humidity and soil moisture at the edge than in the forest interior (Chen et al. 1995; Matlack 1993). Secondary responses to forest edge include changes in vegetation structure and composition that are influenced by available resources and stressors at the edge (Murcia 1995). Regenerating forest edges may create a dense “sidewall” of vegetation (Didham and Lawton 1999; Duelli et al. 2002; Matlack 1994), and herbaceous growth has been shown to increase at anthropogenic edges (Harper and Macdonald 2002).

Forest edge structure and any resulting edge effect can depend greatly on the nature of the edge origin and its maintenance (Didham and Lawton 1999; Larrivee et al. 2008). In particular, linear forest openings, such as roads or powerlines, have been shown in tropical environments to exhibit edge dynamics that are very different from openings of polygonal shape (Pohlman et al. 2007). Narrow linear openings experience less incident wind and solar

radiation than polygonal openings, being sheltered by adjacent forest (Forman 1995). The edges associated with clearcut logging are particularly abrupt, relative to the ragged edges associated with fire, the primary natural disturbance in boreal forests (Harper et al. 2004; McRae et al. 2001). To date, there has not been a comparison of the edge effects of linear and non-linear openings in the boreal forest. Because boreal forests are currently subject to several classes of anthropogenic disturbances that differ in key characteristics such as configuration and maintenance regime, it is important to examine whether these disturbances are equivalent in their edge effects on forest populations.

With this study, we compare the edge effects associated with three common anthropogenic disturbances in the boreal forest of Alberta: logging clearcuts, gravel roads, and buried gas pipelines. We use comparisons between sites located at varying distances from the disturbance edge and sites located within interior forest to detect edge effects on ground-dwelling spider communities, which we explore both in terms of individual species abundances across the edge and in terms of community composition. The widespread clearcuts, roads and pipelines in the Alberta landscape provide the opportunity to compare edge effects based on differences in their configuration (i.e., linear or non-linear), and also in their maintenance: while the gravel roads are used regularly by vehicles, pipeline right-of-ways are only very rarely disturbed by vehicles and are seeded with grass (Tera Environmental Consultants 2003). Therefore our objectives are to detect and compare the extent of edge effects at clearcuts, roads and pipelines on (1) individual ground-dwelling spider species, and on (2) ground-dwelling spider communities.

Methods

Study location and sampling design

Spiders were collected at study sites in Kananaskis Country, Alberta (approximately 50°58'N, 114°43'W) in the summers of 2004 and 2008. Sites were located in mixed-wood coniferous forest, dominated by lodgepole pine (*Pinus contorta*). Other important tree species included white spruce (*Picea glauca*), aspen (*Populus tremuloides*) and subalpine fir (*Abies lasiocarpa*). Mature trees at study sites were roughly 20 m tall. Elevation of study sites ranged from 1,375 to 1,650 m. Transects were set up through edges of differing orientations at logging clearcuts, roads, and gas pipelines (Table 1).

To account for regional differences in vegetation, elevation and topography, a blocked design was used where six blocks each contained one site for each of the three

Table 1 Site characteristics of clearcuts, pipelines and roads where sampling took place

Disturbance type	Block	Size	Orientation (°)	Year of creation
Logging	1	16.8	0	1994
Logging	2	20	179	1991
Logging	3	12.9	303	1988
Logging	4	7.6	45	1988
Logging	5	2.1	200	1987
Logging	6	8.7	192	1987
Pipeline	1	18.9	141	2005
Pipeline	2	16.3	324	2005
Pipeline	3	24.1	248	2005
Pipeline	4	26.1	273	2005
Pipeline	5	20.5	237	2005
Pipeline	6	24.1	343	2005
Road	1	20.8	89	1980s
Road	2	17.6	86	1980s
Road	3	22.7	342	1980s
Road	4	22.8	37	1980s
Road	5	5.3	297	1980s
Road	6	23.1	3	1980s

A total of six replicate blocks each contained one distance transect at the edge of a clearcut, one at the edge of a pipeline, and one at the edge of a gravel road. Size for logging sites refers to clearcut size in hectares, while for roads and pipelines it refers to the width (in meters) of the opening. Orientation describes the direction relative to true north that was exposed at each edge; for example, an edge at angle 0° ran from east to west, with open disturbed area to its north and undisturbed forest to its south, while an edge at 360° also ran from east to west, with open disturbed area to its south and forest to its north

disturbance types (road, logging, or pipeline; Fig. 1). Blocks were usually at least 1 km from a nearest neighbor, and within a block, sites were between 200 and 800 m from a site of the nearest alternative disturbance type. Each site contained four distance levels (“stations”) arranged in a linear transect orthogonal to the disturbance edge: one 10 m into the disturbed area from the forest edge (hereafter the “0 m” station for convenience); one 10 m into the forest; one 45 m into the forest; and a final level 200 m from the disturbance edge. The edge was delineated as the line where mature trees gave way to cleared land or young regenerating trees, and was easy to distinguish. In the case of roads, because sampling directly on the road was impractical, traps at 0 m stations were placed approximately 1 m from the edge of the gravel, on the road verge.

Each station consisted of five uncovered yellow (R: 230, G: 240, B: 80) pitfall traps, 15 cm in diameter and 10 cm deep. Yellow, uncovered traps were used so that a greater diversity of arthropods (including flower-visiting insects that are best sampled with pan traps) could be captured and included for analysis in separate studies. The traps

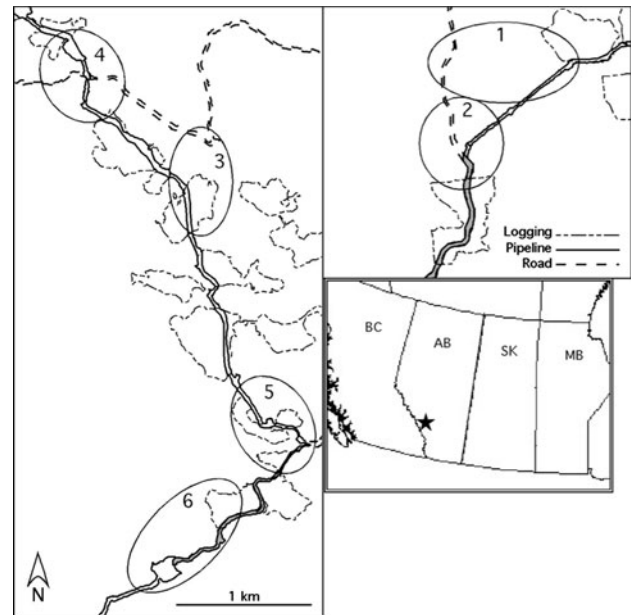


Fig. 1 Map of the study area showing the arrangement of clearcuts, pipelines and roads where sites were located. Grey shaded areas indicate overlap of road and buried pipeline. Numbered ovals show the locations of study blocks (six total), where each block contained a series of pitfall traps laid out in a distance transect from a clearcut edge, a pipeline edge, and a road edge. The areas shown in the two separate panes are separated by roughly 3 km. Bottom-right pane shows the location of the study area in Alberta, Canada

therefore were doubly efficient as yellow pan traps (Leong and Thorp 1999) and as large pitfall traps (Work et al. 2002). To avoid detrimental effects to the many large vertebrates active in the study area, we filled traps halfway with a saturated salt solution and a few drops of detergent to reduce surface tension. The five traps within a station were spaced roughly 1 m apart in a linear row orthogonal to the disturbance edge. Eight additional control stations, each consisting of a line of five pitfall traps, were established at random points in undisturbed forest at least 200 m from any of the three disturbances. These control stations were designed to allow comparison with the 200 m site stations, in case the effects of disturbances extended beyond 200 m. Thus each disturbance-distance combination had six replicates for each year of sampling.

Traps were set twice for 9–11 days at a time between July 3 and July 13 and between July 21 and July 31 of both 2004 and 2008. Although spider species may peak in abundance at widely disparate points during the season, our sampling was timed to approximately coincide with that point during the season when species richness of ground-dwelling spiders is highest (Buddle and Draney 2004; Niemela et al. 1994). The contents of the two trapping periods during each year, and the five samples at each site, were pooled at the station level for analysis (i.e., pooling 10 samples, yielding $n = 80$ stations for each year).

Roughly 1 week after sampling during both summers, percent cover of plant species and ground-cover types was estimated in a 1 m² quadrat around each pitfall trap. Because the pipeline in this area was built in the winter of 2004–2005, sampling on the pipeline disturbance was only conducted in 2008. Sampling in 2004 included sites along the proposed pipeline location (treated in analysis as control sites, or omitted) that were sampled again after pipeline construction in 2008. All other sites (control, clearcut and road edge sites) were sampled identically in 2004 and 2008.

All adult spiders were identified to species or morpho-species by external genitalia using published keys (Dondale and Redner 1978, 1982, 1990, 2003; Platnick and Dondale 1992). Identifications were made in consultation with reference collections at the University of Calgary, the University of Alberta, the Denver Museum of Nature and Science and, in some cases, with assistance from experts in spider taxonomy. Nomenclature followed Platnick (2010). Due to the difficulty of assigning most juvenile spiders to species, juveniles (which represented 12% of 12,796 individuals) were excluded from analysis.

Statistical methods

Except where otherwise noted, analysis was conducted in JMP v.8.0.2 (SAS Institute 2009). Because of some trap losses in the field and slightly unequal trapping times between sites, station-level abundances were standardized for sampling effort to 105 trap-days. We validated this ratio-based adjustment by confirming that total spider abundance was positively and significantly predicted by number of trap-days ($F_{1,158} = 44$, $P < 0.0001$), and that the intercept of the regression line was zero ($t_{158} = 0.00$, $P = 0.99$). To better meet model requirements for normal and homogeneous residuals, abundances were transformed by $\ln(x + 1)$. Because pipeline sites in 2004 were sampled before pipeline construction, we treated them as control sites with identical, arbitrary distances.

Our statistical approach considered edge effects of the three disturbances on individual species; on community metrics such as total spider abundance, species richness, and evenness; and on spider community composition. First, to identify spider species that were predominant within certain levels of the study design, we used indicator analysis (Dufrene and Legendre 1997) in the labdsv package for R v.2.8.1 (R Development Core Team 2008; Roberts 2007). This analysis identified spider species that were significantly associated with disturbance classes, i.e. disturbance type-distance combinations. We tested the statistical significance of indicator values with 1,000 permutations.

To assess whether the three disturbances had a significant edge effect on the abundances of individual species,

we analyzed the abundance of the ten most abundant species in a mixed-model ANOVA with the following categorical X factors: block (random), year, disturbance type, distance, and disturbance type by distance interaction. We also confirmed the lack of a significant year by distance interaction in a model we do not report here. Because the pipeline was constructed in 2005, the unbalanced nature of our design made it impossible to test a year by disturbance type interaction. We compared 10 and 45 m distance levels to the 200 m level within disturbances using Tukey's HSD, to determine the extent of edge effect at each disturbance type, if any. Where there were significant disturbance type by distance interactions, we compared distance levels for each disturbance type using Tukey's HSD to test for edge effects occurring within each disturbance type.

We used an identical model to examine community-level measures: total spider abundance, species richness (rarefacted to a common sample size of 20 individuals), and evenness (using the Δ_1 metric of Olszewski (2004)) at disturbance types and distance levels.

We used PERMANOVA (Anderson 2001), part of the PRIMER-E v.6 package (Clarke and Gorley 2006), to carry out a similar MANOVA-style analysis on spider community assemblages. PERMANOVA partitions multivariate variation on the basis of disturbance factors and analyzes interactions, random, and nested fixed effects. The analysis is performed on a distance matrix and significance of F ratios is assessed through permutation, which allowed for inclusion in the model of species whose residuals from model fits were not normal and homogeneous. We used the Bray–Curtis similarity index (Legendre and Legendre 1998) to analyze $\ln(x + 1)$ -transformed spider species abundances so that the model included the X factors year (fixed), block (random), disturbance type, and distance (fixed; nested within disturbance type).

We again used pairwise comparisons of distance levels within disturbance types to examine at what distance from the edge of each disturbance the spider community became statistically indistinguishable from “interior” communities. Because we were unable to compare specific distance levels (e.g., Logging-0 m) to control sites explicitly, we chose to instead compare distance levels within disturbance types to each other and to consider 200 m sites as equivalent to control, or forest interior. Subsequent ordination of spider communities confirmed that communities at 200 m levels within each disturbance were very similar to control communities. We used Hochberg's (1988) procedure to control the false discovery rate in multiple comparisons.

Although PERMANOVA provides a powerful way to statistically measure the effect of different disturbance factors on community composition, it cannot be graphically displayed. Thus to provide a visual complement to PERMANOVA analysis we used non-metric multidimensional

scaling (NMDS), using the Bray–Curtis similarity index, to ordinate spider community composition within different disturbance classes. We calculated centroids and 95% confidence intervals from individual sampling stations within each disturbance–distance combination. Analysis was performed with the vegan package in R v.2.8.1 (Oksanen et al. 2009; R Development Core Team 2008). To decrease the effect of rare species on analysis in PERMANOVA and NMDS, only those species occurring in at least 5% of traps over both years were included (McCune and Grace 2002).

Similar multivariate community-level analyses were carried out on the plants; percent cover records ($\ln(x + 1)$ -transformed) were combined into an overall percentage across all pitfall traps for each sampling station. We used PERMANOVA on the Bray–Curtis similarity index to explore differences in plant community composition between disturbances and distances.

Results

A total of 12,796 spiders were collected. Of these, 9,091 were adult spiders that could be identified to the species level, comprising 131 species in 16 families (for complete species list see “Appendix”, Table 6). Wolf spiders (Lycosidae), by far the most abundant family, accounted for 53% of individuals identified; individuals in Linyphiidae, the second-most abundant family, accounted for 28% of the total. Some spiders could not be identified and were excluded from analysis: morphospecies that could not be assigned to a species ($n = 1,350$ spiders in 121 morphospecies, nearly all in the family Linyphiidae) were excluded from analysis, except in the case of 63 individuals which were resolved to a single genus and retained as one category (Linyphiidae: *Walckenaeria* spp.) and 52 individuals in the genus *Agyneta* (Linyphiidae) which were separated from other *Agyneta* spp. and retained as a morphospecies (*Agyneta* #1).

Edge effects on individual species

Out of 127 candidate species, indicator analysis identified 16 species as significant indicators of at least one disturbance–distance class (Table 2). While 13 of these species were indicative of on-disturbance sites (5 for Logging 0 m, 6 for Pipeline 0 m, and 2 for Road 0 m), no species were characteristic of forest interior classes (i.e., 45 or 200 m from a disturbance edge). Three wolf spider species were characteristic of “edge” habitat 10 m from disturbances: *Pardosa dorsuncata* (Lowrie and Dondale 1981) was significantly associated with clearcut edges, while

Table 2 Indicator analysis of spider species on distance levels from logging, pipeline and road edges

Species	Level	Indicator value	<i>P</i>	No. recorded
<i>Pardosa moesta</i>	Logging 0 m	0.469	0.001	989
<i>Meioneta simplex</i>	Logging 0 m	0.325	0.002	56
<i>Pardosa hyperborea</i>	Logging 0 m	0.268	0.04	152
<i>Alopecosa aculeata</i>	Logging 0 m	0.248	0.02	463
<i>Pocadicnemis americana</i>	Logging 0 m	0.247	0.01	65
<i>Pardosa dorsuncata</i>	Logging 10 m	0.234	0.03	220
<i>Pardosa groelandica</i>	Pipeline 0 m	0.583	0.001	60
<i>Pardosa xerampelina</i>	Pipeline 0 m	0.572	0.001	157
<i>Xysticus ferox</i>	Pipeline 0 m	0.422	0.001	20
<i>Gnaphosa parvula</i>	Pipeline 0 m	0.326	0.002	11
<i>Zelotes puritanus</i>	Pipeline 0 m	0.303	0.004	19
<i>Xysticus emertoni</i>	Pipeline 0 m	0.247	0.01	26
<i>Pardosa mackenziana</i>	Pipeline 10 m	0.265	0.001	1,897
<i>Pardosa uintana</i>	Pipeline 10 m	0.252	0.02	467
<i>Pardosa tesquorum</i>	Road 0 m	0.579	0.001	168
<i>Pardosa distincta</i>	Road 0 m	0.296	0.007	133

Indicator value ranges from 0 to 1, with 0 indicating a species that is equally abundant at all levels and 1 denoting a perfect indicator of one level (high fidelity and abundance within that level). Level and indicator value are listed for that level for which indicator value was highest for each species. *P* values assessed with 1,000 permutations

P. mackenziana (Keyserling 1877) and *P. uintana* (Gertsch 1933) were indicative of pipeline edges (Table 2). Because abundance within each specified class is incorporated in the indicator analysis algorithm, it is not surprising that many of the indicator species identified were among the most abundant species overall.

The abundances of the ten most abundant spider species were strongly significantly affected by distance from the disturbance edge (Table 3). The abundances of four species differed between years, and of two species were affected by disturbance type. One spider species displayed a significant disturbance type \times distance interaction: *Pardosa moesta* (Banks 1892) was significantly more abundant on clearcuts than within the forest (Fig. 2). Most species were clearly more abundant either on-disturbance or in the forest interior, with the exception of *P. uintana*, which declined in abundance moving from the disturbance edge into the disturbance (Fig. 2), and showed a declining trend in the direction of the forest interior (regression $F_{1,88} = 4.54$, $P = 0.036$). *P. mackenziana* also showed a significant edge effect, peaking in abundance at sites 10 m from the disturbance edge. None of the other abundant species showed a significant edge effect in terms of its abundance at distance levels.

Table 3 Fixed effects tests from an ANOVA on the abundances of ten spider species and on total spider abundance, rarefacted species richness, and evenness

Species	Year		Disturbance type		Distance		Disturbance type × distance	
	$F_{1,102}$	P	$F_{2,102}$	P	$F_{3,102}$	P	$F_{6,102}$	P
<i>Alopecosa aculeata</i>	0.009	0.93	0.34	0.72	4.7	0.004	1.1	0.37
<i>Cryphoea montana</i>	1.8	0.18	5.9	0.004	12.0	<0.0001	1.6	0.15
<i>Diplocentria bidentata</i>	34.2	<0.0001	1.0	0.36	3.3	0.02	2.0	0.07
<i>Lepthyphantes alpinus</i>	5.6	0.02	0.66	0.52	11.6	<0.0001	0.38	0.89
<i>Pardosa distincta</i>	0.05	0.82	2.6	0.08	14.8	<0.0001	0.97	0.45
<i>Pardosa mackenziana</i>	9.4	0.003	0.79	0.46	5.5	0.002	2.1	0.06
<i>Pardosa moesta</i>	3.6	0.06	4.3	0.02	15.7	<0.0001	3.8	0.002
<i>Pardosa uintana</i>	6.4	0.01	0.29	0.75	11.6	<0.0001	1.3	0.25
<i>Sisicottus montanus</i>	3.2	0.08	0.17	0.85	7.7	0.0001	0.56	0.76
<i>Zorncult</i>	3.3	0.07	2.4	0.09	4.7	0.004	0.48	0.82
Abundance	0.4	0.51	0.14	0.87	7.1	0.0002	2.4	0.03
Richness	9.2	0.003	2.1	0.12	3.6	0.02	0.73	0.63
Evenness	6.5	0.01	3.7	0.03	1.9	0.13	2.5	0.03

Block was also included in the model as a random effect. Items in bold are significant at $P < 0.05$

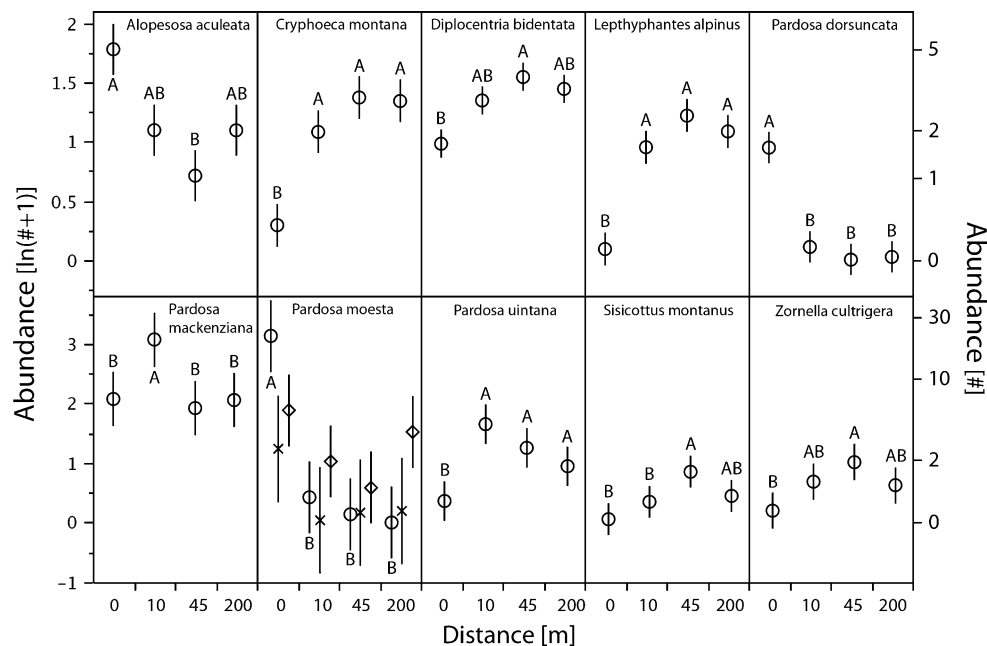


Fig. 2 Least square mean ($\pm 2SE$) abundance of the most abundant species at distance (0, 10, 45, 200 m) levels. Abundances of all spider species were $\ln(x + 1)$ transformed. Capital letters indicate significant differences between levels as determined by Tukey's HSD at $P < 0.05$. *Pardosa moesta* showed a significant interaction of distance with disturbance type, so for this species means are plotted for each disturbance type (circle = logging, cross = pipeline,

diamond = road) and capital letters refer to distances within logging, the only disturbance for which distance levels differed from each other. For all other species, the distance by disturbance type interaction was not significant (Table 3). Sample size for each distance level = 30. Sample sizes for interactions as follows: all logging distance classes = 12; pipeline distance classes = 6; road distance classes = 12

Edge effects on spider communities

Spider community metrics showed generally strong distance effects (Table 3). Rarefacted species richness was significantly affected by distance from the disturbance edge

but not by disturbance type (Table 3). Abundance and evenness both showed significant disturbance type by distance interactions, such that distance explained abundance only in clearcuts, and explained evenness only on pipelines (Fig. 3). Only species richness displayed a significant edge

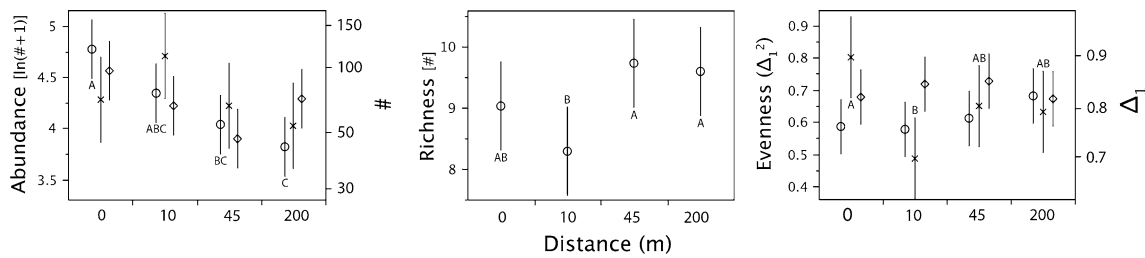


Fig. 3 Least square mean (± 2 SE) abundance, richness and evenness of spiders ($\ln(x + 1)$ -transformed) at distance levels (0, 10, 45, 200 m). Capital letters indicate significant differences between levels as determined by Tukey's HSD at $P < 0.05$. Where there was a

significant disturbance type \times distance interaction, separate plots are given for distance levels within each disturbance type. Sample sizes as follows: Control = 40; all logging distance classes = 12; pipeline distance classes = 6; road distance classes = 12

Table 4 Results of permutational multivariate ANOVA (PERMANOVA) analysis on spider community composition

Source	DF	Pseudo- <i>F</i>	Perm. <i>P</i>
Year	1	7.80	<0.001
Block (random effect)	5	2.45	<0.001
DisturbanceType	3	2.22	<0.001
Distance[DisturbanceType]	9	3.39	<0.001
YearDisturbanceType	2	1.10	0.32
YearDistance[DisturbanceType]	6	0.81	0.85

Significance of *F* statistic was assessed through 9,999 permutations. Error DF = 138

effect: richness dipped to a minimum level at 10 m from disturbance edges, and was significantly lower at 10 m sites than at sites in the forest interior (45 and 200 m).

Viewed multivariately, spider community composition was significantly affected by year, block, disturbance type and distance (nested within disturbance type), and there were no significant interactions between year and disturbance type or distance (PERMANOVA, Table 4). Pairwise comparisons within the PERMANOVA showed a clear decay of differences in spider communities along distance transects with increasing distance from disturbance; within all disturbance types, 0 m sites were strongly different from 200 m sites. In the case of roads and pipelines, 10 and 45 m sites were not significantly different from 200 m; only in the case of logging transects was there a significant difference between distance levels that persisted to 10 m. Logging sites at 10 m were also significantly different from on-disturbance sites.

To visualize these contrasts, unconstrained ordination showed that sampling sites were separated primarily between on- and off-disturbance sites (Fig. 4). Ninety-five percent confidence intervals of centroids for distances of 10, 45 and 200 m within all disturbance types overlapped substantially with those of the control, although the centroid for Logging-10 m diverged from control along NMDS axis 3. Centroids for Logging-45 and 200 m scored

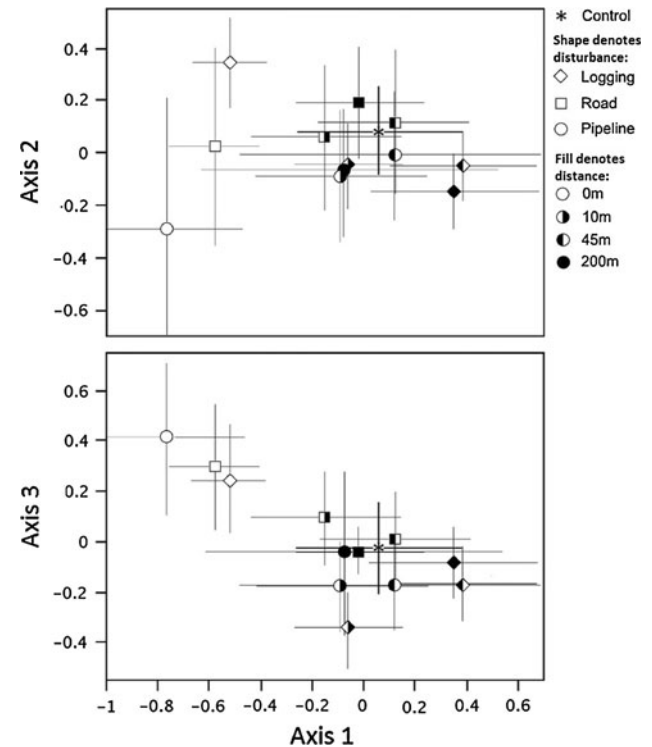


Fig. 4 Three dimensional non-metric multidimensional scaling ordination of the first and second (*top*) and first and third (*bottom*) axes in an analysis of species abundance using the Bray–Curtis similarity index. Only species that appeared in at least 5% of total sampling sites were included ($n = 57$ species), and abundances were $\ln(x + 1)$ -transformed. Stress = 15.6. Points shown are centroids calculated from mean axis scores of disturbance type–distance combination replicates, so that each *centroid* depicts a disturbance type–distance combination (e.g., a *filled circle* represents Pipeline-200 m). Ninety-five percent confidence intervals were calculated from replicates with sample sizes as follows: control = 16; all logging distance classes = 12; pipeline distance classes = 6; road distance classes = 12

higher on NMDS axis 2 than the other within-forest sites. The three on-disturbance centroids (i.e., Logging-0 m, Pipeline-0 m and Road-0 m) showed some separation along NMDS axis 2, although the confidence intervals of the Road-0 m centroid overlapped substantially with those of both Logging-0 m and Pipeline-0 m.

Spider species with the highest scores on NMDS axes were different from those selected by indicator analysis, and included a high proportion of linyphiid spiders (Table 5). Linyphiid species (# 3–9) occupied the positive end of axis 1 and the negative end of axis 2, while wolf spiders and crab spiders (Lycosidae, Philodromidae and Thomisidae, # 10–14) clustered together near zero on axis 2 (Fig. 5). High-scoring species were also significantly less abundant on average than indicator species (NMDS species mean \pm SD: 41 ± 41 individuals; indicator species 474 ± 492 individuals; $F_{1,26} = 11.5$, $P = 0.002$). Hence, indicators of distance classes were not necessarily important descriptors of community-level changes in species abundance across edges.

Edge effects on vegetation

The vegetation in the on-disturbance sites was distinct from corresponding sites at 200 m from the disturbance edge, as determined by pairwise contrasts (Logging: $t_5 = 3.0$, $P = 0.012$; Pipeline: $t_5 = 4.31$, $P = 0.002$; Road: $t_5 = 2.64$, $P = 0.004$). On-disturbance sites in general were dominated by grass and bare ground (average \pm SD percent cover, grass: $40 \pm 28\%$; bare ground: $25 \pm 30\%$), while vegetation at 200 m sites was largely composed of moss ($21 \pm 22\%$) and needles ($20 \pm 26\%$).

At clearcuts, sites 10 m from the forest edge had high levels of wood ($15 \pm 6\%$) and bare ground ($8 \pm 13\%$) compared to sites 10 m from the edges of pipelines and roads, which both had high levels of needles (Pipeline: $40 \pm 26\%$; Road: $17 \pm 21\%$). Clearcut 10 m sites showed a marginally significant (i.e., $0.05 < P < 0.1$) difference compared to sites 200 m from the edge (10 m vs. 200 m:

Table 5 Spider species with the highest loadings on NMDS axes (shown in Fig. 5)

No	Species	Family	No. recorded
1	<i>Anyphaena pacifica</i>	Anyphaenidae	8
2	<i>Gnaphosa parvula</i>	Gnaphosidae	11
3	<i>Agyneta #1</i>	Linyphiidae	52
4	<i>Bathyphantes pallidus</i>	Linyphiidae	126
5	<i>Dismodicus alticeps</i>	Linyphiidae	32
6	<i>Hybauchenidium gibbosum</i>	Linyphiidae	24
7	<i>Sisicottus orites</i>	Linyphiidae	17
8	<i>Tenuiphantes zebra</i>	Linyphiidae	46
9	<i>Walckenaeria karpinskii</i>	Linyphiidae	8
10	<i>Pardosa distincta</i>	Lycosidae	133
11	<i>Pardosa groenlandica</i>	Lycosidae	60
12	<i>Tibellus oblongus</i>	Philodromidae	9
13	<i>Xysticus ferox</i>	Thomisidae	26
14	<i>Xysticus emertoni</i>	Thomisidae	20

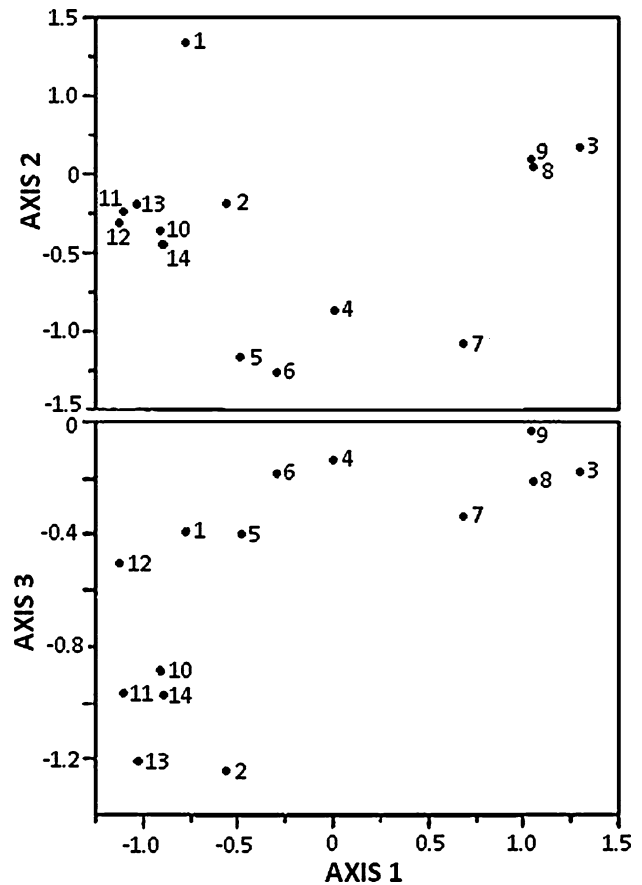


Fig. 5 Spider species loadings on NMDS axes. The five species with the highest loadings on each of the three axes are shown here; species numbers correspond to Table 5. Stress = 15.6

$t_5 = 1.65$, $P = 0.07$), while sites at 10 and 45 m from pipeline and road edges were very similar to 200 m sites (Pipeline 10 m vs. 200 m: $t_5 = 0.725$, $P = 0.69$; 45 m vs. 200 m: $t_5 = 0.732$, $P = 0.76$; Road 10 m vs. 200: $t_5 = 1.173$, $P = 0.25$; 45 m vs. 200 m: $t_5 = 1.31$, $P = 0.19$). Overall, some edge effects on vegetation were apparent at clearcut edges, while edge effects on vegetation at road and pipeline edges were negligible.

Discussion

Our objectives were to detect and compare the depth of edge influence at logging clearcuts, roads, and pipelines on ground-dwelling spider species and communities. We have shown that edge effects do not extend beyond 45 m into interior forest, but in some cases do extend up to 10 m from the disturbance edge. We have also shown that edge effects are more common at the edge of clearcuts than at roads or pipelines.

Indicator analysis, which considered only the abundances of spider species within disturbance classes and did

not account for effects such as year and block, identified three species that were indicative of edge habitat. These three species were significantly associated with clearcut and pipeline edges at 10 m from the respective disturbance, suggesting that some edge effects were present at both of these disturbances. However, when we examined the abundances of ten species across edges in a full model including year and block effects, edge effects on individual species were rare (only 2 of 10 species tested). Two spider species (*P. mackenziana*, *P. uintana*) displayed edge effects up to 10 m from disturbance edges, peaking in abundance at 10 m from the edges of all disturbance types. Thus we did not find strong evidence that any of the abundant species that we examined experienced differing edge effects at the three disturbance types.

Using three univariate community metrics, we did not detect strong edge effects. The strongest was with species richness, which for all disturbances was lower at 10 m from the disturbance edge than within forest interiors. Evenness declined at 10 m from the disturbance edge in the case of pipelines, although this decline was only statistically significant relative to the disturbance. Total spider abundance was significantly higher on-disturbance than at forest interior sites for all three disturbance types, and while spider abundance remained high at 10 m into the forest from clearcuts and pipelines, it was not significantly higher than interior forest levels.

While we found little evidence of differing edge effects at roads, pipelines or clearcuts using abundance of individual spider species or simple community metrics (abundance, richness, evenness), we found that spider community composition viewed multivariately did discriminate between disturbance types. Spider assemblages at clearcut edges remained distinct from those of forest interior sites to a distance of at least 10 m, while at roads and pipelines the spider community became indistinguishable from that at interior sites within 10 m of the edge. Spider assemblages at 10 m from clearcut edges were significantly different from on-clearcut assemblages, suggesting that at 10 m from a clearcut there is a distinct “edge community.” Visualization of these patterns using NMDS ordination showed that spider assemblages at 10 m in the forest were nevertheless close in composition to control sites and sites at further distances from the clearcut edge, suggesting that the edge community at 10 m is the result of faunal mixing between on-disturbance and interior communities.

The penetration of edge influence of between 10 and 45 m, shown here both by an individual species across all disturbances and by community composition at clearcuts, is substantially smaller than many that have been reported for other invertebrates (Haskell 2000; Ries et al. 2004), but it is consistent with Larrivee et al.’s

(2008) estimate of a 30 m edge effect on spider communities from a clearcut edge. It is possible that more edge effects would have been detected had sampling included distances that were smaller than 10 m from the forest edge. Edge effects in the boreal forest have been shown to be shorter in general than those reported in temperate or tropical forests (Harper and Macdonald 2002; Lopez et al. 2006).

It should be noted that only ground-active spiders were considered here and that edge effects may be different for spiders active in aboveground vegetation. Spiders that build webs in above-ground vegetation, because of their affinity with particular physical structure (Uetz 1991), could be expected to respond to changes in vegetation at forest edges to an even greater extent than those that hunt or build their webs on the forest floor. To date, studies that consider edge effects on spiders (e.g., Larrivee et al. 2008; Pajunen et al. 1995; Pearce et al. 2005) have exclusively used pitfall traps and thus are confined in application to ground-active spiders.

Although the study design makes it impossible to attribute differences in edge effects between the three disturbances to any one characteristic exclusively, for example shape, age or maintenance regime, evidence suggests that disturbance shape may be most important. Disturbance shape is important in determining the abiotic effects that are incident on forest edges. Pohlman et al. (2007) found that microclimatic gradients at the edges of linear openings in tropical forests dissipated within 25 m of the edge, which is much shorter than the penetration of microclimatic effects reported for edge effects at non-linear openings in similar forest (Laurance et al. 2002). The open space next to non-linear edges such as clearcuts leaves them more vulnerable to winds that increase in speed over the open area (Forman 1995), and they are exposed to incident solar radiation at more points during the day than are linear openings (Laurance et al. 2009). Although we did not measure abiotic features, we did find that forest edges at 10 m from clearcuts were more different from the forest interior than edges at 10 m from roads and pipelines in terms of their ground vegetation. Thus it seems possible that the greater exposure of forest edges at non-linear openings to abiotic effects causes greater penetration of edge effects on spider communities.

Apart from disturbance shape, the date of the edge origin could also contribute to different edge effects between disturbances. In eastern deciduous forests, edge effects at cut forests have been shown to change greatly over time, following succession and “aging” of the edge (Didham and Lawton 1999; Matlack 1993, 1994). The three disturbances considered here are unequal in age, the clearcuts and roads representing older, regenerating disturbances (12–19 years post-harvest) and the pipelines being much newer (within

2 years). The clearcuts and roads, constructed over the span of 8–10 years, also varied much more in age than the pipeline. Thus although the modulating effect of edge age cannot be explicitly accounted for, the fact that clearcuts and roads had similar average ages but different edge effects, and that roads and pipelines had different average ages but similar edge effects, suggests that disturbance shape is more important than age.

Like several studies of other invertebrates across forest/open space edges, we found that most spider species were clearly associated with either on-disturbance, or forest interior sites; all spider species showed strongly significant distance effects. A rich literature dealing with edge effects on carabid beetles in boreal forests suggests that most carabid species do not penetrate the edge but are likely to adhere either to the forest or the open area (Niemela et al. 2007), and this appears to be true of spiders as well. In addition, several authors have suggested that forest-associated spiders (Galle and Torma 2009; Pearce et al. 2005) and carabid beetles (Yu et al. 2010) “drift” into adjacent open spaces to a greater extent than open-associated species may drift into adjacent forests. This is consistent with our finding that species richness was significantly lower at the disturbance edge, suggesting that forest-associated species avoid the edge.

We have shown here that three common anthropogenic disturbances in the Alberta boreal forest are associated with significant impacts on spider communities. Not only do these disturbances themselves host markedly different spider communities from those that reside in interior forest, the disturbances are associated with edge effects that magnify the spatial extent of the disturbance effects on the landscape. Our finding that clearcuts are more strongly associated with edge effects than are narrow linear openings suggests that modified forestry practices could minimize the impact of tree harvest on forest spider communities. Our data indicate that silvicultural techniques such as variable retention harvest and partial cutting, especially when cut blocks are narrow, may minimize the detrimental impacts of logging on spider communities (Buddle and Shorthouse 2008).

As forests worldwide become increasingly vulnerable to fragmentation through development and deforestation, it is important to understand the ways that these human activities affect forest biota (Ewers and Didham 2008; Spence et al. 2008). The boreal forests of Alberta are subject to many sources of forest loss and disturbance due to their multiple uses as timber sources, oil and gas resources, and recreation (Schneider 2002). Compared to edges produced following forest fire, the edges that accompany clearcutting have been increasing in their extent on the landscape (Perera and Baldwin 2000). In Alberta, clearcuts are applied on the landscape in a checkerboard pattern of roughly evenly spaced 20–30 ha blocks, producing a between-cutblock forest habitat of similar size and shape to the cutblocks. The practiced pattern of imposing many small logging disturbances on the landscape, each with a large proportion of perimeter or edge, suggests that the relatively modest edge effects detected in this study are of broad significance. This study has shown that although spider communities in clearcuts, pipeline right-of-ways, and recreational roads do differ from spider communities in the forest, clearcuts are associated with the most marked edge effect of at least 10 m into undisturbed forests. In addition, this study presents some evidence that the configuration of open-space anthropogenic disturbances may have important consequences for their edge effects on spiders in boreal forests.

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Appendix

See Table 6.

Table 6 Spider species list, sorted alphabetically by family

Species	Family	Authority	No. recorded
<i>Agelenopsis utahana</i>	Agelenidae	Chamberlin & Ivie, 1933	177
<i>Arctobius agelenoides</i>	Amaurobiidae	Emerton, 1919	24
<i>Callobius nomeus</i>	Amaurobiidae	Chamberlin, 1919	20
<i>Anyphaena pacifica</i>	Anyphaenidae	Banks, 1896	8
<i>Araneus corticarius</i>	Araneidae	Emerton, 1884	1
<i>Araneus iviei</i>	Araneidae	Archer, 1951	4
<i>Cyclosa conica</i>	Araneidae	Pallas, 1772	1
<i>Hypsosinga alberta</i>	Araneidae	Levi, 1972	1

Table 6 continued

Species	Family	Authority	No. recorded
<i>Clubiona canadensis</i>	Clubionidae	Emerton, 1890	60
<i>Clubiona furcata</i>	Clubionidae	Emerton, 1919	1
<i>Clubiona kulczynskii</i>	Clubionidae	Lessert, 1905	100
<i>Clubiona opeongo</i>	Clubionidae	Edwards, 1958	6
<i>Clubiona trivialis</i>	Clubionidae	C. L. Koch, 1843	1
<i>Dictyna brevitarsa</i>	Dictynidae	Emerton, 1915	1
<i>Hackmania prominula</i>	Dictynidae	Tullgren, 1948	6
<i>Hackmania saphes</i>	Dictynidae	Chamberlin, 1948	3
<i>Drassodes neglectus</i>	Gnaphosidae	Keyserling, 1887	6
<i>Gnaphosa borea</i>	Gnaphosidae	Kulczynski, 1908	135
<i>Gnaphosa brumalis</i>	Gnaphosidae	Thorell, 1875	4
<i>Gnaphosa microps</i>	Gnaphosidae	Holm, 1939	24
<i>Gnaphosa muscorum</i>	Gnaphosidae	L. Koch, 1866	120
<i>Gnaphosa parvula</i>	Gnaphosidae	Banks, 1896	11
<i>Haplodrassus eunis</i>	Gnaphosidae	Chamberlin, 1922	3
<i>Haplodrassus hiemalis</i>	Gnaphosidae	Emerton, 1909	10
<i>Haplodrassus signifer</i>	Gnaphosidae	C. L. Koch, 1839	5
<i>Micaria aenea</i>	Gnaphosidae	Thorell, 1871	80
<i>Micaria coloradensis</i>	Gnaphosidae	Banks, 1896	3
<i>Micaria gertschi</i>	Gnaphosidae	Barrows & Ivie, 1942	1
<i>Micaria pulicaria</i>	Gnaphosidae	Sundevall, 1831	34
<i>Micaria rossica</i>	Gnaphosidae	Thorell, 1875	2
<i>Orodrassus canadensis</i>	Gnaphosidae	Platnick & Shadab, 1975	2
<i>Orodrassus coloradensis</i>	Gnaphosidae	Emerton, 1877	1
<i>Sergiolus montanus</i>	Gnaphosidae	Emerton, 1890	1
<i>Zelotes fratris</i>	Gnaphosidae	Chamberlin, 1920	31
<i>Zelotes puritanus</i>	Gnaphosidae	Chamberlin, 1922	19
<i>Cryphoeca montana</i>	Hahniidae	Emerton, 1909	466
<i>Neoantistea agilis</i>	Hahniidae	Keyserling, 1887	2
<i>Neoantistea gosiuta</i>	Hahniidae	Gertsch, 1934	5
<i>Agyneta #1</i>	Linyphiidae		52
<i>Agyneta #5</i>	Linyphiidae		1
<i>Agyneta #6</i>	Linyphiidae		4
<i>Agyneta allosubtilis</i>	Linyphiidae	Loksa, 1965	118
<i>Agyneta olivacea</i>	Linyphiidae	Emerton, 1882	143
<i>Bathypantes latescens</i>	Linyphiidae	Chamberlin, 1919	4
<i>Bathypantes pallidus</i>	Linyphiidae	Banks, 1892	126
<i>Bathypantes simillimus</i>	Linyphiidae	L. Koch, 1879	5
<i>Ceraticelus bulbosus</i>	Linyphiidae	Emerton, 1882	3
<i>Ceraticelus crassiceps</i>	Linyphiidae	Chamberlin & Ivie, 1939	1
<i>Ceraticelus fissiceps</i>	Linyphiidae	O. P.-Cambridge, 1874	70
<i>Ceraticelus laticeps</i>	Linyphiidae	Emerton, 1894	30
<i>Ceratinella alaskae</i>	Linyphiidae	Chamberlin & Ivie, 1947	1
<i>Diplocentria bidentata</i>	Linyphiidae	Emerton, 1882	504
<i>Dismodicus alticeps</i>	Linyphiidae	Chamberlin & Ivie, 1947	32
<i>Dismodicus decemoculatus</i>	Linyphiidae	Emerton 1882	3
<i>Erigone aletris</i>	Linyphiidae	Crosby & Bishop, 1928	4

Table 6 continued

Species	Family	Authority	No. recorded
<i>Erigone dentigera</i>	Linyphiidae	O. P.-Cambridge, 1874	1
<i>Grammonota angusta</i>	Linyphiidae	Dondale, 1959	2
<i>Grammonota gentilis</i>	Linyphiidae	Banks, 1898	26
<i>Grammonota gigas</i>	Linyphiidae	Banks, 1896	1
<i>Hybauchenidium gibbosum</i>	Linyphiidae	Sorensen, 1898	24
<i>Hypselistes florens</i>	Linyphiidae	O. P.-Cambridge, 1875	1
<i>Impropantes complicatus</i>	Linyphiidae	Emerton, 1882	40
<i>Lepthyphantes alpinus</i>	Linyphiidae	Emerton, 1882	428
<i>Meioneta fabra</i>	Linyphiidae	Keyserling, 1886	3
<i>Meioneta simplex</i>	Linyphiidae	Emerton, 1926	56
<i>Microlinyphia mandibulata</i>	Linyphiidae	Emerton, 1882	3
<i>Oedothorax #1</i>	Linyphiidae		1
<i>Oreonetides vaginatus</i>	Linyphiidae	Thorell, 1872	2
<i>Pelecopsis bishopi</i>	Linyphiidae	Kaston, 1945	1
<i>Pelecopsis menzei</i>	Linyphiidae	Simon, 1884	132
<i>Pityohyphantes subarcticus</i>	Linyphiidae	Chamberlin & Ivie, 1943	20
<i>Pocadicnemis americana</i>	Linyphiidae	Millidge, 1876	65
<i>Sisicottus montanus</i>	Linyphiidae	Emerton, 1882	181
<i>Sisicottus orites</i>	Linyphiidae	Chamberlin, 1919	17
<i>Tennesseeillum formica</i>	Linyphiidae	Emerton, 1882	1
<i>Tenuiphantes zebra</i>	Linyphiidae	Emerton, 1882	46
<i>Tunagyra debilis</i>	Linyphiidae	Banks, 1892	23
<i>Walckenaeria arctica</i>	Linyphiidae	Millidge, 1983	7
<i>Walckenaeria D3</i>	Linyphiidae		7
<i>Walckenaeria directa</i>	Linyphiidae	O. P.-Cambridge, 1874	3
<i>Walckenaeria exigua</i>	Linyphiidae	Millidge, 1983	4
<i>Walckenaeria II</i>	Linyphiidae		45
<i>Walckenaeria karpinskii</i>	Linyphiidae	O. P.-Cambridge, 1873	38
<i>Walckenaeria lepida</i>	Linyphiidae	Kulczynski, 1885	1
<i>Walckenaeria palustris</i>	Linyphiidae	Millidge, 1983	1
<i>Walckenaeria spiralis</i>	Linyphiidae	Emerton, 1882	1
<i>Walckenaeria tricornis</i>	Linyphiidae	Emerton, 1882	39
<i>Zornella cultrigera</i>	Linyphiidae	L. Koch, 1879	237
<i>Agroeca ornata</i>	Liocranidae	Banks, 1892	32
<i>Alopecosa aculeata</i>	Lycosidae	Clerck, 1757	463
<i>Arctosa alpigena</i>	Lycosidae	Doleschall, 1852	35
<i>Pardosa concinna</i>	Lycosidae	Thorell, 1877	3
<i>Pardosa distincta</i>	Lycosidae	Blackwall, 1846	133
<i>Pardosa dorsuncata</i>	Lycosidae	Lowrie & Dondale, 1981	220
<i>Pardosa groenlandica</i>	Lycosidae	Thorell, 1872	60
<i>Pardosa fuscata</i>	Lycosidae	Thorell, 1875	5
<i>Pardosa hyperborea</i>	Lycosidae	Thorell, 1872	152
<i>Pardosa mackenziana</i>	Lycosidae	Keyserling, 1877	1897
<i>Pardosa modica</i>	Lycosidae	Blackwall, 1846	8
<i>Pardosa moesta</i>	Lycosidae	Banks, 1892	989
<i>Pardosa ontariensis</i>	Lycosidae	Gertsch, 1933	8
<i>Pardosa tesquorum</i>	Lycosidae	Odenwall, 1901	168
<i>Pardosa uintana</i>	Lycosidae	Gertsch, 1933	467

Table 6 continued

Species	Family	Authority	No. recorded
<i>Pardosa xerampelina</i>	Lycosidae	Keyserling, 1877	157
<i>Trochosa terricola</i>	Lycosidae	Thorell, 1856	89
<i>Philodromus mysticus</i>	Philodromidae	Dondale & Redner, 1975	1
<i>Philodromus pernix</i>	Philodromidae	Blackwall, 1846	4
<i>Philodromus placidus</i>	Philodromidae	Banks, 1892	1
<i>Philodromus rufus quartus</i>	Philodromidae	Walckenaer, 1826	2
<i>Thanatus formicinus</i>	Philodromidae	Clerck, 1757	3
<i>Thanatus rubicellus</i>	Philodromidae	Mello-Leitao, 1929	2
<i>Thanatus striatus</i>	Philodromidae	C. L. Kock, 1845	1
<i>Tibellus maritimus</i>	Philodromidae	Menge, 1875	11
<i>Tibellus oblongus</i>	Philodromidae	Walckenaer, 1802	9
<i>Tetragnatha laboriosa</i>	Tetragnathidae	Hentz, 1850	1
<i>Tetragnatha versicolor</i>	Tetragnathidae	Walckenaer, 1842	1
<i>Enoplognatha intrepida</i>	Theridiidae	Sorensen, 1898	18
<i>Robertus fuscus</i>	Theridiidae	Emerton, 1894	1
<i>Steatoda albomaculata</i>	Theridiidae	De Geer, 1778	1
<i>Ozyptila sincera canadensis</i>	Thomisidae	Dondale & Redner, 1975	2
<i>Xysticus acquiescens</i>	Thomisidae	Emerton, 1919	1
<i>Xysticus benefactor</i>	Thomisidae	Keyserling, 1880	11
<i>Xysticus brücheri</i>	Thomisidae	Gertsch, 1934	54
<i>Xysticus canadensis</i>	Thomisidae	Gertsch, 1934	5
<i>Xysticus ellipticus</i>	Thomisidae	Turnbull, Dondale & Redner, 1965	9
<i>Xysticus emertoni</i>	Thomisidae	Keyserling, 1880	26
<i>Xysticus ferox</i>	Thomisidae	Hentz, 1847	20
<i>Xysticus luctuosus</i>	Thomisidae	Blackwall, 1836	62
<i>Xysticus obscurus</i>	Thomisidae	Collett, 1877	17
<i>Xysticus triguttatus</i>	Thomisidae	Keyserling, 1880	2
<i>Titanoeca nivalis</i>	Titanoecidae	Simon, 1874	3

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