Pollinators of the Great Plains: Ecology, Distribution, and Conservation
2022 *PRAIRIE NATURALIST* Special Issue 1:1–10

Pollination Biology and Insect Visitation of Pasqueflower (Ranunculaceae: *Pulsatilla patens* ssp. *multifida*) in the Little Missouri National Grasslands of North Dakota

Joshua W. Campbell[1*] and Alex R. Morphew[1]

Abstract - The Little Missouri National Grassland, located in western North Dakota, is the largest national grassland in the United States. Little is known about pollinator communities within this region of the northern Great Plains. *Pulsatilla patens* ssp. *multifida* (Pasqueflower) is one of the first plants to flower in the early spring. We investigated the pollination biology of the *P. patens* ssp. *multifida* through an insect exclusion study and observational surveys to determine if the species is dependent on insects for setting seed and to document the common insect visitors to open flowers. We found that flowers in which insects were excluded from visiting had a lower chance of producing seed heads and developing mature seeds compared with control flowers. However, flowers that did produce mature seeds from both the control and treatment groups produced similar numbers of seeds per flower. The most common likely pollinators were andrenid and halictid bees, specifically genera *Andrena* and *Lasioglossum*. Thus, the early spring bee community may be dependent on *P. patens* ssp. *multifida* for pollen and nectar due to the lack of other flowering plants during this time period.

Introduction

Pulsatilla patens (L.) Mill ssp. *multifida* (Pritz) Zamels (Pasqueflower or Prairie Crocus), also known as *Anemone patens* (L.) ssp. *multifida* (Pritz) Hulten, is a member of the family Ranunculaceae and is native to mixed and short-grass prairies, sub-alpine meadows, and dry rocky areas in North America. This is one of the first spring flowers to bloom in the northern Great Plains and tundra areas and its range extends broadly from Wisconsin to Alaska and south as far as Texas. A perennial, *P. patens* ssp., *multifida* (hereafter *P. patens*) produces showy, bell-shaped flowers consisting of 5–7 light-blue to purple sepals (Van Bruggen 1983). The center of the flower consists of 150 to 200 yellow stamens and several pistils situated in the middle of the stamens (Dutton et al. 1997). The outer stamens are modified nectaries (Bock and Peterson 1975). Flowers open during the day and close at night and during cold days (Ordway 1986). In general, *P. patens* is shade-intolerant and relies primarily on early-season flowering periods and regular disturbances, such as fire and mild grazing to limit competition for sunlight and nutrients from nearby plant species (Kricsfalusy 2016).

In some portions of the northern Great Plains, *P. patens* is quite common. However, declines at the edges of its range have led to elevated conservation status of *P. patens* in some states, including Washington and Wisconsin, where it is currently classified as threatened and endangered, respectively (Fertig 2021, Wisconsin Department of Natural Resources Bureau of Natural Heritage Conservation 2021). These declines are likely linked to native prairie habitat loss due to agriculture and shifts in disturbance regimes, such as under- or over-grazing and fire suppression (Kricsfalusy 2016, Kricsfalusy and Ponomarenko 2013).

Although *P. patens* can be found in grassland habitats across multiple states/provinces, and despite growing concern for conservation of the species, very little is known about *P. patens* pollination. The few studies documenting insect associates were accomplished in Colorado,

[1]US Department of Agriculture, Agricultural Research Service, Northern Plains Agricultural Research Laboratory, 1500 N. Central Ave., Sidney, MT 59270 USA. [*]Corresponding Author: joshua.campbell@usda.gov.

Associate Editor: Clint Otto, US Geological Survey, Northern Prairie Wildlife Research Center.

Minnesota, North Dakota, and Canada (Ascher and Pickering 2021, Bock and Peterson 1975, Gibbs 2010, Ordway 1986). *P. patens* insect visitors can be readily found during early spring throughout the northern Great Plains. Thus, this plant is important for provisioning pollen and nectar for early season bees and other pollinators. Within this region is the Little Missouri National Grassland (LMNG), which is the largest national grassland in the United States. Administered by the United States Department of Agriculture Forest Service, the LMNG is located in western North Dakota and comprises over 400,000 ha. Primary studies conducted in LMNG have thus far focused largely on grasshoppers, birds, and plants (e.g., Branson 2011, Fontaine et al. 2004). To our knowledge, only one pollinator study has been conducted within the LMNG, which explored pollinators of *Echinacea angustifolia* DC (purple coneflower) (Leuszler et al. 1996). However, one pollinator study was conducted in Theodore Roosevelt National Park, which is surrounded by the LMNG (Larson et al. 2006). In addition to little research on pollinators conducted within the LMNG, extensive knowledge gaps exist regarding pollinators of the northern Great Plains in general (Hanberry et al. 2020).

We investigated *P. patens* pollination in the LMNG where we conducted surveys of flower-visiting insects and an insect exclusion experiment. Our objectives were to (1) document flower-visiting insects and their foraging behavior on *P. patens* blooms and (2) determine if *P. patens* in the LMNG require insect visitation to set seed. Based on prior research, we anticipated that bees in the family Andrenidae, specifically those in the genus *Andrena* Fabricius, would be the most common insect visitors. We hypothesized that insect excluded flowers would produce fewer seeds compared to flowers that were allowed insect visitation.

Methods

Site Description and Insect Exclusion Experiment

We located 4 sites within the LMNG that contained numerous *P. patens* and were separated by at least 2 km to ensure independent populations (Supplemental Table 1, available online at https://eaglehill.us/prnaonline/suppl-files/prna-010h-campbell-s1.pdf). All sites were considered shortgrass prairie, with plant communities composed primarily of *Bouteloua gracilis* (Kunth) Lag. ex Griffiths (blue grama), *Juniperus horizontalis* Moench (creeping juniper), *Schizachyrium scoparium* (Michx.) Nash (little bluestem), and *Bouteloua dachtyloides* (Nutt.) Columbus (buffalo grass). Prior to bloom (6–9 April 2021), we placed 10 mesh cages over *P. patens* plants at each site, and these acted as our insect exclusion treatment. Plants chosen for the caged treatment had a) at least 1 clearly formed flower bud, with no visible anthers or petals (i.e., insect pollination not possible), and b) were within 10 meters of another *P. patens* plant with a clearly-forming flower. Control or open-treatment flowers were thus located within 10 meters of a paired, caged plant and had either a) closed flowers or b) newly-opened flowers. Cages were approximately 30 cm (width) x 30 cm (height), cylindrical, and consisted of aluminum screening with 0.5 mm^2 size mesh. Additionally, at each site, we tagged 10 additional *P. patens* plants to act as our control treatment (insects could freely visit flowers). In total, 81 stems with clearly forming flower buds were caged for the insect exclusion treatment, and 107 stems with either developing or open flowers were tagged for the control treatment.

After flowers senesced, we visited each study plant once every 3 days to assess seed development. We collected developed seed heads when a majority of the seeds were visually determined to be near maturation but not yet liberated from the seed head. For each seed head collected, we counted the number of mature seeds. We considered a seed mature if an achene was at least 2 mm long, 1.5–2 mm wide, and attached to an awn (Fig. 1). At 3 of the 4 sites, extensive herbivory of flowers occurred and we established new control treatments to maintain our 10 replicates per site.

Insect Surveys

We conducted visual insect surveys walking slowly throughout the extent of our focal *P. patens* populations. When possible, 2 people conducted surveys at the same time and location to minimize observer bias. The first surveys began when approximately 10% of the *P. patens* within the site were open and the last surveys were made when approximately 90% of flowers had already senesced. When open *P. patens* were encountered, we collected representative insects that were actively visiting reproductive parts of the flower (anthers/pistils). Insects that could not be collected were recorded. All collected and recorded insects were identified to the lowest taxonomic level possible. All visual surveys were conducted between the hours of 10:30 and 18:30 on 9 days from April 8 to 13 May 2021. Given that sustained wind speeds averaged 10.2 and 11.2 m/s (23 and 25 mph) in April and May (NCEI 2021), respectively, we were logistically unable to limit surveys to periods of minimal wind speeds. Thus, surveys took place when weather conditions were a minimum of 10°C and winds were less than 9 m/s (20 mph). Lengths of individual surveys ranged from 10 to 70 minutes and were largely driven by weather conditions and flower abundance.

In addition to visual insect surveys, on 4 separate days (21, 22, 30 April; 14 May), digital video cameras (Sony HD Handy Cams) attached to tripods recorded blooming *P.*

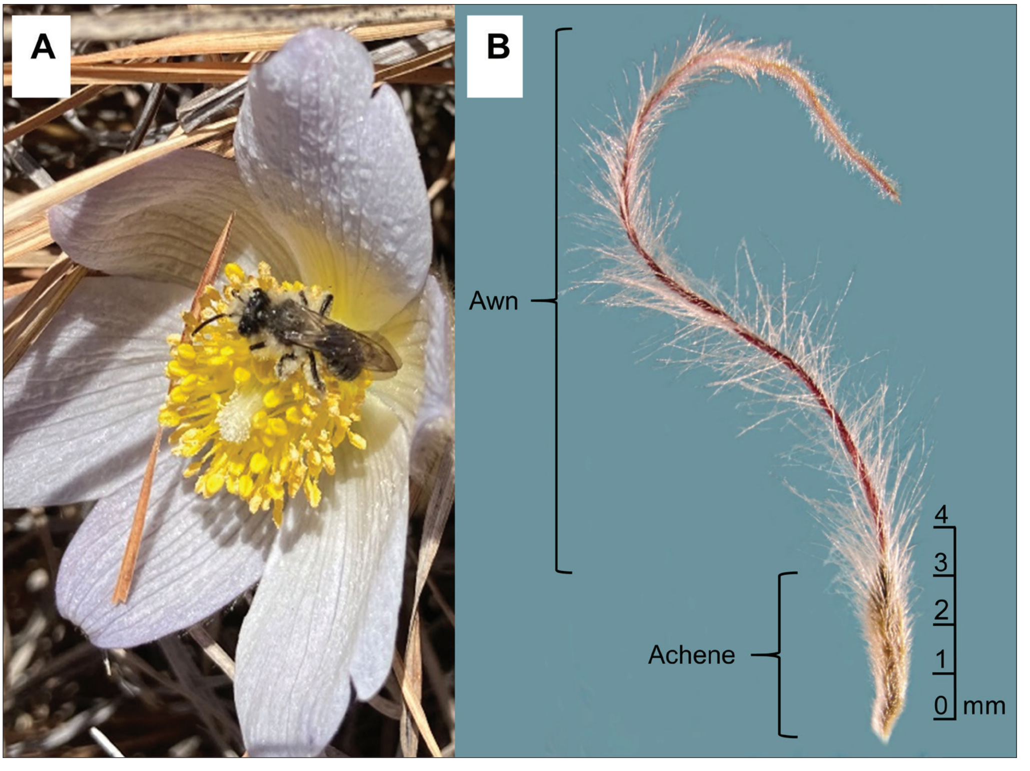

Figure 1. A) *Andrena* sp. visiting the of an early spring *P. patens*. B) *P. patens* achene and plumose awn.

patens. Cameras were placed approximately 30 cm from flowers. We later watched each video and recorded flower visitors and length of time they remained on the flower. Only insects that touched anthers or pistils were counted.

We also conducted a literature search to document all flower-visiting insects previously observed on or collected from *P. patens*. In addition to reviewing primary literature, we searched the Discover Life database (Ascher and Pickering 2021) for digital records of insects collected directly from *P. patens, P. patens* ssp. *multifida, A. patens,* and *A. patens* ssp. *multifida*.

Statistical Analysis

A chi-square test was used to determine if the likelihood of producing a seed head was different between caged and control treatments. Aborted seeds were excluded from these analyses. Due to the non-normality of the data, a Wilcoxon Rank Sum test was used to test for differences between the amount of time *Lasioglossum* Curtis (sweat bees) and *Andrena* Fabricius (mining bees) spent on individual flowers based on the video survey and for the number of mature seeds produced between the caged and control treatments.

Results

Insect Exclusion Experiment

A total of 35 *P. patens* flowers developed on plants within cages, and 71 flowers developed on the plants in the control treatment. However, only 62% of flowers under cages produced seed heads (n = 22) whereas 83.1% of flowers in the control treatment produced seed heads (n = 59). The Chi-square analysis revealed that control plants that were allowed insect visitation to flowers were significantly more likely to produce seed heads ($\chi^2 = 14.72$, df = 1, P = 0.0001) than caged plants. Additionally, only 27.2% of all plants from the insect exclusion treatment produced mature seeds, whereas 38.2% of all plants in the control treatment produced mature seeds (Fig. 2A). An average of 20.1 (SE ±3.5) mature seeds developed from flowers within the insect exclusion treatment and an average of 17.8 (SE ±2.9) mature seeds in the flowers from the control treatment, but this difference was not statistically different (z = 0.78, P = 0.44) (Fig. 2B). Over the course of the study, we observed widespread herbivory of mature flowers at 3 of the 4 sites. At the fourth site, however, we found no evidence of herbivory. A total of 36.4% of the original open treatment flowers were grazed for the other 3 sites.

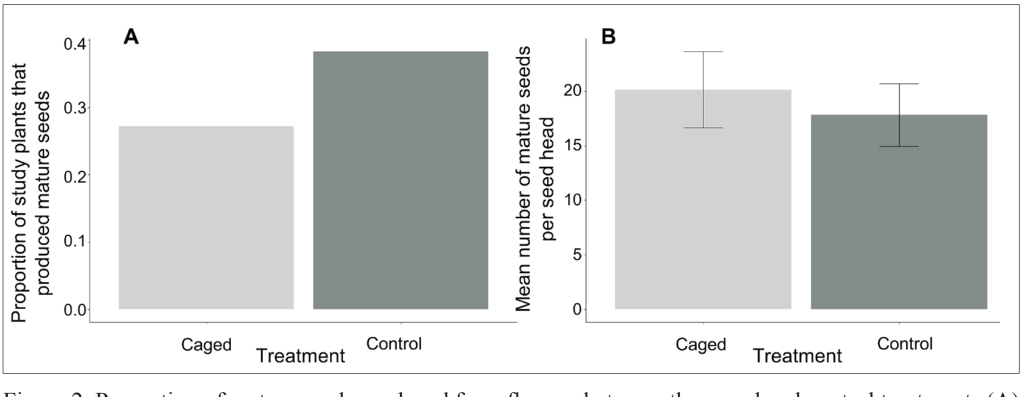

Figure 2. Proportion of mature seeds produced from flowers between the caged and control treatments (A) and the mean number of mature seeds (± SE) produced from insect excluded plants (caged) and plants allowed insect visitation (control) (B).

Insect Surveys

A total of 526 minutes and 117 flower-visiting insects were recorded on video. Bees (Apoidea) were the most common insects recorded (n = 56) followed by ants (Formicidae) (n = 39). Of bees, the genus *Andrena* was most common (N=39) followed by the genus *Lasioglossum* (n = 18). On average, *Lasioglossum* spent more time on individual flowers (92.9 seconds) compared to *Andrena* (46.9 seconds; Z = 3.02, P = 0.0025, Figure 3).

We conducted a total of 640 minutes of visual surveys and collected/observed 81 insects. Again, bees were among the most common flower visitors (n = 43), followed by flies (n = 17), and ants (n = 11). Of the bees, *Andrena* (n = 32) and *Lasioglossum* (n = 10) were the most frequently observed genera, and 15 of the 17 observed flies were tachinids in the genus *Winthemia* Robineau-Desvoidy (Tachinid fly) (N = 15). See Table 1 for a list of all insects documented on video and observational surveys. Diptera and Formicidae individuals were identified by J.W. Campbell (Fisher and Cover 2007, Miranda et al. 2013). Collected *Andrena* and *Lasioglossum* bees were identified to species by A.R. Morphew and M. Arduser (Bouseman and LaBerge 1979; Gibbs 2010, 2011; LaBerge 1985, 1986; LaBerge and Ribble 1975).

P. patens-associated insect records documented in the literature spanned 5 insect orders and included 6 families of Hymenoptera (Table 2). Bees were by far the most common visitors observed in this study and 8 bee genera overall have been reported visiting *P. patens* flowers. Discover Life database records for *P. patens* insect visitors contributed an additional 10 bee species, all of which were collected from *P. patens* between the years 1906 and 1915.

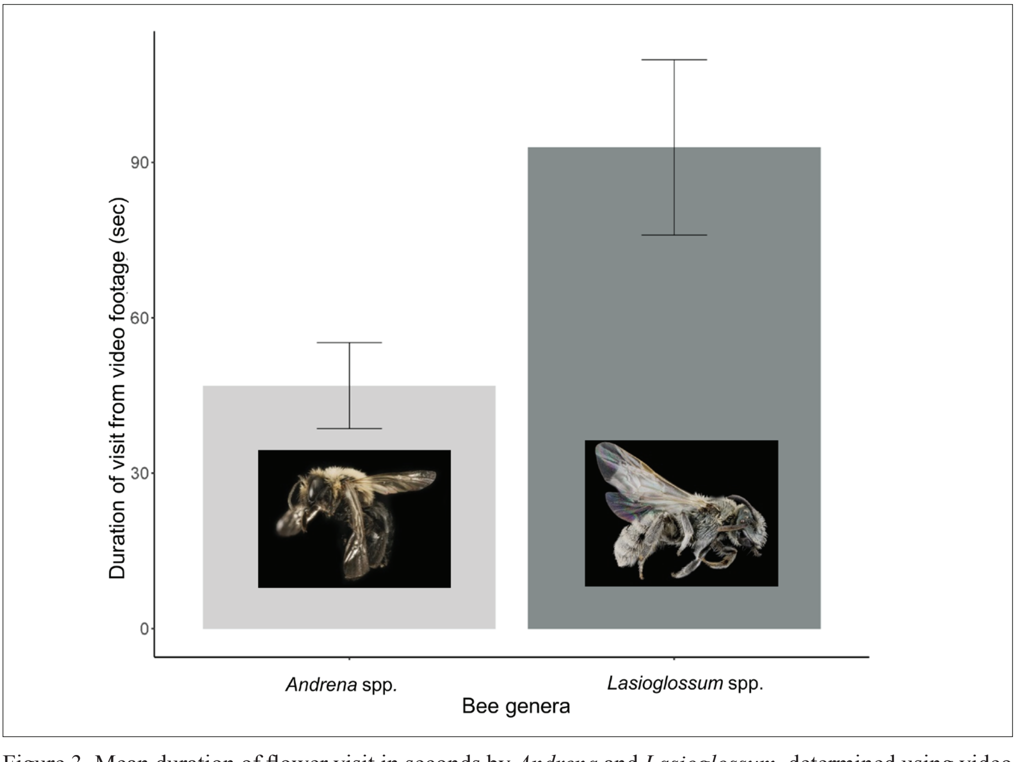

Figure 3. Mean duration of flower visit in seconds by *Andrena* and *Lasioglossum*, determined using video footage. Error bars represent the standard error. Photos of *Andrena carlini* (left) and *Lasioglossum (Dialictus) pruinosum* (right) used with permission from and taken by Sam Droege/www.discoverlife.com.

Discussion

P. patens is one of few species that can be found flowering during early spring in the northern Great Plains, making it an important resource for flower-visiting insects. Despite this, very few studies have assessed the flower-visiting insects and pollination of *P. patens*. In this study, we documented numerous insect visitors to *P. patens* flowers. Overall, the number of developed seeds produced by control (open) *P. patens* was significantly higher than that of caged, insect-excluded plants. Thus, our data suggests that *P. patens* benefit from insect visitation that is probably promoting cross pollination. In addition to the reproductive benefit to *P. patens*, insect visitors are being supplied floral resources that sustain adults and larvae. Only a few *Townsendia* Hook (Townsend daisies) plants were observed flowering during the bloom period for *P. patens*, exemplifying the importance of *P. patens* to early-season bees and other insects dependent on pollen/nectar.

Although bees and other insects undoubtedly contribute to cross pollination, numerous plants within our insect exclusion cages produced seed heads with mature seeds. Due to potential harsh weather conditions, *P. patens* has probably evolved the ability to self-pollinate when insect activity is low. Additionally, andrenid bees were observed visiting *P. patens* on

Table 1. List and numbers of all *P. patens* visitors observed visiting open flowers from digital video and visual/collecting surveys. All insects were observed between 8 April – 14 May 2021 in the Little Missouri National Grassland, North Dakota.

	Family/Taxa	Genera/Taxa	Video	Visual/Collecting Surveys
Coleoptera	Chrysomelidae		4	1
Diptera	muscoids		6	
	Syrphidae	*Copestylum* Mcquart sp.		1
		Paragus Latreille sp.	2	
		Platycheirus Lepeletier and Serville sp.		1
	Tachinidae	*Winthemia* spp.	5	15
Hemiptera	Miridae	*Lygus* Hahn spp.	1	9
Hymenoptera	Andrenidae	*Andrena* spp.	39	16 (not collected)
		Andrena (Euandrena) algida Smith ♀, ♂		8
		Andrena (Melandrena) carlini Cockerell ♀, ♂		6
		Andrena (Holandrena) cressonii Robertson ♂		1
		Andrena (Thysandrena) w-scripta Viereck ♀		1
	Halictidae	*Halictus confusus* Smith ♀	1	1
		Lasioglossum (Dialictus) pruinosum Robertson ♀		4
		Lasiolgossum (Dialictus) laevissimum Smith ♀		1
		Lasioglossum(Dialictus) Robertson sp. 1 ♀		1
		Lasioglossum (Hemihalictus.) sp. 1 ♀		2
		Lasioglossum spp. ♀, ♂	18	2 (not collected)
	Formicidae	includes *Tapinoma sessile* Say and *Formica* L. spp.	39	11
Lepidoptera	Papilionidae	*Papilio polyxenes* Fabricius (Black Swallowtail)	1	
		Total *P. patens* Visitors	117	81

Table 2. Known insect visitors of *P. patens*. Species records associated with entomology collections were taken from the Discover Life database (Ascher and Pickering 2021) and are indicated with an asterisk (*). AMNH_BEE: American Museum of Natural History; CUIC_ENT: Cornell University Insect Collection Database; UCRC_ENT: University of California, Riverside, Entomology, Entomology Research Museum.

Order	Family	Species	State	Reference or Collection	Year collected
Hymenoptera	Andrenidae	*Andrena* spp.	CO	Bock and Peterson 1975	1971-1973
			MN	Ordway 1986	1984
		Andrena (Parandrena) andrenoides Cresson	Unk.	Krombein et al. 1979	Unk.
		Andrena (Euandrena) algida	CO	*AMNH_BEE; *UCRC_ENT	1913; 1906, 1913
			ND	*AMNH_BEE; *CUIC_ENT	1913
		Andrena (Melandrena) carlini	MN	Ordway 1986	1984
		Andrena (Holandrena) cressonii	CO	*AMNH_BEE; *UCRC_ENT	1913; unk.
		Andrena (Tylandrena) erythrogaster Ashmead	MN	Ordway 1986	1984
		Andrena (Trachandrena mariae Robertson	MN	Ordway 1986	1984
		Andrena (Trachandrena) sigmundi Cockerell	MN	Ordway 1986	1984
		Andrena (Scrapteropsis) nigra Provancher	MN	Ordway 1986	1984
		Andrena (Larandrena) miserablis Cresson	MN	Ordway 1986	1984
		Andrena (Scrapteropsis) imitatrix Cresson	MN	Ordway 1986	1984
		Andrena (Micandrena) Ashmead sp.	MN	Ordway 1986	1984
	Apidae	*Apis mellifera* L.	CO	Bock and Peterson 1975	1971-1973
			MN	Ordway 1986	1984
		Ceratina neomexicana Cockerell	CO	*AMNH_BEE	1913
		Ceratina Latreille sp.	MN	Ordway 1986	1984
		Bombus Latreille spp.	CO	Bock and Peterson 1975	1971-1973
		Epeolus Latreille sp.	MN	Ordway 1986	1984
	Halictidae	*Halictus* Latreille sp.	MN	Ordway 1986	1984
		Halictus (Halictus) rubicundus Christ	Unk.	Moure and Hurd 1987	Unk.
			CO	*AMNH_BEE	1906; 1913
			ND	*AMNH_BEE	1913
		Lasioglossum sp.	MN	Ordway 1986	1984
		Lasioglossum Dialictus) admirandum Sandhouse	ND	*AMNH_BEE	1915

Table 2. Continued.

		Lasioglossum Dialictus) cinctipes Provancher	CO	*AMNH_BEE	1913
		Lasioglossum Dialictus) cressonii Robertson	Canada	Gibbs 2010	Unk.
		Lasioglossum Dialictus) laevissimum Smith	ND	*AMNH_BEE	1915
		Lasioglossum Dialictus) pilosum Smith	Canada	Gibbs 2010	Unk.
		Lasioglossum Dialictus) pruinosum	ND	*AMNH_BEE	1915
		Lasioglossum Dialictus) semicaeruleum Cockerell	ND	*AMNH_BEE	1913
		Lasioglossum s.s.) sisymbrii Cockerell	CO	*AMNH_BEE	1913
	Colletidae	*Colletes* Latreille sp.	MN	Ordway 1986	1984
	Formicidae	*Formica obscuripes* Forel	MN	Ordway 1986	1984
	Tenthredinidae		MN	Ordway 1986	1984
Diptera	Syrphidae		CO	Bock and Peterson 1975	1971-1973
	Anthomyiidae		MN	Ordway 1986	1984
	Tachinidae		MN	Ordway 1986	1984
Hemiptera	Miridae		MN	Ordway 1986	1984
	Scutellaridae		MN	Ordway 1986	1984
Coleoptera			MN	Ordway 1986	1984
Thysanoptera			MN	Ordway 1986	1984

cool, windy days suggesting they too have evolved to forage in sub-optimal weather conditions. Indeed, Andrenidae have been documented to forage in cooler weather (Herrera 1995) or weather that is unsuitable for honey bees (Güler and Sorkun 2010).

Published records for *P. patens*-visiting insects included numerous bee species, flies, ants, and many other insects (Table 2). Bees were, by far, the most commonly observed insect-visitors, with *Andrena* bees comprising a majority of these observations. *Andrena* are usually the first bees to emerge from their ground nests in the spring. Due to their larger size (compared to *Lasioglossum*) and their shorter visitation time per flower, and thus increased likelihood of visiting multiple flowers, they are probably the most efficient pollinator of *P. patens*. *Andrena* bees were also the most commonly observed visitors of *P. patens* from other observational studies (Table 2; Bock and Peterson 1975, Ordway 1986). Overall, 12 species of *Andrena* have been documented on *P. patens* (Tables 1 and 2). Of these, 4 *Andrena* species were observed during this study, including *Andrena w-scripta,* a previously unknown *P. patens* association prior to this study.

Lasioglossum and *Winthemia* were also both observed visiting multiple plants, thus probably also contributing to cross-pollination. Ants were also a commonly observed insect visitor to *P. patens*. Although ant pollination has been documented in a few plants (e.g., Abbate and Campbell 2013), ants are generally considered poor pollinators because they secrete chemical substances that decrease pollen viability (Beattie et al. 1984). It is also unlikely that ants carried many pollen grains and visited multiple plants. Other visitors, such as Chrysomelidae Latreille (leaf beetles) and Miridae Hahn (plant bugs) are herbivores and, although they could contribute to pollination, they are likely damaging flowers through herbivory. The extensive herbivory observed in 3 of our sites was not expected. Often, *P. patens* can be found on overgrazed pastures because it is not preferred by livestock (Wildeman and Steeves 1982). In boreal forests where cattle grazing has ceased, *P. patens* can become rare due to increased understory vegetation (Kalliovirta et al. 2006). *Antilocapra americana* Ord (Pronghorn Antelope) and *Odocoileus hemionus* Rafinesque (Mule Deer) were the only large herbivores that were commonly observed near our sites, and we believe they removed many of the *P. patens* during the study. Flowers appeared eaten from above, and often, only the flower stalk was consumed. Our data suggests that *P. patens* were also an important early spring food source for large herbivores.

Our 2 observational methods, visual surveys and video recordings, documented the same common insect genera (e.g., *Andrena*, *Lasioglossum*, etc.) visiting *P. patens*. Our total visual survey time included 100 more minutes over 5 additional days than the video recordings. However, the video recordings documented more insect visits and different insect groups than observational surveys (Table 1). Thus, some insects may have been wary of researcher activity and, thus, were not observed during the visual surveys. Future studies that want to quantify general insect visitation to plants may consider relying on digital recordings of flower visitors. However, visual surveys and insect collection are essential for species-level determinations, as digital recordings may currently be insufficient for the identification of smaller pollinators to species.

Acknowledgements

We thank Avery Pearson and Natalie West for assisting with visual surveys for *P. patens* insects. We thank the McKenzie Ranger District of the US Department of Agriculture Forest Service for granting access and permission to conduct this research and collect insects and *P. patens*. We gratefully acknowledge Mike Arduser for bee taxonomic assistance.

Literature Cited

Abbate, A.P., and J.W. Campbell. 2013. Parasitic beechdrops (*Epifagus virginiana*): A possible ant-pollinated plant. Southeastern Naturalist 12:661–665.

Ascher J.S., and J. Pickering 2021. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Draft-35. Available online at http://www.discoverlife.org/mp/20q. Accessed 31 August 2021.

Beattie, A.J., C. Turnbull, R.B. Knox, and E.G. Williams. 1984. Ant inhibition of pollen function: A possible reason why ant pollination is rare. American Journal of Botany 71:421–426.

Bouseman, J.K., and W.E. LaBerge. 1978. A revision of the bees of the genus Andrena of the Western Hemisphere. Part IX. Subgenus *Melandrena*. Transactions of the American Entomological Society 104:275–389.

Branson, D.H. 2011. Relationships between plant diversity and grasshopper diversity and abundance in the Little Missouri National Grassland. Psyche 2011:748635.

Bock, J.H., and S.J. Peterson. 1975. Reproductive biology of *Pulsatilla patens* (Ranunculaceae). American Midland Naturalist 94:476–478.

Dutton, B.E., C.S. Keener, and B.A. Ford. 1997. *Anemone*. Pp. 139–158, *In* Flora of North America Editorial Committee (Eds.). Flora of North America North of Mexico, Vol. 3. Oxford University Press, New York & Oxford. 590 pp.

Fertig, W. 2021. 2021 Washington vascular plant species of conservation concern. Washington Natural Heritage Program Report Number: 2021–04. Olympia, WA, USA.

Fisher, B.L. and S.P. Cover 2007. Ants of North America. University of California Press, Berkeley, CA. 194 pp.

Fontaine, A.L., P.L. Kennedy, and D.H. Johnson. 2004. Effects of distance from cattle water developments on grassland birds. Rangeland Ecolog and Management 57:238–242.

Gibbs, J. 2010. Revision of the metallic species of *Lasioglossum* (*Dialictus*) in Canada (Hymenoptera, Halictidae, Halictini). Zootaxa 2591:1–382.

Gibbs, J. 2011. Revision of the metallic *Lasioglossum* (*Dialictus*) of eastern North America (Hymenoptera: Halictidae: Halictini). Zootaxa 3073:1–216.

Güler, Y., and K. Sorkun. 2010. Analysis of pollen collected by *Andrena flavipes* Panzer (Hymenoptera: Andrenidae) in sweet cherry orchards, Afyonkarahisar Province of Turkey. Psyche 2010:160789.

Hanberry, B.B., S.J. DeBano, T.N. Kaye, M.M. Rowland, C.R. Hartway, and D. Shorrock. 2020. Pollinators of the Great Plains: Disturbances, stressors, management, and research needs. Rangeland Ecology & Management 78:220-234.

Herrera, C.M., 1995. Floral biology, microclimate, and pollination by ectothermic bees in an early-blooming herb. Ecology 76:218–228.

Kalliovirta, M., T. Ryttäri, and R.K. Heikkinen. 2006. Population structure of a threatened plant, *Pulsatilla patens*, in boreal forests: Modelling relationships to overgrowth and site closure. Biodiversity & Conservation 15:3095–3108.

Kricsfalusy, V. 2016. Variations in the life cycle of *Anemone patens* L.(Ranunculaceae) in wild populations of Canada. Plants 5:1–17.

Kricsfalusy, V.V., and Ponomarenko, Y.P. 2013. Notes on biology and ecology of the Prairie Crocus (*Anemone Patens* L.) and its current status in Saskatchewan. Blue Jay 71:135–148.

Krombein, K.V., P.D. Hurd, D.R. Smith, and B.D. Burks. 1979. Catalog of Hymenoptera in America north of Mexico Vol. 2. Smithsonian Institution Press, Washington, DC. 2735 pp

LaBerge, W.E. 1985. A revision of the bees of the genus *Andrena* of the western hemisphere. Part XI. Minor subgenera and subgeneric key. Transactions of the American Entomological Society 111:441–567.

LaBerge, W.E. 1986. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part XII. Subgenera *Leucandrena*, *Ptilandrena*, *Scoliandrena* and *Melandrena*. Transactions of the American Entomological Society 112:191–248.

Laberge, W.E., and D.W. Ribble. 1975. A revision of the bees of the genus *Andrena* of the western hemisphere. Part VII. Subgenus *Euandrena*. Transactions of the American Entomological Society 101:371–446.

Larson, D.L., R.A. Royer, and M.R. Royer. 2006. Insect visitation and pollen deposition in an invaded prairie plant community. Biological Conservation 130:148–159.

Leuszler, H.K., V.J. Tepedino, and D.G. Alston. 1996. Reproductive biology of purple coneflower in southwestern North Dakota. Prairie Naturalist 28:91–102.

Miranda, G.F.G., A.D. Young, M.M. Locke, S.A. Marshall, J.H. Skevington, and F.C. Thompson. 2013. Key to the genera of Nearctic Syrphidae. Canadian Journal of Arthropod Identification 23:1–351.

Moure, J.S. and P. D. Hurd, Jr. 1987. An annotated catalog of the halictid bees of the Western Hemisphere (Hymenoptera: Halictidae). Smithsonian Institution Press, Washington, DC. 405 pp.

National Centers for Environmental Information (NCEI). 2021. Local Climatological Dataset. United States Department of Commerce: National Oceanic and Atmospheric Administration. Available online at https://www.ncdc.noaa.gov/cdo-web/datatools/lcd. Accessed 10 Nov 2021.

Ordway, E. 1986. The phenology and pollination biology of *Anemone patens* (Ranunculaceae) in western Minnesota. Pp. 181–201, *In* The Prairie: Past, Present and Future: Proceedings of the Ninth North American Prairie Conference. University of Wisconsin-Madison Press: Moorhead, MN. 264 pp.

Van Bruggen, T. 1983. Pp 65. Wildflowers, grasses, and other plants of the Northern Plains and Black Hills. Badlands Natural History Association, Interior, SD. 112 pp.

Wildeman, A.G. and T.A. Steeves. 1982. The morphology and growth cycle of *Anemone patens*. Canadian Journal of Botany 60:1126–1137.

WI DNR Bureau of Natural Heritage Conservation. 2021. Wisconsin Endangered and Threatened Species Laws and Lists. Wisconsin Department of Natural Resources PUBL-ER-001-2004. Madison, WI. 5 pp.