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BEE VISITORS OF SWEETVETCH, HEDYSARUM BOREALE BOREALE (LEGUMINOSAE), AND THEIR POLLEN-COLLECTING ACTIVITIES¹

Vincent J. Tepedino² and Mark Stackhouse³

ABSTRACT.—The native bee fauna visiting and pollinating a population of sweetvetch in Grand Teton National Park was surveyed. The papilionaceous flowers were exploited by 37 bee species, most of which had long mouthparts. Most species collected pollen as well as nectar. Bees foraged most heavily in early afternoon when poflen was most abundant. However, there was no indication that bee species were competing for limited pollen resources: there was no difference among three time periods in percent sweetvetch pollen carried in the scopal pollen loads of bees nor was there any evidence that some species were displacing the foraging times of others. The advantages of developing a native species as a commercial pollinator of sweetvetch are discussed and several potential candidates are mentioned.

Legumes are important components of rangeland ecosystems because of their ability to enrich the soil by fixing nitrogen and because of the nutritional content and palatability of some to livestock and wildlife. These characteristics have led to suggestions that productivity of rangelands can be increased by using mixtures of grasses and legumes rather than grasses alone (Cook 1983, Rumbaugh and Townsend 1985).

Among the many species of legume under study for potential inclusion in the managed rangeland community is sweetvetch, Hedysarum boreale Nutt., a perennial forb of holarctic distribution. Sweetvetch fixes nitrogen and is both nutritious and palatable to grazing animals (Rumbaugh and Townsend 1985). Two subspecies grow in North America: ssp. boreale in the western United States and southern British Columbia and Alberta; and ssp. mackenzii in northern Canada, the Yukon Territory, and Alaska (Northstrom and Welsh 1970). Subspecies *boreale* is likely to be most valuable as a rangeland plant because of its geographic distribution and habitat requirements.

Although sweetvetch is an excellent seed producer (Rumbaugh and Townsend 1985), seed for use in rangeland seedings and in revegetating disturbed sites is both costly and scarce. At present, seed is primarily collected from wild plants in natural habitats; commercial production has hardly begun. Indeed, aside from a study of ssp. *mackenzii* in the Yukon Territory (Kowalczyk 1973), there is little known of the reproductive biology and pollination ecology of sweetvetch. Kowalczyk (1973) reported that in ssp. mackenzii the pinkish to purple papilionaceous flowers were partially self-fertile but required visitation by insects, particularly bumblebees (Bombus), to set seed. The pollination ecology of ssp. boreale may differ because the flowers are smaller than those of ssp. mackenzii (Northstrom and Welsh 1970) and may be less attractive to long-tongued bumblebees.

This study describes the bee fauna visiting a natural population of *Hedysarum* boreale boreale in Grand Teton National Park, Wyoming. In particular, we report on the relative abundances of bee visitors at different times of day and their pollen-collection activities.

METHODS

We selected an undisturbed population of several hundred *Hedysarum boreale* boreale growing among Artemisia tridentata and other subshrubs on the rocky, south- and west-facing slopes of Spread Creek Hill, Teton Co., Wyoming, at about 2,200 m altitude. Systematic collections of bees were made on five days from late June to mid-July during the peak blooming period. To assure a representative temporal sample of flower visitors, two collectors were active during each of

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Т	Total no. bees captured			No. females captured Time period		
		*	1	2	3	No time
	ਰੇ ਹੇ	φç	N (P) % Pollen	N (P) % Pollen	N (P) % Pollen	recorded N (P) % Poller
Andrenidae						
Andrena spp.	1	2				2 (0)
Anthophoridae						
Nomada spp.	1	0				
Tetralonia frater (Cresson)	3	101	27 (18) 79.1	42 (33) 80.7	18 (16) 79.8	14(14)87.1
Apidae						
Apis mellifera Linnaeus	0	7				7 (0)
Bombus appositus Cresson	0	5				5 (0)
Bombus hifarius Cresson	0	11				11 (5)
Bombus fervidus (Fabricius)	0	- 3				3 (1)
Bombus flavifrons Cresson	0	19				19 (5)
Bombus griscocollis (Degeer)	0	7				$7^{-}(0)$
Bombus nevadensis Cresson	0	13				13 (0)
<i>Bombus occidentalis</i> Greene	0	2				2 (0)
Bombus rufocinctus Cresson	0	10				10 (4)
Bombus sylvicola Kirby	()	1				1 - (1)
Psithyrus insularis (Smith)	0	2				$2^{-}(0)$
Halictidae						
<i>Evylaeus</i> spp.	0	2				$2 \langle 0 \rangle$
Halictus spp.	1	0				
Megachilidae						
Callanthidium formosum (Cresso	n) 1	0				
Hoplitis albifrons (Kirby)	1	1				1 - (0)
Hoplitis producta (Cresson)	0	1				1 (0)
Megachile frigida Smith	3	7	0	6 (6) 76.4	1 - (0)	
Megachile gemula Cresson	5	15	2 (2) 76.9	8 (7) 73.7	2 (2) 90.6	3 (3) \$6.7
Megachile inermis Provancher	1	0				
Megachile melanophaea Smith	5	34	S (6) S7.1	15(11)86.3	10 (5) 88.3	1 (1) 89.6
Osmia albolateralis Cockerell	3	17	2(1)96.0	11 (11) 87.6	4 (4) 99.1	
<i>Osmia atrocyanea</i> Cockerell	0	-4	2 (2) 75.2	1 (1) 96.3	$1_{-}(1).67.0_{-}$	
Osmia bruneri Cockerell	0	5	2 (2) 29.3	3 (3) 89.5		
<i>Osmia bucephala</i> Cresson	0	21	3 (3) 65.9	12 (12) 73.8	5 (5) 81.6	1 (1) 90.3
Osmia cockerelli Sandhouse	1	0				
<i>Osmia grindeliae</i> Cockerell	2	9	2(2)98.2	5 (5) 96.4	$1_{-}(1) 99.7$	1(1)99.0
Osmia inermis (Zetterstedt)	0	3		1 (1) 98.3	$I_{-}(1)$ 98.0	1(1)98.3
Osmia longula Cresson	2	5		3 (3) 96.1	1(1) 90.0	1 (1) 94.0
<i>Osmia nifoata</i> Cockerell	1	1		1 (1) 42.6		
Osmia paradisica Sandhouse	0	10	5 (3) 72.5	3 (3) 69.5		2 (1) 79.0
Osmia pentstemonis Cockerell	0	-4	1 (1) 93.6	3 (1) 43.3		
<i>Osmia pusilla</i> Cresson	0	5	1 (1) 88.0	3 (1) 79.6		1 (1) 86.6
<i>Osmia tersula</i> Cockerell	0	2	1 (1) 60.3	1 (0)		
<i>Osmia tristella</i> Cockerell	0	1	1 (1) 1.0			
TOTALS	31	330	57 (43)	118 (99)	44 (36)	110 (40)
$-\frac{101AL3}{X}$	01	000	78.4%	84.0%	86.2%	110 (10)

TABLE 1. Total number of bees captured by species and number of females captured by time period (N). P-number of females carrying pollen; % pollen is the average percent sweetvetch pollen carried in the scopa.

three 80-minute time periods each day, once in the morning from 940 to 1100 hr, once in the afternoon, usually from 1440 to 1600 hr, and once in early evening between 1900 and 2200 hr.

Insects were netted while they foraged on the flowers. After insects were pinned and labeled, pollen slides were made from all solitary bees carrying pollen in their scopae. Pollen from each of the hind legs or venter (in the case of megachilids) was scraped onto a clean slide with an insect pin and stained as described by Beattie (1971). Except where noted, 300 grains from each slide were identified under 450X magnification by comparison with a pollen-reference collection. (For bumblebees, we mercly noted whether they were carrying pollen.)

RESULTS

Sweetvetch proved to be highly attractive

to bees, especially to those with long mouthparts. During 40 man-hours, we collected 37 species of bees, most in the family Megachilidae (21), in the genera *Osmia* (14) and *Megachile* (4) (Table 1). Bumblebees (*Bombus* and *Psithyrus*; Apidae) were also common (10 species). Most abundant was another species with long mouthparts, *Tetralonia frater* (Cresson) (Anthophoridae). Only 3 species (6 individuals) with short mouthparts, in the families Andrenidae and Halictidae, were collected.

The most abundant species captured were collectors of sweetvetch pollen, although a few (e.g., *Bombus griseocollis* (Degeer), *B. nevadensis* Cresson) seemed primarily collectors of nectar. Of 178 pollen samples examined (all from species in the families Anthophoridae and Megachilidae), 147 (82.6%) contained at least 75% sweetvetch pollen. Thus, individuals that foraged on sweetvetch were quite flower constant, at least within individual foraging trips.

The time of day that bees forage for floral rewards is influenced by such factors as ambient temperature, time of nectar and pollen production, and schedule of availability of flower rewards from competing species (Linsley 1978). For any given flower species, bee foraging is not usually spread evenly throughout the day but is restricted to the most rewarding times. In sweetvetch, as in many other legumes (Frankel and Galun 1977), the anthers of the diadelphous stamens dehisce simultaneously in the bud, and pollen is available at anthesis, usually in mid to late morning, after our first collection period. We used this schedule to make two predictions about bee foraging: (1) flower visitation is highest during the second collection period; and (2)because pollen in flowers should be gradually depleted over the course of a day, the percentage of sweetvetch pollen in the pollen loads of bees should be highest during the second collection period and lowest during the first collection period.

The data supported only the first of these hypotheses. Significantly more bees visited the flowers for nectar and/or pollen during the second collection periods ($X^2 = 40.2$, d.f. = 2, P < 0.001; Table 1). The distribution over time of bees collecting pollen followed the same pattern ($X^2 = 42.8$, d.f. = 2, P < 0.001).

There was no difference in the distributions between bees that were collecting pollen and those that were not ($X^2 = 1.8$, d.f. = 2, P > 0.25). These results held for all abundant bee species; there was no indication that any species specialized in foraging at a particular time or that time was a resource which bees were partitioning.

Our second prediction, that the percentage of sweetvetch pollen in the pollen loads would be highest during the second collection period, was not supported by the data; When all pollen-collecting bees were grouped, irrespective of species, there were no differences among time periods in the percentage of sweetvetch pollen in bee pollen loads (ANOV on arcsin transformed data: F = 1.89, d.f. = 2,175, P = 0.15). This result also held when the more abundant species were examined individually: for Tetralonia frater, the mean percentage of sweetvetch pollen ranged only from 78.7% to 80.1% across the three time periods. Results for other species such as Megachile gemula Cresson, M. melanophaea Smith, and Osmia bucephala Cresson were similar.

DISCUSSION

In Grand Teton National Park, sweetvetch flowers are very attractive to a variety of bee species with long mouthparts (Table 1). This is not surprising because the long, narrow, closed corolla tube of papilionaceous legume flowers makes their rewards, particularly nectar, unavailable to species with short mouthparts.

Our collections on ssp. boreale in the Tetons yielded a far more diverse bee fauna than that found by Kowalczyk (1973) on ssp. mackenzii in the Yukon Territory. In the Yukon, ssp. mackenzii was visited and pollinated almost exclusively by bumblebees. Indeed, the Osmia, Megachile, and Anthidium that Kowalczyk (1973) did find were so rare that he did not even bother to have them identified to species. While bumblebees were also abundant on sweetvetch flowers in the Tetons, other species with long mouthparts were more numerous. The most straightforward explanation for this difference is simply that bumblebees comprise an increasing proportion of the bee fauna with increasing latitude (Morse 1982). This transition is a result of April 1987

an increase in bumblebee numbers with latitude but rather to a gradual decline in the diversity and abundance of solitary species, presumably because of their inability to adapt to the harsh climate.

It is not farfetched to speculate that the decline, with increasing latitude, of solitary bee pollinators of sweetvetch has influenced the length of the corolla in ssp. mackenzii and may have played a role in its separation from ssp. boreale. Indeed, pollinators have been implicated as agents of speciation in many plant taxa (Levin 1971). We suggest that the longer corolla in ssp. mackenzii gradually evolved as an adaptation to the larger, and more abundant and reliable, bumblebee pollinators whose mouthparts are generally longer than those of solitary species. As the corolla lengthened over time, the flowers would gradually become less exploitable by solitary species until, eventually, only bumblebees could forage from them with consistent profit. There would be no such selective pressure on ssp. *boreale* because of the size, diversity, and reliability of nonbumblebee populations.

Should sweetvetch prove to be a desirable species for rangeland seedlings or revegetating disturbed areas, commercial seed-growing operations will be needed. Depending on the area and situation under which commercial operations are conducted, it may be necessary to provide a pollinating insect to obtain maximum seed production. If the area under cultivation is small and is adjacent to natural habitat, then it is probable that sweetvetch is sufficiently attractive to native bees to require no special provision for pollination. For example, a three-acre planting surrounded by rangeland in western Wyoming attracted numerous megachilid and apid species and produced copious seed. If plantings are larger or are located in cultivated areas where bees are scarce, it may be necessary, or desirable, to develop a solitary bee species that can be managed as a commercial pollinator. Pollination by solitary species would be especially appropriate for sweetvetch because plantings are likely to be relatively small and bloom lasts only about a month. Thus, a pollinator that has but one generation a year and flies for a short period of time (a few weeks) would be ideal. Small populations should also be readily obtainable, and the bee should be attracted to the plant. Obviously, several species listed in Table 1 possess these characteristics. Of these, some are particularly amenable to manipulation because they nest in existing holes in wood (Parker and Torchio 1980). Examples are *Megachile gemula* and *Osmia albolateralis* Cockerell, *O. bruneri* Cockerell and *O. bucephala*. Such species require minimal care and attention because they spend 10 to 11 months of each year as immatures in their nests. Any attempt to develop a solitary bee as a commercial pollinator for sweetvetch would do well to begin with one of these species.

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