

SHORT COMMUNICATION

Egg sac parasitism of Arctic wolf spiders (Araneae: Lycosidae) from northwestern North America

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Abstract. Parasitoids can have significant impacts on the life history of their hosts, as well as on local population and community dynamics. These effects could be particularly pronounced in the Arctic where the breeding season is short. We studied the incidence and loads of egg sac parasitoids, and whether these varied with body size or among species in three Arctic wolf spider species: *Pardosa sodalis* Holm 1970, *Pardosa lapponica* (Thorell 1872) and *Pardosa moesta* Banks 1892 from the Yukon Territory in northwestern Canada. We found a high incidence of egg sac parasitism (by *Gelis* sp.) and that the incidence of parasitism increased significantly with body size in two of the spider species; however, it did not change in the largest species. Among the three species investigated, parasitism was highest in the largest species (*P. sodalis*). Parasitism loads ranged from one to fourteen individuals per egg sac, and incidence reached 29.6% overall in *P. sodalis*. Parasitism may have significant impacts on the life history of tundra wolf spiders.

Keywords: *Gelis*, *Pardosa*, parasitoid, tundra, Yukon Territory

Parasitoids are efficient predators and can have significant effects on local host population densities (Polis et al. 1998). Parasitoid loads can vary with life history trade-offs and host quality (Fletcher et al. 1994), while their incidence may be influenced by host availability (Le Lan et al. 2012). Wasps belonging to the families Ichneumonidae (e.g., *Gelis* sp.) and Scelionidae (*Baeus* sp.) are known to parasitize the egg sacs of wolf spiders (Edgar 1971; Cobb & Cobb 2004) with the former known to destroy the entire contents of the egg sac (Edgar 1971). Spider densities can be heavily influenced by abiotic factors (Bowden & Buddle 2010), but are also likely affected by local biological factors like predation [i.e., birds and arthropods (Meltote et al. 2007)], and these could be particularly pronounced in Arctic environments.

Spiders are one of the most speciose arthropod taxa in the Arctic, especially in northwestern North America (e.g., Dondale et al. 1997), with wolf spider species often reaching very high densities (Bowden & Buddle 2012). Female wolf spiders are notable in that they invest unusually heavily in their reproduction. They invest not only in production of the egg sac, but because the egg sac is tethered to them as they move about and they also invest in its incubation and protection. This female movement, however, also likely makes the egg sac more conspicuous to parasitoids and predators. To examine if parasitoids could be important to the ecology of arctic wolf spiders we wanted to determine whether the incidence of parasitoids and parasitoid loads varied among species or with body size within species found on the tundra in the Yukon Territory, Canada.

Sampling was conducted from late June to early August 2008 at three tundra sites in the northern Yukon Territory, Canada: Tombstone, 64.36261N, 138.19411W, elev. 1200m; Ogilvie, 65.47404N, 137.46206W, elev. 862m and Richardson, 66.55546N, 136.19874W, elev. 534m. We selected these three sites to maximize the spatial extent of our study and the collection of our focal species. All three sites were very similar in vegetation composition with representatives of *Ledum* sp., *Vaccinium* sp., *Rubus chamaemorus*, *Cladonia rangiferina* (and other lichens), *Empetrum* sp., *Betula glandulosa* and *Salix* sp. We sampled spiders from late June–early July, mid-July and late July–early August at the Tombstone and Richardson sites and mid-July and late July–early August at the Ogilvie site. Each sampling period consisted of three to four days of

collecting in an area of approximately 1 km². Our sampling window represents the majority of the active period for arthropods in the region.

We collected live gravid female spiders by visual surveys and with dry pitfall traps at each site. Pitfall traps consisted of 750ml plastic containers dug into the ground with the rim flush to the substrate. They were emptied every five to six hours for the extent of the each sampling period. Our focal species were *Pardosa lapponica* (Thorell 1872), *Pardosa sodalis* Holm 1970 and *Pardosa moesta* Banks 1892, as they represent 46% (28%, 8%, 11%, respectively) of the activity density (abundance) of all spiders in this region (Bowden & Buddle 2010). Gravid female spiders were collected in the field across most of the active season so as to limit bias (detecting many parasitized late in season or few early in season) in the data (Edgar 1971) and subsequently preserved in 70% ethanol. Following gravid spiders through most of the active growing season also allowed us to document the parasitoids' ontogeny to the imago stage. Spider egg sacs are notably darker and more oval when parasitized by wasps like *Gelis* late in the season when larvae have pupated.

All specimens were returned to the laboratory where carapace width of each female was measured to determine body size and the respective egg sac dissected, and contents evaluated. We collected two genera of wasps: *Gelis* and *Baeus*; however, due to the low presence of *Baeus* sp. (eight in *P. moesta*, two in *P. sodalis* and six in *P. lapponica*; all collected from the Ogilvie site) we did not pursue statistical analyses with this genus. Representatives of the adult wasps were sent to the Canadian National Collection of Insects, Arachnids and Nematodes in Ottawa, Canada for identification/confirmation and could only be identified to the genus level; hence it is possible that multiple species occurred. The morphology (e.g., wings) of *Gelis* wasps is known to differ between the sexes (Edgar 1971) and to be influenced by environment and larval host (Salt 1952), making identification to species cumbersome. As the ecology of known species in the genus *Gelis* is similar, however, in having the same ultimate effect upon the spider progeny, our study is relevant to the spiders' ecology. Measurements were conducted using a Nikon® SMZ1000 stereomicroscope fitted with an ocular micrometer. Voucher specimens can be found at McGill's Lyman Entomological Museum, Sainte Anne de Bellevue, Québec, Canada.

Pardosa lapponica is found in high abundance on tundra and less frequently in sparse boreal forest (Bowden & Buddle 2010). *Pardosa*

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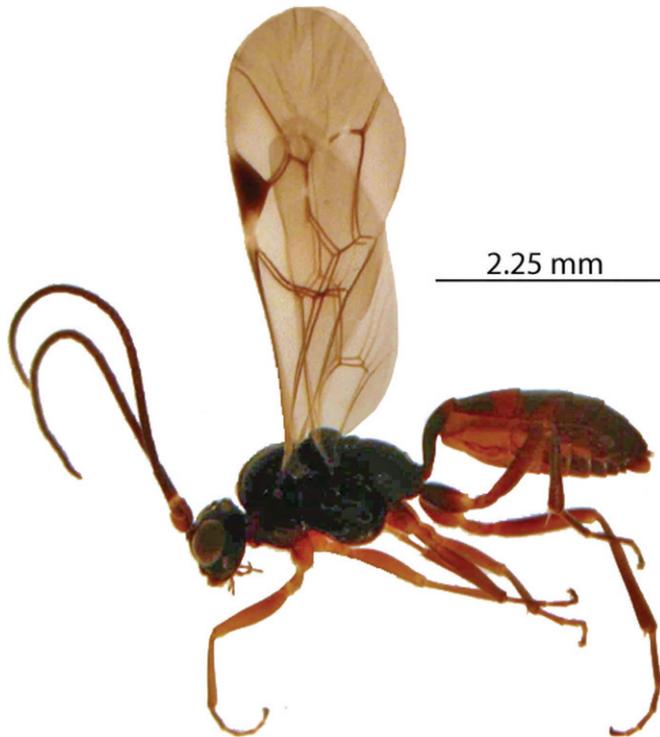


Figure 1.—Adult *Gelis* sp. that emerged from an egg sac of *Pardosa* sp. on the tundra in the Yukon Territory, Canada.

sodalis is likely restricted to moist tundra (Dondale & Redner 1990; Bowden & Buddle 2010). *Pardosa moesta* is a generalist species found throughout much of North America (Dondale & Redner 1990; Buddle 2000) and is the smallest wolf spider collected in this region (Bowden & Buddle 2010).

To determine whether the incidence of *Gelis* (Fig. 1) increased with spider size within species we fitted logistic regressions (presence/absence) of *Gelis* to female body size with site as a random factor using generalized linear mixed models (GLMM) with Laplace approximation and log-likelihood ratio tests to test the significance of body size. We examined the proportion of individuals in each spider species parasitized by *Gelis* and determined if larger spiders, within species, hosted more parasitoids using linear regressions. All regressions and ANOVAs were conducted with the base statistics package and GLMMs using lme4 (Bates et al. 2011) for the R environment version 2.15.0 (R Development Core Team 2012).

We collected a total of 574 *P. lapponica*, 253 *P. sodalis* and 121 *P. moesta* and found high incidences of wolf spiders parasitized by *Gelis* on the Yukon tundra (Table 1). We detected significant variation among sites, with the lowest incidence in all three species at the Richardson site. This site variation did not track differences in spider body size (Table 1) and could reflect a context dependency related to some unmeasured biotic (e.g., hyperparasitoids) or abiotic (e.g., temperature) factor(s).

The incidence of *Gelis* parasitoids increased significantly with body size in two of the three species: *P. lapponica* ($X^2_1 = 4.06$, $P = 0.04$) and *P. moesta* ($X^2_1 = 5.33$, $P = 0.02$), but not in *P. sodalis* ($X^2_1 = 1.08$, $P = 0.29$). The highest incidence of *Gelis*, however, was found in the largest species (*P. sodalis*: Table 1). Interestingly, we also found that *P. sodalis* appears to be the first species of the three to emerge from the egg sac (Bowden 2011). We found no significant effect (all $R^2 \leq 0.01$ and P -values $\gg 0.05$) of body size, a proxy for potential clutch size, on parasitoid load for any of the wolf spider species examined.

Table 1.—Incidence of egg sac parasitoids in three *Pardosa* spp. collected from three tundra sites in the Yukon Territory, Canada. The data for *P. moesta* were not available from the Tombstone site. Body size measured as carapace width in millimeters. F-statistics with degrees of freedom are shown above each species tested for body size variation among/between sites. Significant differences are indicated with letters, using Tukey's HSD or ANOVA (for *P. moesta*) at $\alpha = 0.05$.

		Mean body size (\pm SE)	Percent parasitized
		$F_{2,571} = 119.94$	
<i>P. lapponica</i>	Tombstone	2.175 (\pm 0.007)a	13.55 (N=214)
	Ogilvie	2.334 (\pm 0.009)b	43.90 (N=164)
	Richardson	2.309 (\pm 0.008)c	9.18 (N=196)
		$F_{2,250} = 18.79$	
<i>P. sodalis</i>	Tombstone	2.536 (\pm 0.012)a	48.54 (N=103)
	Ogilvie	2.641 (\pm 0.019)b	51.50 (N=33)
	Richardson	2.641 (\pm 0.014)b	6.84 (N=117)
		$F_{1,119} = 0.14$	
<i>P. moesta</i>	Ogilvie	1.913 (\pm 0.012)a	5.00 (N=40)
	Richardson	1.920 (\pm 0.019)a	1.23 (N=81)

To our knowledge, the percentages of parasitized egg sacs we report are the highest on record and are almost 1.5 times greater than the highest recorded in other populations of wolf spiders (Eason et al. 1967; Edgar 1971; Cobb & Cobb 2004). Edgar (1971) found total egg sac parasitism, by *Gelis* and *Hidryta*, to range from 2.9% to 34.8% of individuals in *Pardosa lugubris* (Walckenaer) in Scotland. The high overall incidence of parasitism by *Gelis* in the region of our study may reflect high resource availability of prey (i.e., spiders) with little refuge. Therefore, high rates of parasitism could also be present in other open habitats (e.g., alpine tundra, coastal barrens) where wolf spiders are abundant.

Our findings suggest that these parasitoids could have important consequences for the reproductive fitness of these northern spider species since *Gelis* destroy the contents of the egg sac, rendering the female's fitness effectively equal to zero (Edgar 1971; pers. obs.). This idea is supported by our data because we collected gravid female spiders throughout most of the active season (active season being late May to late August), and our sampling shows that it takes an entire season to mate, produce the clutch and carry it until the progeny hatch late in the summer (Bowden 2011). Like high elevation species (Schmoller 1970), our study species probably take multiple years to reach maturity, and this is supported by the overlapping generations we collected in pit-fall traps. Hence, in our study area we suspect that females produce just one egg sac per lifetime as it is unlikely that females overwinter to produce subsequent clutches in following seasons (Kiss & Samu 2002).

The fact that we found the highest incidence of *Gelis* parasitoids in egg sacs of *P. sodalis* and the lowest in *P. moesta* suggests that targeting the largest spider species may maximize the parasitoids' fitness. This would make sense from the perspective of the wasp, as it could maximize resources available for the wasp's progeny; however, we did not find that body size (within spider species) significantly predicted parasitoid loads in egg sacs. Perhaps variation in actual clutch size (e.g., larger spiders producing smaller clutches) skews this relation or there is a balance to be struck between host clutch mass and number (Pérez-Contreras & Soler 2004) and its own mass. We did find, at least for *P. moesta* and *P. lapponica*, that the probability of being parasitized increases with body size, and this may reflect increased movement by larger individuals or parasitoids able to assess this trait. We did not find the same with *P. sodalis*, so it is possible that a threshold is reached for the parasitoid where it does not pay or is not possible to produce and lay more eggs in larger spider egg sacs.

Further experiments would have to be employed to fully test these ideas.

Our study shows that egg sac parasitoids are frequent in populations of Arctic wolf spiders from the tundra in the Yukon Territory, Canada. Evidence exists in other high Arctic arthropod groups that parasitoids may have an important influence on the life history of host species (Kukal & Kevan 1987). Although little is known about the parasitoids themselves, we have shown that their phenology seems to track that of the spiders quite well; however, it could vary from year to year. Hence, this study reveals many new questions in the contexts of community, population and behavioral ecology. Understanding more about the parasitoids and their impacts on local population and community dynamics, both spatially and temporally, would be particularly interesting.

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LITERATURE CITED

- Bates, D., M. Maechler & B. Bolker. 2011. lme4: Linear mixed-effects models using Eigen and Eigen. Online at: <http://cran.r-project.org/web/packages/lme4/index.html>
- Bowden, J.J. 2011. Biodiversity, biogeography and life history of spiders (Araneae) in the Yukon Territory, Canada. PhD dissertation. McGill University, Montréal, Québec, Canada.
- Bowden, J.J. & C.M. Buddle. 2010. Determinants of ground-dwelling spider assemblages at a regional scale in the Yukon Territory, Canada. *Écoscience* 17:287–297.
- Bowden, J.J. & C.M. Buddle. 2012. Life history of tundra-dwelling wolf spiders (Araneae: Lycosidae) from the Yukon Territory, Canada. *Canadian Journal of Zoology* 90:714–721.
- Buddle, C.M. 2000. Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in central Alberta, Canada. *Journal of Arachnology* 28:319–328.
- Cobb, L.M. & V.A. Cobb. 2004. Occurrence of parasitoid wasps, *Baeus* sp. and *Gelis* sp., in the egg sacs of the wolf spiders *Pardosa moesta* and *Pardosa sternalis* (Araneae, Lycosidae) in southeastern Idaho. *Canadian Field Naturalist* 118:122–123.
- Dondale, C. & J. Redner. 1990. The wolf spiders, nursery web spiders, and lynx spiders of Canada and Alaska: Araneae: Lycosidae, Pisauridae and Oxyopidae. *Insects and Arachnids of Canada Handbook, Series 17*. Agriculture Canada, Ottawa.
- Dondale, C., J. Redner & Y. Marusik. 1997. Spiders (Araneae) of the Yukon. Pp. 73–113. *In: Insects of the Yukon* (H. Danks & J. Downes, eds.). Biological Survey of Canada, Ottawa, Canada.
- Eason, R.R., W.B. Peck & W.H. Whitcomb. 1967. Notes on spider parasites including a reference list. *Journal of Kansas Entomological Society* 40:422–434.
- Edgar, W.D. 1971. Aspects of ecology and energetics of egg sac parasites of the wolf spider *Pardosa lugubris* (Walckenaer). *Oecologia* 7:155–163.
- Fletcher, J.P., J.P. Hughes & I.F. Harvey. 1994. Life expectancy and egg load affect oviposition decisions of a solitary parasitoid. *Proceedings of the Royal Society B: Biological Sciences* 258:163–167.
- Kiss, B. & F. Samu. 2002. Comparison of autumn and winter development of two wolf spider species (*Pardosa*, Lycosidae, Araneae) having different life history patterns. *Journal of Arachnology* 30:409–415.
- Kukal, O. & P.G. Kevan. 1987. The influence of parasitism on the life history of a high arctic insect, *Gynaephora groenlandica* (Wöckle) (Lepidoptera: Lymantriidae). *Canadian Journal of Zoology* 65:156–163.
- Le Lan, C., B. Visser, J. van Baaren, J.J.M. van Alphen & J. Ellers. 2012. Comparing resource exploitation and allocation of two closely related aphid parasitoids sharing the same host. *Evolutionary Ecology* 26:79–94.
- Meltofte, H., T.T. Høye, N.M. Schmidt & M.C. Forchhammer. 2007. Differences in food abundance cause inter-annual variation in the breeding phenology of High Arctic waders. *Polar Biology* 30:601–606.
- Pérez-Contreras, T. & J.J. Soler. 2004. Egg parasitoids select for larger clutch sizes and covering layers in pine processionary moth (*Thaumetopoea pityocampa*). *Annales Zoologici Fennici* 41:587–597.
- Polis, G.A., S.D. Hurd, C.T. Jackson & F. Sanchez-Piñero. 1998. Multifactor population limitation: Variable spatial and temporal control of spiders on Gulf of California islands. *Ecology* 79:490–502.
- R Core Development Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Online at: <http://www.R-project.org>
- Schmoller, R. 1970. Life histories of Alpine tundra Arachnida in Colorado. *American Midland Naturalist* 83:119–133.
- Salt, G. 1952. Trimorphism in the ichneumonid parasite *Gelis corruptor*. *Quarterly Journal of Microscopical Science* 93:453–474.

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