



Carabid and spider population dynamics on urban green roofs

J. A. COLIN BERGERON¹, JAIME PINZON² & JOHN R SPENCE¹

¹ Department of Renewable Resources, University of Alberta, 442 Earth Sciences Building, Edmonton, AB, T6G 2E3

² Natural Resources Canada, Northern Forestry Centre, 5320-122 street, Edmonton, AB, T6H 3S5

Corresponding author: Colin Bergeron: 442 Earth Sciences Building, Edmonton, AB, T6G 2E3, email: cb1@ualberta.ca, phone: 780-492-6965

Abstract

Green roofs are valuable ecosystems that enhance the biodiversity value of urban landscapes in northern Alberta. Using pitfall traps on green roofs and adjacent ground sites, we show that roof arthropods are characteristic of native grasslands that are threatened in Alberta. Although we found lower abundance of spiders and carabids on roofs, species richness as assessed by rarefaction did not differ between roof and nearby ground sites. Thus, arthropod communities of these extensive green roofs do not seem to be impoverished compared to ground habitats, despite differences in local environmental variables (e.g. substrate depth, surface, vertical isolation). Seasonal distribution of larval and adult captures in pitfall traps, and observation of egg sacs in spiders suggest that a number of species have established reproducing populations on these green roofs. Interestingly, carabid assemblages differed markedly in species composition between roofs and ground sites, but spider assemblages were much more similar. We explain this in relation to differences in dispersal ability between these taxa. Green roofs are likely valuable for urban conservation allowing native species characteristic of native grasslands to permeate through urban landscapes.

Key words: arthropods, vegetated roofs, grasslands, dispersal ability, wing di-morphism, larvae

Introduction

‘Green’ roofs with substrates for growth of vegetation contribute to urban biodiversity conservation and provide numerous additional benefits (Oberndorfer *et al.* 2007). The combination of vegetation, growing substrate, various membranes and irrigation systems installed on buildings is increasingly seen as a functioning ecosystem providing some services usually delivered by natural environments (Sutton 2015). Despite the wide gap in knowledge about the exact value of green roofs for urban biodiversity conservation (Williams *et al.* 2014), plants, birds, reptiles, mammals and many arthropods use these engineered habitats, in addition to prolific communities of bacteria and fungi (McGuire *et al.* 2015). As a result, governments at several levels are starting to include biodiversity conservation objectives among green roof policies and regulations (Sutton 2015; Assemblée Nationale de France 2016).

Design of green roof ecosystems ranges from extensive (shallow soil usually with a mat of *Sedum* spp.) through semi-extensive (shallow soil with higher herbaceous plant diversity) to intensive (deeper soil with diverse plant layers including vegetables, shrubs and trees) (Sutton 2015), and may include structural features creating additional habitat heterogeneity (e.g. woody material, stones, hummock, depressions) and environmental conditions appropriate for sustaining different organisms. Ground-dwelling arthropods are especially well suited for research on the habitat value of green roofs because 1) their life history strongly depends on ground and plant layers (Pearce and Venier 2006), and 2) the restrictions in ecosystem surface and depth on green roofs may be sufficient to satisfy their resource requirements (MacIvor and Ksiazek 2015). Therefore, arthropods have potential to establish viable populations on green roofs, rather than just being itinerant visitors.

With the explosion of enthusiasm for green roofs over the last few decades (Sutton 2015), knowledge

about their value as habitat for arthropods has started to emerge. In general, ground-dwelling arthropods collected from roofs tend to be adapted to hot and dry conditions characteristic of open habitats, and have a strong dispersal ability (MacIvor and Ksiazek 2015). Within roof vegetation cover and diversity (Madre *et al.* 2013), the surrounding landscape (Braaker *et al.* 2014) as well as distance of the roof from the ground (Madre *et al.* 2013) all affect the arthropod fauna of green roofs. Depending on green roof construction and landscape matrix (Kadas 2006), roof ecosystems seem to generally host fewer individuals and species, as well as different assemblages than ground sites nearby (Brenneisen and Hänggi 2006; MacIvor and Lundholm 2011). Although adult arthropods collected on roofs are often taken to imply successful colonization (Kadas 2006; MacIvor and Lundholm 2011; Braaker *et al.* 2014), deeper investigation of species-specific natural histories is required to know whether viable populations could be established on green roofs. Such knowledge would promote better understanding of metapopulation dynamics of species using green roofs in urban areas.

Study of juvenile arthropods associated with adults of species found on the roofs, as well as the seasonal occurrence of adults, eggs and juveniles, should clarify the nature of populations on green roofs. Juvenile invertebrates have been collected from roofs (MacIvor and Lundholm 2011; Rumble and Gange 2013) but have rarely been included in detailed analyses aimed to understanding the dynamics of roof-dwelling populations. Similarly, data about wing-dimorphic species, such as many carabids, may shed more light on green roof population dynamics. For instance, in some species commonly found in urban environments long-winged individuals dominate during the colonization phase, but the proportion of long winged individuals decreases after establishment of populations (Bourassa *et al.* 2011).

In this paper, we use data about adult and juvenile carabid beetles and spiders collected in pitfall traps to answer the three following questions: 1) What species are found on green roofs in Edmonton, Alberta, Canada, and how are these species characterized in terms of typical habitat and dispersal ability? 2) Are there any species that could potentially complete their life cycle on green roofs and establish viable populations? 3) How do assemblages from green roofs compare to those from nearby ground sites in terms of species richness, species composition, dispersal ability, and body size?

Methods

Study site

We studied six green roofs and four adjacent ground sites, all located in Edmonton, Alberta, Canada (Table S1). Edmonton lies within the Central Parkland Natural Subregion, a broad ecosystem type at the junction of boreal forest to the north and grasslands to the south (Natural Regions Committee 2006). The natural vegetation of the Edmonton area is composed of remnant patches of aspen and willow shrublands mixed with grasslands (Natural Regions Committee 2006). The Central Parkland Natural Subregion hosts the highest human population density in Alberta – Edmonton is the northernmost large city in North America, having a population over one million people – and most of the native grasslands have been replaced by extensive agriculture for over a century (Natural Regions Committee 2006).

Edmonton has a cold continental climate. During 1981 - 2010, the average daily temperature recorded at the Edmonton City Centre airport was 4.2 °C and ranged from -10.4 °C in January to 17.7 °C in July with average minimum of -14.8 °C in January and an average maximum of 23.1 °C in July (Environment Canada, 2017). Typically, most of the low annual precipitation (total 455.7 mm) falls as rain (total 347.8 mm) during the short and hot summers while the rest (an average of 123.5 cm of snow) falls during the long and cold winter (Environment Canada, 2017).

Sampling Sites

All of the sampling sites were located within the limits of the City of Edmonton (Table S1), no farther than 1.3 km from the North Saskatchewan River, which is bordered by native vegetation typical of the aspen parklands and by an extensive boreal forest urban park with restricted development. We sampled six green roofs and paired four of them with adjacent ground sites. Green roof size varied between 221 m² and 825 m² and depth of growing medium between 8 cm and 16 cm (Table 1). The oldest roof was established in 2004 and the newest roof in 2013 (Table 1). Three of the ground sites were located within 100 meters of their associated roof, but distance to the fourth was c. 450 meters, given availability of potential habitats in the urban landscape. The ground sites were extensively managed (no repeated mowing, weed control or planting), dominated by grasses, and ranged in size from 281 m² to 722 m² (Table 1).

TABLE 1. Description of green roofs and ground sites.

Site ID (abbreviation) ¹	Total roof area (m ²)	Green area (m ²)	Green roof height (m)	Substrate depth (cm)	Vegetation type	Irrigation	Year planted
ATB east (ATB)	685	407	13	8 to 16	Herb mix and <i>Sedum</i> spp.	No	2010
Immigration Hall (Immig.)	666	334	10	8	Herb mix	No	2009
Stantec Atrium (Stantec)	3968	825	12	8 to 16	Herb mix and <i>Sedum</i> spp.	Yes	2004
Edventure ² (Edv.)	1497	378	3	8 to 16	<i>Sedum</i> spp. with grasses	No	2013
Arctic Shore ² (Arctic)	460	345	3	10	Herb mix mostly grasses	No	2012
John Janzen Nature Centre (JJNC)	1073	221	7	8	<i>Sedum</i> spp. with grasses	Yes	2012
ATB ground (ATB_G)	NA	542	NA	NA	Herb mix mostly grasses	No	NA
Stantec ground (Stantec_G)	NA	434	NA	NA	Herb mix mostly grasses	No	NA
Zoo ground (Zoo_G)	NA	281	NA	NA	Herb mix mostly grasses	No	NA
JJNC ground (JJNC_G)	NA	722	NA	NA	Herb mix mostly grasses	No	NA

¹Abbreviations in parenthesis are used to identify individual sites in the text, figures and tables. ²Corresponding ground level site for Edv. and Arctic is Zoo_G.

Four of the green roofs had been established by spreading a continuous mat of growing medium over the different structural layers (drainage, root barrier, waterproof membrane and insulation (Sutton 2015)) and planted using seeds or seedlings of native species from the Prairies (Sutton *et al.* 2012). The two other green roofs consisted of *Sedum* spp. mats with only a few grasses planted in plastic trays laid out on the roof over the functional layers (Table 1).

Many herb species native to Alberta's prairies were present on the four roofs with continuous growing medium, as it is the case for the ATB roof (Sutton *et al.* 2012; Table 1). These species included *Poa pratensis* Linnaeus, *Poa secunda* Presl, *Hieracium unbellatum* Linnaeus, *Allium schoenoprasum* Linnaeus, *Potentilla gracilis* Douglas ex Hook, *Festuca saximontana* Rydberg, *Taraxacum officinale* Weber, *Elymus trachycaulis* (Link) Gould ex Shinnars, *Bouteloua gracilis* (H.B.K.) Lag. ex Griffith, *Koeleria macrantha* (Ledeb.) J.A. Schultes, *Muhlenbergia cuspidate* (Torr.) Rydberg, *Artemisia* spp., and *Heterotheca villosa* (Pursh) Shinnars. Various *Sedum* species dominated the other two roofs.

Sampling Design

During the summer season of 2014, five pitfall traps were installed at each site in such a way as to maximise spacing between traps and roof coverage. Traps consisted of a white plastic cup (8 cm deep X 11 cm diameter) serving as outer sleeve with an inner white plastic 'collecting cup', which could be removed to minimize disturbance around the trap during visits to service the traps, and a roof made of white corrugated plastic held above the trap by metal wire pushed into the ground (Spence and Niemelä 1994). Use of toxic substances was not desired on the roofs, so we used vinegar to preserve and kill arthropods. Pitfall traps were active on the

roofs from the last week of April until mid-October for a total of 173 days. Ground sites were sampled from mid-June to mid-October for a total of 117 days. Results pertaining to which species are found on the roofs and their life cycle were generated based on the full 173-day trapping season, but all comparisons between ground and roof assemblages were based on the 117 common days of trapping for both ground and roof assemblages.

Data analysis

We compiled overall abundance of each species, including juvenile individuals at the genus (carabids) or family (spiders) level, on each of the six roofs as well as the total abundances of these species from traps on all green roofs. For carabid beetles, we included published habitat associations (open, generalist, or forest) and moisture affinities (dry, mesic/dry, mesic, mesic/moist, moist, or wet) (Larochelle and Larivière 2003). We also noted whether species were native or introduced (Klimaszewski *et al.* 2012), and for each dimorphic species the proportion of short-winged specimens (wing shorter than elytra when fully extended). As equivalent information is not readily available for spiders, we used published information for species for which this information is known.

Life cycle on roofs

To facilitate comparisons among roofs and adult populations, we divided the pooled weekly catches of adult carabids and spiders by the number of effective trapping days on each roof in order to standardize for difference in sampling effort resulting from disturbed traps. The same standardization procedure was applied to juvenile spiders but for carabid larvae we plotted the seasonal raw abundance because the large discrepancy between number of larvae and number of adults hindered detection of patterns if larval abundances were standardized. Because of low rates of capture, pitfall traps are not appropriate sampling tools to assess larval activity-density (Traugott 1998); however, our goal here was simply to detect temporal associations.

We selected individual roofs where abundant species dominated the catches, and plotted the seasonal occurrence of adults and their corresponding juveniles for each taxon. By restricting analysis to single roof, it was frequently possible to restrict association of juveniles to one or very few species of adults. In addition to plotting captures of carabid and spider juveniles, we also plotted temporal presence of spiders with egg sacs.

Ground and green roof assemblages

In order to compare species richness between roof and ground sites, we calculated individual based rarefactions (Simberloff 1979) using the raw number of individuals per species pooled for either roof or ground habitats. Given disparities in sample size, species richness was estimated using coverage-based rarefaction for both roof and ground sites to compare roof and ground species richness at the same sample completeness along the rarefaction curve using the 95% confidence intervals (Chao and Jost 2012). Calculations were done using the iNEXT package (Hsieh *et al.* 2016) in the R statistical platform (R Core Team 2016).

We investigated differences in species composition between roof and ground sites using a Nonmetric Multidimensional Scaling (NMS) ordination based on Bray-Curtis dissimilarity (Legendre and Legendre 2012). For this analysis, we pooled adult catches from the 117-day common trapping season for the roof and ground sites, and standardized the catch in relation to sampling effort. On the ordination diagram, we plotted sites and only included species centroids for those represented by more than 14 individuals (15 carabid and 16 spider species). Based on published information about body size for carabid (Lindroth 1961, 1963, 1966, 1968, 1969) and spider (Peckham and Peckham 1909; Levi 1957; Dondale and Redner 1978, 1990; Paquin and Dupérré 2003; Dupérré and Paquin 2005) species, we used the median body length to calculate centroids for carabid species larger than 10 mm and spider species larger than 5 mm. These lengths allowed us to investigate whether the 30% largest species showed a preference for ground or roof sites. Ordinations were calculated using the vegan package (Oksanen *et al.* 2016) in the R statistical platform (R Core Team 2016).

Results

Carabids and spiders on green roofs

Over all six green roofs, we collected a total of 1,346 adult individuals (carabids: 544; spiders: 802),

representing 87 species (carabids: 34; spiders: 53; Table 2 & 3). Total catches of adults per roof over the 25 trapping weeks varied between 58 and 365 individuals (carabids: 17-217; spiders: 25-190; Table 2 & 3), with 224.3 ± 43.86 (average \pm Standard Error) individuals per roof (carabids: 90.7 ± 29.86 ; spiders: 133.7 ± 24.75). We collected 16 to 40 species of adult arthropods per roof (carabids: 6-20 carabids; 10-24 spiders; Table 2 & 3). We also collected 90 carabid larvae representing three genera, and 395 juvenile spiders representing eight families (Table 2 & 3). Number of juveniles per roof varied between 22 and 153 individuals (carabids: 1-29; spiders: 14-126; Table 2 & 3).

TABLE 2. Abundance and characteristics of carabids caught by pitfall traps between the last week of April and the third week of October on six green roofs in Edmonton, Canada.

Species	Total	Habitat	Moisture	Native	# Brachypterous
<i>Agonum cupreum</i>	169	Open	Dry	Y	1
<i>Amara ellipsis</i>	78	Open	Dry	Y	0
Amara larvae	70	na	na	na	na
<i>Amara cupreolata</i>	49	Open	Dry	Y	0
<i>Pterostichus adstrictus</i>	43	Generalist	Mesic/Dry	Y	0
<i>Amara lunicollis</i>	41	Open	Mesic	Y	0
<i>Amara littoralis</i>	37	Open	Mesic/Dry	Y	0
<i>Amara torrida</i>	34	Open	Dry	Y	0
<i>Stenolophus conjunctus</i>	16	Open	Dry	Y	0
<i>Bembidion quadrimaculatum</i>	15	Open	Mesic/Dry	Y	0
Agonum larvae	12	NA	NA	NA	NA
<i>Dicheirotrechus cognatus</i>	8	Open	Dry	Y	0
Pterostichus larvae	8	NA	NA	NA	NA
<i>Amara convexa</i>	6	Open	Dry	Y	0
<i>Agonum gratiosum</i>	5	Open	Moist	Y	0
<i>Poecilus lucublandus</i>	5	Open	Mesic/Dry	Y	0
<i>Pterostichus melanarius</i>	5	Open	Mesic/Moist	N	2
<i>Harpalus somnulentus</i>	4	Open	Mesic/Dry	Y	0
<i>Agonum placidum</i>	3	Open	Very dry	Y	0
<i>Amara familiaris</i>	3	Open	Mesic/Dry	N	0
<i>Harpalus ventralis</i>	3	Open	Dry	Y	0
<i>Bembidion nitidum</i>	2	Open	Dry	Y	0
<i>Bembidion versicolor</i>	2	Open	Moist	Y	0
<i>Clivina fossor</i>	2	Open	Moist	N	0
<i>Loricera pillicornis</i>	2	Open	Wet	Y	0
<i>Agonum sordens</i>	1	Open	Moist	Y	0
<i>Amara idahoana</i>	1	Open	Mesic/Dry	Y	0
<i>Amara obesa</i>	1	Open	Dry	Y	0
<i>Bembidion concretum</i>	1	Open	Wet	Y	0
<i>Calathus ingratus</i>	1	Generalist	Mesic	Y	1
<i>Carabus granulatus</i>	1	Open	Mesic	N	1
<i>Carabus nemoralis</i>	1	Open	Moist	N	1
<i>Cymindis borealis</i>	1	Open	Dry	Y	0
<i>Harpalus opacipennis</i>	1	Open	Dry	Y	0

...Continued on next page

TABLE 2. (Continued)

Species	Total	Habitat	Moisture	Native	# Brachypterous
<i>Notiophilus aquaticus</i>	1	Open	Mesic/Dry	Y	0
<i>Syntomus americanus</i>	1	Open	Dry	Y	0
<i>Synuchus impunctatus</i>	1	Generalist	Dry	Y	1
Total carabid adults	544				
Total carabid larvae	90				
Total carabids	634				

Life cycles on green roofs

Among the carabid larvae from green roofs, we identified representatives of three genera: *Amara* (70 larvae, 5 roofs), *Agonum* (12 larvae, 4 roofs), and *Pterostichus* (8 larvae, 3 roofs; Table 2). The seven most common carabid species caught (*Agonum cupreum* Dejean, *Amara ellipsis* (Casey), *Amara cupreolata* Putzeys, *Pterostichus adstrictus* Eschscholtz, *Amara lunicollis* Schiodte, *Amara littoralis* Mannerheim and *Amara torrida* (Panzer)) all occurred on roofs from which we collected larvae of the corresponding genus (Table S2). Five of these species (*A. cupreum*, *A. ellipsis*, *A. cupreolata*, *P. adstrictus*, and *A. lunicollis*) showed a first seasonal peak of adult activity during April-May, followed by the presence of larvae of the corresponding genera in June, and a second period of adult activity in June to August (Fig. 1). Adults of *A. torrida* were active from late June to mid-September and occurred on roofs where *Amara* larvae were trapped during May through September-October (Fig. 1b).

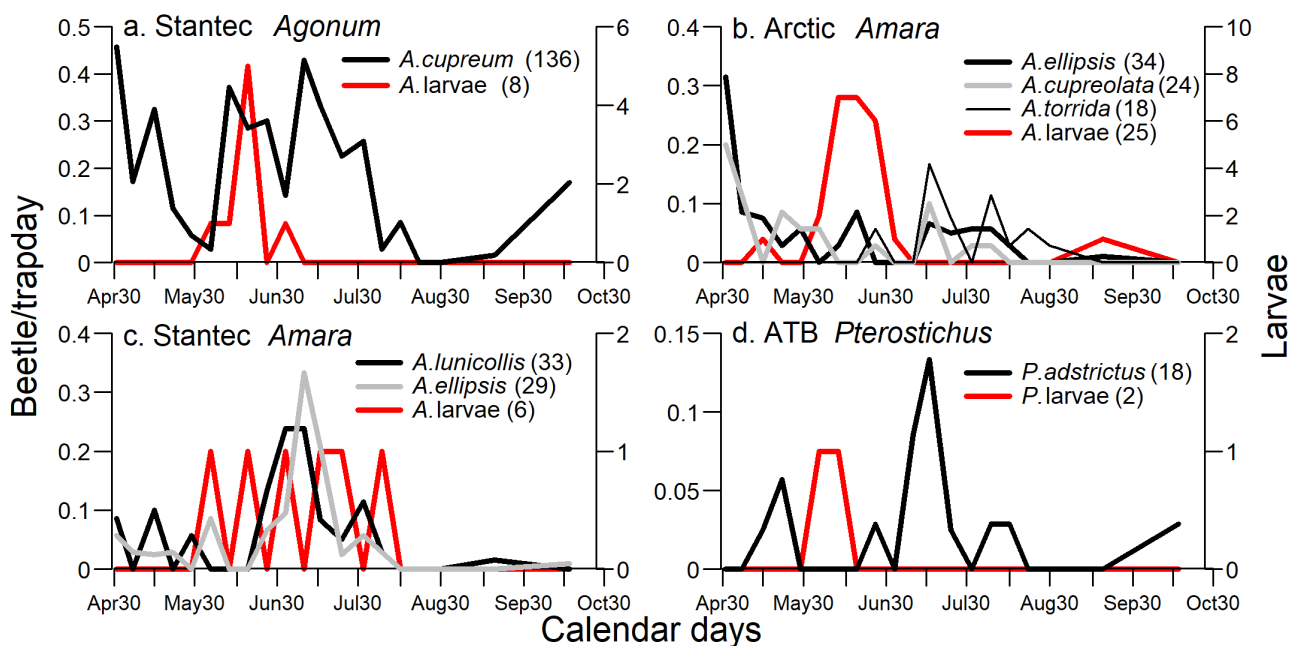


FIGURE 1. Seasonal abundance of the most common adult carabid beetles and their associated larvae from green roofs where they dominated the catches. Note that left axis is for adults and right axis is for larvae. a. *Agonum* from Stantec roof; b. *Amara* from Arctic roof; c. *Amara* from Stantec roof; d. *Pterostichus* from ATB roof

Among the juvenile spiders on green roofs, most represented three families (Linyphiidae: 143 individuals, 6 roofs, Lycosidae: 134 individuals, 6 roofs, and Thomisidae: 111 individuals, 5 roofs). Although juveniles of five other spider families were represented in the captures, no more than three individuals identified from roofs were included in any of them (Table 3). All of the six most abundant spider species caught on green roofs (*Pardosa distincta* (Blackwall), *Erigone blaesae* Crosby & Bishop, *Grammonota gentilis* Banks, *Mermessus trilobatus* Emerton, *Pardosa moesta* Banks and *Xysticus ferox* (Hentz)) occurred on roofs where juveniles of their corresponding families were present (Table S3).

TABLE 3. Abundance of spiders caught by pitfall traps between the last week of April and the third week of October on six green roofs in Edmonton, Canada.

Family	Species	Total
Linyphiidae	Juveniles	143
Lycosidae	Juveniles	134
Lycosidae	<i>Pardosa distincta</i>	128
Linyphiidae	<i>Erigone blaesa</i>	113
Thomisidae	Juveniles	111
Linyphiidae	<i>Grammonota gentilis</i>	108
Linyphiidae	<i>Mermessus trilobatus</i>	72
Lycosidae	<i>Pardosa moesta</i>	57
Thomisidae	<i>Xysticus ferox</i>	51
Linyphiidae	<i>Islandiana princeps</i>	25
Linyphiidae	<i>Meioneta simplex</i>	24
Lycosidae	<i>Pardosa fuscula</i>	23
Lycosidae	<i>Pardosa modica</i>	23
Linyphiidae	<i>Centromerus sylvaticus</i>	18
Thomisidae	<i>Ozyptila gertschi</i>	17
Linyphiidae	<i>Meioneta fabra</i>	13
Thomisidae	<i>Xysticus canadensis</i>	12
Linyphiidae	<i>Collinsia plumosa</i>	10
Theridiidae	<i>Enoplognatha caricis</i>	10
Linyphiidae	<i>Soucron arenarium</i>	8
Philodromidae	<i>Thanatus formicinus</i>	7
Lycosidae	<i>Pirata piraticus</i>	6
Philodromidae	<i>Thanatus striatus</i>	6
Linyphiidae	<i>Erigone alettris</i>	5
Linyphiidae	<i>Erigone atra</i>	5
Linyphiidae	<i>Islandiana flaveola</i>	5
Linyphiidae	<i>Mermessus undulatus</i>	5
Thomisidae	<i>Xysticus emertoni</i>	5
Linyphiidae	<i>Erigone zographica</i>	4
Lycosidae	<i>Pardosa ontariensis</i>	4
Theridiidae	<i>Enoplognatha cf. intrepida</i>	4
Linyphiidae	<i>Allomengea dentisetis</i>	3
Theridiidae	Juveniles	3
Thomisidae	<i>Xysticus discursans</i>	3
Linyphiidae	<i>Bathyphantes canadensis</i>	2
Linyphiidae	Linyphiidae sp1	2
Linyphiidae	Linyphiidae sp2	2
Theridiidae	<i>Asagena americana</i>	2
Clubionidae	<i>Clubiona abbotti</i>	1
Clubionidae	Juvenile	1

...Continued on next page

TABLE 3. (Continued)

Family	Species	Total
Dictynidae	Juvenile	1
Linyphiidae	<i>Aphileta misera</i>	1
Linyphiidae	<i>Bathyphantes concolor</i>	1
Linyphiidae	<i>Microlinyphia mandibulata</i>	1
Linyphiidae	<i>Praestigia kulczynskii</i>	1
Linyphiidae	<i>Sciastes cf. dubius</i>	1
Linyphiidae	<i>Tapinocyba prima</i>	1
Linyphiidae	<i>Walckenaeria castanea</i>	1
Lycosidae	<i>Alopecosa aculeata</i>	1
Lycosidae	<i>Pardosa groenlandica</i>	1
Lycosidae	<i>Pardosa mulaiki</i>	1
Lycosidae	<i>Pardosa tesquorum</i>	1
Lycosidae	<i>Trochosa terricola</i>	1
Philodromidae	Juvenile	1
Philodromidae	<i>Thanatus coloradensis</i>	1
Salticidae	<i>Habronattus captiosus</i>	1
Salticidae	<i>Habronattus cf. americanus</i>	1
Salticidae	Juvenile	1
Theridiidae	<i>Neottiura bimaculata</i>	1
Theridiidae	<i>Theridion cf. frondeum</i>	1
Theridiidae	<i>Theridion petraeum</i>	1
Thomisidae	<i>Xysticus cunctator</i>	1
	Total adult spiders	802
	Total juvenile spiders	395
	Total spiders	1197

Only seven specimens of *P. distincta*, the most abundant spider species, were caught carrying egg sacs on roofs (Fig. 2a) as well as one specimen of *Pirata piraticus* Clerck. Adults of *P. distincta* were trapped from June to September, with egg sacs occurring in July and August, along with a strong presence of lycosid juveniles (Fig. 2a). A few juvenile lycosids were also present on this roof in April-May and September-October.

Although no egg sacs were encountered, captures of other spider adults lined up seasonally with juvenile activity. For example, adults of *P. moesta* were mostly active in June and July with few individuals also caught in May and August-October, and lycosid juveniles were mostly caught at the end of July-early August with few specimens trapped in May and October (Fig. 2b). Part of these juveniles may also be associated with adults of *Pardosa fuscata* Thorell caught on the same roof mostly in May but present in the catch until August (Fig. 2b); however, they might also be associated with the juveniles captured on the roofs. Adults of *E. blaesae*, *M. trilobatus* and *G. gentilis* were all caught at the end of April (Fig. 2c, d, e), and show a first activity period in May-June, and another in July-August with few adults caught in September and October. Juveniles likely associated with these species were present in roof samples from the end of April until October (Fig. 2c, d, e). Thomisid juveniles likely associated with *X. ferox* were caught during the end of April to early May (Fig. 2f), and adult catches of this species were concentrated in May-June, but some until October.

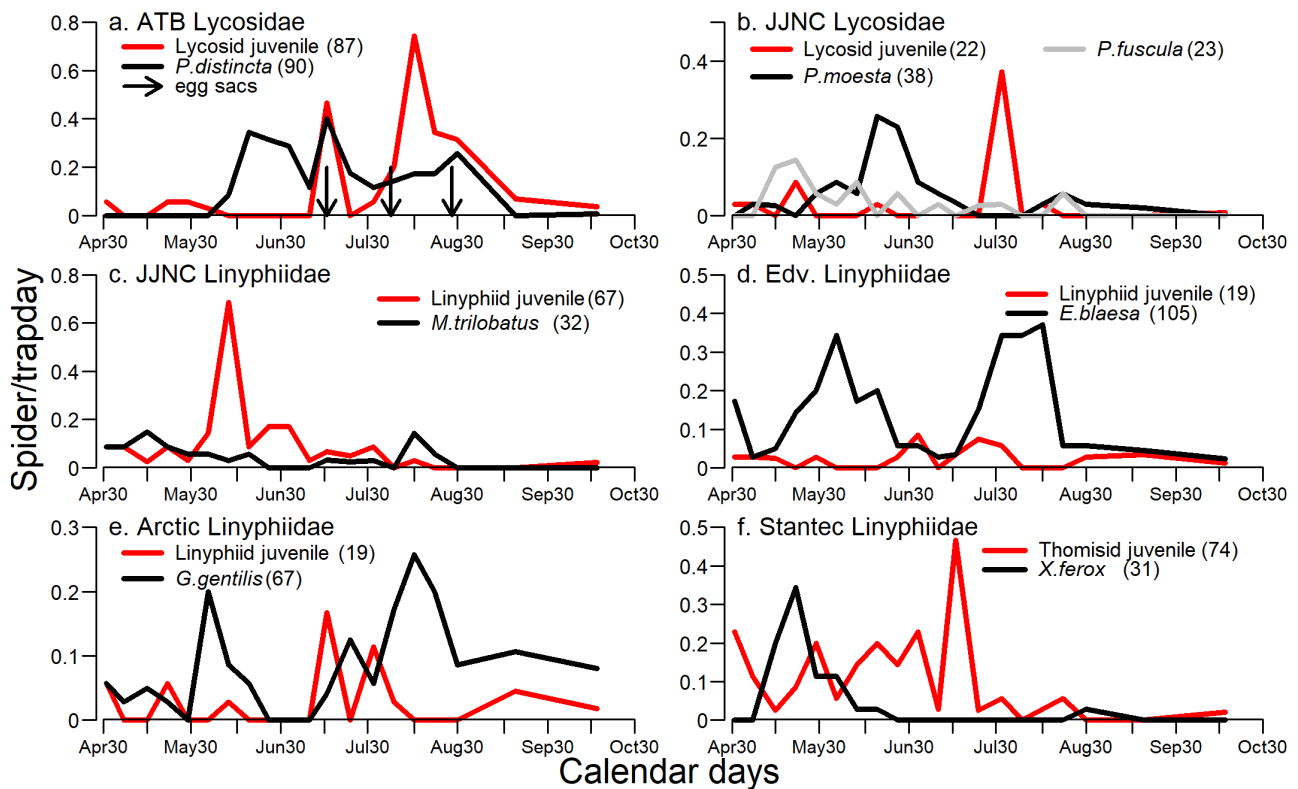


FIGURE 2. Seasonal abundance of the most common adult spiders, their associated juveniles, and presence of individuals carrying egg sacs from green roofs where they dominated the catches. a. Lycosidae from ATB roof; b. Lycosidae from JJNC roof; c. Linyphiidae from JJNC roof; d. Linyphiidae from Edv. Roof; e. Linyphiidae from Arctic roof; f. Linyphiidae from Stantec roof

Arthropods from green roofs vs ground sites

We caught about twice as many individual carabids at ground sites (115.5 ± 36.43) as we did on roofs (57.7 ± 18.94 ; Table 4), and three times as many spiders at ground sites (roofs: 79.7 ± 14.86 vs. ground: 245.8 ± 105.69 individuals; Table 5). Nonetheless, when assessed by rarefaction there was no difference in species richness between roof and ground sites for either carabids or spiders (Fig. 3a, b). The 95% confidence intervals for estimated richness at 96.2% sample coverage for carabids and 97.3% sample coverage for spiders overlapped greatly between ground sites (white error bars) and roofs (black error bars).

TABLE 4. Trapping rate and total catch of carabids caught between mid-June and the third week of October from green roofs and ground sites in Edmonton, Canada.

Species	Ground ¹	Roof ¹	Total ¹
<i>Carabus nemoralis</i>	66.0	0.3	139
<i>Agonum cupreum</i>	1.9	27.4	96
<i>Harpalus ventralis</i>	43.5	0.9	94
<i>Pterostichus melanarius</i>	37.8	1.5	84
<i>Amara ellipsis</i>	1.0	12.2	43
<i>Pterostichus adstrictus</i>	0.5	11.0	38
<i>Amara torrida</i>	1.0	9.8	35
<i>Amara littoralis</i>	0.5	9.5	33
<i>Harpalus somnulentus</i>	13.9	1.2	33

... Continued on next page

TABLE 4. (Continued)

Species	Ground¹	Roof¹	Total¹
<i>Amara cupreolata</i>	4.3	6.3	30
<i>Amara lunicollis</i>	1.0	8.3	30
<i>Carabus granulatus</i>	10.5	0.3	23
<i>Poecilus lucublandus</i>	8.1	1.2	21
<i>Harpalus opacipennis</i>	8.6	0.3	19
<i>Bembidion quadrimaculatum</i>	2.4	3.6	17
<i>Agonum placidum</i>	3.8	0.9	11
<i>Notiophilus aquaticus</i>	4.8	0.3	11
<i>Dicheirotrechus cognatus</i>	0.0	1.8	6
<i>Agonum gratiosum</i>	0.0	1.5	5
<i>Harpalus amputatus</i>	2.4	0.0	5
<i>Stenolophus conjunctus</i>	0.0	1.5	5
<i>Syntomus americanus</i>	1.4	0.3	4
<i>Diplocheila obtusa</i>	1.4	0.0	3
<i>Amara idahoana</i>	0.5	0.3	2
<i>Amara obesa</i>	0.5	0.3	2
<i>Chlaenius purpuricollis</i>	1.0	0.0	2
<i>Clivina fossor</i>	0.0	0.6	2
<i>Harpalus herbivagus</i>	1.0	0.0	2
<i>Harpalus reversus</i>	1.0	0.0	2
<i>Synuchus impunctatus</i>	0.5	0.3	2
<i>Amara familiaris</i>	0.0	0.3	1
<i>Amara latior</i>	0.5	0.0	1
<i>Bembidion concretum</i>	0.0	0.3	1
<i>Bembidion versicolor</i>	0.0	0.3	1
<i>Calathus ingratus</i>	0.0	0.3	1
<i>Carabus chamissonis</i>	0.5	0.0	1
<i>Cymindis borealis</i>	0.0	0.3	1
<i>Harpalus innocuus</i>	0.5	0.0	1
<i>Harplaus ventralis</i>	0.5	0.0	1
<i>Tachypachus holmbergi</i>	0.5	0.0	1
Total (# individuals)	462	346	808
% Macropterous	51.5	98.3	71.6
Number of sites	4	6	10
Average catch per site (S.E.) ²	115.5(36.43)	57.7(18.94)	80.8(19.64)
Min. catch per site	14	13	13
Max. catch per site	181	137	181

¹Species level trapping rate for roof and ground sites represent the number of carabids per 1000 trap days. All other values are number of individuals. ²S.E.: Standard Error.

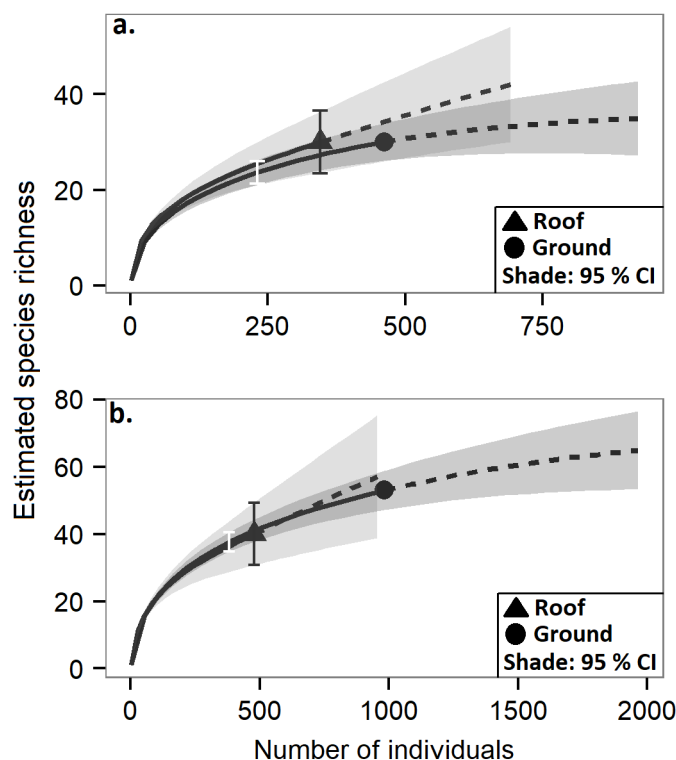


FIGURE 3. Rarefaction curves comparing estimated species richness between green roofs and ground sites for carabids (a.) and spiders (b.). Solid lines: interpolated species richness; dotted lines: extrapolated species richness; black and white error bars: 95 % confidence interval for roof and ground, respectively, compared at equal sample completeness (Chao and Jost, 2012)

Species assemblages of both carabids and spiders from green roofs, however, differed fundamentally from those at ground sites (Fig. 4 and 5). For carabids, ground sites grouped together on the upper right side of the ordination plot while roof sites grouped on the lower left side (Fig. 4a). *Carabus nemoralis* Müller, *Carabus granulatus* Linnaeus, *Pterostichus melanarius* (Illiger), *Harpalus ventralis* Leconte, *Harpalus somnulentus* Dejean, *Harpalus opacipennis* Haldeman and *Poecilus lucublandus* (Say) characterized the ground assemblages, while *A. cupreum*, *A. lunicollis*, *A. ellipsis*, *A. littoralis*, *P. adstrictus*, *A. torrida* and *Bembidion quadrimaculatum* Say were associated with green roof habitats (Fig. 4b). In the ordination, *A. cupreolata* is somewhat closer to the roofs than the ground sites (Fig. 4b), but catch rate did not differ much between roofs and ground sites (Table 4). Carabid assemblages from the ground sites, tended to be dominated by larger-bodied species than on the roofs (Fig. 4a), and ground sites also had a much higher proportion of brachypterous individuals (48.5%) compared to the roofs (1.7%; Table 4).

For spider assemblages, ground sites were found on the right side of the ordination space, while roof sites were found on the left side (Fig. 5a). Many spider species were clearly associated with ground sites (*P. moesta*, *Pardosa tesquorum* (Odenwall), *Trochosa terricola* Thorell, *Bathyphantes concolor* (Wider), *Neottiura bimaculata* (Linnaeus), *Zelotes fratris* Chamberlin, *Alopecosa aculeata* (Clerck) and *Castianeira descripta* (Hentz); Fig. 5b) with catches significantly higher at these sites (Table 5). However, catches of *G. gentilis* and *E. blaesa* were clearly higher on roof sites (Fig. 5b, Table 5). Other species, such as *P. distincta*, *X. ferox* and *M. trilobatus*, were caught at similar rates at both roof and ground sites (Fig. 5b; Table 5). Most of the largest-bodied spider species are found in association with ground sites (Fig. 5a).

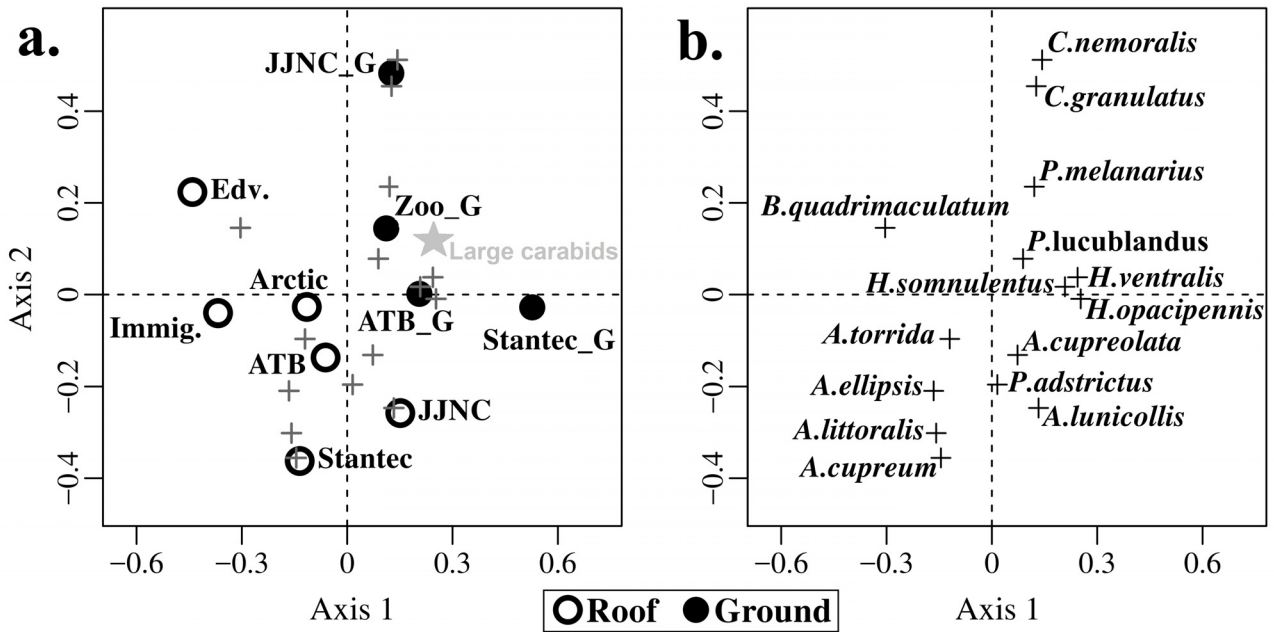


FIGURE 4. NMS ordination illustrating the carabid species composition in each site (stress: 0.11). a. Position of each site and species centroid, star: centroid for species larger than 10 mm; b. Species name related to each species centroid.

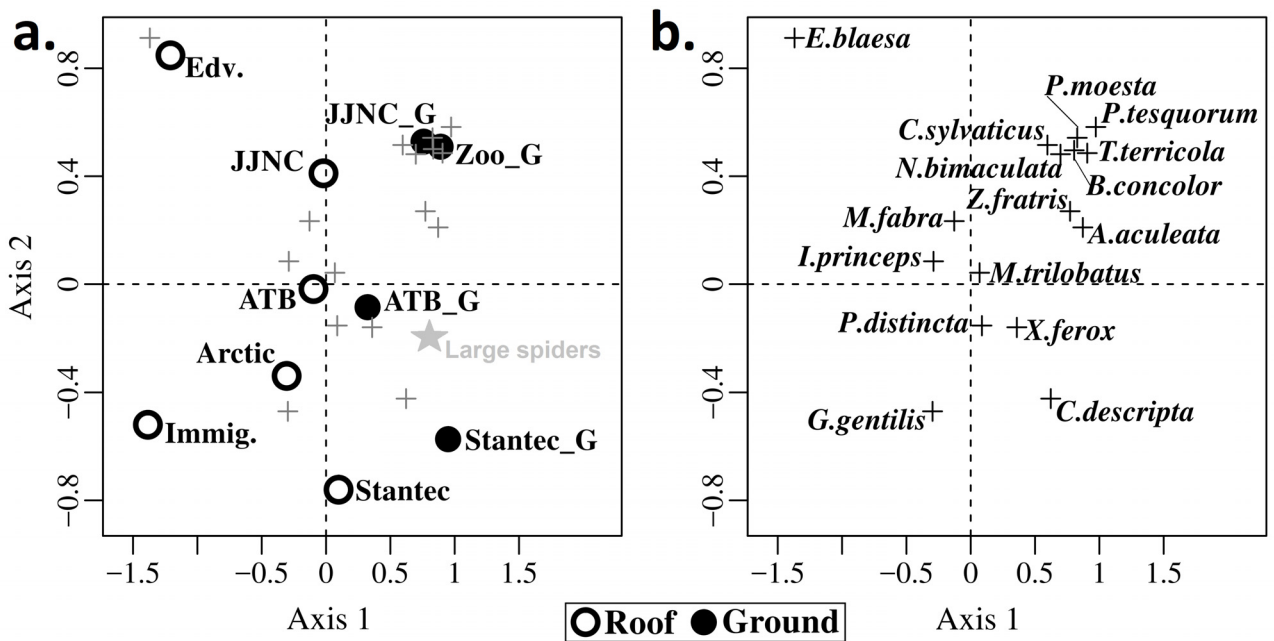


FIGURE 5. NMS ordination illustrating the spider species composition in each site (stress: 0.11). a. Position of each site and species centroid, star: centroid for species larger than 5 mm; b. Species name related to each species centroid.

TABLE 5. Trapping rate and total catch of spiders caught between mid-June and the third week of October from green roofs and ground sites in Edmonton, Canada.

Family	Species	Ground ¹	Roof ¹	Total ¹
Lycosidae	<i>Pardosa moesta</i>	184.6	11.9	426
Lycosidae	<i>Pardosa distincta</i>	24.9	36.7	175
Linyphiidae	<i>Bathypantes concolor</i>	56.9	0.3	120
Lycosidae	<i>Trochosa terricola</i>	40.2	0.0	84
Linyphiidae	<i>Grammonota gentilis</i>	0.5	22.9	78
Linyphiidae	<i>Erigone blaesa</i>	0.5	21.2	72
Linyphiidae	<i>Mermessus trilobatus</i>	12.4	10.4	61
Linyphiidae	<i>Centromerus sylvaticus</i>	18.7	5.4	57
Corinnidae	<i>Castianeira descripta</i>	24.9	0.0	52
Lycosidae	<i>Alopecosa aculeata</i>	21.5	0.0	45
Lycosidae	<i>Pardosa tesquorum</i>	10.5	0.0	22
Thomisidae	<i>Xysticus ferox</i>	6.2	2.1	20
Linyphiidae	<i>Islandiana princeps</i>	1.4	3.9	16
Theridiidae	<i>Neottiura bimaculata</i>	7.2	0.3	16
Linyphiidae	<i>Meioneta fabra</i>	2.9	2.7	15
Gnaphosidae	<i>Zelotes fratris</i>	6.7	0.0	14
Linyphiidae	<i>Allomengea dentisetis</i>	4.8	0.9	13
Lycosidae	<i>Pardosa fuscula</i>	1.9	2.1	11
Philodromidae	<i>Thanatus formicinus</i>	3.3	1.2	11
Thomisidae	<i>Ozyptila gertschi</i>	0.0	3.3	11
Thomisidae	<i>Xysticus emertoni</i>	4.8	0.3	11
Theridiidae	<i>Enoplognatha caricis</i>	0.5	2.4	9
Linyphiidae	<i>Meioneta simplex</i>	1.0	1.8	8
Theridiidae	<i>Asagena americana</i>	2.9	0.6	8
Mimetidae	<i>Mimetus eperoides</i>	2.9	0.0	6
Corinnidae	<i>Castianeira longipalpa</i>	2.4	0.0	5
Gnaphosidae	<i>Zelotes puritanus</i>	2.4	0.0	5
Hahniidae	<i>Neoantistea agilis</i>	2.4	0.0	5
Liocranidae	<i>Scotinella pugnata</i>	2.4	0.0	5
Linyphiidae	<i>Erigone aletris</i>	0.5	1.2	5
Linyphiidae	<i>Erigone atra</i>	0.0	1.5	5
Lycosidae	<i>Pirata piraticus</i>	0.0	1.5	5
Thomisidae	<i>Xysticus canadensis</i>	0.0	1.5	5
Linyphiidae	<i>Erigone zographica</i>	0.0	1.2	4
Linyphiidae	<i>Grammonota</i> cf. <i>capitata</i>	1.9	0.0	4
Linyphiidae	<i>Islandiana flaveola</i>	1.9	0.0	4
Lycosidae	<i>Hogna frondicola</i>	1.9	0.0	4
Thomisidae	<i>Xysticus discursans</i>	0.0	0.9	3
Clubionidae	<i>Clubiona kastoni</i>	1.0	0.0	2

...Continued on next page

TABLE 5. (Continued)

Family	Species	Ground ¹	Roof ¹	Total ¹
Dictynidae	<i>Cicurina</i> cf. <i>intermedia</i>	1.0	0.0	2
Gnaphosidae	<i>Drassodes neglectus</i>	1.0	0.0	2
Gnaphosidae	<i>Micaria pulicaria</i>	1.0	0.0	2
Linyphiidae	Linyphiidae sp2	0.0	0.6	2
Linyphiidae	<i>Microneta viaria</i>	1.0	0.0	2
Theridiidae	<i>Theridion</i> cf. <i>frondeum</i>	0.5	0.3	2
Thomisidae	<i>Ozyptila sincera canadensis</i>	1.0	0.0	2
Thomisidae	<i>Xysticus luctuosus</i>	1.0	0.0	2
Hahniidae	<i>Neoantistea magna</i>	0.5	0.0	1
Linyphiidae	<i>Bathyphantes canadensis</i>	0.0	0.3	1
Linyphiidae	<i>Bathyphantes pallidus</i>	0.5	0.0	1
Linyphiidae	<i>Collinsia plumosa</i>	0.0	0.3	1
Linyphiidae	<i>Helophora insignis</i>	0.5	0.0	1
Linyphiidae	Linyphiidae sp1	0.5	0.0	1
Linyphiidae	<i>Mermessus undulatus</i>	0.0	0.3	1
Linyphiidae	<i>Praestigia kulckzynskii</i>	0.0	0.3	1
Linyphiidae	<i>Scotinotylus sanctus</i>	0.5	0.0	1
Linyphiidae	<i>Soucron arenarium</i>	0.0	0.3	1
Linyphiidae	<i>Walckenaeria digitata</i>	0.5	0.0	1
Liocranidae	<i>Phrurotimpus borealis</i>	0.5	0.0	1
Lycosidae	<i>Arctosa rubicunda</i>	0.5	0.0	1
Lycosidae	<i>Pardosa groenlandica</i>	0.5	0.0	1
Lycosidae	<i>Pardosa modica</i>	0.0	0.3	1
Lycosidae	<i>Pardosa mulaiki</i>	0.0	0.3	1
Philodromidae	Philodromidae sp.	0.5	0.0	1
Philodromidae	<i>Thanatus coloradensis</i>	0.0	0.3	1
Salticidae	<i>Habronattus captiosus</i>	0.0	0.3	1
Salticidae	<i>Habronattus</i> cf. <i>americanus</i>	0.0	0.3	1
Theridiidae	Theridiidae sp1	0.5	0.0	1
Theridiidae	<i>Theridion petraeum</i>	0.0	0.3	1
Thomisidae	<i>Xysticus cunctator</i>	0.0	0.3	1
	Total	983	478	1461
	Number of sites	4	6	10
	Average catch per site (S.E.) ²	245.8 (105.69)	79.67(14.86)	146.1(47.94)
	Min. catch per site	78	16	16
	Max. catch per site	548	126	548

¹Species level trapping rate for roof and ground sites represent the number of spiders per 1000 trap days. All other values are number of individuals. ²S.E.: Standard Error.

Discussion

Carabids and spiders from green roofs

The green roofs that we studied in Edmonton, Canada host carabid and spider species commonly found in open habitats such as grasslands, prairies and meadows typical of the aspen parkland ecosystem surrounding the city, as well as anthropogenically disturbed habitats. In carabids for example, 16 of the 18 most abundant species (except *A. torrida* and *B. quadrimaculatum* which are nonetheless typical of open habitats; Table 2) are reported to naturally occur in grassland and prairie habitats by Lindroth (1961, 1963, 1966, 1968, 1969) or Laroche and Larivière (2003). Typical habitats are not known as well for spider species as for carabids, but all lycosid species represented by more than 2 individuals on the roofs are associated with open habitats (Dondale and Redner, 1990; Table 3). Many of the most abundant spider species on roofs (*P. distincta*, *E. blaesae*, *G. gentilis*, *M. trilobatus*, *P. moesta*, *X. ferox*, *Islandiana princeps* Braendegaard, *P. fuscata*, *Pardosa modica* (Blackwall), *Centromerus sylvaticus* (Blackwall), *Ozyptila gertschi* Kurata, *Collinsia plumosa* Emerton; Table 3) occur naturally in grassland and prairie habitats, although some of these species (i.e., *M. trilobatus*, *P. fuscata*, *O. gertschi*) may be more commonly encountered in forested regions (Carcamo *et al.* 2014). Carabid and spider populations established in prairies, grasslands and disturbed habitats seem to act as a source for the arthropod species pool that occupies green roofs in Edmonton.

Many of the species collected on roofs are also associated with dry habitats. Carabids found on green roofs have a tendency toward xerophily; in fact, 23 of the 34 species have an affinity for dry to moderately dry habitats, including the 11 most abundant carabid species (Laroche and Larivière, 2003; Table 2). However, some of the carabids (e.g. *A. gratiosum*, *L. pillicornis*, *A. sordens*, *B. concretum*) and spiders (*E. blaesae*, *P. fuscata*, *P. modica* and *P. piraticus*) caught on a subset of the roofs are also known to be associated with moist to wet habitats (Dondale and Redner 1990; Laroche and Larivière 2003; Table 2 & 3; Carcamo *et al.* 2014). Six of the eight aforementioned species were found on the JJNC roof, which was irrigated (Table 1), near a wetland, and partly shaded by trees. Of special interest, all the 26 specimens of *P. piraticus*, a pronouncedly semi-aquatic species (Graham *et al.* 2003), including the only specimen of this species carrying egg sac, were found on the JJNC roof. Wetter roof conditions and availability of source populations from nearby wetlands seem to affect the species composition of at least carabids and spiders found on green roofs. When designing green roofs for biodiversity purposes, factors such as irrigation and water retention will likely contribute to create heterogeneity within and between roofs that will attract a diverse set of species.

It appears that arthropods colonize green roofs in a relatively short time period after roof establishment. Our system of roofs is relatively young; they range in age from 1-10 years. The carabid and spider fauna of these new urban ecosystem islands is almost completely composed of species that can disperse aerially either by flight or ballooning (Table 2 & 3). Of the 544 carabids caught on the roofs, only seven adult specimens had wings shorter than the elytra (brachypterous; Table 2). The three spider families represented most abundantly on roofs (Linyphiidae, Lycosidae, and Thomisidae; Table 3) are all known to readily balloon at least as spiderlings (Foelix 2011). Furthermore, linyphiids and lycosids are, with carabids, known to be among the first organisms to establish populations in primary colonization of new islands and after volcanic eruptions (Thornton 2007). Good dispersal is also characteristic of species established in unstable environments (Den Boer 1970), where population maintenance is favoured by continuous influx from surrounding habitats.

Carabids and spiders may colonize green roofs by flying (carabids) or ballooning (spiders), climbing buildings, or arriving with the building material used to develop green roofs or, perhaps, with visitors (MacIvor and Ksiazek 2015). We believe that most of the carabid and spider species probably colonized green roofs while dispersing by flight or ballooning. Vertical isolation of these habitat islands, however, acts as a filtering mechanism that restricts the colonization of these relatively new ecosystems to species with higher mobility (Braaker *et al.* 2014).

The carabid and spider fauna from green roofs comprise a wide array of feeding habits, ranging from strictly carnivorous species (the spiders (Foelix 2011)) to omnivorous and mainly herbivorous carabid species. Because green roofs include a vegetative layer in their design (Sutton 2015), herbivorous animals that reach them have access to food sources from their time of arrival. In our study, about half (47.4 %) of the adult carabids caught on roofs (including five of the seven most abundant species) belonged to the genera *Amara* and *Harpalus* (Table 2) which are known to feed largely on seeds, fruits and vegetable matter (Lindroth, 1968); however, most of the other carabid species are mostly carnivorous (Laroche and Larivière 2003). Despite the fact that most organic matter included in the original growing medium is at least partly sterilized

(Best *et al.* 2015), a wide array of potential arthropod prey such as Collembola, Diptera, Hymenoptera, Lepidoptera, Heteroptera, Coleoptera, Psocoptera, and Arachnids are known to occur on green roofs (MacIvor and Lundholm 2011; Rumble and Gange 2013; MacIvor and Ksiazek 2015; Páll-Gergely *et al.* 2015). In addition to arriving with the building material (MacIvor and Ksiazek 2015), many of these taxa may themselves arrive on roof tops by direct dispersal (e.g. flying and ballooning) or passive aeolian fallout (Hawes 2008), serving as important links in the trophic webs in these communities.

Life cycle on green roofs

Presence of carabid larvae (incapable of flight and with poor mobility), and rare brachypterous adults, as well as spiders with egg sacs suggests that at least some species can reproduce, complete a full life cycle and, thus, establish resident populations on green roofs. We found that seasonal occurrence of adult beetles and associated larvae in the pitfall traps often matched expectations given understanding of their natural life cycles. For example, *A. ellipsis*, *A. cupreolata*, *A. lunicollis*, and *P. adstrictus* show spring breeding activity pattern (Niemelä *et al.* 1992) with high early spring activity for breeding, followed by strong presence of larvae in June, and a second period of adult activity in late summer (Fig. 1b, c, d) typical of these species in nature (Lindroth 1968). Breeding season of *A. cupreum* is not well known, but seasonal activity is similar to what described for spring breeders with a strong second activity period (Fig. 1a) and it is very likely that this species may complete a full life cycle on roofs as well. Furthermore, adult catches at the end of April and in October when snow is present suggests that adults overwinter on the roofs, as adult overwintering is known in nature for all the aforementioned carabid species (Larochelle and Larivière 2003). *A. torrida* is known as a summer breeder (Bousquet 2010) and its activity from June to the end of August, as well as the presence of associated larvae all summer including May and September (Fig. 1b) suggest that this species may also complete a full life cycle on the roofs.

Because ballooning of sub-adult and adult lycosids is very uncommon (Richter 1970), and that *Pardosa* species overwinter as sub-adults in Alberta (Buddle 2000), the presence of numerous *P. distincta*, *P. moesta*, and *P. fuscula* adults on single roofs (Table S3) indicates that sub-adults probably overwintered, emerged and reached maturity on the roof. Furthermore, the presence of seven *P. distincta* and one *P. piraticus* with egg sacs suggests that at least some adult lycosids breed on roofs. The observed occurrences of *P. distincta* with egg sacs coincide temporally with a strong presence of lycosid juveniles in pitfall traps (Fig. 2a). Thus, most of the numerous lycosid juveniles caught in July and August are likely new spiderlings coming out of the egg sacs, rather than juveniles from last year. These early juvenile stages account for the majority of ballooning in *Pardosa* (Richter, 1970). Furthermore, large-bodied juvenile lycosids caught in late April and early May could very well have overwintered on the roofs, especially those that were sub-adults. We do show here that all life stages of at least *P. distincta* are encountered on the roofs, and thus it is likely that this species can complete a full two-year life cycle (Dondale and Redner 1990) on roofs. Because we did not find individuals *P. moesta* and *P. fuscula* with egg sacs on any of the roofs, the evidence for completing a full life cycle is somewhat more equivocal. However, these two species assuredly complete part of their life cycle on the roofs, including overwintering, and the fact that we did not find female with egg sacs could be related to a combination of lower abundance and behavioral change that affect probability of capture when caring for egg sacs (Foelix 2011).

It is also very likely that *E. blaesae*, *M. trilobatus* and *G. gentilis*, the most abundant linyphiid species on the roofs, are able to complete a full life cycle on green roofs. Adults and related juveniles of these three species occur throughout the full sampling season (with a simultaneous drop in catches in late June-early July; Fig. 2c, d, e). This temporal pattern of abundance suggests a bivoltine life cycle, with overlapping generations and continuous reproduction that characterizes many linyphiids occurring in young, frequently disturbed and unstable environments (Draney and Crossley 1999; Blandenier *et al.* 2013). Furthermore, most linyphiid spiders are small web builders living in the litter or at its surface, and feeding on soft bodied insects, such as flies and springtails (Draney and Buckle 2005), which are abundant on green roofs (Rumble and Gange 2013; MacIvor and Ksiazek 2015). We cannot be certain that these spiders exist as self-sustaining populations on green roofs as linyphiids may balloon even as adults (Foelix 2011) and pitfall trap catches may reflect influx of dispersing spiders. However, the activity patterns reflected in our catch closely match those known for other linyphiid species in agricultural landscapes (Draney and Crossley 1999; Blandenier *et al.* 2013) where they reproduce and overwinter (Wheeler 1973; Royauté and Buddle 2012).

Finally, *X. ferox* populations on roofs seem to have a life cycle similar to those in Manitoba with one peak of activity during the first part of the summer, and a two-year life cycle (Aitchison 1984). Individuals of this

species are similar in body-size to *P. moesta* and *P. distincta* (Paquin and Dupérré 2003) and therefore, less likely to disperse by ballooning as adults and sub-adults. Thus, presence of numerous adults indicate that at least sub-adults may overwinter on the roofs. Furthermore, the presence of juveniles at the end of April-early May (Fig. 2f) could represent both sub-adults and spiderlings from the previous year that overwintered on the roofs. The peak of adult abundance during May-June followed by presence of juveniles until October (Fig. 2f) also suggest that both new spiderlings and juveniles from the previous years may stay on the roofs for the full summer. This is consistent with the natural history described by (Aitchison 1984) and provides evidence that *X. ferox* may also complete full life cycle on green roofs.

Brachypterous carabids cannot fly. Curiously, six of the seven brachypterous specimens we collected were the only individuals of their species caught on individual roofs and thus must have climbed or been transported to the roof. However, the single brachypterous individual of *A. cupreum* caught on the Stantec green roof occurred together with 135 macropterous individuals of this wing-dimorphic species (Table S2). While it is not impossible that this specimen was brought to the roof, it is also likely that this brachypterous individual actually comes from macropterous parents present on the roof and that carried a gene for brachyptery (Lindroth 1946). At least a few wing-dimorphic carabid species are known to fly as macropters, and with time after colonization, proportion of macropters decreases in newly established populations (Den Boer 1970; Bourassa *et al.* 2011). Thus, it will be interesting to follow such possible changes in populations on these islands of urban habitats.

Ground and roof assemblages

Carabids and spiders found on extensive green roofs are not just a subset of what is found in extensively managed ground sites located near the roofs, but generally support distinct species assemblages (Fig. 4 & 5). This is especially true for the beetles, among which all species, except *A. cupreolata*, were markedly more abundant in trap catches, either on the roof or on the ground (Table 4). In contrast, many of the most abundant spider species from the roofs were also abundant on ground sites, except for *G. gentilis* and *E. blasea* (Table 5). The power of dispersal by ballooning together with the tendency of spiders to be more generalist about habitat support the fact that spiders found on green roofs are more strongly affected by immigration from surrounding populations than are carabids (Braaker *et al.* 2014). Ground sites are located close to their associated roofs for JJNC, ATB and Stantec on the spider ordination (Fig. 5), but not on the carabid ordination (Fig. 4). This suggests that landscape effects are more important for spiders than for carabids, which in turn, are more strongly affected by local environmental conditions prevailing on roofs. Thus, local environmental selection should be stronger in carabid populations, while the species pool available locally to colonize roof tops seems more important in determining spider species assemblages (Braaker *et al.* 2014).

Variation in both dispersal ability and natural history seem to be important drivers of differentiation of roof and ground assemblages for both carabids and spiders. The high percentage of macropterous carabid individuals on the roof (98.3%) compared to that on the ground (51.5%; Table 4) suggests that carabid assemblages on roofs should be more similar to those of intensively managed and other highly disturbed open habitats. These assemblages generally have a higher proportion of macropterous specimens compared to extensive urban green areas (Hartley *et al.* 2007). However, even in intensively managed ground sites, Hartley *et al.* (2007) found a relatively high proportion of brachypterous specimens compared to our study and their species list is more similar to what we found on extensive ground sites than green roofs. Thus, it is possible that green roofs support carabid assemblages that are somewhat similar to those of remnant natural grasslands surrounding Edmonton. This underscores the opportunity for these species to permeate urban landscapes as suggested by (Braaker *et al.* 2014) and establish thriving populations in the absence of large introduced competitors.

Large-bodied carabids with short wings (*C. nemoralis*, *C. granulatus* and *P. melanarius*) and large cursorial spiders less likely to balloon (*P. moesta*, *T. terricola*, *A. aculeata*, *P. tesquorum*) were strongly associated with ground sites in our study (Figs. 4 & 5). Clearly, lack of access to the roofs could be largely responsible. However, of course these sites are more stable and do not need constant reintroduction to insure population maintenance. In contrast, roof populations may require metapopulation connections to enhance resilience to stochastic disturbances in these limited areas (Fahrig and Merriam 1994). It is also possible that resources such as food, overwintering sites or microclimate heterogeneity on the roofs are insufficient to support larger-bodied carabid and spider species at this point. Even if the occasional individual of these species might arrive, dispersal rates are likely too low for population establishment.

The introduced species *P. melanarius* is especially interesting in an urban island context because after local colonization by macropterous individuals, proportions of brachypterous individuals are known to increase with time in established populations (Niemelä and Spence 1991; Bourassa *et al.* 2011). We caught very few *P. melanarius* on roofs (five individuals from the six roofs compared with 82 individuals from the four ground sites; Table 4), corroborating findings about this species from roofs in Halifax, Nova Scotia (MacIvor and Lundholm 2011). At ground sites 34 % of *P. melanarius* individuals were macropterous, whereas three of five (60%) were macropterous on roofs. The data are slim but clearly it is possible for some individuals of this species to arrive on green roofs. However, it seems that the local environment of green roofs does not clearly support establishment of *P. melanarius* as a maximum of two individuals were caught on an individual roof. It seems most likely that the two brachypterous individuals caught on green roofs (40 % of the roof catch) were brought there. Similarly, presence of one brachypterous individual of each *C. nemoralis* and one *C. granulatus* in our sample from green roofs, suggests that large-bodied short-winged species are able to arrive on green roofs, but have not been able to establish populations thus far. Roof populations of smaller-bodied native species, however, may benefit from release from competition associated with the inability of large-bodied introduced species (Table 4) to establish roof populations.

Finally, arthropod communities of green roofs do not seem to be impoverished compared to ground habitats, despite differences in local environmental variables (e.g. substrate depth, surface, vertical isolation). Although we found lower abundance of spiders and carabids on roofs (Table 4 and 5), species richness as assessed by rarefaction did not differ between roof and nearby ground sites (Fig. 3). Other studies have reported lower number of species from roofs (Brenneisen and Hänggi 2006; Kadas 2006), but we show that when statistical procedures adjusting for effort and faunal coverage are used there were no significant differences in species diversity between roof and ground sites as reported by (MacIvor and Lundholm 2011).

Conclusions

Extensive green roofs provide interesting islands of urban ecosystem that are valuable as habitat for carabid and spider species characteristic of prairies, grasslands and naturally disturbed habitats that are threatened by urbanization in the Edmonton region. We have shown that at least some native carabid and spider species are able to reproduce and establish viable populations on green roofs. Extensive green roofs and corresponding urban ground areas seem equivalent in term of species richness but host different species composition. Dry conditions and resource stochasticity fostered by shallow roof substrates, as well as vertical isolation seem to act as filters for larger-bodied species that are poor dispersers and more demanding of resources. Plants used in the vegetative component of green roofs and aeolian arthropod fallout provide resources needed for establishment of herbivorous, omnivorous and carnivorous species shortly after green roof construction. Our results suggest that a diverse set of native arthropods readily colonize and use green roofs, even in our northern city. Thus, these low impact urban infrastructures may be strategically used in conservation planning related to species of threatened native prairie and grasslands habitats. Furthermore, these habitat islands provide an interesting basis for tests of various ecological theories about the significance of dispersal and species interactions in structuring arthropod communities.

Acknowledgements

We thank the Green Roof Working Group of the Alberta Low Impact Development Partnership for facilitating communication with building owners and site selection. Stantec Inc., Triovest Realty Advisors Inc, Hope Mission and The City of Edmonton kindly allowed us to access and sample the green roofs. Leonie Nadeau provided comments on an early version of the paper. Zoe Crandall, Matthew Brachmann and Cari McGillivray participated in field and laboratory work. The National Sciences and Engineering Research Council of Canada provided support through funding for a summer student through the USRA program, and an operating grant to J. Spence.

Literature cited

- Aitchison, C.W. (1984) The Phenology of Winter-Active Spiders. *The Journal of Arachnology*, 12: 249–271.
- Assemblée Nationale de France (2016) Loi n° 2016-1087 du 8 août 2016 pour la reconquête de la biodiversité, de la nature et des paysages. *Journal Officiel de la République de France*. Available from: <https://www.legifrance.gouv.fr/affichTexte.do?cidTexte=JORFTEXT000033016237&dateTexte=20170814> (accessed 19 January 2018)
- Best, B.B., Swadek, R.K. & Burgess, T.L. (2015) Soil-based green roofs. *In: Sutton, R.K. (Ed.), Green roof ecosystems*, Springer International Publishing, Switzerland, pp. 139–174.
https://doi.org/10.1007/978-3-319-14983-7_6
- Blandenier, G., Bruggisser, O.T., Rohr, R.P. & Bersier, L.F. (2013) Are phenological patterns of ballooning spiders linked to habitat characteristics? *The Journal of Arachnology*, 41, 126–132.
<https://doi.org/10.1636/P12-48>
- Bourassa, S., Spence, J.R., Hartley, D.J. & Lee, S.I. (2011) Wing-dimorphism and population expansion of *Pterostichus melanarius* (Illiger, 1798) at small and large scales in central Alberta, Canada (Coleoptera, Carabidae, Pterostichini). *ZooKeys*, 545–558.
<https://doi.org/10.3897/zookeys.147.2097>
- Bousquet, Y. (2010) *Illustrated Identification Guide to Adults and Larvae of Northeastern North American Ground Beetles (Coleoptera, Carabidae)*. Pensoft, Sofia, Bulgaria, 562 pp.
- Braaker, S., Ghazoul, J., Obrist, M.K. & Moretti, M. (2014) Habitat connectivity shapes urban arthropod communities: the key role of green roofs. *Ecology*, 95, 1010–1021.
<https://doi.org/10.1890/13-0705.1>
- Brenneisen, S. & Hänggi, A. (2006) Begrünte Dächer–ökofaunistische Charakterisierung eines neuen Habitattyps in Siedlungsgebieten anhand eines Vergleichs der Spinnenfauna von Dachbegrünungen mit naturschutzrelevanten Bahnarealen in Basel (Schweiz). *Mitteilungen der Naturforschenden Gesellschaften beider Basel*, 9, 99–122.
- Buddle, C.M. (2000) Life History of *Pardosa Moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in Central Alberta, Canada. *The Journal of Arachnology*, 28, 319–328.
[https://doi.org/10.1636/0161-8202\(2000\)028\[0319:LHOPMA\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2000)028[0319:LHOPMA]2.0.CO;2)
- Carcamo, H.A., Pinzon, J., Leech, R. & Spence, J.R. (2014) Spiders (Arachnida: Araneae) of the Canadian prairies. *In: Carcamo, H. & Giberson, D.J. (Eds.), Arthropods of Canadian grasslands (volume 3): biodiversity and systematics Part 1*. Ottawa: Biological Survey of Canada, pp. 75–137.
- Chao, A. & Jost, L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, 93, 2533–2547.
<https://doi.org/10.1890/11-1952.1>
- Den Boer, P.J. (1970) On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). *Oecologia*, 4, 1–28.
<https://doi.org/10.1007/BF00390612>
- Dondale, C.D. & Redner, J.H. (1978) *The insects and arachnids of Canada, Part 5. The crab spiders of Canada and Alaska, Araneae: Philodromidae and Thomisidae*. Agriculture Canada, Ottawa, Canada, Publication 1663, 225 pp.
- Dondale, C.D. & Redner, J.H. (1990) *The insect and arachnids of Canada, Part 17. The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska (Aranea: Lycosidae, Pisauridae, and Oxyopidae)*. Agriculture Canada, Ottawa, Canada, Publication 1858, 383 pp.
- Draney, M.L. & Buckle, D.J. (2005) Linyphiidae. *In: Ubick, D., Paquin, P., Cushing, P.E. & Roth, V. (Eds.), Spiders of North America: an identification manual*, American Arachnological Society, pp. 124–161.
- Draney, M.L. & Crossley, D.A. (1999) Relationship of Habitat Age to Phenology among Ground-Dwelling Linyphiidae (Araneae) in the Southeastern United States. *The Journal of Arachnology*, 27, 211–216.
- Dupérré, N. & Paquin, P. (2005) A new species of *Tapinocyba* (Araneae, Linyphiidae) with a redescription of *Tapinocyba minuta* (Emerton). *Zootaxa*, 1069 (1), 13.
<https://doi.org/10.11646/zootaxa.1069.1.2>
- Environment Canada (2017) *Climate normals and averages, 1981–2010*. Available from: http://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?searchType=stnName&txtStationName=edmonton&searchMethod=contains&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=1867&dispBack=0 (accessed 19 January 2018)
- Fahrig, L. & Merriam, G. (1994) Conservation of Fragmented Populations. *Conservation Biology*, 8, 50–59.
<https://doi.org/10.1046/j.1523-1739.1994.08010050.x>
- Foelix, R.F. (2011) *Biology of Spiders, third edition*. New York, USA: Oxford University Press USA/Georg Thieme Verlag, 419

pp.

- Graham, A.K., Buddle, C.M. & Spence, J.R. (2003) Habitat affinities of spiders living near a freshwater pond. *Journal of Arachnology*, 31, 78–89.
[https://doi.org/10.1636/0161-8202\(2003\)031\[0078:HAOSLN\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2003)031[0078:HAOSLN]2.0.CO;2)
- Hartley, D.J., Koivula, M.J., Spence, J.R., Pelletier, R. & Ball, G.E. (2007) Effects of urbanization on ground beetle assemblages (Coleoptera, Carabidae) of grassland habitats in western Canada. *Ecography*, 30, 673–684.
<https://doi.org/10.1111/j.2007.0906-7590.05199.x>
- Hawes, T.C. (2008) Aeolian fallout on recently deglaciated terrain in the high Arctic. *Polar Biology*, 31, 295–301.
<https://doi.org/10.1007/s00300-007-0357-0>
- Hsieh, T.C., Ma, K.H. & Chao, A. (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7, 1451–1456.
<https://doi.org/10.1111/2041-210X.12613>
- Kadas, G. (2006) Rare invertebrates colonizing green roofs in London. *Urban Habitats*, 4, 66–86.
- Klimaszewski, J., Langor, D.W., Batista, R., Duval, J.A., Majka, C.G., Scudder, G.G.E. & Bousquet, Y. (2012) *Synopsis of adventive species of Coleoptera (Insecta) recorded from Canada Part I: Carabidae*. Pensoft Publishers, Sofia, Bulgaria, 96 pp.
- Larochelle, A. & Larivière, M.C. (2003) *Natural history of the ground-beetles (Coleoptera: Carabidae) of America north of Mexico*. Pensoft, Sofia, Bulgaria, 583 pp.
- Legendre, P. & Legendre, L. (2012) *Numerical ecology*. Elsevier, Amsterdam, The Netherlands, 853 pp.
- Levi, H.W. (1957) The spider genera Enoplognatha, Theridion, and Paidisca in America north of Mexico (Araneae, Theridiidae). *Bulletin of the American Museum of Natural History*, 112, 1–124.
- Lindroth, C.H. (1946) Inheritance of wing dimorphism in *Pterostichus anthracinus* Ill. *Hereditas*, 32, 37–40.
<https://doi.org/10.1111/j.1601-5223.1946.tb02769.x>
- Lindroth, C.H. (1961) The ground-beetles (Carabidae excl. Cicindelinae) of Canada and Alaska. *Opuscula Entomologica, Supplementum XX*, 1–200.
- Lindroth, C.H. (1963) The ground-beetles (Carabidae excl. Cicindelinae) of Canada and Alaska. *Opuscula Entomologica, Supplementum XXIV*, 201–408.
- Lindroth, C.H. (1966) The ground-beetles (Carabidae excl. Cicindelinae) of Canada and Alaska. *Opuscula Entomologica, Supplementum XXIX*, 409–648.
- Lindroth, C.H. (1968) The ground-beetles (Carabidae excl. Cicindelinae) of Canada and Alaska. *Opuscula Entomologica, Supplementum XXXIII*, 649–944.
- Lindroth, C.H. (1969) The ground-beetles (Carabidae excl. Cicindelinae) of Canada and Alaska. *Opuscula Entomologica, Supplementum XXXIV*, 945–1192.
- MacIvor, J.S. & Ksiazek, K. (2015) Invertebrates on Green Roofs. In: Sutton, R.K. (Ed.) *Green Roof Ecosystems*, Springer International Publishing, Cham, pp. 333–355.
https://doi.org/10.1007/978-3-319-14983-7_14
- MacIvor, J.S. & Lundholm, J. (2011) Insect species composition and diversity on intensive green roofs and adjacent level-ground habitats. *Urban Ecosystems*, 14, 225–241.
<https://doi.org/10.1007/s11252-010-0149-0>
- Madre, F., Vergnes, A., Machon, N. & Clergeau, P. (2013) A comparison of 3 types of green roof as habitats for arthropods. *Ecological Engineering*, 57, 109–117.
<https://doi.org/10.1016/j.ecoleng.2013.04.029>
- McGuire, K.L., Payne, S.G., Orazi, G. & Palmer, M.I. (2015) Bacteria and fungi in green roof ecosystems. In: Sutton, R.K. (Ed.), *Green roof ecosystems*, Springer International Publishing, Switzerland, pp. 175–191.
https://doi.org/10.1007/978-3-319-14983-7_7
- Natural Regions Committee (2006) *Natural regions and subregions of Alberta*. Edmonton, Government of Alberta, 254 pp.
- Niemelä, J. & Spence, J.R. (1991) Distribution and Abundance of an Exotic Ground-Beetle (Carabidae): A Test of Community Impact. *Oikos*, 62, 351–359.
<https://doi.org/10.2307/3545500>
- Niemelä, J., Spence, J.R. & Spence, D.H. (1992) Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. *The Canadian Entomologist*, 124, 521–540.
<https://doi.org/10.4039/Ent124521-3>
- Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R.R., Doshi, H., Dunnett, N., Gaffin, S., Köhler, M., Liu, K.K.Y. & Rowe, B. (2007) Green Roofs as Urban Ecosystems: Ecological Structures, Functions, and Services. *Bioscience*, 57, 823–833.
<https://doi.org/10.1641/B571005>
- Oksanen, J., Blanchet, F.J., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L.,

- Solymos, P., Stevens, M.H.H., Szoecs, E & Wagner, H. (2016) Vegan: Community Ecology Package. R Package Version 2.4-0.
- Páll-Gergely, B., Kyrö, K., Lehvävirta, S. & Vilisics, F. (2015) Green roofs provide habitat for the rare snail (Mollusca, Gastropoda) species *Pseudotrachia rubiginosa* and *Succinella oblonga* in Finland. *Memoranda Societatis pro Fauna et Flora Fennica*.
- Paquin, P. & Dupérré, N. (2003) Guide d'identification des araignées (Araneae) du Québec. *Fabriques*, 11, 251.
- Pearce, J.L. & Venier, L.A. (2006) The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. *Ecological Indicators*, 6, 780–793.
<https://doi.org/10.1016/j.ecolind.2005.03.005>
- Peckham, G.W. & Peckham, E.G. (1909) Revision of the Attidae of North America. *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters*, 16, 355–665.
- R Core Team (2016) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Available from: <https://www.R-project.org/> (accessed 22 January 2018)
- Richter, C.J.J. (1970) Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). *Oecologia*, 5, 200–214.
<https://doi.org/10.1007/BF00344884>
- Royauté, R. & Buddle, C.M. (2012) Colonization dynamics of agroecosystem spider assemblages after snow-melt in Quebec (Canada). *Journal of Arachnology*, 40, 48–58.
<https://doi.org/10.1636/P11-16.1>
- Rumble, H. & Gange, A.C. (2013) Soil microarthropod community dynamics in extensive green roofs. *Ecological Engineering*, 57, 197–204.
<https://doi.org/10.1016/j.ecoleng.2013.04.012>
- Simberloff, D. (1979) Rarefaction as a distribution-free method of expressing and estimating diversity. In: Grassle, J.F., Patil, G.P., Smith, W.K. & Tailie, C. (Eds.), *Ecological diversity in theory and practice*, International Cooperative Publishing, Burstonville, Maryland, pp. 159–176.
- Spence, J.R. & Niemelä, J.K. (1994) Sampling carabid assemblages with pitfall traps: the madness and the method. *The Canadian Entomologist*, 126, 881–894.
<https://doi.org/10.4039/Ent126881-3>
- Sutton, R.K. (2015) Introduction to green roof ecosystems. In: Sutton, R.K. (Ed.) *Green roof ecosystems*, Springer International Publishing, Cham, Switzerland, pp. 1–25.
https://doi.org/10.1007/978-3-319-14983-7_1
- Sutton, R.K., Harrington, J.A., Skabelund, L., MacDonagh, P., Coffman, R.R. & Koch, G. (2012) Prairie-based green roofs: litterature, templates, and analogs. *Journal of Green Building*, 7, 143–172.
<https://doi.org/10.3992/jgb.7.1.143>
- Thornton, I.W.B. (2007) *Island colonization : the origin and development of island communities*. Cambridge: Cambridge University Press, 302 pp.
<https://doi.org/10.1017/CBO9780511618710>
- Traugott, M. (1998) Larval and adult species composition, phenology and life cycles of carabid beetles (Coleoptera: Carabidae) in an organic potato field. *European Journal of Soil Biology*, 34, 189–197.
[https://doi.org/10.1016/S1164-5563\(00\)86661-3](https://doi.org/10.1016/S1164-5563(00)86661-3)
- Wheeler, A.G. (1973) Studies on the arthropod fauna of alfalfa: spiders (Araneida). *The Canadian Entomologist*, 105, 425–432.
<https://doi.org/10.4039/Ent105425-3>
- Williams, N.S.G., Lundholm, J. & MacIvor, J.S. (2014) FORUM: Do green roofs help urban biodiversity conservation? *Journal of Applied Ecology*, 51, 1643–1649.
<https://doi.org/10.1111/1365-2664.12333>