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Epigeal Spider (Araneae) Communities in Moist Acidic and Dry Heath Tundra at Toolik Lake, Alaska

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Abstract

For the 2004–2006 growing seasons, we trapped a total of 6980 spiders (5066 adults, 1914 immatures) using pitfall traps at the Arctic Long Term Experimental Research (LTER) site in Toolik Lake, Alaska. We found 10 families and 51 putative species, with 45 completely identified, in two distinct habitats: Moist Acidic Tundra (MAT) and Dry Heath (DH) Tundra. We captured spiders belonging to the following families (number of species captured): Araneidae (1), Clubionidae (1), Dictynidae (1), Gnaphosidae (4), Linyphiidae (26), Lycosidae (11), Philodromidae (2), Salticidae (1), Theridiidae (1), and Thomisidae (3). Statistical comparisons of families captured at MAT and DH Tundra indicate that the habitats have significantly different spider communities (Chi Square Test: $p < 0.0001$, and Fisher's Exact Test: $p = 0.0018$). This finding is further supported by differences in similarity, diversity, evenness, and species richness between the two habitats. In this report, we present eight new state records and five extensions of previously described ranges for spider species. The following species are new state records for Alaska: *Emblyna borealis* (O.P.-Cambridge 1877), *Horcotes strandi* (Sytschevskaja 1935), *Mecynargus monticola* (Holm 1943), *Mecynargus tungusicus* (Eskov 1981), *Metopobactrus prominulus* (O.P.-Cambridge 1872), *Poeciloneta theridiformis* Emerton 1911, and *Poeciloneta vakkhanka* (Tanasevitch 1989). The following five species have been reported previously in Alaska, but not near Toolik Lake: *Hypsosinga groenlandica* Simon 1889, *Gnaphosa borea* Kulczyn'ski 1908, *Gnaphosa microps* Holm 1939, *Haplodrassus hiemalis* (Emerton 1909), and *Islandiana cristata* Eskov 1987. Pairwise similarity indices were calculated across 13 other arctic and subarctic spider communities and statistical tests show that all sites are dissimilar ($p = 0.25$). These results fit the general pattern of both the patchiness and habitat specificity of arctic spider fauna.

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Introduction

Taxonomic knowledge and descriptive reports of northern arctic spider faunas have lagged behind those made in temperate latitudes (Dondale et al., 1997). Within the Arctic, reports of spider assemblages from the northern Nearctic regions (e.g., northern Alaska and Canada) are outnumbered by reports from the Palearctic and southern Nearctic regions (e.g., Cotton, 1979; Cutler and Saltmarch, 1986; Koponen, 1992; Dondale et al., 1997; Pickavance, 2006). Of the assemblages from the Nearctic, the arctic spider fauna is best described from Greenland, where historical connections to European scientists, naturalists, and universities have resulted in a well-documented spider fauna (Danks, 1981; Pickavance, 2006). Despite the existence of Alaska spider species lists and small collections of specimens (*see* Jackson, 1933; Davis, 1936; Chamberlin and Ivie, 1947; Holm, 1960, 1970; Cutler and Saltmarch, 1986; Slowik, 2006; Paquin et al., 2010), the spider fauna of northern Alaska is still largely unknown except near Barrow (Weber, 1949, 1950). Furthermore, reports focused on large collections of arctic Nearctic spiders are scarce (Pickavance, 2006).

The material reported here represents the culmination of a three year, intensive sampling effort at Toolik Lake in the North Slope Borough, which encompasses 230,510 km^2 of territory across northern Alaska. Toolik Lake is located north of the Brooks Range at the Arctic Long Term Ecological Research (LTER) site. To the authors' knowledge, this study is the first of its kind for this area. Large collections, made over multiple habitat areas in the Arctic, are valuable because they can record changes in the range of species, report new taxa, compile biogeographical data of previously known taxa, and contribute to our overall understanding of arctic biodiversity (Pickavance, 2006).

In this paper, we report on spider species, captured via pitfall trap, from two distinct tundra habitat types, Moist Acidic Tundra (MAT) and Dry Heath (DH) Tundra in northern Alaska. We compare the community structure of ground spiders of the two tundra types in terms of species richness, evenness, and diversity in relation to soil and vegetation features. We then extend our analysis of epigeal spider community comparisons to include published data sets for communities from other arctic and subarctic sites from within the Nearctic zone.

Methods

SITE DESCRIPTION

We conducted surveys in the summers of 2004–2006 at the Arctic Long Term Ecological Research (LTER) site at Toolik Lake, Alaska (Fig. 1). Toolik Lake is located in the northern

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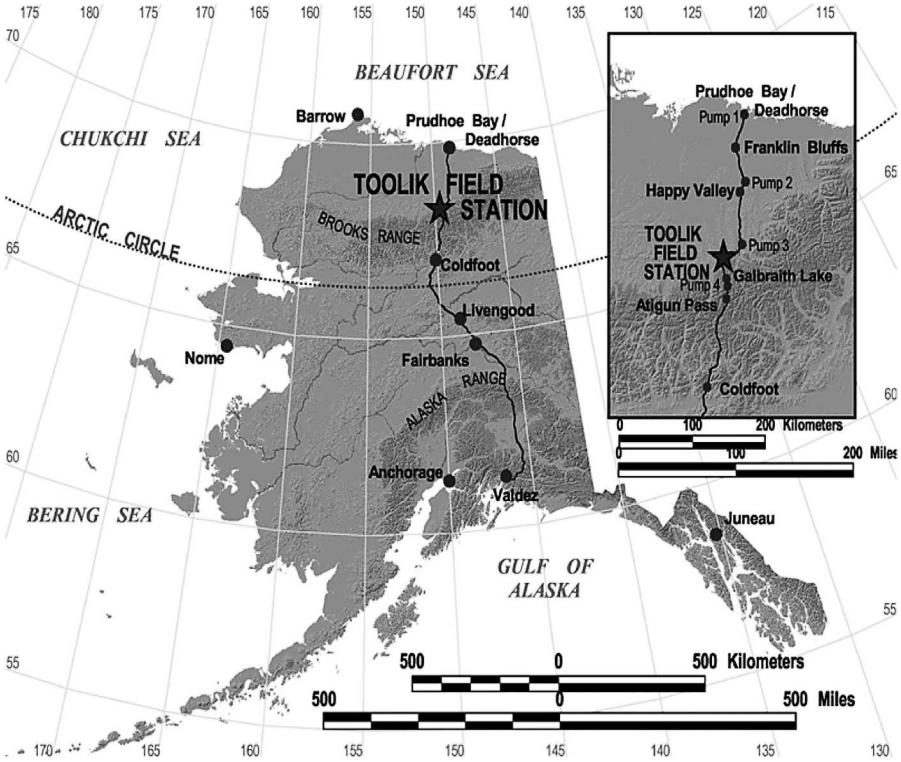


FIGURE 1. The Moist Acidic Tundra (MAT) and Dry Heath (DH) Tundra study sites are located at Toolik Lake LTER, Alaska, which is located on the north slope of the Brooks Range along the Dalton Highway.

foothills of the Brooks Range (68°38′N and 149°43′W, elevation 760 m) approximately 240 km north of the Arctic Circle. The site is maintained by the Toolik Field Station operated by the Institute of Arctic Biology of the University of Alaska–Fairbanks and was formally established as a site within the LTER network in 1987. The mean annual air temperature at Toolik Lake is −7 °C. The growing season is approximately 50–70 days. The mean temperature during the growing season is 10 °C (Hobbie and Chapin, 1998). Annual precipitation ranges from 200 to 400 mm with 50% falling as snow. Distribution of snow cover is highly dependent on wind and topographical relief.

The Toolik Lake LTER site is typical of the northern foothills region near the Brooks Range. This area has continuous permafrost, no large trees, complete snow cover and ice for most of the year, and cessation of river flow during winter. Waterlogged soils are commonplace as the permafrost prevents the downward drainage of water. At the landscape scale, the tundra vegetation is composed of sedges, grasses, dwarf birches, low willows, mosses, and lichens. The presence and combinations of these plant types is dependent on age since glaciation, soil type, soil moisture, exposure, drainage, and topography (Doles, 2000). Abiotic properties, coupled with the vegetative community, give rise to four unique ecosystem types surrounding Toolik Lake. These include moist acidic, dry heath, wet sedge, and shrub tundra. Ecosystem types discussed here are Moist Acidic Tundra (MAT) and Dry Heath (DH) Tundra.

MAT is the most common vegetation type surrounding Toolik. This vegetation type constitutes 38.7% of the total land cover near Toolik Lake (Walker, 1998). The MAT habitats generally have moist soils and are covered by an organic layer 0–30 cm thick (Shaver and Chapin, 1991). The MAT vegetation type occurs on rolling topography with silt to gravely soils with varying glaciation histories. Maximum thaw depth is 30–50 cm and, in many locations, the soil does not thaw to the mineral layer (Doles, 2000). The plant community is dominated by an equal biomass of graminoids (*Eriophorum vaginatum* and *Carex bigelowii*), shrubs (*Betula nana*), evergreens, and mosses (Chapin et al., 1995). Of particular note, the grass species *E. vaginatum* forms dense, compact tufts called tussocks, which are typical of moist acidic tundra. Average plant species density is 11 species/m^2 (Gough et al., 2007). This habitat type is named for the slightly acidic soil and high soil water content. Net primary productivity (NPP) is estimated at 145 g m^{-2} y^{-1} (Gough et al., 2007).

DH Tundra is an arctic vegetation type compromising 7.8% of the land cover near Toolik Lake (Walker, 1998). DH Tundra is characterized by drier conditions, a predominance of dwarf shrubs (*B. nana*), fruticose-lichen plant biomass, and graminoids (*Hierochloe alpine* and *Carex microchaeta*, (Shaver and Chapin, 1991; Gough et al., 2007). Average plant species density is 6 species/m^2 (Gough et al., 2007). This type of tundra occurs on exposed, rocky interfluve areas with thin organic layers (0–10 cm) that retain little snow cover during winter because of wind exposure (Nadelhoffer et al., 1991; Cheng et al., 1998). These areas are well drained and have a deeply thawed mineral layer (>2 m). NPP is estimated at 60 g m^{-2} y^{-1} (Gough et al., 2007). The two sites used in this study are roughly 3.2 km apart.

PITFALL TRAPPING

We estimated the diversity and total abundance of surface active invertebrate populations over the growing season (June–August) with pitfall traps in both the MAT and DH Tundra. The traps were 10 cm deep with an 8 cm opening diameter. Traps were one-third filled with 70% ethanol and collected and emptied after 3 days following each date listed in Table 1. We chose pitfalls traps for epigeal spider sampling because of the need for passive, minimally destructive sampling techniques on long term ecological research plots.

At the MAT and DH Tundra sites, plot size measured 5 × 5 m, with 4 plots per block. The MAT site had four blocks while the design in the DH site had three due to space constraints. This resulted in 16 total plots at the MAT and 12 plots at the DH

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TABLE 1

Sample dates for pitfall traps for this study. All dates include Moist Acidic Tundra (MAT) and Dry Heath (DH) Tundra sites, unless noted. Traps were set and left open three days following the collection date listed below.

Sample Dates
Year: 2004
14 June, 25 June, 03 July, 10 July, 31 July, 19 August
Year: 2005
06 June, 13 June, 20 June, 27 June, 11 July, 18 July, 04 August, 15 August, 18 August
Year: 2006
11 June (DH only), 14 June, 17 June, 20 June (DH only), 15 July, 25 July, 28 July, 31 July

Tundra. We placed the traps roughly 1 m from each other on the east (MAT) or south (DH) sides of the plots. In 2004, we placed three traps within each plot. We increased the number of traps to four per plot in 2005 and 2006 and repeated for each block. This resulted in 84 (2004) and 112 (2005 and 2006) total samples per date. We sampled 6 dates in 2004 and 2006, and 9 dates in 2005 during the arctic growing season (May–August). Furthermore, for 2006, we sampled an additional two times in DH before snowmelt allowed sampling at the MAT site. This resulted in 2280 total possible samples (1248 total MAT samples; 1032 total DH samples). However, we lost a few traps and samples due to wind, precipitation events, animal disturbance, and shipping error. We lost 66 (2.89% loss of the total) samples between 2004 and 2006 (34 missing samples in the MAT and 32 samples in the DH). This represents a loss of 2.72% of possible total MAT samples and 3.1% loss of total DH Tundra samples. Thus, the data analyzed here are from 2214 total samples (1214 samples in the MAT and 1000 samples in the DH Tundra) representing 6642 total trap days of effort. At each site, there were 3642 total trap days of effort in the MAT site and 3000 trap days of effort in the DH Tundra.

Contents were preserved in 70% ETOH and identified to species when possible using appropriate keys (Dondale and Redner, 1978, 1990; Platnick and Dondale, 1992; Buckle et al., 2001, Dondale et al., 2003, Ubick et al., 2005). We followed Platnick (2010) for taxonomy, except for Linyphiidae, where Buckle et al. (2001) was preferred. Maturity of specimens was determined by the presence of sclerotized genitalia. The first author identified most of the material; second author identified most of the individuals belonging to the family Linyphiidae. Mr. Don Buckle also helped in the identification and confirmation of linyphiid species. We identified the early instars to family level or genus when possible and these data are not presented here, as this information is not appropriate for our species list and richness calculations. Range information was derived from Dondale and Redner (1978, 1990), Platnick and Dondale (1992), Dondale et al., (2003), Ubick et al. (2005), Buckle et al. (2001), Paquin et al. (2010), and Platnick (2010). Vouchers are in the collections of the first and second author. Furthermore, vouchers will be deposited at Field Museum of Natural History, Chicago, Illinois, U.S.A. (FMNH), and the University of Alaska Museum Insect Collection (UAM) by the second author. The pitfall trap by-catch (non spiders) was stored in vials of ethanol for future work.

ESTIMATION OF SPECIES DIVERSITY AND COMMUNITY SIMILARITY

Total abundance of spiders and community indices were calculated from pooled data for each site over all sampling dates for both Moist Acidic Tundra (MAT) and Dry Heath (DH) Tundra. Total abundances were calculated for the years 2004–2006 for mature specimens only. We calculated Shannon's Diversity Index, evenness, richness, and Sørensen's Similarity Index for the years 2004–2006 using data for all of the species found in this study.

The indices used were all based on standard forms. Shannon's Diversity Index (H) (Shannon, 1948) was calculated using the following equation:

$$H = -\sum_{i=1}^{S} p_i * (\ln * p_i) \quad (1)$$

with S = number of species present in sample (Species Richness) and p_i = the proportion of individuals made up of the ith species.

Species Evenness (E) was calculated using the following (Brower et al., 1998):

$$E = H/H_{max} \quad (2)$$

with H = Shannon's Diversity Index and H_{max} = theoretical H if all the species in the community had an equal number of individuals. H_{max} is found by taking the natural log of the species richness.

Sørensen's similarity index (C_s) (Magurran, 2004) was used to measure the similarity in species composition for two sites, A and B, given by the following equation:

$$C_s = 2 * c/(a+b) \quad (3)$$

where a is the number of species found in site A, b is the number of species in site B, and c is the number of species shared in common by sites A and B. Several arctic and subarctic sites were chosen based on their analyses being restricted to epigeal spider fauna and similarity of trapping method.

Species rarefaction curves were calculated using PAST software (Hammer and Harper, 2005).

STATISTICS

Total overall family abundance differences between MAT and DH were tested using the Chi-Square test for families with >5 total spiders (significant difference when $\alpha \leq 0.05$) (SAS Institute, 2000). For families with <5 total spiders, we used Fisher's Exact Test (significant difference when $\alpha \leq 0.05$). Significant differences between individual families in the MAT and DH were tested using a binomial proportion T-test with a Bonferroni correction ($p \leq 0.05$) (R Development Core Team, 2005). Pairwise site similarity was analyzed using the ANOVA analysis package in Microsoft Excel (version 2007).

Results

SPECIES LIST AND TOTAL ABUNDANCE

We trapped a total of 6980 spiders (5066 adults, 1914 immatures and juveniles) from moist acidic tussock tundra and dry heath tundra from June to August during 2004–2006. Families and species identified are shown in Table 2. We captured 3404 adult spiders in the MAT (67.2% of the total) and 1662 adult spiders (32.8% of the total) in the DH. Analyses of the species list using Chi Square and Fisher's Exact tests indicates that, overall, there are significant differences between the spider families found in the MAT and DH Tundra (Chi Square $p < 0.001$; Fisher's Exact test $p = 0.0018$). The relative abundance (proportions) of

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TABLE 2

List of spider species found in Moist Acidic Tundra (MAT) and Dry Heath (DH) Tundra at Toolik Lake LTER, Alaska, from 2004 to 2006. We captured 51 morphospecies, of which 45 were identified to the species level. Note that an immature spider from the family Tetragnathidae and one from the superfamily Amaurobioidea are not included in this table. Furthermore, immature and juvenile spiders are not included in this table. Bold numbers indicate a cumulative total at the family level and across both sites.

Family/Species	# Collected per Site	# Collected per Site	
Site	Moist Acidic Tundra	Dry Heath Tundra	Total Collected
Araneidae	**11**	**0**	**11**
Hypsosinga groenlandica Simon 1889	11	0	**11**
Clubionidae	**11**	**0**	**11**
Clubiona praematura Emerton 1909	11	0	**11**
Dictynidae	**0**	**1**	**1**
Emblyna borealis (O.P.-Cambridge 1877)	0	1	1
Gnaphosidae	**97**	**32**	**129**
Gnaphosa borea Kulczyn'ski 1908	15	11	**26**
Gnaphosa microps Holm 1939	46	7	**53**
Gnaphosa orites Chamberlin 1922	5	11	**16**
Haplodrassus hiemalis (Emerton 1909)	31	3	**34**
Linyphiidae	**246**	**229**	**475**
Agyneta pseudosaxatilis Tanasevitch 1984	43	0	**42**
Agyneta simplex (Emerton 1926)	1	7	**8**
Bathyphantes simillimus (L. Koch 1879)	18	0	**18**
Gonatium crassipalpum Bryant 1933	18	1	**19**
Hilaira herniosa (Thorell 1875)	72	0	**72**
Hilaira leviceps (L. Koch 1879)	12	0	**12**
Horcotes strandi (Sytschevskaja 1935)	13	1	**14**
Hybauchenidium aquilonare (L. Koch 1879)	1	0	**1**
Islandiana cristata Eskov 1987	8	0	**8**
Mecynargus monticola (Holm 1943)	11	2	**13**
Mecynargus tungusicus (Eskov 1981)	22	0	**22**
Metopobactrus prominulus (O.P.-Cambridge 1872)	0	210	**210**
Microlinyphia m. mandibulata (Emerton 1882)	2	0	**2**
Microlinyphia pusilla (Sundevall 1829)	1	0	**1**
Poeciloneta theridiformis (Emerton 1911)	2	0	**2**
Poeciloneta vakkhanka (Tanasevitch 1989)	1	0	**1**
Poeciloneta variegata (Blackwall 1841)	1	0	**1**
Scotinotylus alienus (Kulczyn'ski 1885)	1	0	**1**
Walckenaeria clavicornis (Emerton 1882)	9	6	**15**
Walckenaeria fraudatrix Millidge 1983	6	0	**6**
Walckenaeria karpinskii (O.P.-Cambridge 1873)	1	0	**1**
Walckenaeria sp. cf. *arctica* Millidge 1983	1	0	**1**
Linyphiidae sp. 4	0	1	**1**
Linyphiidae sp. 6	0	1	**1**
Linyphiidae sp. 7	1	0	**1**
Linyphiidae sp. 8	1	0	**1**
Lycosidae	**2859**	**1272**	**4131**
Alopecosa aculeata (Clerck 1758)	2	0	**2**
Alopecosa hirtipes (Kulczyn'ski 1907)	2	5	**7**
Alopecosa pictilis (Emerton 1885)	17	215	**232**
Arctosa alpigena Doleschall 1852	125	63	**188**
Arctosa insignata (Thorell 1872)	555	307	**862**
Pardosa concinna (Thorell 1877)	118	34	**152**
Pardosa furcifera (Thorell 1875)	0	2	**2**
Pardosa lapponica (Thorell 1872)	1289	282	**1571**
Pardosa moesta Banks 1892	1	0	**1**
Pardosa podhorskii (Kulczyn'ski 1907)	379	363	**742**
Pardosa sodalis Holm 1970	371	1	**372**
Philodromidae	**41**	**22**	**63**
Apollophanes margareta Lowrie & Gertsch 1955	1	0	**1**
Thanatus arcticus Thorell 1872	40	22	**62**
Salticidae	**0**	**1**	**1**
Chalcoscirtus glacialis Caporiacco 1935	0	1	**1**

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TABLE 2

Continued.

Family/Species	# Collected per Site	# Collected per Site	
Site	Moist Acidic Tundra	Dry Heath Tundra	Total Collected
Theridiidae	**10**	**0**	**10**
Robertus sp. 1	10	0	10
Thomisidae	**129**	**105**	**234**
Ozyptila arctica Kulczyn'ski 1908	38	12	**50**
Xysticus britcheri Gertsch 1934	86	3	**89**
Xysticus deichmanni Sørensen 1898	5	89	**94**
Total Spiders	**3404**	**1662**	**5066**

Araneidae, Clubionidae, Lycosidae, Linyphiidae, Theridiidae, and Thomisidae within the spider communities differed significantly between the MAT and DH Tundra (Table 3). Araneidae, Clubionidae, Lycosidae, and Theridiidae are significantly more abundant in MAT, whereas Linyphiidae and Thomisidae are significantly more abundant in DH Tundra. The proportions of the families Dictynidae, Gnaphosidae, Philodromidae, and Salticidae did not differ significantly between the MAT and DH Tundra.

RANGE EXTENSIONS AND STATE RECORDS

We present eight new state records and five extensions of previously reported species ranges (not implying any movement due to climate change), representing 25.5% of the total species captured. *Agyneta pseudosaxatilis* Tanasevitch 1984 has only been described in the Old World in Kazakhstan (Marusik et al., 2000) and is represented here, for the first time, as occurring in the Nearctic (Table 4). The following species are new state records for Alaska: *Emblyna borealis* (O.P.-Cambridge 1877), *Horcotes strandi* (Sytschevskaja 1935), *Mecynargus monticola* (Holm 1943), *Mecynargus tungusicus* (Eskov 1981), *Metopobactrus prominulus* (O.P.-Cambridge 1872), *Poeciloneta theridiformis* Emerton 1911, and *Poeciloneta vakkhanka* (Tanasevitch 1989). Interestingly, while the previously listed spider species have not been found in Alaska, they have been found across Canada, Greenland, and into the Palearctic zone (e.g., Finland, Siberia, etc.). Thus, these records represent westward extensions of known occurrences. The following five species have been reported previously in Alaska, but not in the North Slope, and so are northern extensions of known occurrences: *Hypsosinga groenlandica* Simon 1889, *Gnaphosa borea* Kulczyn'ski 1908, *Gnaphosa microps* Holm 1939, *Haplodrassus hiemalis* (Emerton 1909), and *Islandiana cristata* Eskov, 1987. Of the records described here, spiders belonging to the family Linyphiidae made up 61.5% of the total, followed by Gnaphosidae (23.1%), Dictynidae (7.7%), and Araneidae (7.7%).

FAMILY AND SPECIES RICHNESS, EVENNESS, AND DIVERSITY

We captured 51 putative species, of which 45 were identified to the species level. Six species, belonging to Linyphiidae and Theridiidae, did not match published descriptions and may represent species that are undescribed. We feel that these unconfirmed species are important to include in our richness, evenness, diversity, and similarity calculations because it reflects the actual richness of our samples more accurately than if we only included taxonomically well-known species. These undescribed species should be noted to show the extent of how poorly known spider diversity is in the Toolik Lake region.

We captured 10 spider families in our traps within the MAT and DH Tundra sites, and 12 spider families if we include the immature Tetragnathidae and Amaurobioidea specimens that were captured and identified as immature by a lack of sclerotized genitalia. When the study sites were considered separately, the MAT site yielded 8 spider families and the DH Tundra site yielded 7 (Table 5). When the study sites were considered separately, the MAT had 45 spider species and the DH had 27. The most speciose family, the linyphiids, constituted ~51% of the 51 species recorded (Table 6). Families Lycosidae, Gnaphosidae, Thomisidae, and Philodromidae composed 21.6%, 7.8%, 5.9%, and 3.9% of the species recorded, respectively. The remaining families (Araneidae,

TABLE 3

Total abundances as a percentage of total ground spiders collected per family from 2004 to 2006 in Moist Acidic Tundra (MAT) and Dry Heath (DH) Tundra at Toolik Lake, Alaska, for Whole Site (MAT + DH), MAT only, DH only.

	MAT + DH (%)	With MAT Total Only (%)	Within DH Total Only (%)	Point Estimate for Proportion Difference	Confidence Interval Lower and Upper Range	
Araneidae *	0.22	0.32	—	−0.344	−0.579	−0.108
Clubionidae *	0.22	0.32	—	−0.344	−0.579	−0.108
Dictynidae	0.02	—	0.06	—	—	—
Gnaphosidae	2.55	2.85	1.93	—	—	—
Linyphiidae *	9.38	7.23	13.78	0.065	0.038	0.092
Lycosidae *	81.54	83.99	76.53	−0.082	−0.116	−0.048
Philodromidae	1.24	1.20	1.32	—	—	—
Salticidae	0.02	—	0.06	—	—	—
Theridiidae *	0.20	0.29	—	−0.313	−0.542	−0.082
Thomisidae *	4.62	3.79	6.32	0.025	0.006	0.044

* Indicates a statistically significant difference in familial proportion between the MAT and DH for a binomial proportion *T*-test. A dash indicates non-significance.

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TABLE 4

Reported range extensions and Alaska state records for species collected at Toolik Lake, Alaska. Abbreviations used to indicate range change are NE (new to the Nearctic Region), AK (new to the state of Alaska but it has been found elsewhere in the Nearctic), and N (species has been found in southern portions of Alaska).

Family/Species	Range Change	Reported Range and References
Araneidae		
Hypsosinga groenlandica Simon 1889	N	Yukon Territory and western Northwest Territories, southern British Columbia and Quebec, Greenland (Dondale et al., 2003); southern Alaska (Slowik, 2006); U.S.A., Canada, Greenland (Platnick, 2010)
Dictynidae		
Emblyna borealis (O.P.-Cambridge 1877)	AK	Nunavut (Jackson, 1933; Davis, 1936); Greenland (Leech, 1966); Russia (Platnick, 2010)
Gnaphosidae		
Gnaphosa borea Kulcyznski 1908	N	Southern Alaska to Labrador, south to New Mexico and to northern New England; Siberia (Platnick and Dondale, 1992); Yukon Territory (Dondale et al., 1997); western Alaska (Holm, 1970); Holarctic (Platnick, 2010)
Gnaphosa microps Holm 1939	N	Southern Alaska to Newfoundland, south to Colorado and northern New England; Europe; U.S.S.R. (Platnick and Dondale, 1992; Holm, 1970); Yukon Territory (Dondale et al., 1997); Holarctic (Platnick, 2010)
Haplodrassus hiemalis (Emerton 1909)	N	Middle to southern Alaska to Newfoundland, south to Colorado and New Jersey; U.S.S.R. (Platnick and Dondale, 1992); Yukon Territory (Dondale et al., 1997); Holarctic (Platnick, 2010)
Linyphiidae		
Agyneta pseudosaxatilis Tanasevitch 1984	NE	Northwest Kazakhstan (Marusik et al., 2000)
Horcotes strandi (Sytschevskaja 1935)	AK	Yukon Territory, Palearctic (Buckle et al., 2001); Finland, Russia, Canada (Platnick, 2010)
Islandiana cristata Eskov 1987	N	Yukon Territory, Siberia. (Buckle et al., 2001); Russia, Alaska, Canada (Platnick, 2010)
Mecynargus monticola (Holm 1943)	AK	British Columbia, Northwest Territory, Yukon Territory, Palearctic (Buckle et al., 2001); Sweden, Finland, Russia, Mongolia, Canada (Platnick, 2010)
Mecynargus tungusicus (Eskov 1981)	AK	Yukon Territory, eastern Palearctic (Buckle et al., 2001); Russia, Kyrgyzstan, China, Canada (Platnick, 2010)
Metopobactrus prominulus (O.P.-Cambridge 1872)	AK	Maine, Massachusetts, Michigan, New Hampshire, Alberta, New Brunswick, Nova Scotia, Northwest Territories, Ontario, Quebec, Saskatchewan, Greenland, Palearctic (Buckle et al., 1998); Holarctic (Platnick, 2010)
Poeciloneta theridiformis (Emerton 1911)	AK	New Hampshire, New Brunswick, Quebec, Saskatchewan, eastern Palearctic (Buckle et al., 2001); Russia, North America (Platnick, 2010)
Poeciloneta vakkhanka (Tanasevitch 1989)	AK	Northwest Territories, eastern Siberia (Buckle et al., 2001); Russia (Platnick, 2010)

Clubionidae, Dictynidae, Salticidae, and Theridiidae) were rare and each contributed one species to the list.

Estimates of family level and species evenness (E) for the MAT and DH Tundra are presented in Table 5. Overall, the study area (the combined MAT and DH sites) had a family level evenness of $E = 0.313$. At the species level, the pooled data had an evenness calculation of $E = 0.598$. When the sites are considered separately, the family evenness for the MAT and DH was $E = 0.322$ and $E = 0.408$, respectively. The species level evenness for the MAT and DH was $E = 0.572$ and $E = 0.651$, respectively. Shannon's Diversity Index (H) was calculated for spiders captured in MAT and DH (Table 5). Overall, (MAT + DH), the familial diversity for the whole study area was estimated at $H = 0.724$. The diversity of epigeal spider community at the species level, for both sites combined, measured $H = 2.352$. When the MAT and DH spider communities are considered separately, the familial diversity for both sites study sites are $H = 0.669$ and $H = 0.794$ for MAT and DH, respectively (Table 5). The diversity index is $H = 2.17$ for the MAT and $H = 2.14$ for the DH at the species level.

SITE SIMILARITY

Familial and species similarity based on the Sørensen's similarity index (C_s) was calculated for the MAT and DH Tundra. The MAT and DH had a family level similarity measurement of $C_s = 0.655$ and a species-level similarity of $C_s = 0.453$ (Table 5). The MAT and DH shared the following families: Gnaphosidae, Linyphiidae, Lycosidae, Philodromidae, and Thomisidae. The similarity index for the species within each of these shared families are $C_s = 0.40$, $C_s = 0.046$, $C_s = 0.52$, $C_s = 0.73$, and $C_s = 0.17$, respectively. The families Araneidae, Clubionidae, Dictynidae, Salticidae, and Theridiidae were unique to only one site (MAT or DH).

The pooled Toolik Lake, Alaska, spider fauna, identified here from within the MAT and DH Tundra, was compared with previous studies performed across arctic and subarctic sites in the Nearctic ranging from the Canadian Arctic Archipelago to southern Alaska by pairwise species-level similarity comparisons (Table 7). We included a wide latitudinal range for our similarity study because we wanted to address the similarity of spider fauna using similar methods (e.g., pan traps and pitfall traps). Furthermore, we wanted to investigate the similarity of studies across a poorly known region. For all sites, pairwise similarity indices (C_s) measurements ranged from 0.00 to 0.944 with an average measurement of $C_s = 0.127 \pm 0.121$ (Table 8). The results of an ANOVA test did not return any significant differences in similarity between all sites. The similarity between arctic sites (collection locales north of the 10 °C July isotherm) is $C_s = 0.162 \pm 0.168$ and not significant in an ANOVA test ($p = 0.14$). These sites

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TABLE 5

Diversity metrics arranged by site, Moist Acidic (MAT) and Dry Heath (DH) tundra and across the whole site (MAT + DH).

Diversity Metrics – By Site	MAT	DH
Family Richness	8	7
Family Evenness	0.322	0.408
Shannon's Index – Family Level	0.669	0.794
Sørensen's Index – Family Level	0.655	
Species Richness	45	27
Species Evenness	0.572	0.651
Shannon's Index – Species Level	2.17	2.14
Sørensen's Index – Species Level	0.453	

Diversity Metrics – Total	MAT + DH
Whole Site Family Richness	10
Whole Site Family Evenness	0.313
Whole Site Shannon's Index – Family Level	0.721
Whole Site Species Richness	51
Whole Site Species Evenness	0.598
Whole Site Shannon's Index – Species Level	2.352

include Southhampton Island, Baffin Island, Toolik Lake, the arctic portion of the Yukon Territory, Hazen Camp, Devon Island, and the two Akpatok Island studies.

Discussion

Over the course of 2004–2006, we found 10 spider families and 45 confirmed species and 6 incompletely identified species. The majority of species found during the course of this study have been reported for the arctic Nearctic region (*see* Dondale and Redner, 1978, 1990; Platnick and Dondale, 1992; Dondale et al., 2003; Paquin et al., 2010) except for one species previously unreported to the Nearctic region, *Agyneta pseudosaxatilis* (Tanasevitch 1984). The number of total spiders captured here was dominated by the family Lycosidae, particularly in the genera *Pardosa*, *Arctosa*, and *Alopecosa*. Spiders belonging to the family Linyphiidae made up the bulk of the species in the collection. Spiders belonging to the families Lycosidae and Linyphiidae are the most abundant families reported in descriptions of northern epigeal spider communities (Danks, 1981; Marusik and Koponen, 2002). Linyphiids tend to be the most speciose spider family across the Nearctic (see Leech, 1966; Cotton, 1979; Cutler and Saltmarch, 1986; Koponen, 1992; Dondale et al., 1997; Pickavance, 2006; Paquin et al., 2010). This was the case for samples taken in this study. Other families were all much less abundant. This fits the general pattern that most families, other than Lycosidae and Linyphiidae, tend to decline in the Nearctic regions (Dondale et al., 1997).

The spider species richness reported here is higher than numbers reported by other studies of Alaskan and Canadian Nearctic spider faunas collected in a singular location. For example, Hillyard (1979) described 2 families with 10 species from his work on Baffin Island, Canada. On the North Slope, Weber (1949) described a small collection taken near Barrow, Alaska, that included six families and 18 putative species. However, it remains unclear as to whether Toolik Lake, Alaska, has a larger number of epigeal spider species than other arctic areas or if this pattern is a result of historic undersampling in the region.

Large collections made in geographically widespread regions (e.g., Yukon Territory from Dondale et al., 1997) or studies in more temperate regions (e.g., Chichagof Island, Alaska, from Slowik, 2006) reported higher family and species richness compared to the spider fauna captured at Toolik Lake (*see* references in Table 9). This is not surprising given the limited collection area included in this study when compared to a survey of arctic fauna occurring in Yukon Territory. Furthermore, Slowik (2006) reported 95 spider species on Chichagof Island, Alaska. However, this island is located in a temperate rainforest in SE Alaska and a direct comparison of spider fauna might not be appropriate due to differences in rainfall pattern, temperature regimes, etc. We feel that these studies are worth mentioning because of the dearth of large collections made in the northern Nearctic.

TABLE 6

Species richness of spiders collected, arranged by family, from 2004 to 2006 in Moist Acidic Tundra (MAT) and Dry Heath (DH) Tundra at Toolik Lake, Alaska, for Whole Site (MAT + DH), MAT only, and DH only.

	MAT + DH	MAT Only	DH Only
Araneidae	1	1	–
Clubionidae	1	1	–
Dictynidae	1	–	1
Gnaphosidae	4	4	4
Linyphiidae	26	23	8
Lycosidae	11	10	9
Philodromidae	2	2	1
Salticidae	1	–	1
Theridiidae	1	1	–
Thomisidae	3	3	3

We are aware that our method of capture, pitfall trapping, does have drawbacks and is heavily biased towards fauna that are actively moving on the soil surface. We made an effort to supplement pitfall trapping with a second collection method, as recommended by Uetz and Unzicker (1976), to address criticisms in using pitfall trap methods. Sweep netting of tundra vegetation around the pitfall traps in moist acidic and dry heath research plots was conducted in the summer of 2007 within a 0.5 m diameter of each pitfall trap for one minute. We did not capture any arboreal or stem/trunk dwelling spiders (Araneidae, Dictynidae, Salticidae, Tetragnathidae, and Theridiidae) via sweep netting. However, we found them in our pitfall traps, albeit in very low numbers, as less than 0.5% of the total number of specimens collected over the three growing seasons belonged to these families. Lack of sweep netting success could be attributed to a variety of factors, including disturbance of plant canopy from vegetation measurements, cold temperatures, etc.

Despite these criticisms, we did capture a large number of species compared to other studies made in the region. We attribute our high species richness to persistence in trapping effort over time (3 years) and efforts made to trap over the growing season (June–August) when spiders are most active. Our collection efforts yielded a species richness estimate in the upper 95% confidence limit of a rarefaction curve, which leads us to conclude that our collection of fauna captured by pitfall trap is fairly complete and our sampling methods are justified (Fig. 2).

Newcomers to the Arctic are initially presented with what appears a uniform biome in which species are widely distributed (Pickavance, 2006). However, patchiness in distribution of arctic Nearctic spider species has been identified (discussed in Pickavance, 2006). For example, of a collective 55 spider species in six arctic locations, over 50% of species were found in only one location and 90% were found in half or fewer of the sites studied (Pickavance, 2006). In his discussion, Pickavance argues that this

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TABLE 7

Pairwise Sørensen's similarity index calculated for Toolik Lake LTER, Alaska, and 13 arctic and subarctic study sites in Alaska (AK) and Canada (CAN). Similarity Indices > 0.25 are shaded.

	Belcher Island, CAN	Chichagof Island, AK	AK – VEGA Expedition, 1878	AK – Lindroth Expedition, 1958	Akpatok Island, CAN, Part 1, 1933	Akpatok Island, CAN, Part II, 1936	Mt. Wrangell, AK (Alpine tundra)	East Bay, South-hampton Island, CAN	Yukon Territory, CAN	Baffin Island, CAN	Toolik Lake, AK, U.S.A., 2004–2006	Devon Island, CAN	Hazen Camp, CAN
Spiders of Alaska	0.057	0.181	0.076	0.201	0.023	0.023	0.061	0.030	0.449	0.008	0.101	0.016	0.015
Belcher Island, CAN		0.047	0.187	0.211	0.308	0.280	0.125	0.118	0.127	0.047	0.119	0.000	0.043
Chichagof Island, AK			0.000	0.068	0.000	0.000	0.036	0.018	0.179	0.000	0.041	0.000	0.000
AK – VEGA Expedition, 1878				0.211	0.262	0.271	0.070	0.267	0.136	0.077	0.237	0.200	0.182
AK – Lindroth Expedition, 1958					0.180	0.163	0.104	0.121	0.206	0.066	0.152	0.045	0.085
Akpatok Island, CAN, Part 1, 1933						0.944	0.000	0.000	0.000	0.069	0.086	0.000	0.188
Akpatok Island, CAN, Part II, 1936							0.063	0.171	0.083	0.074	0.088	0.000	0.200
Mt. Wrangell, AK (Alpine tundra)								0.000	0.000	0.08	0.121	0.000	0.071
East Bay, Southhampton Island, CAN									0.070	0.286	0.058	0.462	0.452
Yukon Territory, CAN										0.026	0.201	0.033	0.039
Baffin Island, CAN											0.066	0.111	0.348
Toolik Lake, AK, U.S.A., 2004–2006												0.000	0.125
Devon Island, CAN													0.667

Study sites referenced, from left to right, Chamberlin and Ivie (1947); Koponen (1992); Slowik (2006); Holm (1970); Holm (1960); Jackson (1933); Davis (1936); Cutler and Saltmarch (1986); Pickavance (2006); Dondale et al. (1997); Hillyard (1979); Leech and Ryan (1972); Leech (1966). Toolik Lake, Alaska, data are taken from current study.

TABLE 8

Mean Sørensen's pairwise similarity index calculated for Toolik Lake LTER, Alaska, and 13 arctic and subarctic study sites in Alaska (AK) and Canada (CAN). *P*-value for the ANOVA test was $p = 0.25$ and $f = 1.245$, indicating no statistically significant differences between sites.

Site and Reference	Mean Sørensen's Index	S.D. ±
Spiders of Alaska – Chamberlin and Ivie (1947)	0.160	0.123
Belcher Island, CAN – Koponen (1992)	0.128	0.095
Chichagof Island, AK – Slowik (2006)	0.044	0.065
AK – VEGA Expedition 1878 – Holm (1970)	0.167	0.088
AK – Lindroth Expedition 1958 – Holm (1960)	0.139	0.061
Akpatok Island, CAN, Part 1, 1933 – Jackson (1933)	0.182	0.249
Akpatok Island, CAN, Part II, 1936 – Davis (1936)	0.109	0.099
Mt. Wrangell, AK – Cutler and Saltmarch (1986)	0.063	0.043
East Bay, South Hampton Island, CAN – Pickavance (2006)	0.159	0.162
Yukon Territory, CAN – Dondale et al. (1997)	0.119	0.123
Baffin Island, CAN – Hillyard (1979)	0.104	0.113
Toolik Lake, AK, USA, 2004–2006 – current study	0.107	0.064
Devon Island, CAN – Leech and Ryan (1972)	0.118	0.211
Hazen Camp, CAN – Leech (1966)	0.186	0.196

patchiness is a result of dispersion difficulties and localized habitat and microclimate preference, not sampling artifact.

Our results show that this pattern can, again, be seen across 14 separate studies examining the spider fauna of arctic and subarctic sites. The mean similarity index for shared spider species was quite low ($C_s = 0.127$) for all sites. This result suggests that, on average, the epigeal spider species for the sites were 0.873 *dissimilar*. Mean similarity by site ranged from $C_s = 0.044$ (Chichagof Island, Alaska; Slowik, 2006) to $C_s = 0.186$ (Hazen Camp, Canada; Leech, 1966). Interestingly, collection sites located on island features or ''islands'' of habitat (e.g., alpine tundra habitat) returned lower similarity measures compared to their mainland counterparts. This supports the notion that island areas support fewer species and also have less species diversity. However, our data shows that even large-scale, mainland studies (e.g., Chamberlin and Ivie, 1947; Dondale et al., 1997) have low similarity values ($C_s = 0.16$ and $C_s = 0.119$, respectively). However, these similarity comparisons should be interpreted with caution as the spiders faunas, compared here, were derived from studies taken from a wide range of habitats and latitude, and are therefore not standardized to a similar Nearctic locale.

However, spider faunas in the same collection locality show a strong trend of dissimilarity. While the MAT and DH Tundra sites are only ~3.2 km apart in distance, they have different spider communities. For instance, the species level similarity between the two sites is less than half ($C_s = 0.453$). That is, the two sites share ~45% of the total spider species collected. For this study, the habitats (MAT and DH) each represent a distinct, unique microclimate with differences in plant community, primary production, canopy height, litter layer, and insulation from extreme weather events. The two habitats share only about half of the Toolik Lake species of the most abundant family, Lycosidae ($C_s = 0.518$). Interestingly, the family Linyphiidae was the most speciose (26 species out of 51 collected). However, when the similarity between the linyphiids collected at the MAT and DH is compared, they share less than 5% in common ($C_s = 0.046$). Our interpretation is that the Linyphiidae are specialists to their given habitat. For example, the spider *Metopobactrus prominulus* was collected in over 200 instances in the DH but none were sampled in the MAT. This species makes up most (91.7%) of all linyphiids collected at the dry heath.

Spider species that are unique to only one site make up more than half (~59%) of the collection. Spiders belonging to family Linyphiidae make up the bulk of the unique, one-site-only species found at Toolik Lake. However, it is important to note that we collected 15 singleton species, 11 belonging to the family Linyphiidae, and clearly, these can only be represented from one habitat or the other, regardless of their true habitat distribution. Therefore, this unique status may be premature and requires more investigation. However, the fact remains that, when we compared our species list across the arctic and subarctic areas of the Nearctic zone, and even locally at Toolik Lake, a strong trend of dissimilarity emerges. At the local scale, the MAT and DH Tundra are statistically different in terms of family abundance and distribution and this claim is further supported by the differences in species richness, evenness, and diversity indices. Pickavance (2006) argued that this patchiness and community divergence is indeed the norm with northern spider communities. This is in contrast to the idea that spider faunas are relatively similar across the northern arctic region (Marusik and Koponen, 2000). The question remains as to why these spider communities are so habitat and locale specific.

Numerous studies have detailed the relationship between vegetative structure and the composition of spider communities, and it is often argued that this is the most important parameter involved in retreat and web site selection (Wise, 1993). Habitat requirements vary according to foraging strategy. Epigeal spiders, especially active hunters belonging to the family Lycosidae, are generally most numerous in warmer, open habitats which do not have a closed canopy (Pajunen et al., 1995). Furthermore, an open canopy is important for the Lycosidae because females maintain optimum temperature for their egg sacs by sunning (Humphreys, 1974). These requirements for a thermally favorable environment, especially given the Arctic's limited growing season, must reasonably extend to the other families mentioned in this study.

The influence of variation in litter on ground-spider communities must also be considered. In one experiment, both litter depth and structural complexity were manipulated on a temperate forest floor (Uetz, 1979). More species of epigeal spiders were present in areas of greater depth and/or litter complexity in all sites studied (Uetz, 1979). Relative familial abundance in the study by Uetz (1979) changed over a gradient of increasing litter depth and complexity, with Lycosidae decreasing and Clubionidae, Thomisidae, and Gnaphosidae increasing. Thus, heterogeneity of the plant community will influence the ground-spider community by the input of different amounts and types of plant litter. Arctic spider communities also change when litter shape, structure, and depth is manipulated, and the community responds differentially in terms of abundance and diversity when the plant community is altered by long-term fertilization experiments at both the MAT and DH Tundra sites (Wyant, 2008).

Conclusion

Long-term, intensive sampling efforts, as used here, can reveal information concerning undescribed species, range extensions of species, and community level information (e.g., species evenness (*E*), species richness (*S*), and species diversity (*H*). Interestingly, the epigeal spider community at Toolik Lake is more

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TABLE 9

Number of spider families and species in 14 arctic and subarctic localities in Alaska (AK) and Canada (CAN).

Place	Belcher Island, CAN, 1992	Chichagof Island, AK, 2006	Akpatok Island, CAN, Part 1, 1931	Akpatok Island, CAN, Part 2, 1936	Matanuska Valley, AK, 1947 (Spiders of AK)	Mt. Wrangell, AK (Alpine tundra), 1986	Vega Expedition, AK, 1878–1880
Latitude North	56	58.1	60	60	62	62	Collections made in Norway, Siberia, and AK
Total Specimens	1065	1239	125	Not Reported	Not Reported	Not Reported	677
Total Families	8	16	3	3	16	8	8
Total Species	33	95	19	17	247	16	42
Sample Method	Hand Picking, Litter Seiving, Pitfall	Beat Sheets, Head Lamps, Pitfalls Traps, casual collection	Not Reported	Not Reported	Not Reported	Hand Picking, Sweep Netting	Not Reported

Place	Lindroth Expedition of 1958	East Bay, South Hampton Island, CAN, 2006	Yukon Territory, CAN (Arctic Zone), 1997	Baffin Island, CAN, 1979	Toolik Lake, AK, 2004–2006	Devon Island, CAN, 1972	Hazen Camp, CAN, 1966
Latitude North	Throughout AK	64	Throughout Yukon Territory	66.71	68.38	76	81.5
Total Specimens	Not Reported	22,816	Not Reported	65	5066	2375	20,600
Total Families	9	2	9	2	10	2	4
Total Species	81	18	297	10	51	8	13
Sample Method	Not Reported	Pitfall traps	Not Reported	Pitfall Trap	Pitfall Traps	Pitfall Traps	Pan Traps

Study sites referenced, from left to right, Koponen (1992); Slowik (2006); Jackson (1933); Davis (1936); Chamberlin and Ivie (1947); Cutler and Saltmarch (1986); Holm (1970); Holm (1960); Pickavance (2006); Dondale et al. (1997); Hillyard (1979); current study; Leech and Ryan (1972); Leech (1966).

Note: Devon Island, Southhampton Island, Hazen Camp, Akpatok Island: total numbers include immature specimens; for Baffin Island, Chichagof Island, Toolik Lake, and the Belcher Islands, numbers are adults only. Table modified from Pickavance (2006).

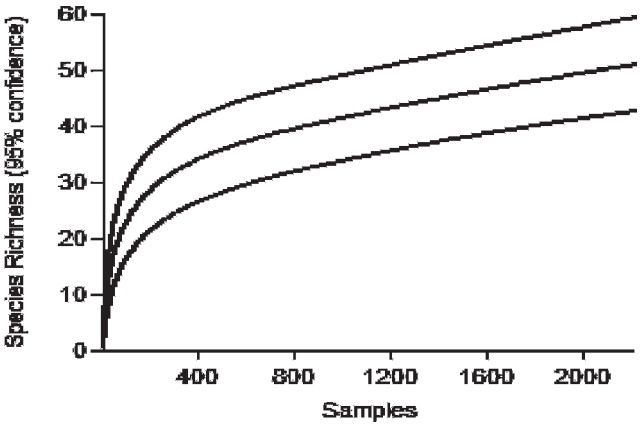


FIGURE 2. Spider species richness estimates for number of samples taken from 2004 to 2006 in Moist Acidic Tundra (MAT) and Dry Heath (DH) Tundra at Toolik Lake, Alaska. 95% confidence intervals (LCI—43; UCI—60) are shown on top and bottom and the mean estimate is in the middle. The ground spider species richness for this study is 51 which approaches the upper 95% confidence limit calculated by rarefaction for 2114 total pitfall traps (PAST Software; Hammer and Harper, 2005).

species rich than generally reported for the Arctic. Moreover, habitat specific spider communities have also been documented for Moist Acidic Tundra and Dry Heath Tundra. Our report of the northward range extension of *Hypsosinga groenlandica*, *Gnaphosa borea*, *Gnaphosa microps*, and *Haplodrassus hiemalis* is intriguing and also confounding, given the recent warming and lengthening of the growing season in the Arctic (Oechel et al., 2000; Serreze et al., 2000, Chapin et al., 2005). Whether these records indeed reflect a northward extension of ranges in response to trends in warming or is due to the fact that the region had not been surveyed extensively, remains unclear, but warrants further study. Arctic areas may have higher spider richness than generally reported but intensive sampling efforts must be used to detect the signal of this trend. Natural history studies that document faunal composition and fundamental community patterns will contribute to baseline data with regards to biotic response to future climate change.

Research over the past three decades indicates that the arctic Nearctic region is fragile and highly susceptible to disturbance such as warming (Hinzman et al., 2005). This region is experiencing dramatic environmental changes that are likely to have profound impacts on the local flora and fauna. Documenting the response of the biotic community to changes in temperature is an important part of monitoring and characterizing possible ecosystem level responses to warming. However, much of the arctic fauna remains poorly studied and much natural history work remains, especially for the invertebrate community. Future efforts should focus on documenting the northern Alaska spider community with active searching (e.g., overturning stones and collecting spiders), hand sorting, quadrat sampling, sweep netting, and the use of beat sheets to address potential gaps in describing the spider community.

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