



Links between floral morphology and floral visitors along an elevational gradient in a *Penstemon* hybrid zone

Sarah Kimball

S. Kimball (kimballs@email.arizona.edu), *Ecology and Evolutionary Biology*, 321 Steinhaus Hall, Univ. of California, Irvine, CA 92697, USA. Present address: *Ecology and Evolutionary Biology*, PO 210088, Univ. of Arizona, Tucson, AZ 85721, USA.

Hybrid zones can form when two species of plants hybridize along an environmental gradient. Changes in floral morphology across such a gradient and the degree of reproductive isolation can be influenced by pollinator behavior, but little is known about pollinator visitation to hybridizing species that receive visits from a diverse array of animals. I studied floral morphology, nectar rewards and pollinator visitation for *Penstemon newberryi*, *P. davidsonii* and their hybrids along an elevational gradient in the Sierra Nevada of California. Sixty-two floral visitor species were observed visiting plants, making this system highly generalized compared to previous studies of visitation in hybrid zones. Morphological measurements were used to construct a plant hybrid index and examine the correlation with elevation and with floral visitors. Using observations of floral visitors along the gradient, I performed an ordination to determine whether the pollinator community changed along with plant morphology. Plants varied in a clinal pattern along the elevational gradient. The visitor community varied incrementally with altitude, although visitors to *Penstemon davidsonii* were separated from those to *P. newberryi* and hybrids along the main ordination axis. Hummingbirds were only found at low and middle elevations, and small halictid bees were relatively more abundant at high elevations. Although there is some potential for ecological isolation in the pollinator community, 11 common pollinator species visited both parent species and could be contributing to hybrid formation.

Plant hybrid zones occur in regions where there has been a breakdown in reproductive isolating mechanisms that were formerly strong, or where the process of developing reproductive isolation was never complete. Pollinators can contribute to reproductive isolation and reduce the amount of hybridization in three ways. First, different sets of pollinators may preferentially visit different species (ethological isolation, Grant 1949). Second, pollinators may be more effective at transferring pollen within a species than between species due to floral morphology (mechanical isolation, Grant 1949). Third, when the parent species occupy different habitats, pollinators may prefer the habitat of one species (ecological isolation). Pollinator-mediated selection has been shown to help structure plant hybrid zones (Chase and Raven 1975, Arnold 1997, Campbell et al. 1997, 2002, Schemske and Bradshaw 1999, Chari and Wilson 2001, Ramsey et al. 2003), but all of the above cases involved a small set of pollinators. A much larger community of pollinators, which are potentially more generalized, visits some hybridizing plant species. The network links between communities of pollinators and plants in the absence of hybridization have received much recent attention (Memmott 1999, Olesen and Jordano 2002). However, the behavior of a large community of pollinators in plant hybrid zones has rarely been studied (Kephart and Theiss 2003), and it is not clear that the patterns of

reproductive isolation seen in cases with a few pollinator species would be followed in such a situation.

In principle, pollinator community composition can influence the evolution of floral characters. Depending on the system, flowers may specialize on one or a few pollinators, may generalize on a diverse array of pollinators, or, more frequently, may fall somewhere on the spectrum between specialization and generalization (Waser et al. 1996). Specialization can lead to distinct ‘pollination syndromes’, or suites of floral traits that reflect adaptations to a particular type of pollinator (Grant 1949, Fenster et al. 2004). For example, in the genus *Penstemon*, hummingbird-pollinated plants tend to have red tubular flowers with exerted stamens that produce large quantities of dilute nectar, while hymenopteran-pollinated plants tend to have blue flowers with wide corolla mouths and inserted stamens that produce smaller amounts of more concentrated nectar (Wilson et al. 2004). Natural selection can favor traits that attract efficient visitors whose morphology maximizes pollen removal and deposition (Stebbins 1970, Campbell and Waser 1996, Fulton and Hodges 1999, Castellanos et al. 2003), but it does not necessarily do so. Flowers that encounter a diverse array of floral visitors through space and time may be selected instead to generalize on several different pollinator species, and may even specialize on a less effective pollinator if that specialization entails little loss

in the fitness contribution of a more effective pollinator (Aigner 2001).

Pollinator community composition changes depending on geographic location, time of day and season. Different suites of pollinators may be found visiting the same plant species at different locations and times (Dilley et al. 2000, Moeller 2005, Price et al. 2005). Studies of visitation to the same plant at different geographic locations indicate shifts in pollinator community composition and diversity (Eckert 2002, Herrera 2005, Moeller 2005). Along an elevational gradient, pollinator community composition may be expected to change with the changing environment. Pollinator community studies conducted along elevational gradients indicate that pollinator species richness, visitation rate and connectance (the percentage of all possible interactions within a plant–pollinator food web) decrease with increasing altitude (Kalin Arroyo et al. 1982, Totland 2001, Olesen and Jordano 2002). Very few studies have investigated whether flower morphology changes along with pollinator community composition and elevation (Galen and Cuba 2001, Scobell and Scott 2002), and these studies did not focus on hybridization. However, selective pressures would be expected to change along with pollinator community composition through space, possibly leading to evolutionary changes in floral morphology and nectar reward.

To understand how pollinator community composition and floral morphology change with elevation in a plant hybrid zone, I measured floral morphology, nectar production and visitation by a large suite of potential pollinators on pure parental and hybrid populations of *Penstemon* along an elevational gradient. I addressed the following questions: (1) How does plant morphology change with increasing altitude? (2) How do floral visitors change with altitude? (3) Are those changes related? (4) What do the changes in plants and floral visitors tell us about the role of reproductive isolation imposed by pollinator visitation patterns? Unlike the few previous studies of elevational changes in both floral morphology and pollinators, this study examines a highly diverse group of pollinators of *Penstemon* species and their hybrids. Such a large group of potentially more generalized pollinators may be less likely to contribute to reproductive isolation.

Methods

Study system

My study system is a hybrid zone between two species of perennial wildflowers, *Penstemon newberryi* and *P. davidsonii*. *Penstemon newberryi* occurs in the montane zone of the Sierra Nevada. Its close relative, *P. davidsonii*, is found in the alpine zone of the Sierra Nevada and Cascade ranges. Hybrids are abundant at intermediate elevations, where the ranges of the two parent species overlap (Clausen et al. 1940, Chabot and Billings 1972, Datwyler and Wolfe 2004). Crosses between the species and natural hybrids produce as many seedlings as crosses within a species, indicating that there is no strong intrinsic reproductive isolation (Kimball 2007). Both species grow in rocky outcrops, and are locally abundant. I studied plant

morphology and animal visitation along an elevational transect in the eastern Sierra Nevada of California. The transect was along the Piute Pass trail above Bishop, from 2400 m to 3800 m elevation (37°14'22"N, 118°36'24"W to 37°14'44"N, 118°40'36"W).

Morphological measurements

During the summers of 2002 and 2003, I took measurements on 262 individuals along the study transect. Measurements were conducted on traits known to differ between the parent species, including number of leaf teeth, inflorescence height, floral tube length, short stamen length, floral circumference at the opening of the floral tube, leaf area and leaf perimeter. All plants located below 3025 m elevation were considered to be pure *P. newberryi*. Plants located above 3450 m elevation were considered to be pure *P. davidsonii*, and plants between those elevations to be hybrids. These elevational divisions correspond with the characters measured and also with flower color. To determine whether morphology varied depending on the type of plant measured (*P. davidsonii*, *P. newberryi* or hybrid), I performed a MANOVA with plant type as a fixed factor. I also performed a canonical discriminant analysis (CDA) on plants considered to be pure parents to develop a function based on morphological characters that best differentiates the two species. Next, I applied the function to all plants measured along the elevational transect to generate a hybrid index score for each individual. The index was then scaled between 0 and 1 by subtracting the minimum value and dividing by the range.

I compared morphological traits associated with pollination syndrome to determine whether the plant types have traits that are thought to be associated with separate suites of pollinators. Hummingbird-pollinated penstemons generally have exerted stamens and narrower corolla tubes, while bee-pollinated penstemons generally have inserted stamens and wider corollas (Wilson et al. 2004). Hummingbirds preferred plants with taller inflorescences in *Penstemon barbatus* and *P. pinifolius* (Lange et al. 2000), and birds, but not bees, favored taller inflorescences in *Lobelia* (Johnston 1991). Stamen exertion, floral circumference, and inflorescence height were analyzed by separate ANOVAs with plant type as a fixed factor. ANOVAs were supplemented with two planned comparisons: (1) *P. newberryi* versus *P. davidsonii*, and (2) the mid-parent value (mean of *P. newberryi* and *P. davidsonii*) versus natural hybrids. Plant type was assigned according to the elevation at which the plant was found using the previously mentioned elevational divisions.

Nectar

I measured the amount and sugar concentration of nectar produced by 1–6 flowers on 67 individuals from three locations along the elevational transect. The locations, at 3014, 3325 and 3659 m in altitude, were selected to represent pure parental and hybrid populations. I placed pollinator exclusion bags sewn from bridal veil over one to three inflorescences on 14–29 plants per location (depending on availability) with several unopened flowers. After

flowers inside the pollinator exclusion bags had opened and the anthers had dehisced (24–72 h later), the bags were removed. I used 3 and 5 μl microcapillary tubes to collect nectar from flowers. The length that the tube was filled with nectar was measured and converted to volume to determine the amount of nectar produced by each flower. The sugar concentration of the nectar was measured with a refractometer. The *P. newberryi* population was bagged on 25 and 26 June and measured on 26 and 28 June. The hybrid population was bagged on 9 July and measured on 10–11 July. The *P. davidsonii* population was bagged on 15 July, and measured on 17–18 July. These dates represented times when the populations were in full bloom. All measurements were conducted on dry and clear days.

To distinguish differences in nectar due to date in the season from differences due to plant type, I also measured nectar of potted plants grown in common conditions. Cuttings were taken from pure *P. newberryi*, pure *P. davidsonii*, and natural hybrids at low, middle and high elevations. The cuttings were rooted in water and then transplanted into 3.8 l pots with a 1:1 mixture of potting soil mix and pumice. Plants were grown outside at Univ. of California, Irvine, near sea level, for one year until they flowered in early April. For both the field data and the potted plant data, the average quantity and concentration of nectar produced by each plant were analyzed by separate ANOVAs with plant type (*P. newberryi*, *P. davidsonii* or natural hybrid) as a fixed factor. For the field data, I also performed linear regressions of nectar amount and concentration on the hybrid index score of the plant (calculated as described above).

Pollinator community

I observed floral visitors to both species and hybrids to see how the visitor community changed with elevation. Animals were considered to be floral visitors if they made physical contact with the flowers, either by entering or hovering above flowers. I conducted ninety 30-min censuses during the summers of 2002, 2003 and 2004. Censuses were made between 08:00 and 18:00 during June and July, when the plants were in bloom, on the largest flower patches available. An effort was made to collect data from a large elevational range each day and to begin each day collecting at a different elevation. During each census, I estimated the abundance of visitors using a 4 point scale where 0 = not present; 1 = one visitation bout on a few adjacent flowers; 2 = 2–5 visitation bouts; 3 = 6–15 bouts; and 4 = > 15 bouts in 30 min (methods from Wilson et al. 2004). At least one specimen of every insect visitor was collected for identification. I noted the orientation by which the visitor entered the flower (right-side-up, up-side-down, hovering over flowers, etc.) and the presence of any visible pollen on the visitor. I scored the amount of pollen on the body on a 3 point scale, where 1 = no visible pollen or only a few grains; 2 = some obviously visible pollen; and 3 = large amounts of pollen clearly visible. For each census, I recorded the date, time of day and weather. I later coded the weather on a three point scale where 0 = rainy or very windy; 1 = partly cloudy, breezy, or sunny and cool; and 2 = sunny and warm.

To indicate how the floral visitor censuses differed from one another, I used non-metric multi-dimensional scaling (NMDS) to ordinate all censuses based on dissimilarity in floral visitors. The dissimilarity measure used was Sorenson (Bray–Curtis) distance. The resulting ordination was rotated to maximally correlate elevation with axis 1. Correlations of the species with position in ordination space were calculated. Floral visitors were grouped into nine ‘functional groups’ according to their size and their method of visiting the flowers (Fenster et al. 2004). The abundance values for pollinators in each functional group were summed to calculate group abundance. The abundance values of all functional groups were then entered into the secondary matrix of the ordination to enable correlations of the abundance of functional groups with position in ordination space.

To determine whether the pollinator community was correlated with plant morphology, I grouped the censuses into seven elevational zones based on obvious geographic features such as lakes or steep, actively eroding slopes that provide unsuitable habitat, and calculated the average hybrid index score of plants in each zone. Next, I calculated the average abundance of each functional group in each elevational zone, and calculated the correlation of hybrid index score with functional group abundance. I also used the pollinator census data to calculate species richness (S), Shannon–Weaver diversity index (H) and evenness (E_H) for each elevational zone, and correlated S, H and E_H with hybrid index score of the plants.

Results

Morphological measurements

Morphological measurements indicated that the plants changed gradually along the elevational gradient in a clinal pattern (Fig. 1). Short stamen exertion decreased gradually with elevation such that plants at lower altitudes had exerted stamens while those at the highest elevations had included stamens. Floral circumference increased with elevation, and inflorescence height decreased with elevation (Fig. 1). The MANOVA indicated that morphology differed significantly depending on whether the plant was *Penstemon newberryi*, hybrid, or *P. davidsonii* (Wilks’ lambda = 0.143, $F_{14,418} = 49.079$, $p < 0.0001$). Floral circumference, inflorescence height, and short stamen exertion (calculated as floral tube length minus short stamen length) all differed significantly depending on the plant type ($F_{2,217} = 303.054$, 84.344 and 64.701 respectively, all $p < 0.0001$). The CDA separated the two parental species with a function with positive coefficients for number of leaf teeth (0.42), leaf area (1.88), and inflorescence height (0.01), and negative coefficients for floral tube length (–0.09), short stamen length (–0.02), floral circumference (–0.25), and leaf perimeter (–0.69).

The first planned comparison indicated that the two parent species had different stamen lengths, where *P. davidsonii* had included stamens, while the stamens of *P. newberryi* were exerted (Fig. 1, *davidsonii* vs *newberryi* $F_{1,217} = 160.349$, $p < 0.0001$). Hybrid stamen exertion was closer to *P. newberryi* values, and significantly differed

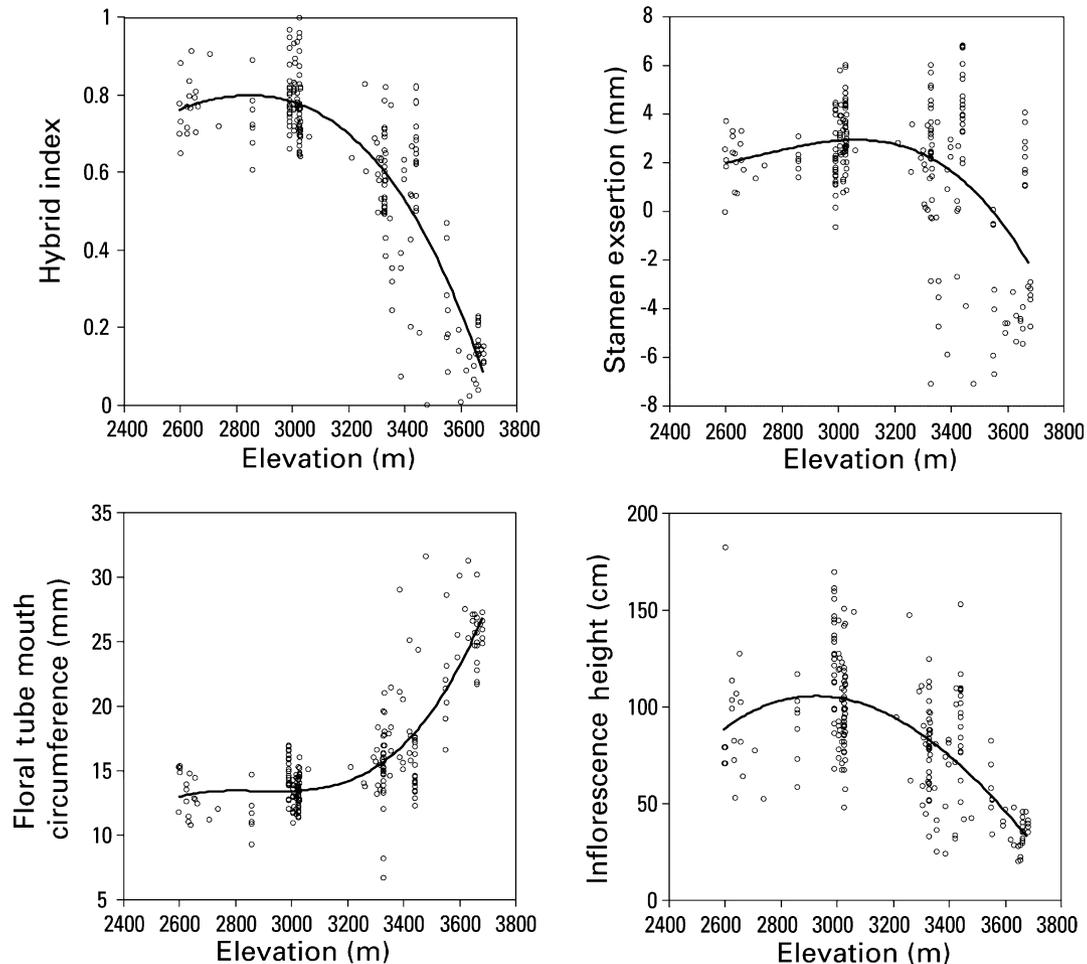


Figure 1. Morphological measurements of plants along an elevational gradient. Each circle represents an individual plant. The curves are third degree polynomials. Top left: hybrid index score calculated from a canonical discriminant analysis on seven morphological characters (number of leaf teeth, inflorescence height, floral tube length, short stamen length, floral circumference, leaf area, and leaf perimeter). Top right: stamen exertion calculated as the length of the short stamen minus the floral tube length. Bottom left: circumference of the floral tube mouth. Bottom right: average height of five inflorescences.

from the mid-parent value (hybrid vs parent $F_{1,217} = 55.639$, $p < 0.0001$). *Penstemon davidsonii* flowers had significantly wider mouths than *P. newberryi* flowers (*davidsonii* vs *newberryi* $F_{1,217} = 786.901$, $p < 0.0001$). Natural hybrids had values close to *P. newberryi* and different from the mid-parental mean (hybrid vs parent $F_{1,217} = 133.938$, $p < 0.0001$). Inflorescences of *P. newberryi* were significantly taller than those of *P. davidsonii* (*davidsonii* vs *newberryi* $F_{1,217} = 216.662$, $p < 0.0001$). Natural hybrids, once again, had values closer to *P. newberryi* (hybrid vs parent $F_{1,217} = 10.015$, $p = 0.002$).

Nectar

The amount of nectar produced by plants in the field differed markedly depending on the plant type (Fig. 2, $F_{2,66} = 22.878$, $p < 0.0001$). *Penstemon newberryi* produced more than three times as much nectar as *P. davidsonii*, while hybrids produced an amount similar to that of *P. davidsonii*. There was no difference in the sugar concentration of nectar produced by the different plant types (Fig. 2,

$F_{2,66} = 0.353$, $p = 0.704$). Nectar quantity increased with an increase in hybrid index value ($r = 0.457$, $p < 0.0001$), but there was no relationship between sugar concentration and hybrid index ($r = 0.065$, $p = 0.601$). In pots at UC Irvine, *P. newberryi* produced more nectar than *P. davidsonii* (Fig. 2, $F_{2,57} = 11.941$, $p < 0.0001$), just as they had in the field. Only in pots, however, did *P. newberryi* and hybrid plants produce nectar with higher sugar concentration than *P. davidsonii* ($F_{2,57} = 8.468$, $p = 0.001$).

Pollinator community

Sixty-two different species of animals were observed visiting *Penstemon newberryi*, *P. davidsonii*, and hybrids along the elevational transect, including hummingbirds, hawkmoths, megachilid bees, small halictid bees and dipterans. Some of the observed visitors are known to specialize on *Penstemon*, including *Pseudomasaris vespoides* (a wasp), and some bee species in the genus *Osmia* (Wilson et al. 2004). Ninety censuses were adequate for sampling the majority of visitor species. In a species-'area' curve generated by randomized

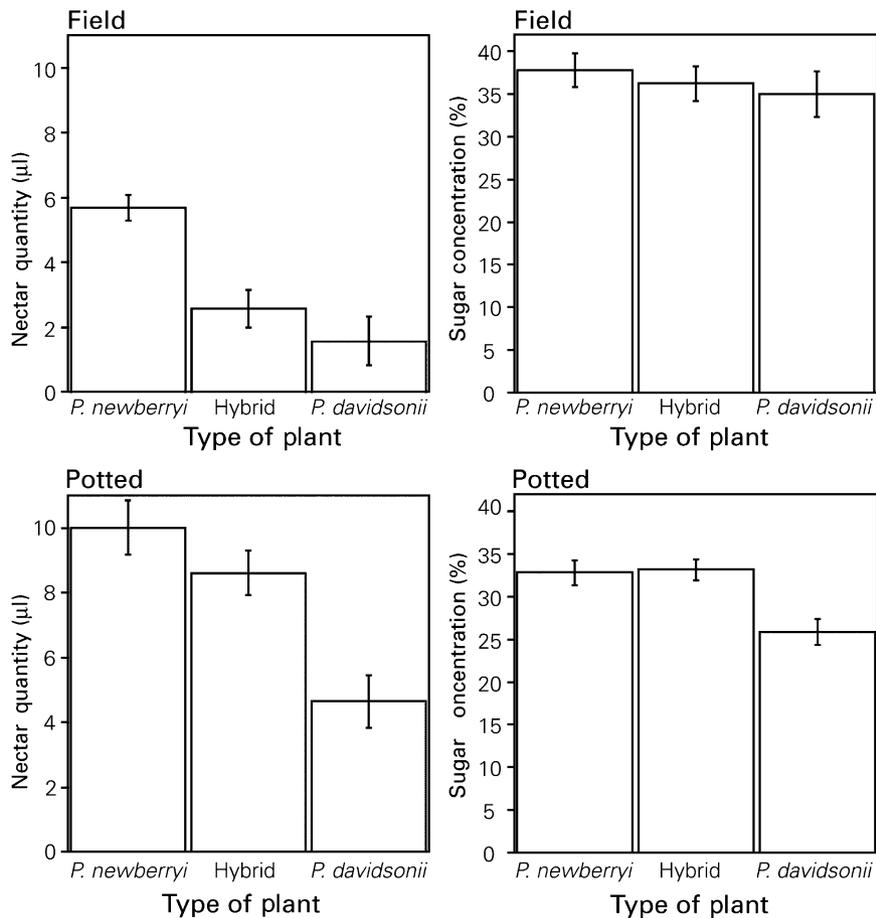


Figure 2. The amount and sugar concentration of nectar produced by *Penstemon newberryi*, *P. davidsonii*, and natural hybrids in the field (above) and in the greenhouse (below). Values are means \pm SE.

sub-sampling, the curve continued to increase only slightly, and half of the species were identified after only ten censuses. The abundance of floral visitors decreased with elevation (Fig. 3). Hummingbirds, nectar-collecting flies and *Pseudomasaris vespoidea* were all only found at low and intermediate elevations (Fig. 3).

The ordination of censuses uncovered little distinction between visitor censuses of *P. newberryi* and hybrid populations. In contrast, the *P. davidsonii* censuses (grouped to the right side of axis 1 of the ordination) were composed of a distinct community (Fig. 4). When censuses were coded according to weather, they were scattered evenly, indicating that weather was not an important factor in determining community composition. Date and time were also not well correlated with ordination space (Table 1). In contrast, elevation correlated well with the ordination ($r = 0.62$, $n = 90$, $p < 0.01$ uncorrected for multiple tests, Table 1). Examining the correlations of individual pollinator species with ordination axes (Appendix 1) reveals that hummingbirds were more abundant at lower elevations ($r = -0.627$ with axis 1 rotated to correspond with elevation). The individual species with the next highest correlation with axis 1 was *Bombus silvicola* ($r = 0.408$, $p < 0.01$), indicating that its abundance increased with elevation. Small bees in the family Halictidae were also more abundant at higher elevations (Table 1).

Species richness (S) and diversity (H) of visitors decreased with elevation over the seven elevational zones (S $r = -0.950$, $p = 0.004$; H $r = -0.936$, $p = 0.006$, Fig. 3). Evenness was not significantly correlated with elevation ($r = 0.271$, $p = 0.604$). Small halictids and bees in the genus *Bombus* increased in frequency with elevation (Halictidae $r = 0.877$, $p = 0.022$, *Bombus* $r = 0.850$, $p = 0.032$, Fig. 3). The changes in visitor community correlated with changes in plant morphology, such that *P. newberryi* and hybrid populations (with higher hybrid index scores) were visited by a diverse community that included hummingbirds, wasps and flies, while *P. davidsonii* populations were visited primarily by hymenopterans (correlations with hybrid index score = 0.972 and 0.987 for S and H respectively, $p < 0.001$, Fig. 3). Evenness was not significantly correlated with hybrid index score ($r = -0.240$, $p = 0.647$).

Hummingbirds, by far the most abundant visitor, were only observed visiting *P. newberryi* and hybrids. There were six other species found in 10 or more censuses that only visited *P. newberryi* and hybrids. Out of species found in 10 or more censuses, only two species, *Bombus silvicola* and *Hylaeus*, only visited *P. davidsonii* and hybrids. Eleven species of abundant visitors visited both parents and hybrids (Fig. 5). These 11 species have the potential to move pollen between the species and form hybrids.

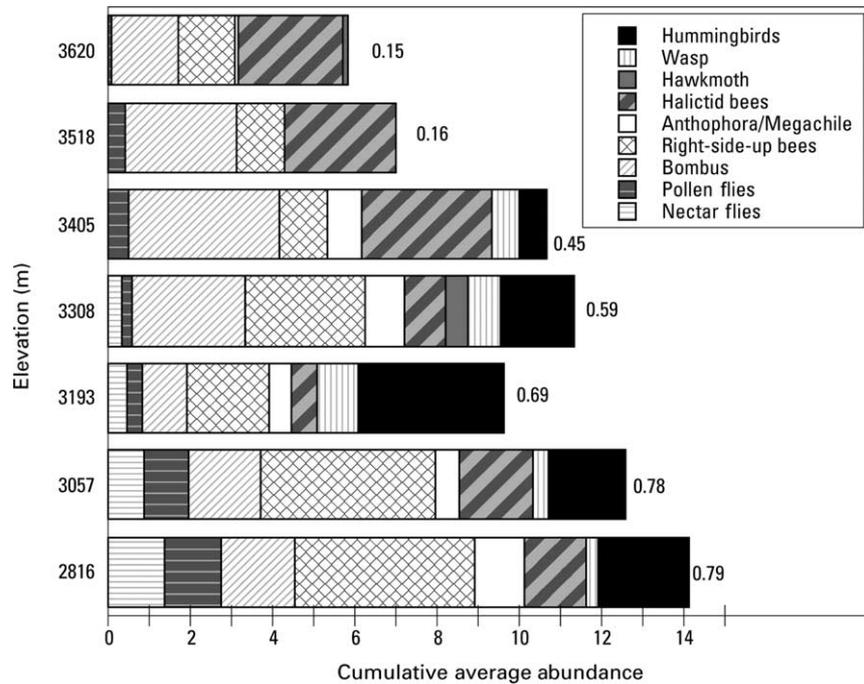


Figure 3. Summary of 90 visitor censuses. The censuses are divided into seven elevational groups and the 62 visitor species are grouped into nine different functional groups. The average abundance of each functional group is plotted cumulatively for each elevational group. The average hybrid index values for each elevational group are to the right of each bar.

Discussion

Previous studies on the role of pollinators in reproductive isolation in hybrid zones have focused on a small number of relatively specialized pollinators compared to those studied here (Chase and Raven 1975, Arnold 1997, Campbell et al. 1997, 2002, Schemske and Bradshaw 1999, Chari and

Wilson 2001, Ramsey et al. 2003). I observed 62 different floral visitors in this *Penstemon* hybrid zone, so it seems likely that these plants are more generalized. Generalization is fairly unusual in the genus *Penstemon*, where most species fit clearly into distinct pollination syndromes (Wilson et al. 2004). It may be this generalization that allows for frequent hybrid formation. When hybridizing taxa are visited by a diversity of animals, pollinator preference is more difficult to study, but is also less likely to play an important role in reproductive isolation.

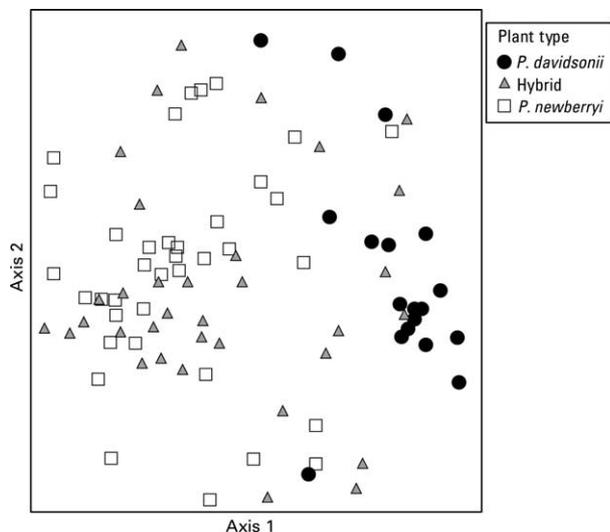


Figure 4. Ordination of censuses in visitor space. The census symbols are coded according to the type of plant (*Penstemon newberryi*, hybrid or *P. davidsonii*). The distance between the censuses is proportional to their dissimilarity. Note that the *P. davidsonii* censuses are grouped together on the right side of the ordination. The final stress for the ordination of all censuses was 30.57.

How does plant morphology change with increasing altitude?

Plants had morphological characters that more closely resembled *P. davidsonii* with an increase in elevation. The clinal pattern of gradual morphological change suggests that

Table 1. Correlations of the secondary matrix variables with ordination space.

	Axis 1 r	Axis 2 r
Date	0.319	-0.218
Time	0.185	0.185
Elevation	0.642	-0.011
Hummingbirds	-0.627	-0.443
<i>Pseudomasaris</i>	-0.306	0.095
Hawkmoths	-0.209	0.11
Halictid bees	0.413	0.075
<i>Anthophora</i> and <i>Megachile</i>	-0.074	-0.06
<i>Osmia</i>	-0.154	-0.001
<i>Bombus</i>	0.159	-0.118
Pollen-collecting flies	-0.034	0.097
Nectar-collecting flies	-0.292	-0.111

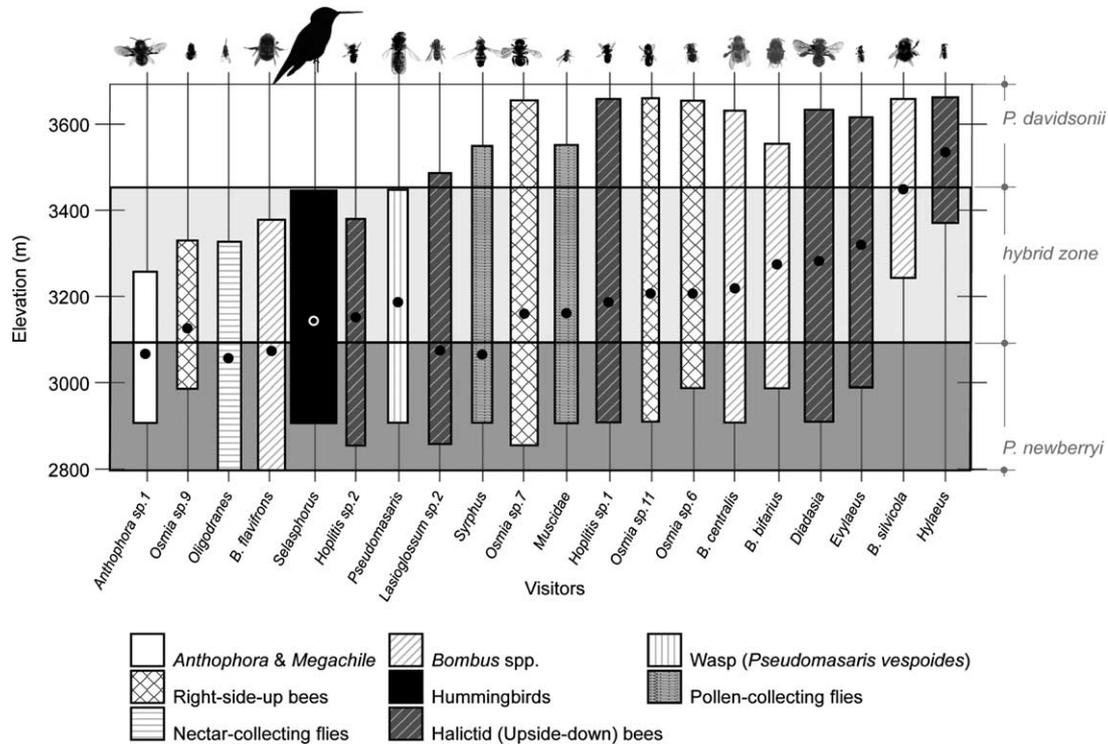


Figure 5. Elevational ranges for visitor species found in more than ten censuses. The thickness of each bar is proportional to the average abundance of each visitor. Black dots indicate the average elevation of censuses in which each visitor was found.

P. newberryi and *P. davidsonii* have hybridized beyond the F_1 generation (Endler 1973, Slatkin 1973, Fig. 1). The shape of a cline, in theory, depends on the distance of gene flow and the strength of selection (Endler 1973, Slatkin 1973, Barton and Gale 1993). Many of the hybrid individuals had morphological traits that more closely resembled *P. newberryi*, suggesting that: (1) there may be more gene flow between *P. newberryi* and hybrid populations, (2) the selectional pressures in the hybrid zone may be more similar to those at lower elevations, or (3) F_1 hybrids may more closely resemble *P. newberryi* due to dominance (Fig. 1).

Many of the morphological characters of *P. newberryi*, such as exerted stamens, narrow corolla tubes and tall inflorescences, are similar to other *Penstemon* species that are hummingbird-pollinated (Lange et al. 2000, Wilson et al. 2004). In contrast, the inserted stamens, wide corolla mouths and short inflorescences of *P. davidsonii* are similar to other bee-pollinated penstemons (Tepedino et al. 1999, Wilson et al. 2004). *Penstemon newberryi* produced more nectar than *P. davidsonii*, which is also consistent with hummingbird- vs bee-pollinated flowers (Grant and Grant 1968). Since the three plant types were measured on different days and nectar is highly variable depending on weather, it is also possible that the detected differences were due to day of the season (Leiss et al. 2004). However, *P. newberryi* also produced more nectar than *P. davidsonii* when measured in potted plants kept under common conditions. Hummingbird-pollinated flowers average 20–25% sucrose concentration, less than the average concentration for bee-pollinated flowers (Roberts 1995). Although *Penstemon newberryi* showed morphology similar to hummingbird-pollinated plants, it produced more concentrated

nectar with an average sucrose concentration of 37% in the field, close to *P. davidsonii* (Fig. 2). The high sucrose concentration combined with the pink corolla color suggests that *P. newberryi*, like its congener *P. pseudospectabilis*, may be adapted to both hummingbird and bee pollination (Lange and Scott 1999).

How do floral visitors change with altitude?

The visitor community in the montane and sub-alpine zones was fairly similar, but the alpine community contained fewer species and included some species that were not present in the montane zone (Fig. 3–5). It was not surprising that visitor species richness and diversity decreased with altitude, because other studies have documented a lack of pollinators in the alpine (Totland 2001, Fabbro and Korner 2004). In this case, the decrease in diversity with increasing elevation was due to the loss, or near loss, of hummingbirds, *Pseudomasaris vespoides*, nectar-collecting flies, pollen-collecting flies and anthophorine and megachilid bees (Fig. 3).

Hummingbirds were particularly important in the montane and sub-alpine zones, while the alpine visitor community consisted primarily of bees. Hummingbird flight at high altitudes is metabolically possible, but extremely demanding (Altshuler et al. 2004). Although some studies have documented an increase in hummingbird visitation from lowland to montane regions (Scobell and Scott 2002, Kay and Schemske 2003), a decrease in hummingbird visitation has been observed from montane to alpine regions (Campbell et al. 1997). Other studies in the Sierra Nevada, on *Mimulus* and *Aquilegia* hybrid zones,

also documented hummingbirds as important pollinators at mid-elevations but not at higher elevations (Fulton and Hodges 1999, Schemske and Bradshaw 1999).

Are the changes in plant morphology and visitor community related?

Correlations between hybrid index score and visitor abundance indicate that the changes in plant morphology and visitor community are related (Fig. 3). *Penstemon newberryi* had many morphological characters that fit bird-syndrome penstemons and was visited frequently by hummingbirds. However, nectar concentration and flower color of *P. newberryi* do not fit the bird-syndrome, and that species was indeed visited by a diverse community. Hybrid populations, with intermediate morphological characters, were visited by a diverse community consisting of birds, bees, flies, moths and *Pseudomasaris vespoides*. *Penstemon davidsonii* populations, with morphological characters typical of bee-syndrome penstemons, were visited by a less diverse community that consisted primarily of bees (Lange and Scott 1999, Wilson et al. 2004).

What do the changes in plants and floral visitors tell us about the role of reproductive isolation imposed by pollinator visitation patterns?

Differences in visitor community composition indicate possible barriers to gene flow. Such differences could be due to ethological isolation or ecological isolation, depending on whether visitors prefer to visit one species or whether they prefer the habitat of one species. An array experiment in which the two plant species are interspersed would be necessary to distinguish between these two types of isolation. The visitor censuses indicated greater similarity in the community visiting hybrids and *P. newberryi* than the community visiting *P. davidsonii*, raising the possibility of increased gene flow and similar pollinator-mediated selection for *P. newberryi* and hybrid populations (Fig. 3–5). Such asymmetrical gene flow through pollen has been described in other hybrid zones (Broyles 2002, Campbell et al. 2002, Buggs and Pannell 2006). When pollinators preferentially visit and transfer pollen between one species and hybrids, increasing gene flow in that direction, it can lead to an ‘advancing wave’ dynamic, where morphological traits of one parent are favored and spread through the hybrid zone (Campbell et al. 1997). Although I did not directly measure pollinator effectiveness, I did note the visitation frequency, the amount of pollen on visitors’ bodies, and the manner in which they visited the flowers (Appendix 2). Frequent visitors have often been shown to contribute more to plant reproduction than less frequent visitors, even if they are not as effective on a per-visit basis (Vasquez et al. 2005, Sahli and Conner 2006).

Hummingbirds, the most abundant visitor, were only observed visiting *P. newberryi* and hybrid populations, so they may limit hybrid formation at lower altitudes by not transferring pollen to or from *P. davidsonii* populations. It is unclear whether hummingbirds avoid *P. davidsonii* or whether they do not occur in the alpine habitat of *P. davidsonii*. Another visitor that may limit hybridization

through habitat or floral preference at lower altitudes is the wasp, *Pseudomasaris vespoides*. It was found visiting *P. newberryi* and hybrid populations only, specializes on *Penstemon*, and is known to be an effective pollinator of other *Penstemon* species (Torchio 1974, Tepedino et al. 1999).

The pollinator community included hummingbirds for *P. newberryi* and hybrids, but consisted primarily of bees for *P. davidsonii*. Small bees in the family Halictidae increased in frequency with altitude (Fig. 3, Table 1). These bees do transfer pollen in other *Penstemon* species (Lange et al. 2000), and their high frequency as well as the large amount of pollen observed on their bodies suggests that they are important pollinators in this system as well (Appendix 2). *Bombus silvicola* was abundant at high altitudes and had a large amount of pollen on its body, suggesting that it is likely to be an important pollinator (Fig. 5). Halictids and *B. silvicola* may limit hybridization at high altitudes by only visiting *P. davidsonii* populations.

Despite the presence of some visitors that may limit hybridization at elevational extremes, eleven abundant potential pollinators visited both species, potentially forming F₁ hybrids (Fig. 5). These included species in the genera *Bombus* and *Osmia*, both important *Penstemon* pollinators (Crosswhite and Crosswhite 1966, Tepedino et al. 1999, Castellanos et al. 2003). The degree to which floral visitors influence hybrid formation is ultimately determined by the frequency and effectiveness of interspecific visits within a visitor’s foraging bout (Campbell et al. 2002), which are as yet unknown. At this point, it is clear that reproductive isolation based on pollinator visitation (ethological and/or ecological isolation) is not complete. However, if the shared floral visitors make mostly conspecific visits when presented with arrays offering choice between species, these aspects of behavior could still contribute to reproductive isolation (Aldridge and Campbell 2007).

Other mechanisms that may maintain these species as distinct include post-pollination reproductive isolation through, for example, reductions in hybrid seed set or low hybrid fitness (Arnold 1997, Chari and Wilson 2001, Ramsey et al. 2003, Johansen-Morris and Latta 2006). However, in hand-pollination experiments, hybrid crosses did not result in few seeds or less viable seeds (Kimball 2007). Other possible reproductive isolating mechanisms include adaptations to distinct environments (McArthur et al. 1998, Schwarzbach et al. 2001, Campbell et al. 2005). *Penstemon newberryi* and *P. davidsonii* do have distinct physiological traits that are appropriate for the specific elevation at which they occur, so it is likely that such habitat specialization is partially responsible for maintaining the species as distinct entities (Kimball 2007).

In conclusion, pollinator differences may only partially explain the maintenance of *P. newberryi* and *P. davidsonii* at elevational extremes, because shared pollinators visit both species and hybrids. Plant morphology gradually changed in a clinal pattern from plants that had some, but not all, characteristics typical of ‘bird-syndrome’ penstemons at lower altitude to those that resembled ‘bee syndrome’ penstemons in the alpine. Floral visitors also changed gradually with altitude, from a diverse assemblage including many different functional groups such as birds, wasps, and different types of flies and bees to a less diverse assemblage

consisting primarily of bees. The floral morphology and visitor community of hybrids more closely resembled *P. newberryi* than *P. davidsonii*. Some important groups of pollinators, like hummingbirds, were only found visiting *P. newberryi* and hybrids, and *P. davidsonii* populations were visited by a somewhat distinct community. Thus, pollinator visitation can produce some degree of reproductive isolation in a hybrid system with a diverse and large community of pollinators, which has been shown previously for some more specialized systems. At the same time, there were eleven abundant visitors that have the potential to form hybrids. Future studies should investigate the floral preferences and effectiveness of conspecific and interspecific visits of these 11 visitors to determine their role in structuring this *Penstemon* hybrid zone.

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Appendix 1. Floral visitors, the functional group to which each visitor belongs, and their correlations with axes 1 and 2 of the ordination. Visitors are listed in order of their abundance. The functional groups are coded, where bird = hummingbirds, rube = right-side-up bees, psve = *Pseudomasaris vespoides* (wasp), udbe = upside-down bees in the Halictidae, bomb = *Bombus* spp., pofl = pollen-collecting flies, anme = bees in the genera *Anthophora* and *Megachile*, nefl = nectar-collecting flies, and hyl1 = *Hyles lineata* (hawkmoth).

Visitor	Functional group	Axis 1	Axis 2
Hummingbirds	bird	–0.627	–0.443
<i>Osmia</i> sp. 7	rube	–0.039	–0.701
<i>Pseudomasaris</i>	psve	–0.306	0.095
<i>Hoplitis</i> sp. 1	udbe	–0.168	0.016
<i>Oligodranes</i>	nefl	–0.327	–0.125
<i>Evyllaesus</i>	udbe	0.334	–0.089
<i>Osmia</i> sp. 11	rube	0.103	0.062
<i>Bombus bifarius</i>	bomb	0.138	–0.036
<i>Bombus silvicola</i>	bomb	0.408	–0.223
<i>Dialictus</i>	udbe	0.283	0.043
<i>Bombus centralis</i>	bomb	–0.124	–0.291
<i>Lasioglossum</i> spp. 2	udbe and rube	–0.1	–0.095
<i>Bombus flavifrons</i>	bomb	0.003	0.123
<i>Bombus</i> sp.	bomb	–0.162	0.074
<i>Hoplitis</i> sp. 2	rube	–0.124	0.068
<i>Hylaeus</i>	udbe	0.552	–0.164
<i>Syrphid</i> sp. 1	pofl	–0.134	–0.041
Apis-like <i>Anthophorine</i>	anme	–0.11	–0.007
<i>Osmia</i> sp. 6	rube	–0.169	0.024
<i>Osmia</i> sp. 9	rube	–0.014	–0.058
Muscoid fly	pofl	0.039	–0.042
<i>Anthophora terminalis</i>	anme	–0.03	–0.038
<i>Halictid</i> spp.	udbe	–0.212	0.402
Black and pearly <i>Anthophorine</i>	anme	0.031	–0.062
<i>Bombus vosnesenskii</i>	bomb	–0.03	–0.034
<i>Osmia</i> sp. 8	rube	–0.136	0.037
<i>Hoplitis albifrons</i>	rube	–0.016	0.057
<i>argentifrons</i>			
<i>Megachile</i> sp. 1	anme	–0.016	–0.027
<i>Platycheirus</i> sp.	pofl	–0.028	0.076
<i>Syrphid</i> sp. 2	pofl	–0.004	0.305
Hawkmoth	hyl1	–0.209	0.11
<i>Lasioglossum</i> sp. 1	udbe	0.178	0.046
<i>Osmia</i> spp.	rube	–0.155	0.335
<i>Osmia</i> sp. 10	rube	0.166	–0.158
<i>Bombylus</i>	nefl	–0.037	0.033
<i>Syrphus opinator</i>	pofl	0.03	0.151
<i>Diadasia</i>	anme	0.283	0.043
<i>Bombus nevadensis</i>	bomb	0.287	–0.007
<i>Osmia</i> sp. 3	rube	–0.043	–0.079
Black wasp	rube	–0.058	–0.034
<i>Anthidium</i>	anme	–0.092	–0.036
<i>Bombus vandykei</i>	bomb	0.036	0.103
<i>Syrphid pipiens</i>	pofl	0.089	–0.032
<i>Stelis</i> sp.	pofl	0.042	0.096
Beetle	pofl	0.044	0.027
<i>Anthophora terminalis</i> , black	anme	–0.022	–0.046
<i>Psithyrus insularis</i>	bomb	0.057	0.054
Coocoo wasp	rube	–0.029	0.196
<i>Osmia</i> sp. 1	rube	–0.032	0.014
<i>Osmia</i> sp. 2	rube	–0.089	–0.034
<i>Osmia</i> sp. 5	rube	–0.1	–0.095
<i>Osmia</i> sp. 12	rube	–0.015	–0.057
<i>Hoplitis fulgida platyura</i>	rube	–0.09	–0.024
<i>Hemipenthes</i>	nefl	–0.006	–0.062
<i>Eupeodes</i> sp.	pofl	–0.052	–0.116
Red fly	parasitoid	0.158	–0.025
Black bee	upbe	0.078	0.028
<i>Syrphus</i> sp.	pofl	–0.048	–0.023
<i>Sphecodes</i> sp.	upbe	0.007	0.065
<i>Hoplitis</i> sp. 3	rube	0.057	0.054
<i>Hoplitis</i> sp. 4	rube	–0.126	–0.018
<i>Syrphid</i> sp. 3	pofl	0.045	–0.181

Appendix 2. Floral visitors, the percentage of censuses in which a visitor was found, abundance, visitation, resource collected, pollen quantity on body, direction of visit and average elevation. Abundance is the average of the four-point abundance scale for the censuses in which visitors were found. Visitation is the proportion of censuses in which the visitor was found \times average abundance per census. The pollen or nectar column indicates whether the visitor was observed collecting nectar, pollen, or both. The next column indicates the amount of pollen observed on the visitors' bodies where 3 = high, 2 = medium, and 1 = low. Direction of visit indicates the orientation in which the visitor entered the flowers, where R = right-side-up, Up = up-side-down, H = hovering above the flower, and In = walking around inside the flower. Elevation is the average elevation of all censuses in which the visitor was observed.

Visitor	% censuses	Abundance	Visitation	Pollen or nectar	Pollen quantity	Direction of visit	Elevation
Hummingbirds	47.8	3.37	1.61	N	3	R	3144
<i>Osmia</i> sp. 7	32.2	2.00	0.64	BOTH	2	Usually R	3161
<i>Pseudomasaris</i>	31.1	1.46	0.46	N	2	R	3186
<i>Hoplitis</i> sp. 1	28.9	1.77	0.51	P	2	Up&R	3188
<i>Oligodranes</i>	27.8	1.72	0.48	N	1	In	3049
<i>Evylaeus</i>	26.7	1.71	0.46	P	3	Up	3326
<i>Osmia</i> sp. 11	26.7	1.25	0.33	BOTH	2	Usually R	3204
<i>Bombus bifarius</i>	23.3	1.81	0.42	BOTH	3	Up&R	3277
<i>Bombus silvicola</i>	22.2	1.90	0.42	BOTH	3	R&Up	3458
<i>Dialictus</i>	20.0	2.11	0.42	P	3	Up	3284
<i>Bombus centralis</i>	20.0	1.56	0.31	BOTH	3	R&Up&Robbing	3225
<i>Lasioglossum</i> spp. 2	18.9	1.65	0.31	N	3	Up&R	3075
<i>Bombus flavifrons</i>	18.9	2.00	0.38	BOTH	3	Up&R	3069
<i>Bombus</i> sp.	14.4	1.85	0.27	N	3	R	3224
<i>Hoplitis</i> sp. 2	14.4	1.38	0.20	P	2	Up	3142
<i>Hylaeus</i>	13.3	1.92	0.26	P	3	Up	3543
<i>Syrphid</i> sp. 1	13.3	1.50	0.20	P	1	H	3063
Apis-like <i>Anthophorine</i>	12.2	1.73	0.21	N	2	R	3063
<i>Osmia</i> sp. 6	11.1	1.70	0.19	BOTH	2	Usually R	3211
<i>Osmia</i> sp. 9	11.1	1.50	0.17	BOTH	2	Usually R	3124
Muscoid fly	11.1	1.70	0.19	P	1	R	3165
<i>Anthophora terminalis</i>	10.0	1.33	0.13	N	2	R	3322
<i>Halictid</i> spp.	8.9	2.75	0.24	P	3	Up	3112
Black and pearly <i>Anthophorine</i>	7.8	1.86	0.14	N	2	R	3130
<i>Bombus vosnesenskii</i>	7.8	1.29	0.10	BOTH	3	R&robbing	3156
<i>Osmia</i> sp. 8	7.8	1.14	0.09	BOTH	2	R	2961
<i>Hoplitis albifrons argentifrons</i>	7.8	1.43	0.11	N	2	R	3076
<i>Megachile</i> sp. 1	7.8	1.14	0.09	P	2	Up	3185
<i>Platycheirus</i> sp.	5.6	1.40	0.08	P	1	H	3050
<i>Syrphid</i> sp. 2	5.6	1.40	0.08	P	1	H	3019
Hawkmoth	4.4	3.25	0.14	N	1	H	3439
<i>Lasioglossum</i> sp. 1	4.4	1.50	0.07	P	3	Up	3430
<i>Osmia</i> spp.	4.4	1.75	0.08	BOTH	2	R	3092
<i>Osmia</i> sp. 10	4.4	1.50	0.07	BOTH	2	R	3471
<i>Bombylius</i>	4.4	1.25	0.06	N	1	H	3012
<i>Syrphus opinator</i>	4.4	1.00	0.04	P	1	H	3251
<i>Diadasia</i>	3.3	1.00	0.03	BOTH	2	R&robbing	3284
<i>Bombus nevadensis</i>	3.3	1.33	0.04	BOTH	3	R	3559
<i>Osmia</i> sp. 3	3.3	1.00	0.03	BOTH	2	R	2976
Black wasp	3.3	1.33	0.04	N	1	R	3101
<i>Anthidium</i>	2.2	1.00	0.02	BOTH	2	Up&R	3134
<i>Bombus vandykei</i>	2.2	1.50	0.03	BOTH	3	Up&R	3057
<i>Syritta pipiens</i>	2.2	1.00	0.02	P	1	H	2973
<i>Stelis</i> sp.	2.2	1.00	0.02	P	1	H	3309
Beetle	2.2	1.00	0.02	unknown	1	In	3243
<i>Anthophora terminalis</i> , black	1.1	1.00	0.01	N	2	R	3326
<i>Psithyrus insularis</i>	1.1	1.00	0.01	N	2	R	2988
Cocoon wasp	1.1	1.00	0.01	N	2	R	3026
<i>Osmia</i> sp. 1	1.1	1.00	0.01	BOTH	2	R	2988
<i>Osmia</i> sp. 2	1.1	1.00	0.01	BOTH	2	R	2907
<i>Osmia</i> sp. 5	1.1	1.00	0.01	BOTH	2	R	2988
<i>Osmia</i> sp. 12	1.1	1.00	0.01	BOTH	2	R	3309
<i>Hoplitis fulgida platyura</i>	1.1	1.00	0.01	BOTH	2	R	3026
<i>Hemipenthes</i>	1.1	2.00	0.02	N	1	H	2908
<i>Eupeodes</i> sp.	1.1	1.00	0.01	P	1	H	3306
Red fly	1.1	1.00	0.01	neither	1	H	3484
Black bee	1.1	1.00	0.01	P	1	Up	3486
<i>Syrphus</i> sp.	1.1	1.00	0.01	P	1	H	3087
<i>Sphecodes</i> sp.	1.1	1.00	0.01	P	1	H	3045
<i>Hoplitis</i> sp. 3	1.1	2.00	0.02	BOTH	2	R	2988
<i>Hoplitis</i> sp. 4	1.1	1.00	0.01	BOTH	2	R	3026
<i>Syrphid</i> sp. 3	1.1	1.00	0.01	P	1	H	2858