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A multivariate search for pollination syndromes among penstemons

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The seeming ubiquity of spatio-temporal variation in pollination regime suggests that flowers ought to be adapted to a wide range of pollinators, yet many comparative biologists perceive that in groups with complex flowers there is considerable specialization onto pollination syndromes. Statistical documentation of such syndromes has been presented for very few groups of flowers. Accordingly, we measured, for 49 species of *Penstemon* and close relatives, both the morphology of the flowers and visitation by pollinators. We describe the mechanics of pollination for representative species. Ordinations show a distinct difference between hummingbird-pollinated species and hymenopteran-pollinated species. Flower color is particularly good at separating hummingbird- from hymenopteran-flowers. Other characters are also correlated with this dichotomy. Within the hymenopteran-pollinated species, there are additional relationships between floral morphology and the size of the principal pollinators. Flowers frequented by large bees, such as *Xylocopa*, have large open vestibules and relatively short floral tubes. Flowers frequented by smaller bees, such as *Osmia*, have long narrow floral tubes. Unlike nectar-collecting bees, pollen-collecting bees tend to be attracted to flowers of the hummingbird syndrome. The overarching pattern was that syndrome characterizations were successful at predicting pollination by hummingbirds versus Hymenoptera, two types of animals that are profoundly different, but less successful at predicting visitation by one kind of bee versus another.

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Pollination syndromes are often the starting point for students learning about the functional diversity of flowers (Buchmann and Nabhan 1996, Proctor et al. 1996, Raven et al. 1999). For instance, it is said that hummingbird-pollinated flowers tend to be red, to have narrow tubes, to be inclined, to lack landing platforms, and to have large quantities of dilute nectar, whereas bee-pollinated flowers are said to be blue or yellow, to have vestibules into which the animals can crawl, to be held rigidly horizontal or upright, to provide landing platforms, and to offer concentrated nectar. Such characterizations can involve long lists of features (Fægri and van der Pijl 1979, Wyatt 1983, Pellmyr 2002). Students are usually taught a series of syndromes, and then cautioned not to take them too literally: there is a great deal of overlap among them (Ollerton and Watts 2000); the morphological "solutions" that have evolved in plants are only roughly convergent, with various structures co-opted in various ways (Stebbins 1974, Ollerton 1998); and other animals can be found pollinating flowers besides the ones implicated by the syndrome (Waser et al. 1996). One must remember as many caveats as rules. We have discussed these logical caveats elsewhere (Thomson et al. 2000, Armbruster et

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al. 2000, Fenster et al. in press). Here, we provide an empirical exercise, searching for syndrome patterns in the morphology of flowers and the visitation activity of pollinators.

Surrounding the topic of pollination syndromes, there is a seeming paradox between the perspectives of evolutionary ecology and of comparative biology (Herrera 1996, Ollerton 1996). The data of evolutionary ecology seem to reveal great variation in pollinator assemblage among sites and from year to year (C. Herrera 1988, J. Herrera 1988, Eckhart 1992, McCall and Primack 1992, Fishbein and Venable 1996, Campbell et al. 1997). This suggests that plants encounter fluctuating selection regimes. For a time, flowers are selected to work well with one kind of pollinator, but before a response to that selection can be fully realized, another pollinator gains prominence, and the plants face different selection pressures (Wilson and Thomson 1996, Dilley et al. 2000). By this view, there should be pervasive forces against adaptations that exclude some pollinators over others, and there is an expectation that a large proportion of plant species ought to be generalists (Waser et al. 1996, Aigner 2001). Moreover, many flowers are expected to be visited and even pollinated by animals other than the ones that evolutionarily shaped them (Lamborn and Ollerton 2000).

In contrast, the descriptions of comparative biology focus on the results of evolution rather than extrapolating up from day-to-day processes. Comparative biologists see striking patterns of convergent evolution and the maintenance of adaptive zones in which multiple floral traits are associated with particular classes of pollinators (Stebbins 1974, Brown and Kodric-Brown 1979, Armbruster 1990, Dafni et al. 1990, Johnson et al. 1998, Bernhardt 2000, Goldblatt and Manning 2000). Admittedly, the majority of animal-pollinated flowers fall into a generalized entomophilous "syndrome" involving many bees, flies, beetles, and Lepidoptera (Hingston and McQuillan 2000). Still, if one considers only the remaining minority of complex flowers, syndrome characterizations seem highly explanatory (Fulton and Hodges 1999, Johnson and Steiner 2000). In other words, for those groups of plants that have the capacity for floral specialization because of such features as recessed nectaries, unusual reward systems, and restrictive perianths, the comparative biologist contends that syndromes summarize modes of pollination (Goldblatt et al. 2001, Fenster et al. in press). To date, however, the comparative biology of pollination syndromes has been almost entirely anecdotal. Hundreds of angiosperm species have been described with reference to how their features match the classical characterizations (Armstrong 1979, Rebelo et al. 1985, Bernardello et al. 2001). This body of information is systematic in the sense of attempting to be thorough and in that it is implicitly thought of as being comparative. However, there have been very few numerical analyses that have described correlations between floral characters and pollinator types among many related plant species of multiple supposed syndromes (Sakai et al. 1999 for a study like ours; Borba et al. 2002 with reference to Borba and Semir 2001 for five species of orchids pollinated by three kinds of flies). Here, we use multivariate methods to address correlations between floral characters and visitation by pollinators of various types.

We do this for a group of flowers we refer to as "penstemons," by which we mean to include *Keckiella* and *Nothochelone* as well as members of the genus *Penstemon* s.s. (technically members of the monophyletic Cheloneae of the Scrophulariaceae; Wolfe et al. 2002). There are about 284 such "penstemon" species. They have flowers that are bilaterally symmetrical, with anthers and stigma positioned for pollination via the backs and upper heads of pollinators. Nectar is produced near the base of a tubular corolla, and is accessed through two shafts that are separated by a staminode (Castellanos et al. 2002). In hymenopteran-pollinated species, the staminode aids in the mechanics of pollination in various ways, levering the anthers down onto the bee's back, forcing the bee to probe repeatedly, and pressing small-bodied bees against the anthers and stigmas (Walker-Larson and Harder 2001, Dieringer and Cabrera 2002). In hummingbird-pollinated species, the staminode is thought to be vestigial (Walker-Larson and Harder 2001).

We will treat the animals that visit penstemon flowers in terms of "functional groups" (Armbruster et al. 2000, Fenster et al. in press). On the one hand, we lump together similar species that we think interact with the flowers all in a similar manner. For instance, there are dozens of species of *Osmia* bees that visit penstemons (Crosswhite and Crosswhite 1966). They are very nearly the same size and behave in the same way as one another. Since it seems unlikely that they differ much in how they affect selection on floral traits, we pool them together as a way of bolstering statistical power. On the other hand, we distinguish animals that manipulate the flowers differently even when they belong to the same species. For example, most individual bumblebees visit flowers right-side-up, probing for nectar and removing pollen only by incidental contact with the anthers, but a few individuals turn up-side-down and actively extract pollen from the anthers, frequently ignoring the nectaries (Thomson and Chittka 2001). We consider these two types of visitors as belonging to different functional groups. Ideally, one would categorize visitors based on rigorous counts of pollen removal from anthers and deposition on stigmas (Wilson and Thomson 1991, Thomson and Thomson 1992). For penstemon visitors, careful counts have been done for only a few species. Castellanos et al. (in press) found that hummingbirds and nectaring bumblebees remove and deposit similar amounts of pollen in *P. strictus*, whereas pollen-collecting bumblebees remove far more pollen than either nectaring bees or birds. Dieringer and Cabrera (2002) found that *Osmia* and similarly sized bees remove and deposit a great deal of pollen, medium-sized *Anthophora terminalis* remove pollen well but deposit it poorly, and *Bombus* and similarly sized bees remove little but deposit effectively. In the absence of quantitative effectiveness data on pollinators visiting many penstemons, our functional groupings are based on the mode of contact with anthers and stigmas (Armbruster 1988). Such characterizations should be viewed as working hypotheses.

We address the following questions; 1. After floral-syndrome features are reduced from many characters to a few synthetic axes of variation, are the synthetic axes correlated with visitation by particular groups of animals? 2. To what degree are bird-flowers phenotypically distinct from hymenopteran-flowers among penstemons? 3. Are there any correlations between floral characters and visitor types within the hymenopteran-pollination syndrome? 4. For each type of animal, which floral characters are best at predicting visitation? 5. Do hymenopteran pollen collectors follow the same syndrome rules as nectar collectors?

Data

Penstemons were studied at numerous sites in the western United States and Mexico from 1997 to 2001. For each species encountered, we measured floral morphology and recorded pollinator attendance at the flowers.

Floral characters

In the field, we measured five flowers on each penstemon species for the inclination of the tube from the horizontal (I), the distance from the lowest point on the anthers to the floor of the corolla (A), the exsertion or inclusion of the anthers from the corners of the mouth to the most distal point (E), the length of the floral tube to the corners of the corolla mouth (T), the length of the staminode divided by the length of the corolla tube (S), and the circumference (width) of the corolla at its mouth (W). We also preserved flowers in FAA for further measurements, and we pressed specimens that have been deposited at the herbarium of California State University Northridge (SFV). From the preserved flowers, one observer scored additional "subjective" characters, including corolla morphotype (vestibular, tubular, etc.), the degree (coded on a 4-point scale) to which the lower lip was held out as a landing platform or reflexed away from the mouth (R, "lower lip reflexion"), and the degree (on a 4-point scale) to which the anthers and stigmas were exserted, taking into account the position of the rear anthers and the lower lip as well as the corners of the mouth (X, "functional exsertion"). Finally, the color (C) of fresh flowers to the human eye was coded from 1 to 4, with 1 representing the extreme end of the hymenopteran-pollination syndrome (either yellow or blue-violet), 4 representing the most extreme orange and scarlet of the hummingbird-pollination syndrome, and intermediate values representing intermediate colors. Appendix 1 gives the medians of the floral characters of the 49 species for which we will present visitor data.

Visitor censuses

Diurnal flower visitors were observed during 30-min censuses in which we noted the various species of visitors, if and where they got pollen on their bodies, and whether they were turning up-side-down to primarily collect pollen or were primarily collecting nectar. We favored doing censuses at large patches of flowers when available, often watching hundreds of flowers at a time. We collected representatives of each species of insect visitor and identified them to the lowest taxonomic level feasible. These identifications do not enter into our statistical analyses, which are based on functional groups. The specimens have been deposited in the insect collection at California State University Northridge. Hummingbird identification was done without capturing the animals, and was generally certain only for mature males. During each visitor census, abundance of each kind of visitor was classified on a 0 to 4 point scale, with 0 being not present, 1 point being a single bout of visitation on a few adjacent flowers, 2 being from two to five such bouts, 3 being from 6 to 15 bouts generally with several visitors, and 4 points being more than 15 bouts in 30 minutes. Although crude, these categories were expedient and seemed to capture much of the variation in visitation rates.

We did 284 such 30-min visitor censuses in which we observed at least one visit. For some but certainly not most of the species, censuses were done throughout the flowering season, in various years, and in various geographic locales. Here we report on the species for which we have more than 5 points of visitation data. For instance, we would include a plant species for which we had two censuses both with vigorous hummingbird visits $(3+3)$. Similarly, we would include a species for which we had one census if there were multiple visits by each of three groups of insects $(2+2+2)$. Our goal was to summarize the visitors at each species of plant. We have different numbers of censuses for the various penstemons. Even if the number of censuses were uniform, the number of visitors that were observed varied from one census to the next. Our sample size, therefore, is not the number of censuses but the number of visitation points accrued over all censuses. For instance, *Keckiella cordifolia* was censused four times. On three of the censuses we observed abundant hummingbird visits (3 points each), and on one census we also observed one small pollen-collecting bee (1 point). Thus, for *K. cordifolia*, we accrued 10 visitation points. In most analyses, we express the 9 points of hummingbird visitation as a proportion of the 10 points of observation, so in this example, we would rate hummingbirds at 0.9. These relative visitor abundances are summarized for the 49 species in Appendix 2.

Descriptions of visitors and flowers

Visitors, provisionally grouped by effects on flowers

Hummingbirds (HB) of various species visit certain penstemons. In some cases, pollen visibly accumulates on the beak or forehead while the birds are drinking nectar. At other penstemons, such as those with narrowly dehiscent anthers (Thomson et al. 2000), patches of pollen are less apparent on the birds, but judging from our studies with *P. strictus*, considerable pollen may nevertheless be transferred (Castellanos et al. in press). Vestibular flowers do not force the bird to push its head against the anthers. Some pollen probably gets on the beak, but contact between the anther or stigma and the bird does not appear to be ensured when the flowers are large and vestibular.

Pseudomasaris vespoides (PV) is a wasp that acts like a bee. When we refer to "hymenopteran-pollination" we could more casually say "bee-pollination", but we mean to include *Pseudomasaris*. *Pseudomasaris vespoides* is a specialist on penstemons, and a common pollinator of many of them. It sucks nectar and gets pollen on the back of its thorax and on its wings. The girth of a *P. vespoides* is about that of a honeybee, though they are much longer. The tempo of foraging is different for males and females (Longair 1987). Females more actively work a patch of flowers than the slower males. Also, females may move in and out of a flower several times, thereby rubbing against the anthers to gather pollen. Pollen is groomed from the back and ingested with nectar to be eventually regurgitated and used to provision egg cells (Gess 1996).

Osmia bees (OS) of many species are more or less specialized on penstemon, and many penstemons seem to receive the majority of their flower visits from these bees (Crosswhite and Crosswhite 1966). The most common are metallic blue-green and green species that are about half the thoracic diameter of a honeybee. They are very important pollen carriers that forage primarily for nectar but get pollen on their backs, sometimes by active rubbing against the anthers (Lawson et al. 1989, Tepedino et al. 1999). Every few dozen flowers, they fastidiously groom, often while standing on the ground. We presume this is responsible for considerable pollen wastage from the plants' perspective. Some individuals can be seen carrying pollen in the scopa on the ventral side of the abdomen. Not included in this functional group were those few *Osmia* that actively collect pollen, which we treat as "small pollen collecting bees."

Anthophora and similar-sized nectar-collecting bees (AN), such as *Melissodes*, *Centris*, and *Diadasia*, we pool together. These are all quick hairy bees that are as big as a honeybee or slightly larger. Mostly these bees do not actively accumulate pollen, but they almost always come into firm contact with the anthers or stigma and carry pollen on their backs. Some of them may groom it into their scopae, which they generally do while flying. Included in this group is *Anthophora terminalis*, a species that we have seen in great abundance on *Penstemon strictus*. When visiting *Penstemon digitalis*, *A. terminalis* wastes more pollen than *Osmia* (Dieringer and Cabrera 2002).

Xylocopa carpenter bees (XY) are common nectar feeders on certain species of penstemons, such as *Penstemon grinnellii* and *Keckiella breviflora*. The most frequent *Xylocopa* we observed was *X. tabaniformis orpifex*, which is the size of a large bumblebee worker. We also occasionally observed visits by the larger *X. californica*. We did not count visits by *Xylocopa* when they were robbing nectar from the outside of the corolla. When they legitimately visit the flowers, they get abundant pollen on their backs. They do not accumulate penstemon pollen in their scopae, which are on their legs.

Nectar-collecting *Bombus* (BN) is a category from which we exclude those individual bumblebees who turned up-side-down and grasp the anthers. Nectaring *Bombus* generally get pollen on their bodies, and often groom it into their corbiculae, which are on their hind legs.

Pollen-collecting *Bombus* (BP) were individuals that turned up-side-down and actively collected pollen. *Bombus* species varied in the proportions of individuals that were collecting nectar versus pollen. In Colorado populations of *P. strictus*, for example, *B. flavifrons* seldom collected pollen, while *B. bifarius* often did. We have always found pollen collectors to be the minority of bumblebees foraging in a patch.

Pollen-collecting *Lasioglossum* (LA) are relatively large sweat bees, such as *L.* (*L.*) *sisymbrii* and *L. (L.) mellipes*, about the size of a medium-sized *Osmia*. They typically turn up-side-down to manipulate the anthers with their mouthparts and legs. They accumulate pollen in the scopae on their legs.

Small pollen-collecting bees (PC) comprise a taxonomically diverse set of small sweat bees, such as *Halictus*, and small megachilids, such as *Hoplitis* (e.g. *H. producta*), *Chelostoma* (e.g. *C. cockerelli*), *Ashmeadiella* (e.g. *A. australis*), and *Protosmia* (e.g. *P. rubifloris*) that actively manipulate anthers.

Eulonchus and *Bombylius* (EU) are large long-tongued flies that probably remove relatively small amounts of pollen when compared to an *Osmia*, but they might deliver a high proportion of that pollen. They are vigorous foragers that contact anthers and stigmas, and they do not seem to groom off pollen.

Oligodranes (OD) is a smaller long-tongued bombyliid fly that rests inside of some penstemon flowers. It is not a particularly common visitor, but we separate it from other long-tongued flies because its size makes it less likely to contact anthers for many penstemons.

Small nectaring bees (SB) is a category for left-over bees that were not collecting pollen and are smaller than a blue-green *Osmia*. Compared to such an *Osmia*, they were probably not as effective at pollination. We include in this functional group *Ceratina* and *Mexalictus*, as well as many other occasional species of similar size and behavior.

In our analyses, we did not include small dasytine melyrid beetles, which are sometimes very common but are dubious pollinators because they move between flowers very seldom and do not seem to carry much pollen. We also ignored the small number of honeybees that we saw because they are alien and we presume the flowers are not adapted to them. Lastly, Lepidoptera are not included. They were very rarely visitors, except in 2001 in Colorado when the hawkmoths *Hyles lineata* visited *Penstemon strictus* (and many other plants) during an unusually large emergence event. They did not appear to be getting much pollen on their bodies. We did not attempt nocturnal censuses, although casual observations suggest that visitation at night is limited to an occasional moth.

Representative flowers

Next, we describe the flowers and pollination mechanics of representative species of penstemon that span the variation in pollination-syndrome space (Fig. 1). The

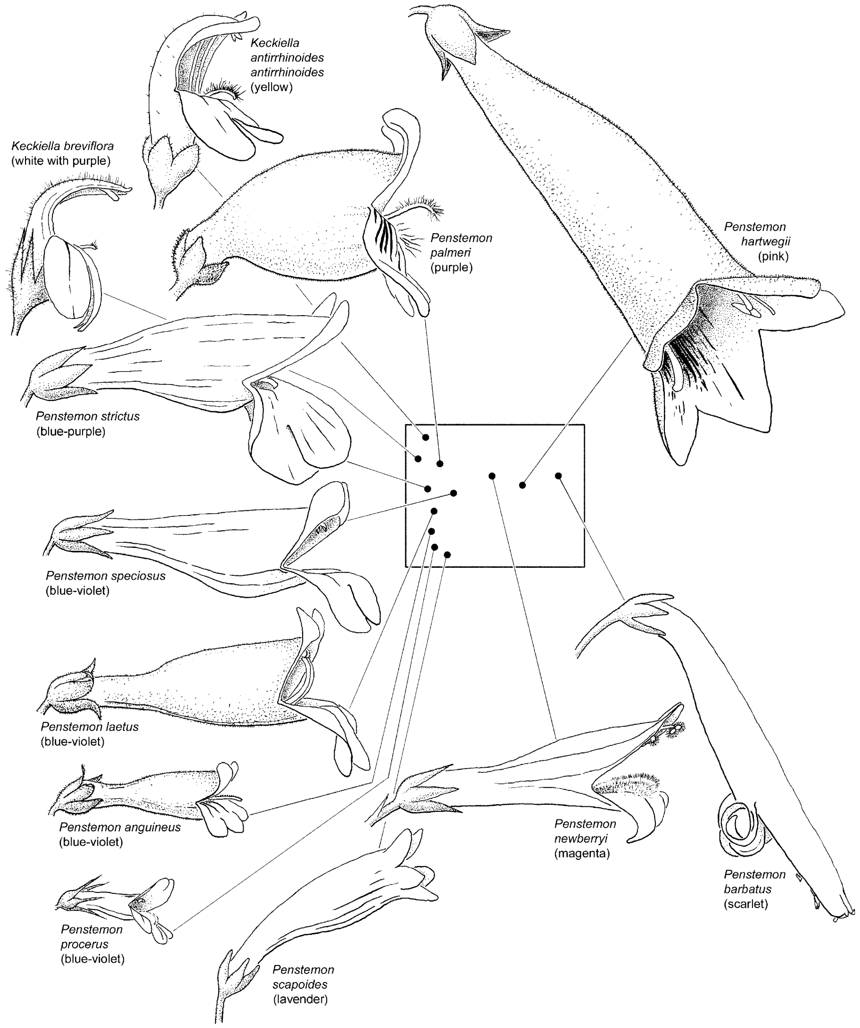


Fig. 1. Representative flowers arranged by pollinator spectra and floral characters that have been suggested to be involved in pollinator specialization. The diagram in the center represents our informal ordination. Flowers on the left are mostly bee-pollinated; flowers on the right are more or less hummingbird-pollinated. Flowers in the upper left fit large bees; flowers in the lower left fit smaller bees or the tongues of larger bees. Drawings traced from photographs or from figures in Holmgren (1993).

first six form a gradient from the most exclusively hummingbird-pollinated to the most exclusively hymenopteran-pollinated (right to left on Fig. 1).

1. *Penstemon barbatus* has bright red flowers that are inclined downward. The staminode is somewhat reduced. The lower lip is strongly recurved, and the anthers and stigma are strongly exserted. The floral tube is so narrow that bumblebees cannot easily fit inside and do not visit the flowers, even in gardens where bumblebees are ardently visiting various blue-violet penstemons. *Penstemon barbatus* produces abundant nectar, but we have never seen a visit through the mouth of the corolla by a nectar-collecting insect (Lange et al. 2000). The anthers are attractive to various pollen collectors.

2. *Penstemon hartwegii* has huge pink flowers with a gradual, trumpet-like flare. In contrast to other penstemons, the corolla opens and the anthers dehisce before the corolla tube has finished expanding. When it is fully expanded, it is 4 to 5 cm long. The flower is inclined downward, has exserted anthers, and the nectar flow is copious, but the lower lip does not reflex backward, unlike in more extreme hummingbird-syndrome penstemons. We saw only hummingbirds and pollen-collecting bees, but Straw (1962) recorded visits by *Bombus*.

3. *Penstemon newberryi* has a magenta corolla that is broad enough to allow a bumblebee to squeeze inside, although it's a tight fit. The anthers are exserted, but the lower lip is only weakly reflexed, the flower is held slightly raised from the horizontal, and the staminode is not reduced relative to hymenopteran-pollinated species of *Penstemon* sub-genus *Dasanthera*. The amount of nectar produced is more abundant than in hymenopteran-pollinated *Dasanthera*. We have seen considerable hummingbird visitation but just as much activity from nectaring bees, especially worker bumblebees.

4. *Penstemon speciosus* fits the hymenopteran-pollination syndrome in being blue-violet, having a vestibular corolla, a lower lip in the position of a landing platform, and relatively included anthers. The flowers are large, however, and hummingbirds can easily reach the nectaries. The nectar is unusually dilute (13% sugar) for a hymenopteran-pollinated penstemon, and hummingbirds visit these flowers, although we have not seen much pollen on their bills or foreheads. Much more frequent are visits by *Osmia*, *Pseudomasaris*, nectar-collecting and pollen-collecting *Bombus*, and various other bees.

5. *Penstemon laetus* has blue-violet vestibular flowers that are held upright from the horizontal. They have a well developed staminode. The anthers dehisce very narrowly, and pollen seems to be shaken out when a *Pseudomasaris* or bee rubs against them, producing audible vibrations (Torchio 1974). A small amount of nectar is produced. Hummingbirds rarely visit *P. laetus*, and we have never seen them working this species assiduously. *Pseudomasaris* and *Osmia* frequently move pollen. Other bees also visit. Pollen collectors are rare, perhaps owing to how narrowly the anthers dehisce.

6. *Keckiella breviflora* has a very short floral tube that is held nearly upright, then the lips abruptly flare into a galea and landing platform upon which a bee can stand and probe for nectar. The corolla is white with small purple blotches. The staminode is narrow but long, and hangs out of the mouth of the corolla. Very small amounts of very concentrated nectar ($>50\%$ sugar) are produced. This is a flower that seems "built for" *Xylocopa* and they can almost always be found visiting it.

The second set of six species represents a gradient, within hymenopteran-flowers, from flowers pollinated by large bees to flowers pollinated by small bees or the tongues of large bees (top to bottom on Fig. 1).

1. *Keckiella antirrhinoides* var. *antirrhinoides* is bright yellow and waxy. It has a short, almost upright corolla base that nearly completely encloses the nectary, which is at the base of the ovary. Nectar can only be reached through slits that are obstructed by hairs between the expanded bases of the filaments. As with other hymenopteran-pollinated keckiellas, the corners of the corolla mouth are positioned proximally and the galea arches over a horizontal landing platform formed by the rim of the mouth and lower lip. These flowers are visited by nectar-seeking *Bombus* and *Xylocopa*.

2. *Penstemon palmeri* has very strongly vestibular flowers. A narrow short base contains the nectaries, then the corolla very abruptly expands into a huge vestibule. The lips often extend forward from the corners of the mouth. The anthers are well inside the vestibule, even though at their farthest extremity they are technically exserted from the corners of the mouth. This makes the corners of the mouth rather poor landmarks for anther position, aggravating our attempts at "objective" measurements. The prominent staminode is densely bearded and lolls out of the mouth. Nectar guides are apparent, and this is the only penstemon flower that we have observed to have a sweet scent to the human nose. *Penstemon palmeri* is visited by nectaring *Bombus*, *Xylocopa* and various anthophorine bees.

3. *Penstemon strictus* has large flowers, but they are deeper and more closed-mouthed than in *P. palmeri*. The landing platform is prominent, and at least the rear anthers are well included within the corolla tube. *Penstemon strictus* flowers are blue-purple. Bumblebees are very important pollinators, along with *Anthophora terminalis*, *Pseudomasaris vespoides* and many species of *Osmia*. On occasion, we have seen hummingbirds visit dense patches when other nectar sources were scarce.

4. *Penstemon anguinius*, with blue-violet flowers, has a corolla much like many larger vestibular-flowered species, just scaled down in size. *Osmia* fit inside nicely. *Bombus* can also visit by inserting their heads without having to fit their bodies inside.

5. *Penstemon procerus* has small flowers that are inclined downward and lower lips that are expanded into a bowl-shaped landing platform. These two characters are peculiarities of the species. In other ways it is representative of many penstemons that we view as "tongue-flowers," i.e., small flowers that bumblebees can drink from by merely inserting their tongues. Such tongue-flowers are also pollinated by small *Osmia* that can crawl inside the corolla. This represents one way for a penstemon flower to be pollinated by small bees and small body-parts of large bees.

6. *Penstemon scapoides*, which is lavender-colored, typifies a second way for a penstemon flower to be pollinated by small bees. The corolla is long and narrow. The anthers and stigma are strongly included. Along with some relatives like *P. caesius*, *P. scapoides* is our best candidate for flowers that have specialized on *Osmia* and the smaller anthophorines to the exclusion of *Bombus*-sized bees.

In Fig. 1, we have arranged the above plant species along the two above-numbered pollination gradients based on flower characters and visitor spectra. Many other species could be added, but the species chosen span the full range for the two axes. This figure can be viewed as an informal ordination.

Statistical methods

Formal ordinations were done using non-metric multidimensional scaling (MDS), carried out in PC-ORD (McCune and Mefford 1999). We did a series of ordinations of plant species based on floral characters. In preparation for ordination, each variable was standardized by subtracting the minimum and dividing by the range. This standardization gives the variation in each character the same weight. Next, we calculated a Euclidean distance (dissimilarity) matrix. Finally, MDS was used to find the best two-dimensional representation of the distance matrix. MDS starts with a random ordination and then randomly adjusts the ordination iteratively, choosing any improvements in the match between the graph and the distance matrix. The resulting orientation of the ordination is completely arbitrary. For ease of communication, we rotated it to maximize the correlation between axis 1 and, for instance, hummingbird visitation. For each ordination, we present correlations between floral characters and the axes of the ordination, and correlations between visitation by various animals and the axes.

We also ordinated penstemons based on visitation data. The visitation points were standardized to be proportions of the points accrued for each plant species (as given in Appendix 2). We used Bray-Curtis distances here instead of Euclidean distances because many of the cells in the data matrix were zeros (Beals 1984). MDS was used to find the best two-dimensional ordination, and this was rotated onto hummingbird visitation. Then correlations were calculated.

The ordination based on visitors combined the data on all visitor groups. We next took each functional group in turn and asked which floral characters are good at "predicting" (in a statistical sense) visitation by that kind of visitor. We did this by a series of stepwise multiple regressions (backwards-deletion, exit criterion $\alpha = 0.25$) using SYSTAT (Wilkinson 1999). The visitation data were treated as dependent variables one visitor group at a time. To improve (but not entirely meet) the assumption of normally distributed residuals, we multiplied the relative visitation points times 244 (the maximum) and then square-root transformed. We will present standardized partial regression coefficients. These indicate the strength of the effect of the character, holding constant the other characters that were retained in the model.

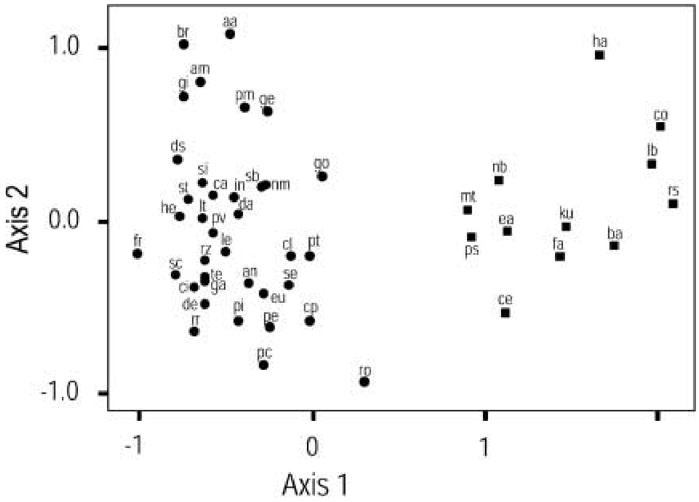
In order to study correlations among floral characters, we calculated Pearson's correlation coefficients between characters two at a time and we calculated Kendall's coefficient of multiple concordance on sets of characters collectively. It should be noted that these correlations do not take into account phylogeny, so they are potentially caused by a combination of convergent evolution and phylogenetic conservatism.

Statistical results

Ordinations based on flower characters: bird- vs bee-syndromes

The MDS ordination of plant taxa based on the degree of similarity in their floral characters is shown in Fig. 2, which also gives the correlations between the axes and both floral characters and visitation activity by various pollinator groups. There is a strong separation of plant species by hummingbird visitation. Also along axis 1, there are negative correlations with various nectaring bees (*Osmia*, *Xylocopa*, *Anthophora*, nectaring *Bombus*), and weak positive correlations with pollen-collecting bees (*Lasioglossum*, pollen-collecting *Bombus*, small pollen collectors). Axis 2 is not as informative; nevertheless, it separates flowers that appeal to large *Xylocopa* from those that appeal to smaller *Osmia*.

How sensitive is this pattern to our inclusion of "subjective" characters? The three characters that correlate best with axis 1 were those that were "subjectively" scored on a four-point scale, i.e. color (C), lower lip reflexion (R), and functional exsertion (X). When we delete R and run a new ordination, a gap between the syndromes remains. Similarly, when we delete only X and run a new ordination, a slightly narrower gap remains. When we delete only C, the space between the syndromes disappears, but the hymenopteran- and



Correlations with Floral Characters

	Axis 1	Axis 2
C	0.941	0.117
R	0.842	-0.148
X	0.918	0.107
E	0.519	0.498
I	-0.640	0.128
W	-0.044	0.712
S	-0.213	0.518
T	0.419	0.315
A	0.492	0.853

Correlations with Floral Visitors

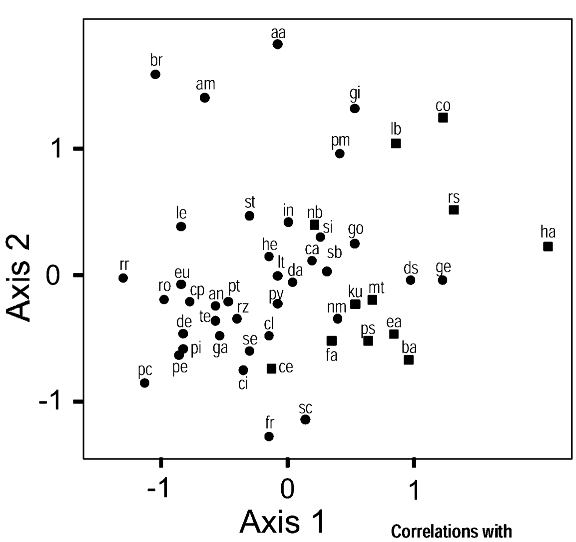
	Axis 1	Axis 2
HB	0.823	0.152
PV	-0.225	-0.087
OS	-0.421	-0.482
BN	-0.344	0.091
BP	0.114	0.054
XY	-0.205	0.526
AN	-0.293	0.091
LA	0.358	0.107
PC	0.179	0.042
EU	-0.280	-0.195
OD	-0.140	-0.074
SB	-0.132	-0.124

Fig. 2. Ordination of plant species based on flower characters. Non-metric multidimensional scaling of Euclidean distances calculated from nine floral characters. Circles are penstemons visited mainly by Hymenopterans; squares are species visited mostly by hummingbirds. Correlations are given between the axes and floral characters (upper right) and pollinator groups (lower right). Codes are as follows: C = color, R = lower lip reflexion, X = functional exsertion, E = exsertion, I = inclination, W = circumference, A = anthers to floor, T = tube length, S = relative staminode length; HB = hummingbirds, PV = *Pseudomasaris vespoides*, OS = *Osmia*, AN = *Anthophora* and similar bees, XY = *Xylocopa*; BN = Nectaring *Bombus*; BP = pollen-collecting *Bombus*, LA = pollen-collecting *Lasioglossum*, PC = small pollen collecting bees, EU = large long-tongued flies, OD = *Oligodranes* flies, SB = small nectaring bees. See Appendix 1 for plant species codes.

hummingbird-syndromes are still non-overlapping. When we delete any two of these characters, the gap similarly closes, but the syndromes remain non-overlapping. This is also the case when we delete R, X and C: the gap disappears but the two syndromes continue to represent separate modes (Fig. 3). There are still strong correlations between the visitation rates and morphology as synthesized in the axes of the ordination based only on "objective" characters, but there is no longer a space between the syndromes.

Ordination of species within the hymenopteran-syndrome

Having established that the principal axis of floral variation is between "hymenopteran-flowers" and "bird-flowers," we now ask if there are also relationships between floral characters and types of visitors within the bee flowers. We deleted the 12 bird-pollinated species (ha, co, nb, mt, lb, ps, ku, rs, ea, ce, ba, fa; see Appendix 1 for complete names), leaving 37 hymenopteran-pollinated species, and we ran a new MDS ordination (Fig. 4). There are no distinct groups of species (i.e. no discrete syndromes), but there are correlations between the axes and visitation by various animals. Most notably, the correlations with nectaring pollinators are arranged along a size gradient: *Osmia* at − 0.44 with axis 1, *Pseudomasaris* at − 0.17, *Anthophora* at 0.13, *Bombus* at 0.16 and *Xylocopa* at 0.67.



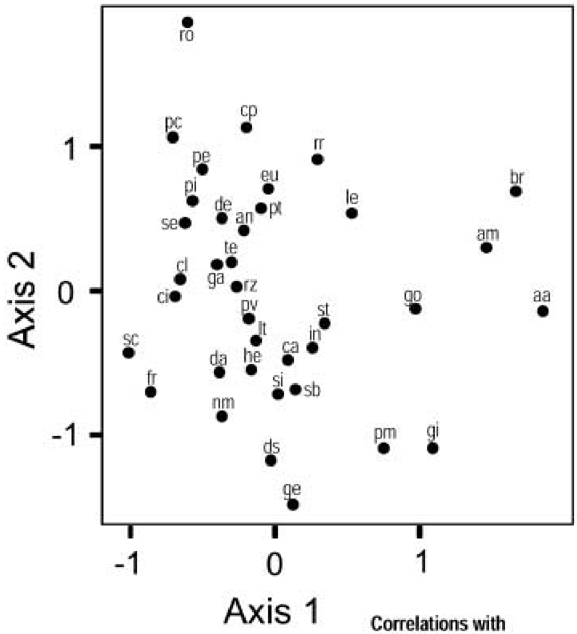
Correlations with Floral Characters

	Axis 1	Axis 2
C	0.626	0.011
R	0.351	-0.037
X	0.433	0.134
E	0.267	0.713
I	-0.561	0.409
W	0.689	0.335
S	-0.145	0.674
T	0.829	-0.181
A	0.726	0.755

Correlations with Floral Visitors

	Axis 1	Axis 2
HB	0.596	0.046
PV	-0.114	-0.079
OS	-0.517	-0.290
BN	-0.152	0.140
BP	0.133	0.102
XY	-0.116	0.595
AN	-0.016	0.046
LA	0.247	-0.059
PC	0.042	0.013
EU	-0.341	-0.162
OD	-0.097	-0.082
SB	-0.045	-0.179

Fig. 3. Ordination based on 6 "objective" morphometric characters. Circles are of the Hymenopteran-pollination syndrome; squares of the hummingbird-pollination syndrome. Codes are as in Fig. 2.



Correlations with Floral Characters

	Axis 1	Axis 2
C	-0.078	-0.151
R	-0.249	0.596
X	0.213	0.654
E	0.797	0.153
I	0.455	0.088
W	0.282	-0.924
S	0.872	0.060
T	-0.292	-0.831
A	0.836	-0.517

Correlations with Floral Visitors

	Axis 1	Axis 2
HB	0.052	-0.438
PV	-0.166	-0.061
OS	-0.438	0.339
BN	0.158	-0.166
BP	-0.077	-0.165
XY	0.671	-0.053
AN	0.134	-0.134
LA	0.098	0.038
PC	0.108	0.225
EU	-0.170	0.160
OD	-0.094	-0.027
SB	-0.067	-0.037

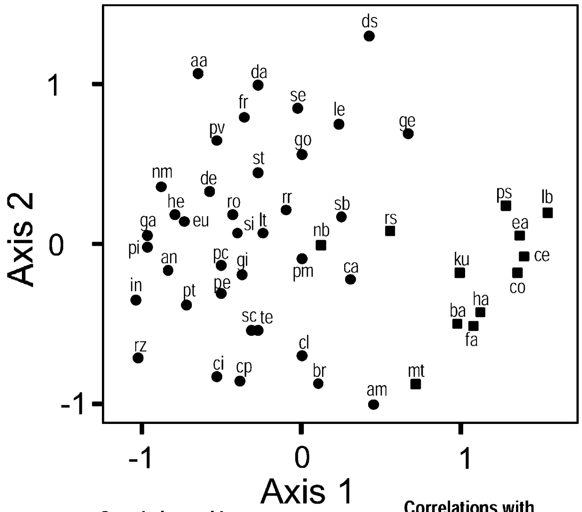
Fig. 4. Ordination of the 37 bee-syndrome species based on all 9 characters, rotated to maximize the correlation between axis 1 and *Xylocopa*. Codes are as in Fig. 2.

Ordination based on visitors

The ordination based on visitation data is shown in Fig. 5. The hummingbird-visited flowers are on the right, and the hymenopteran-visited flowers are on the left. The correlations between axes and floral characters are similar to those found in previous ordinations. Axis 1 is strongly correlated with color and functional anther exsertion. Axis 2 is only weakly correlated with floral characters, with larger and shorter flowers high on the graph and smaller flowers lower on the graph. The ordination shows no obvious gaps between groups.

The value of floral characters at “predicting” visitors

The results of the stepwise multiple regressions are given in Table 1, with each line in the table corresponding to a pollinator functional group. To the right of the “ = ” sign is the set of floral characters that stepwise multiple regression found “predicted” visitation activity along with the standardized partial regression coefficients. The first line indicates that hummingbird activity is predictable by color with a strong positive coefficient (+ 0.64) and predictable to a lesser degree by several other variables, including tube length and anther exsertion. In the opposite direction, color and the presence of a well-developed staminode are predictors of visitation by *Pseudomasaris*. Functional anther inclusion and the shortness of the distance from anthers to floor of the floral tube are good predictors of *Osmia* activity. The shortness of the flower and the width of the flower predict *Bombus* nectaring activity. Pollen collecting *Bombus* are predicted by anther exsertion and staminode length. *Xylocopa* are encouraged by a prominent staminode. Visitation by *Anthophora*-sized bees is not related in a linear manner to any of the floral characters that we measured (although this does not address whether or not they are attracted disproportionately to intermediate floral types). Pollen collecting *Lassioglossum* are attracted to narrow flowers with long tubes that tend to be reddish, i.e. hummingbird-syndrome flowers. Likewise, small pollen collecting bees



Correlations with Floral Characters

	Axis 1	Axis 2
C	0.807	-0.165
R	0.504	-0.226
X	0.735	-0.169
E	0.438	-0.128
I	-0.492	0.134
W	0.157	0.250
S	-0.025	-0.088
T	0.491	0.037
A	0.544	0.071

Correlations with Floral Visitors

	Axis 1	Axis 2
HB	0.850	-0.054
PV	-0.242	0.296
OS	-0.701	-0.397
BN	-0.358	0.645
BP	0.071	0.316
XY	-0.069	-0.104
AN	-0.004	0.210
LA	0.421	-0.221
PC	0.273	-0.579
EU	-0.436	0.081
OD	-0.265	-0.208
SB	-0.117	0.131

Fig. 5. Ordination of plants based on relative visitation rates by various functional groups of pollinators. Non-metric multidimensional scaling of Bray-Curtis distances. Rotated onto HB. Circles are of the hymenopteran-pollinated species; squares of the hummingbird-pollinated species. Codes are as in Fig. 2.

Table 1. Results of step-wise multiple regression, searching for good floral predictors of visitation by each group of pollinators. Following the " = " sign, letters refer to floral characters and numbers refer to standardized partial regression coefficients. Character codes are given under "Data" and in Fig. 2.

Flower visitor	Multiple regression results
Hummingbirds	= +0.64C − 0.13R + 0.27E − 0.16I − 0.13W + 0.29T
Pseudomasaris	= −0.69C + 0.28E − 0.40S + 0.25T
Osmia	= +0.36R − 0.68X + 0.28E − 0.15T − 0.53A
Nectaring *Bombus*	= −0.21E + 0.51W − 0.64T
Pollen-collecting *Bombus*	= −0.23R + 0.46E − 0.41S
Xylocopa	= +0.35E + 0.33W + 0.73S − 0.36A
Anthophorine bees	= +0.28I
Pollen-collecting *Lasioglossum*	= +0.35C − 0.32R − 0.62W + 0.42S + 0.78T
Small pollen collectors	= +0.37R + 0.26S
Eulonchus and *Bombylius*	= −0.19T − 0.23A
Oligodranes	= −0.20R
Small bees	= −0.19X

come to flowers with relatively reflexed lower lips. Floral characters are minimally good at predicting visitation by long-tongued flies and small bees.

These interpretations may be influenced by the overall rate of visitation because our pollinator spectra are summarized as relative numbers of visitation points. For example, suppose that all penstemons get equal numbers of visits from pollen-collecting *Lasioglossum*, that reddish flowers get a small total number of visits dominated by birds, and that blue flowers get many visits by nectar-collecting bees resulting in a large total number of visits. *Lasioglossum* visitation would then be predicted by the color red but not because of an absolute increase in activity. An analysis of absolute visitation numbers has many problems, so we will not present it here. But, as a point of special interest, we correlated color against the absolute number of visitation points for *Lasioglossum* plus small pollen-collecting bees, and we found a Spearman's rank correlation of $r_s = +0.29$ ($N = 49$, $P < 0.05$). Bees, when they are collecting pollen, are weakly attracted to reddish flowers.

Correlations of syndrome characters with each other

Pollination syndromes are often defined as correlations of characters with each other and with the principal pollinators (Thomson et al. 2000, Fenster et al. 2003). So far, we have focused on the correlations of characters with visitors. The correlation of floral characters with each other would presumably be due to the characters each being shaped by natural selection to fit their pollinator, so we might view this type of relationship as less direct. (Correlations could alternatively be the result of a genetic architecture that is maintained across species; Armbruster 2002.) Considering color, lip reflexion, measured anther exsertion, functional anther exsertion, inclination, circumference at the mouth, relative staminode length, floral tube length, and the distance from the anthers to the floor, Kendall's coefficient of multiple concordance is 0.536. If we drop the "subjective" characters (C, R, and X), it is 0.552. Not every correlation, however, is high. Table 2 shows the pairwise rank correlations between floral characters. Many of these relationships are remarkably weak, even though they collectively make for a strong multiple concordance.

Discussion

Interpretation

Among our 49 penstemons there were correlations between floral characters and types of pollinators in the direction suggested by the literature on syndromes (Fægri and van der Pijl 1979, Wyatt 1983), a literature partially formulated from previous work on penstemons (Straw 1956, Bateman 1980, Freeman et al. 1984,

Table 2. Matrix of Spearman's correlation coefficients between floral characters. See "Data" or Fig. 2 for character codes.

C								
0.607	R							
0.669	0.672	X						
0.334	0.253	0.555	E					
−0.535	−0.498	−0.304	0.168	I				
0.118	−0.235	−0.209	0.081	0.076	W			
−0.237	−0.186	−0.058	0.235	0.134	0.001	S		
0.534	0.196	0.117	−0.058	−0.413	0.643	−0.355	T	
0.443	0.119	0.303	0.597	−0.083	0.566	0.344	0.267	A

Thomson et al. 2000, Walker-Larson and Harder 2001). The discriminations were not absolute, however. The only distinct syndromes were hummingbird-pollination versus all other flowers. This bi-modality is largely accounted for by color, but the distinction between bird-flowers and bee-flowers is supported by many other characters. Because color was coded on a four-point scale, it is possible the bi-modality is an artifact of the crudeness of categories. However, if discrete characters that are uncorrelated and varying without regard to one another are combined, a more continuous distribution is produced for the synthetic characters, not a discontinuous bi-modal distribution. So, the suggestion of distinct syndromes remains prominent, despite the existence of species like *P. pseudospectabilis* that are partially hummingbird- and partially bee-pollinated (Mitchell 1988, Reid et al. 1988, Lange and Scott 1999). The more robust result is that there are relationships between floral characters and types of visitors, even if the syndromes grade into one another.

Hummingbird behavior, beak shape, and the texture of feathers and beak are dramatically different from the corresponding features of insect visitors, so it is not surprising that the largest floral differences among flowers were between bird-pollinated species and insect-pollinated species. The characteristics of hummingbird-flowers may be adaptations to the birds or away from the bees, or both (Fægri and van der Pijl 1979, Tadey and Aizen 2001). For example, exserted anthers and stigmas may be an adaptation to increase pollen transfer by birds or to avoid contact with wasteful bees (Wilson et al. in press). Even the red and orange colors of hummingbird-syndrome flowers may have value to the plants both in drawing special attention by birds and in making the flowers inconspicuous to Hymenoptera (Raven 1972, Chittka et al. 2001).

Within the hymenopteran-pollinated species, correlations between floral characters and types of visitors were more subtle, and the ones we were able to detect seemed to be associated with the size of the animal. It makes sense that there is less opportunity for syndromes to arise when the pollinator types are relatively similar and indistinct. Specialization onto birds versus bees may result in well-differentiated syndromes (Fig. 2), specialization onto one order of insects or another may yield less distinct groups (McCall and Primack 1992), adapting to particular genera of bees differing in size and behavior may yield only continuous variation (Petanidou and Vokou 1993; Fig. 3), and adaptation to specific species of the same body size and behavior may result in only idiosyncratic floral divergence (Dilley et al. 2000). As far as we can tell, many of the species of penstemon in the middle of the ordination of insect-pollinated species are generalists, in the sense of being adapted to many species of bees and *Pseudomasaris vespoides*. These species differ from one another in floral characters, but there is no reason to attribute the differences to specialization onto disparate pollinators.

Pollen collectors do not follow the syndrome generalizations. If anything, they are attracted to hummingbird-syndrome flowers over hymenopteran-syndrome flowers. This may be because the anthers are exserted and therefore accessible. It may also be because the hummingbird-pollinated species tend to have anthers that open widely and present pollen more generously (Thomson et al. 2000). Although we have not yet compared pollen movement by pollen collectors and nectar collectors visiting *Penstemon*, data from other systems suggests that pollen collectors deposit a relatively small proportion of the pollen that they remove (Bertin 1982, Wilson and Thomson 1991, Vaughton 1996, Thomson and Goodell 2001). When total visitation rates are high, as is almost always the case for penstemons, it would be in the plant's interest to have the pollen removed by more effective nectar collectors (Thomson in press). Pollen-collecting bumblebees remove more pollen than nectar-collecting bumblebees (Castellanos et al. in press). It will be interesting to see if they deposit less of it on stigmas. We also plan to compare pollen-collectors like *Lasioglossum* to primarily nectar-collecting *Osmia* and *Bombus*.

Finally, we found no evidence that any of our 49 species of penstemon are adapted specifically to pollinators other than Hymenoptera and hummingbirds. This was not surprising given the species included. There is good evidence that *P. tubaeflorus*, with its white tubular corolla, is partly pollinated by butterflies, as well as by small bees (Clinebell and Bernhardt 1998). Long-tongued flies are fairly common visitors to some penstemons, and they end up with pollen on their bodies. We believe that they are efficient pollinators (Ashman and Stanton 1991, Thompson and Pellmyr 1992 for the effectiveness of long-tongued flies). We have not found any populations of penstemon that seem to be principally pollinated by flies; that is, when flies have been observed, bees have also been observed. More to the point, we have not seen floral phenotypes that seemed adapted for long-tongued flies to the exclusion of bees. However, outside of our sample of 49, Straw (1963) suggested that the peculiarities of *Penstemon ambiguus* are adaptations to pollination by *Oligodranes* and *Mythicomyia* (small flies in the Bombyliidae), and he suggested that its sister species *Penstemon thurberi* is pollinated by larger bombyliids "of the hovering kinds" as well as by bees. These species deserve additional study in a comparative context.

Further limitations of the study

Measurement error

We measured soft flower parts, looking for differences on the order of a millimeter, and the measurements were done by numerous observers. Measurement error could be high relative to the differences we detected.

Furthermore, measurement error is unlikely to be the same for all characters. Some characters, such as corolla tube length, are easy to measure. Others, like the distance from the bottom of the anthers to the floor of the corolla, are difficult to measure. Some of the characters that capture the essence of pollination syndromes the best (e.g. the degree to which the flowers are vestibular versus tubular) could not be measured objectively and were merely treated descriptively (Appendix 1). Only with caution should one conclude that a certain character matches syndrome expectations better than another character. In the case of color, however, even our crude categories indicate that reds are highly predictive of hummingbird visitation, more so than, for instance, the circumference of the floral tube at the mouth of the corolla.

Quantification of visitation rates

Records of visitors throughout the range of each species over evolutionary time would be ideal. A 30-minute local visitor census is a meager assay of what kinds of animals a species of plant attracts. Any one census may have been on a cold day, or early in the season, or in a bad habitat for one kind of pollinator. This is why we did not treat visitor censuses as a unit of replication but instead added up visitation points. The downside of summarizing visitation in this way is that we were in effect pooling information across censuses, so we have no way of testing how homogeneous our visitor data are within species. The pollinator spectrum for any one plant species was estimated only with great uncertainty.

The gauge of similarity

Measuring similarity in convergent characters is onerous. One wants a coarse gauge of similarity. Take, for instance, the staminode. We hypothesize that it is ‘‘reduced’’ in hummingbird-pollinated species. There are, however, many ways for a staminode to be reduced. It may be shorter, thinner, moved forward out of the way of the nectaries, or merely less hairy or less rigid. We only measured relative length. Next, consider anther exsertion. Sometimes, by our ruler measurement the anthers are exserted when functionally they are very much included. This situation occurred when the corners of the mouth were positioned well back from the lips of the corolla. In subjectively scoring functional exsertion, we took into account the position of the lips and the degree to which the rear anthers were included as well as the exsertion of the forward anthers beyond the corners of the corolla's mouth. In effect, we were recognizing a synthetic character, combining several more detailed characters.

Phylogenetic effects

Since we have made no attempt to separate convergent evolution from phylogenetic conservatism, caution is warranted as regards the causal significance of the patterns we have reported (Westoby et al. 1995). Elsewhere, we have reported significant convergence: for pairs of closely related penstemons in which one member of the pair is visited primarily by Hymenoptera and the other member of the pair primarily by hummingbirds, we found significant tendencies for the later to be redder, to have a narrower tube, to have more exserted anthers and stigmas, to have a less pronounced landing platform, to be more inclined or to have a more flexible pedicel, to produce more nectar, to have less concentrated nectar, and to have less restricted pollen presentation (Thomson et al. 2000). At present, our most parsimonious phylogenetic analysis suggests that there have been 14–25 independent evolutionary shifts between hymenopteran and hummingbird pollination (Wilson et al. in press). This number may stabilize as the phylogeny becomes better resolved, but we are confident that there has been considerable homoplasy in principal pollinator type. We hope eventually to present an analysis in which we trace, on a well resolved phylogeny, evolutionary changes in floral characters, the aptness of which we are separately studying. Such work has been attempted in very few groups for which there has been enough replicated convergence to study statistical correlations using modern comparative methods (Armbruster 1992, 2002, Bruneau 1997).

Conclusion

Syndromes exist among penstemons but in a limited way. If one takes the classical literature on syndromes as a guide for choosing characters and character states, there is a multivariate gap that separates hymenopteran-flowers from hummingbird-flowers. Many of the characters form associations with one another and are weakly associated with the kind of pollinator. Though these relationships are significant between hymenopteran- and hummingbird-flowers and even for flowers that appeal to various sizes of Hymenoptera, the variation in floral characters remains far from 100% explained, except perhaps for blues and yellows versus reds and oranges. Evolutionary divergence in penstemon flowers sometimes occurs via shifts in pollination ecology, but many species have arisen and diverged in floral characters without permanent shifts between principal pollinators.

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Appendix 1. Pollination-syndrome characteristics of 49 species of flowers. Generally values are medians of 5 or more flowers from different individuals. C, R, and X were subjectively scored from 1 to 4 by a single observer.

Abbreviation	Plant taxon	Morphotype	Color	Color code	Lower lip reflexion	Functional exsertion	Anther exsertion	Inclination up from horizontal	Circumference at mouth	Relative staminode length	Floral tube length	Anthers to floor
				C	R	X	E	I	W	S	T	A
an	*P. anguineus*	vestibular	blue-violet	1	2	1	2	0	13	0.92	13	2.5
aa	*K. antirrhinoides a.*	galeate-well	yellow	1	1	2	10	40	25	1.45	9	8
am	*K. a. microphylla*	galeate-well	yellow	1	1	2	9	60	20	1.36	8	6
ba	*P. barbatus*	broadly tubular	scarlet	4	4	4	7.84	−58	18.9	0.63	25	4.61
br	*K. breviflora*	galeate well	white with purple	1	1	2	9	50	13	1.60	6	6
cp	*P. caespitosus*	sub-vestibular	blue-violet	1	3	2	1.4	7	12.2	0.97	9.05	2.4
ci	*P. caesius*	narrow sub-vestibular	blue-violet	1	1	1	−2	0	16	0.57	19	1.5
ca	*P. campanulatus*	vestibular	blue-violet	1	1	1	0.5	15	25	0.81	20	5
ce	*P. centranthifolius*	narrowly tubular	fire engine red	4	3	3	1.75	−10	14	0.57	24.25	2
cl	*P. clevelandii*	sub-vestibular	purple	2	2	1	0	−5	16	0.60	19	3
co	*K. cordifolia*	tubular	orange	4	4	4	15.5	7	26.29	0.49	20.5	max
ds	*P. dasyphyllus*	vestibular	blue-violet	1	1	1	−3.5	2	34.4	0.73	23.2	5.5
da	*P. davidsonii*	large vestibular	blue-violet	1	1	2	2.5	30	28	0.44	21	3
de	*P. deustus suffrutescens*	tongue flower	yellow with guides	1	1	1	1	0	9.5	0.84	9	2
ea	*P. eatonii*	broadly tubular	crimson	4	1	3	8.5	−45	17	0.67	22	5
eu	*P. euglaucous*	tongue flower	blue-violet	1	2	2	2	32	12.3	0.81	8.9	2.5
fa	*P. fasciculatus*	tubular	bright red	4	3	4	2	−30	18	0.71	24	4
fr	*P. fruiticosus*	large vestibular	blue-violet	1	1	1	−0.9	50	25.9	0.39	26	1.2
ge	*P. gentianoides*	open vestibular	purple	2	1	1	−3	0	36	0.88	27	6
go	*P. gormanii*	vestibular	blue-violet	1	3	1	3	−20	23.4	1.01	16	6
ga	*P. gracilentus*	narrow sub-vestibular	blue-violet	1	1	1	0	10	13	0.68	15	2
gi	*P. grinnellii*	open vestibular	purple on white	1	1	1	6	20	37	1.23	18	7
ha	*P. hartwegii*	trumpet-shaped	red with pink	3	3	4	6	−35	36	0.80	39.5	8
he	*P. heterophyllus*	large vestibular	blue-violet	1	1	1	−1	35	28	0.80	21	3
in	*P. incertus*	large vestibular	pastel lavender	1	2	1	6	40	27	0.54	20	4
ku	*P. kunthii*	broadly tubular	crimson	4	3	4	3.5	−27.5	19.75	0.78	24.5	5
lb	*P. labrosus*	tubular	scarlet	4	4	4	12.1	17	15.4	0.63	22.9	max
lt	*P. laetus*	large vestibular	blue-violet	1	1	1	2.5	25	23.5	0.73	21.75	3
le	*K. lemmonii*	small galeate-well	yellow	1	1	2	4	40	14	1.11	8	3.5
mt	*P. miniatus townsendianus*	sub-vestibular	red with pink	3	3	3	2	−30	23	0.74	25	5.5
nm	*N. nemorosa*	vestibular	purple	2	1	1	−2	0	29	0.58	23	4
nb	*P. newberryi*	sub-vestibular	magenta	3	3	4	8	20	23.5	0.62	21.5	5
pm	*P. palmeri*	open vestibular	purple	2	1	1	4	20	36	1.13	19	6
pv	*P. parvulus*	vestibular	blue-violet	1	1	1	0	10	20	0.62	17	4
pt	*P. patens*	sub-vestibular	purple	2	2	2	2	20	14.75	0.62	13	3
pe	*P. peckii*	tongue flower	blue-violet	1	2	2	1.2	0	8.7	0.65	9.7	1.4
pc	*P. procerus*	tongue flower	blue-violet	1	2	2	0	−10	6.2	0.72	7.09	0.53

Appendix 1. (Continued).

Abbre-viation	Plant taxon	Morphotype	Color	Color code C	Lower lip reflexion R	Functional exsertion X	Anther exsertion E	Inclination up from horizontal I	Circumference at mouth W	Relative staminode length S	Floral tube length T	Anthers to floor A
pi	*P. pruinosus*	tongue flower	blue-violet	1	2	1	1.3	0	10.1	0.68	9.9	1.4
ps	*P. pseudospectabilis*	sub-tubular	purple-pink	3	3	3	3	−48	19.7	0.77	23.5	4.5
rz	*P. roezlii*	vestibular	blue-violet	1	1	1	−1	10	17	0.77	15	2.5
rs	*P. rostriflorus*	tubular	red	4	4	4	7.5	−50	16	0.98	20	max
rr	*K. rothrockii r.*	small galeate well	yellow	1	1	2	4	56	11	0.87	9	1
ro	*P. rydbergii oreocharis*	tongue flower	blue-violet	2	4	2	1.5	40	11	0.67	9.5	2
sc	*P. scapoides*	long sub-tubular	lavender	1	2	1	−3	0	26	0.75	28.5	1
se	*P. secundiflorus*	narrow sub-vestibular	blue-violet	1	2	2	0.315	−21.5	15.385	0.68	14.615	2.445
si	*P. speciosus*	large vestibular	blue-violet	1	1	1	7	20	28	0.68	26	3.5
sb	*P. spectabilis*	vestibular	purple and blue	2	1	1	2	0	25	0.77	21	5
st	*P. strictus*	large vestibular	blue-purple	1	1	1	4.5	50	22.5	0.91	18.5	4
te	*P. teucrioides*	small vestibular	blue-violet	1	1	1	1.98	17.5	13.4	0.62	13.45	2.23

Appendix 2. Amounts of visitation by various types of animals (columns) at 49 species of plants (rows). Intensity of observation and activity varied greatly among species of plants, as indicated by sum of visitation points (rightmost column). Visitation points for each type of animal were divided by this sum to make plant species comparable. Animals are grouped in terms of functional groups (codes in text). For plant species codes, see Appendix 1.

Plant species	HB	PV	OS	BN	BP	XY	AN	LA	PC	EU	OD	SB	Sum of visitation points
an	0	0	0.67	0.17	0	0	0	0	0	0	0	0.17	6
aa	0	0	0	0.63	0	0.25	0	0	0	0.13	0	0	8
am	0	0	0	0	0	0	0.55	0	0.45	0	0	0	11
ba	0.34	0	0	0	0.09	0	0	0.25	0.31	0	0	0	32
br	0	0	0.07	0.05	0	0.53	0.02	0.12	0.16	0.05	0	0	43
cp	0	0	0.67	0	0	0	0	0	0.33	0	0	0	6
ci	0	0	0.68	0	0	0	0	0.15	0.07	0	0.10	0	41
ca	0	0	0	0.16	0	0	0.28	0.09	0.44	0	0.03	0	32
ce	0.86	0	0.04	0	0	0	0	0.08	0.02	0	0	0	51
cl	0.09	0	0.35	0	0	0	0	0.21	0.32	0	0	0.03	34
co	0.90	0	0	0	0	0	0	0	0.10	0	0	0	10
ds	0	0	0	0	0	0	0.80	0	0	0	0	0.20	10
da	0	0.17	0	0.39	0.33	0	0.11	0	0	0	0	0	18
de	0	0	0.27	0.36	0	0	0.36	0	0	0	0	0	11
ea	0.82	0	0	0	0	0	0	0.09	0	0	0	0.09	11
eu	0	0	0.42	0.33	0	0	0	0	0	0	0	0.25	12
fa	0.42	0	0	0	0	0	0	0.33	0.25	0	0	0	24
fr	0	0.10	0	0.20	0	0	0.20	0	0	0.20	0	0.30	10
ge	0.29	0	0	0.71	0	0	0	0	0	0	0	0	14
go	0	0	0	0.25	0	0	0.42	0	0.08	0	0	0.25	12
ga	0	0	0.33	0.22	0	0	0	0	0	0.22	0.22	0	9
gi	0.04	0	0.34	0.15	0	0.32	0.09	0	0.04	0	0	0.02	47
ha	0.50	0	0	0	0	0	0	0.33	0.17	0	0	0	6
he	0	0.19	0.29	0.24	0	0	0	0	0	0.19	0	0.10	21
in	0	0.43	0.43	0	0	0	0	0	0	0	0	0.14	7
ku	0.54	0	0	0	0	0	0	0.15	0.10	0	0	0.21	39
lb	0.80	0	0	0	0.20	0	0	0	0	0	0	0	5
lt	0.03	0.21	0.25	0.09	0.05	0.01	0.18	0.05	0.02	0.08	0.02	0.02	133
le	0	0	0	0.50	0	0	0.17	0.33	0	0	0	0	6
mt	0.14	0	0	0	0	0	0	0	0.71	0	0	0.14	7
nm	0	0	0.33	0.67	0	0	0	0	0	0	0	0	6
nb	0.17	0	0.18	0.25	0.06	0.01	0.06	0.03	0.16	0	0.06	0	93
pm	0.05	0	0.12	0.20	0	0.15	0.10	0.05	0.17	0.07	0.10	0	41
pv	0	0.24	0.12	0.35	0.24	0	0	0.06	0	0	0	0	17
pt	0	0	0.30	0	0	0	0.40	0	0	0.20	0	0.10	10
pe	0	0	0.50	0.17	0	0	0	0	0.17	0.17	0	0	6
pc	0	0.17	0.33	0.17	0	0	0	0	0.17	0.17	0	0	6
pi	0	0	0.44	0.22	0	0	0	0	0	0.33	0	0	9
ps	0.86	0	0	0	0	0	0.14	0	0	0	0	0	7
rz	0	0	0.40	0	0	0	0	0	0	0	0.60	0	5
rs	0.41	0	0.02	0.15	0.10	0	0.12	0.05	0.12	0	0.02	0	41
rr	0	0	0.17	0.30	0.07	0.03	0.20	0	0.17	0	0	0.07	30
ro	0	0	0.29	0.35	0	0	0.21	0	0.06	0.03	0	0.06	34
sc	0	0	0.40	0	0	0	0.40	0	0.20	0	0	0	5
se	0	0.67	0	0.17	0	0	0	0	0.17	0	0	0	6
si	0.05	0.14	0.36	0.19	0.10	0	0.10	0.03	0	0.04	0	0	80
sb	0.23	0.03	0.08	0.25	0.05	0	0.15	0.08	0.08	0.03	0	0.03	65
st	0	0.28	0.12	0.34	0.07	0	0.09	0.01	0.06	0	0	0.05	244
te	0	0	0.40	0	0	0	0.10	0	0.20	0	0	0.30	10