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NECTAR FLOWER USE AND ELECTIVITY BY BUTTERFLIES IN SUB-ALPINE MEADOWS

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ABSTRACT. Nectar flowers are an important resource for most adult butterflies. Nectar flower electivity was evaluated for the pierid butterflies *Pontia occidentalis* (Reak.), *Colias nastes* Bdv., *Colias christina* Edw., *Colias meadii* Edw., *Colias philodice* Godt., and *Pieris rapae* (L.), and the nymphalid *Nymphalis milberti* (Godt.). Butterflies were observed in a series of sub-alpine meadows in Kananaskis Country, Alberta, Canada. A total of 214 observations of nectar feeding were made over four years. The butterflies were found to nectar on a range of species of flowering plants. Despite the variety of flower species used, there was relative consistency in use among butterfly species. Tufted fleabane (*Erigeron caespitosus* Nutt.) and false dandelion (*Agoseris glauca* (Pursh) Raf.) were the flowers most frequently elected by these butterflies.

Additional key words: Alpine, habitat quality, preference, Pieridae, Nymphalidae, host plants, Kananaskis Country, Alberta

INTRODUCTION

For most species of butterflies, nectar is the main source of food energy in the adult stage. Access to nectar resources can affect many aspects of the ecology of butterflies. For example, flowers have been shown to affect the movement of butterflies. Butterflies often disperse to areas or patches with an abundance of nectar flowers (Peterson 1997; Brommer & Fred 1999; Matter & Roland 2002). Similarly, butterflies may emigrate from areas low in nectar resources (Kuussaari *et al.* 1996), although emigration and immigration need not respond in kind, even to the same resource (Matter & Roland 2002). These changes in movement patterns can in turn affect local abundance and potentially population growth.

Nectar resources may also directly influence population growth. For species that continue oogenesis during the adult stage (Boggs 1997), lifetime fecundity can increase with the amount and quality of nectar (Murphy *et al.* 1983; Fischer & Fiedler 2001; Mevi-Schütz & Erhardt 2005). For species that do not continue to mature eggs as adults, nectar may have a positive effect on fecundity by increasing lifespan and decreasing egg resorption (Boggs & Ross 1993).

Despite the importance of nectar for butterfly ecology, nectar flower use by individual species is often poorly known, particularly in specific localities. Nectar flower use can vary by region and can depend on the availability of flowers and on relative nectar quality (Scott 1986). Nectar species use and, in particular electivity, is an important aspect of habitat quality. Use of a flower species only indicates that a butterfly may acquire resources from that species. On the other hand, electivity indicates that a species chooses or "elects" to feed on particular species in greater frequency than its availability. Thus, electivity may indicate that a nectar resource is particularly valuable having appropriate viscosity, sugar content, amino acids or other nutrients. Alternatively, an elected resource may simply be enticing without offering any substantial or consistent benefit. Here, we examine nectar flower use and electivity by several species of butterflies within sub-alpine meadows in the Rocky Mountains of Alberta, Canada.

MATERIALS AND METHODS

Study site. Nectar feeding observations and flower surveys were conducted during the summers of 2003 to 2006 in 17 meadows along Jumpingpound Ridge, Alberta, Canada (51°57'N, 114°54'W). The meadows are at tree-line (~2500 m) and are comprised of grasses, sedges, mountain avens, and many other species of wildflowers. The lower slopes of the meadows are bordered by forest consisting of *Pinus contorta* Dougl., *Abies lasiocarpa* (Hook.) Nutt., and *Picea engelmannii* Parry ex Engelm., which may be a barrier to the dispersal of some species (Ross *et al.* 2004).

Study species. The butterflies examined in this study all inhabit sub-alpine meadows and use the flowers occurring there as nectar sources. Each species depends on the meadows to a varying degree. For some species, both host plants and nectar flowers are only present within the meadows. Other species have host plants and nectar flowers occurring in the meadows and elsewhere. Some species only use these meadows for nectar flowers and hilltopping as their larval host plants occur in other habitats.

Nymphalis milberti – Eggs are normally laid on nettles (*Urtica* sp.) Nettles are not found in the meadows we studied. There are dubious reports of larvae on *Helianthus*, *Ulmus*, and *Salix* (Bird *et al.* 1995). A variety of flowers as well as rotting fruit and tree sap have been reported as adult energy sources in other areas (Austin & Austin 1980; Iftner *et al.* 1992; Reed 1997). This species uses the meadows primarily for nectaring; *Salix glauca* L. is found in the meadows and is a possible, but unlikely, host plant.

Colias christina – Fabaceae in the genera *Hedysarum*, *Lupinus*, and *Thermopsis* are reported host plants for this butterfly (Bird *et al.* 1995; Guppy & Shepard 2001). *Hedysarum sulphurescens* Rydb. is common in these meadows and is a likely host plant. To our knowledge, nectar flowers for this species have not been reported.

Colias philodice – Larvae use a variety of herbaceous Fabaceae, particularly *Trifolium* spp. and *Medicago sativa* L. as host plants (Scott 1986; Bird *et al.* 1995; Guppy & Shepard 2001). A range of flowers, mainly legumes and asters, has been reported as nectar sources (Shields 1972; Iftner *et al.* 1992). This species uses the meadows for nectaring and legumes occurring in the meadows likely are used as host plants.

Colias meadii elis – Larvae of *Colias meadii elis* feed on Fabaceae found in low alpine meadows and valleys in the Rocky Mountains of Alberta and British Columbia. Roland (1982) reports *Erigeron aureus* Greene and *Tonestus* (=*Haplopappus*) *lyallii* (A. Gray) A. Nelson as preferred nectar flowers at a near-by location. In Colorado, Watt *et al.* (1974) detail nectaring of *C. meadii* on several species in the Asteraceae. This species is a meadow resident using local plants for both larval and adult resources. At our site, oviposition on *Astragalus miser* has been recorded (B. Christian Schmidt, personal observation).

Colias nastes – *Astraglus alpinus* L., *Oxytropis campestris* (L.) Dc., and *O. splendens* Dougl. ex Hook. are reported as larval host plants (Bird *et al.* 1995; Guppy & Shepard 2001). Other Fabaceae are used in Europe and elsewhere (Scott 1986; Guppy & Shepard 2001). *A. alpinus* and *O. splendens* can be found in the meadows we studied. Wyatt (1957) describes nectaring on *Arnica alpina* (L.) Olin near Aklavik in the Northwest Territories and Roland (1982) indicates that *Erigeron aureus* and *Tonestus* (=*Haplopappus*) *lyallii* are preferred nectar flowers near our study site. This species is a meadow resident using plants within some meadows for both larval and adult resources.

Pieris rapae – Larvae of this species feed on many Brassicaceae, as well as on *Raphanus raphanistrum* L. and *Tropaeolum majus* L. (Scott 1986; Bird *et al.* 1995; Guppy & Shepard 2001). *P. rapae* prefer agricultural areas, especially those rich in Brassicaceae crops, particularly cabbage (Bird *et al.* 1995; Guppy & Shepard 2001), but can be found in many open habitats. A wide range of nectar flowers have been reported for this species (Iftner *et al.* 1992). It is likely that the meadows contain both local butterflies using mustards found within the meadows as well as immigrants from outside habitats using the abundant nectar flowers.

TABLE 1. Butterfly species and the number of times they were observed nectar feeding on different species of flowers. All observations were made in meadows along Jumpingpound Ridge during the summers of 2003–2006.

Flower	*Nymphalis milberti*	*Colias christina*	*C. meadii*	*C. nastes*	*C. philodice*	*Pieris rapae*	*Pontia occidentalis*
Achillia millifolium					2	2	20
Agoseris glauca			1	5	6	2	18
Arnica angustifolia					1		
Campanula uniflora				1	1	2	
Castilleja occidentalis							1
Delphinium bicolor						1	1
Epilobium angustifolium				1		1	4
Erigeron caespitosus		2	5	2	4	7	61
Erigeron peregrinus			1		5		3
Gaillardia aristata							3
Gentianella amarella					1		
Hedysarum sulpurescens					1		
Potentilla fruticosa				1	1	3	10
Potentilla gracilis				1			2
Rhinanthus minor							2
Sedum lanceolatum		1		1	1	2	2
Senecio canus	1						1
Senecio lugens							1
Solidago multiradiata	1	2	2	1	1	3	9

Pontia occidentalis – Brassicaceae are the primary larval host plants (Bird *et al.* 1995; Guppy & Shepard 2001). *Chrysothamnus nauseous* (Pallas) Britt. is reported as a nectar source (Opler 1995). At our site *P. occidentalis* is an eruptive species. In most years they are common but not abundant. In 2003 they were extremely numerous. These butterflies use the meadows for nectar flowers and hilltopping when abundant, but there is also likely an endemic fraction using mustards found in the meadows as larval host plants.

Nectar feeding and floral abundance. Observations of butterflies were conducted as part of an on-going mark-recapture study. This study primarily focuses on the spatial population dynamics and effects of rising tree-line for *Parnassius smintheus* Doubleday, but we also observe and conduct mark-capture for the butterflies listed above and a few other species. Results and effects of nectar flowers for *P. smintheus* will be presented in detail elsewhere. Meadows were censused for butterflies 3–5 times each year from 2003–2006. Censusing took place between July 15 and August 25 each year. As a part of normal observations, we recorded the species of flowers on which butterflies were observed. In most instances these are cases of nectar feeding, but occasionally butterflies may simply be alighting on flowers. Each captured butterfly was identified using a unique three-letter code on both hind wings with a permanent felt pen. This method ensured that we were using multiple individuals in our estimates of flower electivity. If the same butterfly was observed feeding within a short period of time, only the first observation was considered.

The abundance of flowers was estimated 1–2 times in each meadow, each year. We counted the number of flowers of all species within a varying number of 2 × 10 m, randomly placed transects. The number of transects per meadow varied to provide approximately proportional coverage. In 2003 and 2004 all flowers in bloom were quantified, while in other years we only quantified flowers used by *Parnassius smintheus* and the other butterflies.

Analyses. To examine nectar flower use we simply tallied the number of times that butterflies of each species were observed feeding on different species of flowers. To examine electivity in nectar flower use, we compared the observed number of feeding events to an expected number, based on the relative abundance of each flower species. The expected number assumed that nectar flowers should be used in proportion to their abundance if there is no electivity. Over-use in comparison to the expected indicates electivity while under-use would indicate repulsion. Statistical tests of observed versus expected nectaring events were based on a χ^2 distribution (Zar 1999). All tests were conducted within meadows and only when flower counts and feeding observations were made within seven days. We also limited analysis to cases where there were five or more independent observations of nectar feeding for each butterfly species and used a significance level of $\alpha = 0.01$, as cases where $N^2/k < 10$ may show bias. To examine finer-scale electivity, we restricted analyses to only those species of flowers on which feeding had been observed during the study. For an occasion where nectar feeding was observed on a species of flower that was not present in any flower survey, we added one

TABLE 2. Electivity among flowering species. A varying number of nectar feeding events (N) were observed for different species in different meadows on different dates. The first test (χ^2 and df on the left) was for electivity among all species in flower. The second test and the preferred species was for electivity only among flowers used (Table 1). Note that degrees of freedom can vary among meadows within dates due to differences in species use (see Methods). Significant values ($P < 0.01$) are shown in bold.

Species	Meadow	Date	N	χ^2	df	χ^2	df	Preferred species
Colias meadii	S	1 Aug. 2003	7	**77.8**	14	**10.9**	2	*Erigeron caespitosus*
C. nastes	Z	4 Aug. 2003	6	**54.9**	11	**22.7**	5	*Agoseris glauca*
C. philodice	L	6 Aug. 2003	6	**32.0**	5	**11.5**	2	*Agoseris glauca*
Pieris rapae	S	1 Aug. 2003	5	**91.0**	14	**51.7**	7	*Delphinium bicolor**
Pieris rapae	L	6 Aug. 2003	8	**35.0**	9	11.7	6	
Pontia occidentalis	S	1 Aug. 2003	60	**195.0**	19	**66.7**	12	*Erigeron caespitosus*
Pontia occidentalis	Z	4 Aug. 2003	10	**45.8**	11	7.6	5	
Pontia occidentalis	Y	3 Aug. 2003	5	**98.3**	10	**58.3**	6	*Agoseris glauca*
Pontia occidentalis	M	7 Aug. 2003	18	**3117.9**	16	**669.1**	10	*Erigeron caespitosus*
Pontia occidentalis	L	7 Aug. 2003	7	**35.1**	7	**24.1**	5	*Agoseris glauca*

**Delphinium bicolor* was not observed in the flower surveys in which nectar feeding was observed.

occurrence of this species to the flower abundance counts when calculating expected values.

RESULTS

Over the four years we observed 214 independent nectar feeding events on nineteen species of flowers (Table 1). *Erigeron caespitosus* had largest number of nectaring events, while *Solidago multiradiata* Ait. was used by the greatest number of butterfly species (Table 3). Only two feeding events for *Nymphalis milberti* and five for *Colias christina* were observed. Although there were small differences, overall nectar flower use by the five most frequently observed butterfly species did not differ significantly among the nineteen species of plants (G = 82.1, df = 72, P = 0.20).

Only in 2003 were there sufficient observations to meet our criteria for analysis of electivity. Among all species flowering within meadows, all butterflies showed electivity for nectar flowers (Table 2). When restricted to only those species of flowers on which each species had been observed feeding, there was still a high degree of electivity.

DISCUSSION

The butterflies investigated here nectar on a diversity of flowers, but as a group they showed similar patterns in their use and preference of nectar flowers. Tufted fleabane (*Erigeron caespitosus*) and False dandelion (*Agoseris glauca*) were preferred species in these subalpine meadows. Strong electivity in combination with the wide range of "usable" flowers suggests that nectar resources are not particularly limiting at this site, thus allowing butterflies to be discriminating in their selection of nectar flowers. The result also indicates that there are differences among nectar flowers in characters that are potentially important to the butterflies.

There are many reasons why certain nectar sources may be preferred, ranging from the accessibility and reliability of the source to the quality and quantity of the nectar (Heinrich and Raven 1972, Watt *et al.* 1974). That the butterflies investigated here showed similar electivity suggests that they are responding to the same characters of these flowers. It is interesting that butterflies restricted to these meadows and more generalist species selected similar flowers. Watt *et al.* (1974) found that flowers used by *Colias alexandra* and *C. meadii* in alpine meadows in Colorado shared similar ultraviolet reflectance patterns and generally had dilute nectar containing simple sugars. A comparison of the UV patterns and nectar chemistry of the flowers in the current system will be profitable.

It would be tempting to equate the presence and abundance of *E. caespitosus* and *A. glauca* with high quality meadow habitat for these butterflies. While it is true that butterflies prefer these flowers and their presence would increase habitat quality, they are not ubiquitous or highly abundant at our site (Table 3). Thus, they are a component of habitat quality for adults

TABLE 3. Nectar flower preferences by each butterfly species as determined by the number of feeding observations on each flower in proportion to the number of flowers of each species. Preferred flowers are in bold. Data shown were collected in 2003. The mean density for each flower species is over all meadows and surveys during 2003.

		Butterfly Species				
Flower Species	Density (mean #/20m^2)	*Colias meadii*	*Colias nastes*	*Colias philodice*	*Pieris rapae*	*Pontia occidentalis*
Erigeron caespitosus	11.2	9	2	4	7	61
Agoseris glauca	6.2	1	5	6	2	18
Solidago multiradiata	163.3	2	1	1	3	9
Potentilla fruticosa	20.1		1	1	3	10
Erigeron peregrinus	10.1	1		5		3
Sedum lanceolatum	15.3		1	1	2	2
Potentilla gracilis	114.3		1			2
Senecio lugens	0.5					1
Senecio canus	0.1					1
Arnica angustifolia	27.6			1		
*Delphinium bicolor**	55.7				1	

**Delphinium bicolor* was not observed in the meadow surveys in which nectar feeding was observed.

but not the sole contributor. Other less preferred flowers that are abundant such as alpine goldenrod (*Solidago multiradiata*) likely are necessary to provide sufficient nectar resources. It is also important to note that while nectar flower use was evaluated throughout the flight season and over several years, electivity could only be examined in 2003 between 1 and 7 August. There are phenological changes in the composition and abundance of nectar flowers. Species such as *Dryas* whose flowers are not usually present after late-July, may be important for the earlier emerging adults, such as *N. milberti.*

Nectar-feeding is an important aspect of butterfly ecology. We have shown what flowers are used and preferred by several species inhabiting sub-alpine meadows. It is our hope that further studies such as this will provide information essential for habitat assessment as well as insight into the evolution of nectar plant use.

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