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Pollen presentation and pollination syndromes, with special reference to *Penstemon*

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Abstract

Pollen presentation theory (PPT) allows for a re-examination of some classic themes in pollination biology. Here, we outline its implications in the context of bee- and bird-adapted species of *Penstemon* and *Keckiella* (Scrophulariaceae). PPT models the optimal schedule of pollen presentation, based on the frequency of visits by pollinators, and the capacities of those pollinators to remove and deposit pollen. High visitation rates, high removal and low deposition all favor plants that present pollen in many small doses. Dosing is achieved through gradual opening of anthers and through anthers opening only narrowly. We hypothesize that bees have higher rates of removal and lower rates of deposition than birds; therefore, bee-pollinated species should have anthers that open more gradually and less completely than bird-pollinated species. Before presenting preliminary results that affirm this prediction, we critically discuss the characterization of species by pollination syndrome. PPT sheds new light on why plants may specialize on particular pollinators. Stebbins' most effective pollinator can be recast as the pollinator that deposits more of the pollen that it removes, thereby making other visitors into conditional parasites. Pollinator shifts might occur when a pollinator with low removal and high deposition becomes abundant; the plants would then be selected to discourage their previous pollinators who are now parasites. Bird-pollination may favor anthers that open quickly and widely, thereby making bees wasteful parasites. Bee-pollination may favor anthers that open slowly and narrowly, thereby making birds ineffective pollinators. In paired comparisons of closely related species, the hummingbird-visited species were redder, had narrower or longer floral tubes, more exserted anthers and stigmas, less pronounced landing platforms, more inclined orientation, produced more nectar of a lower concentration, and had anthers that dehisce faster and more extensively.

Keywords: anther, bee, dehiscence, hummingbird, *Keckiella*, *Penstemon*, pollen deposition, pollen removal, pollinator shifts.

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Extending pollen presentation theory to syndromes

This paper attempts to link classical themes in floral evolution to a new body of theory, using examples from the large genus *Penstemon* and its segregate genus *Keckiella*. Adaptation of flowers to pollinators traditionally has been considered in terms of characters such as corolla shape, color, and the placement of sexual organs, but 'pollen presentation theory' (PPT) (Percival 1955) suggests that the scheduling and control of pollen release to visitors should also reflect selection for successful pollination. We first outline the most relevant insights from PPT then review the classical notion of pollination syndromes, to which we add new characters derived from PPT. Turning to organisms, we consider seven pairs of plant species that probably represent independent evolutionary transitions between bee pollination and hummingbird pollination. We gauge the conformity of each

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pair to the expected syndromes, considering both familiar and PPT characters. Then we show how PPT can help explain the mechanisms by which pollinator shifts evolve. Finally, we consider the technical difficulties of measuring the schedules of pollen dosing, and provide preliminary data from new methods.

Pollen presentation theory

Percival (1955) first focussed attention on the ecologic importance of pollen presentation schedules, but it is only more recently that consequences of these schedules for reproductive success have been modeled. These models measure pollination success as the delivery of pollen from a focal plant to the stigmas of others. The essence of PPT is that for a plant that will receive some expected number of pollinator visits there will be an optimal schedule for presenting pollen to those pollinators. That optimum depends on the amounts of pollen visitors remove from anthers and on the amount they deliver to stigmas, as well as other parameters. Generally speaking, plants that receive many visits can maximize the amount of pollen that they donate to other stigmas by presenting their pollen in many small doses rather than all at once. PPT is not a mature body of theory but rather a developing one. It has motivated the gathering of new types of data, and conclusions drawn from those data are driving further development of the theory.

Pollen presentation theory was formalized by Harder and Thomson in 1989. They synthesized the comments of several previous authors, particularly those of Lloyd and Yates (1982; see also Lloyd 1984), into an analytical model describing the circumstances under which pollen should be presented all at once, as opposed to being presented gradually. The value of gradual pollen presentation rests on a central assumption of PPT: that there is a decelerating relationship (‘diminishing returns’) between the amount of pollen removed in a visit (*R*) and the amount of that pollen that is deposited on stigmas (*D*). The assumption can be shown graphically by a $D \bullet R$ curve, such as in Fig. 1. For simplicity, we can use the model $D = R^g$, where $g < 1$. The coefficient g describes how strongly the curve attenuates. LeBuhn and Holsinger (1998) call it ‘pollinator efficiency’ because it reflects the effectiveness of a pollinator at transferring increasing amounts of pollen without increasing the proportion of pollen wastage. For $g < 1$, PPT predicts that plants with high visitation rates should present their pollen gradually. This conclusion holds true whether each visitor removes a fixed number of pollen grains or a set proportion of the grains presented and whether visitors arrive at flowers at regular or random times or even when individual flowers vary in the rate at which they receive visits.

Unfortunately, we have only two empirically derived $D \bullet R$ curves. One is for bumble bees visiting glacier lilies (Thomson & Thomson 1989). In that case, g was 0.33 for the best fit to a power curve. The other is for hummingbirds visiting scarlet gilia in a flight cage (Campbell *et al.* 1996). Each bird was presented with two male-phase flowers followed by 20 female-phase flowers; g was 0.68. Neither data set provides much statistical confidence in the estimates of g nor even for the conclusion that the curves are decelerating. Nevertheless, it is very likely that the $D \bullet R$ curve is more or less strongly decelerating, based on first principles, as discussed by Lloyd (1984). In fact, only a few of the grains that are removed from anthers reach stigmas; frequently fewer than 1% (Levin & Berube 1972; Holsinger & Thomson 1994). The pollen grains that do not reach stigmas are said to be wasted. Pollen wastage occurs because pollinators knock pollen to the ground when they are removing it, because they groom it into scopae for transport to their brood, because they groom it off of their bodies and discard it, or because they deposit it on surfaces other than stigmas. There are many ways for pollen to end up in places other than receptive stigmas. Although pollen grains that are eaten by pollinators may contribute indirectly to plant fitness in the same way that nectar rewards do, in our arguments we still consider them wasted. In bees at least, grooming

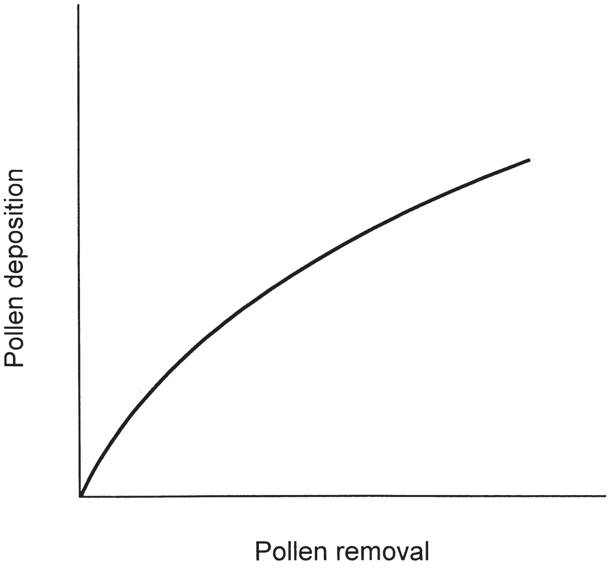

Fig. 1 The $D \times R$ curve is assumed to be decelerating. Pollen removal is the amount removed from the anthers of a flower; pollen deposition is the total amount of that removed pollen that is subsequently deposited on stigmas. As the amount of pollen that is removed in a visit increases, the proportion that reaches stigmas decreases. Thus, it is generally better to dispense a few pollen grains on each of many pollinators than many pollen grains on one pollinator.

is stimulated by pollen pick-up (Harder 1990a,b), so if a plant places too many grains on a bee, most of those will be removed quickly from circulation by grooming. This point is central to our later arguments. More generally speaking, a decelerating $D \times R$ curve will result if wasted pollen grains tend to be wasted together – namely, they are non-independent of one another by being aggregated – and it is most likely that pollen falls to the ground in clumps or is groomed in clumps. Still another way to think about a g-value <1 is to say that deposition of pollen exported to stigmas scales allometrically with low variation on the removal of pollen from anthers.

Pollen presentation theory can also illuminate what happens when a plant receives two types of pollinators that differ in their effectiveness at removing pollen from anthers or depositing it on stigmas. As an example, Wilson and Thomson (1991) studied *Impatiens capensis* flowers visited by nectar-collecting bumble bees and pollen-collecting honey bees. The nectar collectors removed far less pollen from anthers than did the pollen collectors but they deposited far more pollen on stigmas. As the visitation rate of good nectar collectors was high, we concluded that visits by pollen collectors must be detrimental to overall pollen transfer in this situation. Importantly, however, those same pollen collectors did transport some pollen. If no nectar collectors had been visiting, the pollen collectors would have been mutualists with a net beneficial effect on pollen transport. In the presence of better pollen deliverers, however, the pollen collectors became parasites with a net negative effect on transport. This context dependence in the value of visitors arose through depletion of the supply of pollen: pollen collectors were removing pollen from the system that would otherwise have been transported to stigmas by nectar collectors.

Thomson and Thomson (1992) studied these interactions by computer simulations which can be investigated in our interactive package, BeeVisit for Windows (Thomson & Thomson 1998). This program allows the user to specify a function for pollen presentation by a focal plant, plus other functions for removal and delivery by up to three pollinator types; it then calculates the total delivery of pollen from the focal plant to stigmas of others, given a simulated set of stochastically timed visits by some mix of the pollinators. Thomson and Thomson (1992) ran the simulations with various combinations of three types of visitors, whimsically named 'good,' 'bad,' and 'ugly.' Feeling that more sober names were preferable, Goodell and Thomson (1997) rechristened them, respectively, high-removal–high-deposition visitors (HRHD visitors), low-removal–low-deposition visitors (LRLD visitors) and high-removal–low-deposition visitors (HRLD visitors). The most striking result was that a particular pollinator may be beneficial to a plant when it visits alone but may be detrimental when it visits in the company of a better pollinator (Fig. 2). In the presence of HRHD, such as our nectar-collecting bees, HRLD such as our pollen-collecting bees, are detrimental to the plants because the HRLD take away pollen that would otherwise have been delivered by HRHD. This context-dependent parasitism accounts for the name 'ugly.' It is the basis of our later discussion of pollinator shifts.

Thomson and Thomson (1992) did not consider the LRHD category because they were concerned with comparing one natural pollinator of *Erythronium grandiflorum* – bumble bees, assumed to be HRHD – with two hypothetical visitors that were inferior in particular ways. Relatively speaking, however, LRHD visitors can be postulated; in *Penstemon*, we believe that hummingbirds may frequently fall into this category.

Generally speaking, different visitors to a plant can be assigned to locations in $D \bullet R$ space (Fig. 3). For a given value of R, higher values of D always make for a better pollinator (Fig. 3a). If R is not constant, the benefits depend on additional parameters. Generally, a higher removal rate will confer greater benefits to a plant if visits are few, because otherwise pollen may never leave the anthers. If visits are frequent, a low removal rate characterizes a better pollinator (Fig. 3b).

Factors not considered in the simplest forms of PPT

Thomson and Thomson (1992) showed that limits on pollen viability also affect optimal presentation schedules. *Erythronium grandiflorum* (Liliaceae) seems to violate PPT by having a low visitation rate but gradual pollen

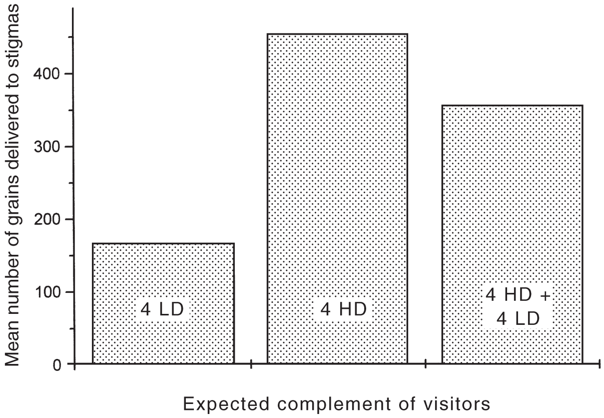

Fig. 2 Context-dependent parasitism. Illustration of numerical simulations (BeeVisit) to show that a low-deposition visitor, which is beneficial to a plant when it visits alone, may be detrimental when a higher-deposition pollinator is also visiting. By taking pollen out of circulation, the LD species prevents that pollen from being delivered by the HD species.

presentation. To resolve the paradox, we suggested that the pollen of this species was short-lived after being exposed by anther dehiscence (but see Thomson *et al.* 1994 for further discussion). This meant that if the plants were to present their pollen all at once, much of it would be dead by the time it got to stigmas. Therefore, the gradual pollen presentation observed in *Erythronium grandiflorum* could be an adaptation to having low visitor frequency combined with having short-lived pollen. In other words, restricted pollen presentation can be favored even when visitor frequencies are low. (BeeVisit includes a parameter for pollen longevity.)

Drosera tracyi (Wilson 1995a) presented a different paradox: high visitation but simultaneous presentation of pollen. All of its flowers for a particular day open between 07.00 and 08.00 hours and the anthers all dehisce simultaneously. Bees arrive promptly to collect the pollen and although pollinator visitation rates in our sites varied, they were generally high. In the site where we studied scheduling, 100% of stigmas had pollen loads by 09.00 hours. The reason why simultaneous pollen presentation is apt for *Drosera tracyi* is because in this plant all of the stigmas in the population are simultaneously exposed. Anthers are therefore under strong selection to have their pollen dispersed immediately no matter how wasteful. We also measured the speed of pollen tube growth and estimated that pollen grains reaching stigmas even 1 h ahead of other pollen grains would have an overwhelming advantage in siring seeds. (In contrast, BeeVisit, and other models of PPT to date, assume that the supply of stigmas is constant throughout anthesis.)

Extensions of PPT

Klinkhamer *et al.* (1994) and Harder and Barrett (1995) extended PPT-like arguments to consider the relationship between the attractiveness of a focal plant and the amount of pollen it exports to other plants. ('Attractiveness' in this context refers to characters such as inflorescence size, rather than to arbitrary signals that bear no relation to the profitability of visiting.) They studied several factors that might affect male fitness when plants are either self-incompatible or when there is inbreeding depression. Their models show how the number of pollinator visits, proportion of pollen removed and deposited and number of flowers per plant relate to floral attractiveness and fitness. If a plant is visited infrequently, attractiveness is advantageous. In such cases, selection should favor rewards that induce visitors to probe many flowers per plant. If, on the other hand, pollinators are abundant, a plant with high nectar rewards and prolonged plant visits would have more pollen grains transferred geitonogamously within the plant; fewer grains would be exported to other plants. Pollen export would not increase linearly with increases in the number of flowers presented per individual plant. Thus, plants should have mechanisms to limit the number of flowers probed within plants by having flowers and anthers open sequentially over time rather than synchronously, at least when visitation rates are high.

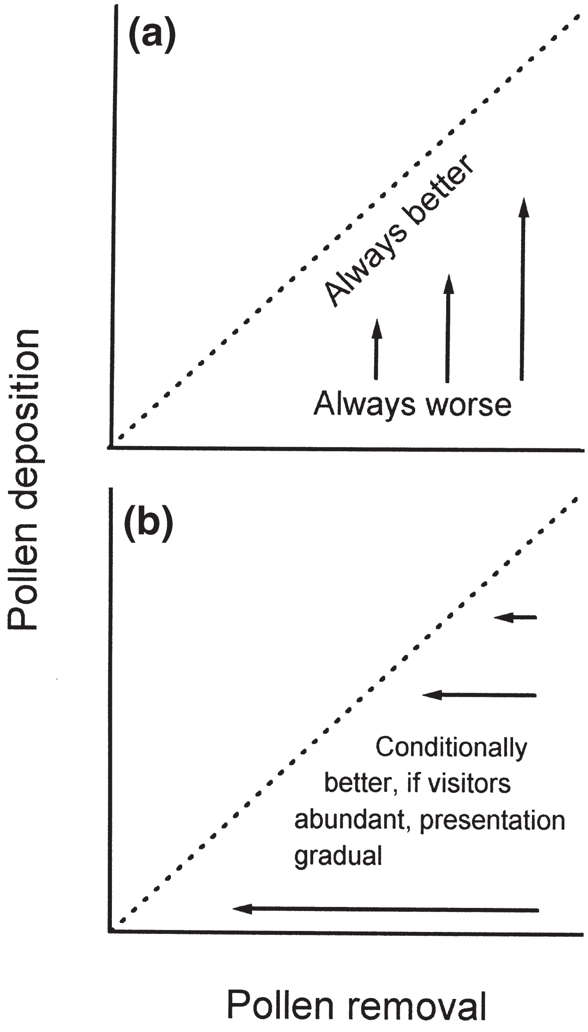

Fig. 3 A pollinator can be thought of as occupying a position in $D \times R$ space, where the axes show pollen removal and deposition, respectively. The dotted line shows the maximum possible deposition, so all points must fall below it. (a) For a given value of removal, a pollinator with a higher deposition is always more beneficial to the plant. (b) For a given value of deposition, whether higher removal is more beneficial depends on the visitation rate and on the pollen presentation schedule.

Farther afield, Warner *et al.* (1995) proposed for fishes a model of optimal sperm presentation that parallels PPT. They suggested that given resource limitations, a male fish should partition the release of gametes over the few to several mating bouts that it accrues. They found that the number of eggs fertilized is a decelerating function of the number of sperm released. Therefore, the optimum amount of sperm released in a mating bout is below the individual's maximum capacity. The optimum is something less than the maximum, and it depends on the number of daily matings. Warner *et al*. found a negative relationship between the number of matings per day and the amount of sperm released per mating. The male fish minimized wastage and maximized his siring rate by partitioning his sperm.

The fullest formulation of PPT is given by Harder and Wilson (1994, 1997, 1998 a, b). They take postpollination processes into account, as well as the diminishing returns from pollen removal to pollen deposition. As with pollen transfer, it is also likely that there are diminishing returns from pollen deposition to ovule fertilization. In addition, Harder and Wilson attempted to incorporate realism into their algebra, including variation in the visitation rate at flowers and the way in which pollen removal might depend on the amount of time since the last visit. These added considerations yield additional predictions, but they also show that the original predictions of Harder and Thomson (1989) are very robust to dynamic pollen removal and random variation in many parameters: values of $g < 1$ in conjunction with visitation rates well above one visit during the life of a flower cause selection for gradual pollen presentation. Just how gradual depends on the typical number of visits, variation in number of visits, the proportion of pollen removed in a visit, and the degree of deceleration in the curves. Harder and Wilson also point out that flowers may have a kind of apt plasticity in the presentation of their pollen; specifically, when the flower has just received a visit it does well to present a small amount of pollen, whereas when it has languished unvisited for a long period of time it does well to present a large accumulation of pollen to the next visitor. Such dynamic dispensing with more and more pollen accumulating between visits may be a by-product of gradual pollen presentation; it need not be selected for in order to exist.

To put PPT in perspective, LeBuhn and Holsinger (1998) explored the strength of selection on the pollen presentation schedule relative to the strength of selection on characters that determine the visitation rate and the quality of pollinators. They found that selection to gradually dispense a little pollen at a time was much weaker than selection to increase the number of visits a flower might expect to receive (by increasing nectar secretion rates, for instance) or to increase the value of g (by encouraging visitors with, say, $g = 0.7$ over visitors with $g = 0.3$). This line of thinking is compatible with that presented by Wilson *et al*. (1994), who suggested that 'attractiveness characters', such as showy petals and sweet nectar, are selected for when pollinator abundances are low. This makes flowers highly attractive to pollinators even during times when pollinator abundances are high. This in turn results in high visitation rates that favor gradual pollen presentation. LeBuhn and Holsinger cleverly bring up the issue of selection for characters that encourage highly effective pollinators, namely those with high values of g. Pollinators might also differ in effectiveness at removing the pollen that is presented. In particular, a pollinator that removes a small proportion of the pollen will tend to be a good pollinator when its visitation rate is high even without the anthers having any special features for gradual release of pollen, whereas a pollinator that removes a large proportion of the pollen presented will select for special features of the anthers that gradually dispense pollen onto those high-removal animals.

Distilling a testable prediction from PPT

We propose a test using the comparative method. We postulate that classes of pollinators – beetles, moths, bees, birds, bats, etc. – differ systematically in their tendencies to remove pollen, waste pollen and deposit it. Therefore, flowers adapted to these different classes of pollinators should tend to differ in the rate at which they present their pollen. That classes of pollinators should have varying capacities for pollen transfer seems likely based on simple generalizations concerning their natural history. Beetles and syrphid flies, for example, eat pollen in quantity. On the other hand, many long-tongued flies mostly forage for nectar and may have relatively low pollen wastage (for example Pellmyr & Thompson 1992). Butterflies and moths also primarily seek nectar. Although some passerines deliberately consume pollen in quantity (Grant 1966), hummingbirds seek nectar exclusively. They seem fairly oblivious to the pollen that gets on their bodies. In contrast, the whole economy of bees is based on gathering pollen. We therefore make the specific hypothesis that bee plants should have more restricted pollen presentation than hummingbird plants. The rationale is two-fold.

First, bees are probably better at removing whatever pollen is presented than are birds. Bees have branched body hairs that facilitate pollen removal. Sometimes pollen removal is done very deliberately by rubbing bristly body parts back and forth against anthers, by manipulating anthers with mouth parts or legs, or by buzzing flowers. Even nectar-seeking bees that do not collect pollen actively will frequently brush against the anthers firmly enough to remove much of the pollen. Electrostatic attraction may increase removal (Thorp 1979; Erickson & Buchmann 1983). Bees that have been airborne are thought to take on a positive charge. Pollen grains are grounded with a negative charge. When a bee dislodges pollen from anthers, airborne pollen is drawn to the bee's body. It seems likely that neither the smooth beak of a bird nor its appressed feathers would interact with pollen so strongly. Thus, a bee flower that restricts pollen removal will still have its pollen removed. In contrast, birds have no interest in pollen, and if a bird flower were to restrict pollen removal, it might put almost no pollen into circulation.

Second, bees use all six legs to groom pollen grains from their bodies. In stereotyped grooming movements, they drag specialized rakes or combs through their pile, gathering the loose pollen into their scopae or corbiculae (Michener *et al*. 1978; Thorp 1979). Such grooming is triggered by large doses of pollen – the more pollen a plant puts on a bee, the more likely the bee is to remove that pollen from circulation (Thomson 1983, 1986; Harder 1990b). Therefore, if a plant doses a bee with a large load, most of that pollen will be packed away immediately. At least in apid bees, the corbicular loads are not capable of donating grains to stigmas, whereas grains applied in small doses tend to remain longer on active sites on the animal. (In other bees, loose scopal loads may in fact constitute active pools of pollen for donation.) In other words, we believe g is very much less than 1 for bees (Harder & Thomson 1989). Because birds are larger and have no dietary interest in pollen, they are less likely to react to a large load in this way, and should therefore produce less saturating curves. For birds, g might be rather closer to 1.

We hypothesize that bees are usually HRLD and birds are LRHD, comparatively speaking. This is consistent with the few data that exist. For bumble bees, if the anthers are prevented from being visited until they are fully dehisced after a bee visit is allowed, then that bee will generally remove 50–80% of the pollen presented (Galen & Stanton 1989; Harder 1990a; Young & Stanton 1990; Wilson 1995b; all critiqued by Wilson 1994). Of course, these conditions may represent unnatural accumulation of exposed pollen for plants that are used to high visitation rates. Still, this result suggests that bees are very good at removing pollen, even when they are primarily collecting nectar. The only paper on pollen removal by birds that we know of is that of Mitchell and Waser (1992). For *Ipomopsis aggregata*, they found the first visit by a bird removed about 20% of the pollen, the second visit removed another 15%, and the third visit removed another 4%. These visits were all in quick succession and probably more time between visits would allow more than 40% to be removed. Mitchell and Waser also mentioned that first visits by hummingbirds to *Penstemon centranthifolius* removed about 30% of the pollen presented. They concluded, 'Low rates of removal may be common for hummingbird-visited flowers because of short probe duration and comparative lack of movement within flowers while probing.' For g-values, more data are urgently needed but the two existing estimates ($g = 0.33$ for bumble bees; $g = 0.68$ for hummingbirds) are consistent with our characterization of pollen carriage by these animals.

On evolutionary shifts between pollination syndromes

The notion of pollination syndromes dates back to the 19th century (Delpino, cited by Faegri & van der Pijl 1979). Most authors who have treated them in any detail have also criticized them (Baker & Hurd 1968; Stebbins 1974; Wyatt 1983). Although Faegri and van der Pijl are widely considered the champions of pollination syndromes, even they frequently warn against over interpreting the concept. Consider the following excerpts.

> It will be found that . . . blossom types are . . . characterized by definite pollination mechanisms. However, this does not mean that all the 'typical' features are present in all cases; there is a certain syndrome of blossom characteristics corresponding to each pollination type, but in any given case any feature belonging to the syndrome may be missing just in the blossom under consideration (p. 23).
>
> It cannot be too strongly stressed that the generalizations inherent in the blossom-type concept must not become a mental straitjacket and preclude the appreciation of visits by other groups of visitors, the adaptations of and to whom are less apparent. Such visitors may pollinate or not; in the latter case they may deplete the blossom of attractants and play a negative role in the pollination game (p. 98).
>
> The general syndrome of beetle pollination is rather uncharacteristic; owing to their lack of specialization, beetle flowers are frequently overlooked and the visits of beetles in blossoms considered accidental – which they sometimes, but far from always, are (p. 99).
>
> Many small hymenopters, in most cases beetles and lepidopters as well, frequent the same blossoms as flies (p. 103).
>
> [The bee–flower] syndrome should not be accepted without some very important reservations . . . social bees – perhaps more than any other group – will visit any blossom type that yields sufficient nectar (p. 114).
>
> Some bird blossoms are of the brush type, others belong to the gullet type with oblique profile, the tube type, and some papilionaceous blossoms are also typical ornithophiles (p. 126).

We too will place many caveats on the idea of floral evolution by syndrome shifts. Our purpose in this section is to define our terms, point out difficulties with the classical view of floral evolution and rephrase the question of whether there is anything at all to the notion of pollination syndromes. In the section following this one, we will conclude that syndromes have some applicability in *Penstemon*; at least there is a number of systematic rules that we have been able to verify concerning the difference between bee- and bird-pollinated flowers.

Definitions

A pollination syndrome is a suite of floral adaptations that have come to fit a class of pollinators or a mode of pollination and that therefore are associated with one another. In addition, one may refer to the group of plants that have those characters as belonging to that syndrome. Pollination syndromes have names based on the root *–phily*; for example, ornithophilous flowers are adapted to birds. Semantically, the syndrome refers to the associations of characters with each other and with classes of pollinators, and the set of plants that have those characters would be considered a syndrome group.

A class of pollinators is a group of animals that move pollen and that are similar to one another in such features as body size, mouth parts, the way that they handle the flowers and their sensory abilities. These are groups such as bees (a superfamily), hummingbirds (a family), small flower-visiting beetles (bits and pieces of an order) and long-tongued flies (a group united by a mixture of one convergent character and many symplesiomorphies). These classes are circumscribed in various ways. Some comprise one or a few species, others many. Some are homogeneous in terms of features important to the flowers; others are loose groupings of disparate organisms. Some are phylogenetic lineages whose evolution has been greatly colored by adaptations to use flowers; others are opportunists whose involvement with flowers is incidental.

Because classes of pollinators come in small, medium and large, pollination syndromes likewise come in all degrees of exclusivity. Many, if not most, flowers have not evolved into any syndrome more specific than insect pollination (entomophily). Others might have specialized to be pollinated by bees in general (mellittophily), to bumble bees generically, or to *Bombus consobrinus* specifically. Likewise, the hummingbird syndrome and the sunbird syndrome are more specialized than ornithophily in general. Flowers adapted to hummingbirds tend to be inclined or to have weak pedicels. They are frequently red (Grant 1966). They are held away from the rest of the plant to ease access by hoverers, and their nectar has low amino acid concentrations and high sucrose:hexose ratios. In contrast, flowers adapted to sunbirds tend to be more firmly held in place near perches with broader floral tubes, and the nectars are rich in amino acids with low sucrose:hexose ratios (Baker & Baker 1983; Martínez del Rio *et al*. 1992). Bruneau (1997) has mapped the hummingbird syndrome versus the passerine syndrome onto a phylogeny of *Erythrina*, concluding that the nectar distinctions arose with hummingbird visitation four times.

The existence of syndromes implies some level of specialization. Specialization is the condition of using, or the evolutionary process of coming to use, a narrower spectrum of resources (pollinators) than some possible reference spectrum. For a diagnosis of specialization to carry meaning, we must indicate what the organism is specialized to use and what it does not use (or cannot use well) because of that specialization. A character that is adaptive no matter who the pollinator is does not contribute to the flower's syndrome. It is only because having exserted anthers is favored by the use of hummingbirds while having inserted anthers is favored by the use of bumble bees that a distinction arises between ornithophilous and melittophilous flowers. In other words, a pollination syndrome exists only in relation to other syndromes from which it differs. Diversity through specialization is based on there being an interaction between the character and the class of pollinator in how they affect fitness (Wilson & Thomson 1996). Some sort of trade-off is considered a precondition for evolutionary specialization for all aspects of the organism, not just its pollination system (Futuyma & Moreno 1988).

One misconception is that flowers that fit very well into a syndrome and that are, by evolution, specialized to use a particular class of pollinators, are visited only by that class of pollinators. Actually, they may be visited by many other animals as well, and they may be pollinated by animals that they are not particularly adapted to. Curiously, many flowers seem adapted to a narrower range of animals than actually pollinate them. This led Stebbins (1974) to postulate that flowers are adapted to their principal pollinators. Precise definitions are elusive but subsequent authors have considered that both abundance and pollen-transfer capability should be important (Armbruster 1988). A flower's principal pollinator has usually been spoken of in the singular as though it were one species or one type of pollinator, like hummingbirds, bumble bees or sphinx moths. It would usually be more proper, though perhaps awkward, to speak of a plant as being adapted to a principal class of pollinators.

If syndromes exist, it must indicate that the classes of pollinators have some fixity throughout the recurring evolutionary drama. Plant lineages arise from time to time always adapting to their pollinators, and to the extent that a class of pollinators (hummingbirds) differs from other classes of pollinators (bees, flies, moths), the many characters of the syndromes are selected for over and over again. In the case of hummingbird plants, flowers tend to become red with narrow tubes, exserted anthers, reduced landing platforms, floppy pedicels, copious dilute nectar that has a high sucrose:hexose ratio, and (we think) rapid pollen presentation. Repeated convergence of this sort argues for the reality of an 'adaptive peak' for ornithophily.

It would seem that pollination by the 'wrong' pollinator is important in the process of floral evolution. Baker (1963) reasoned that it is a precondition for a lineage to undergo a pollinator shift. A pollinator shift is a change from using one class of pollinators to using a different class of pollinators. Such shifts would seem to be unlikely in principle: if a plant's phenotype is well adapted to one pollinator, and the pollinator is well adapted for extracting food from the flowers, how do we envision gradual selection changing the phenotype to something that is adapted to a different pollinator and that now discourages the visits of the formerly effective pollinator? Thompson (1994) speaks of a 'selective sieve' as being necessary for a plant to make an evolutionary choice among a number of animals, but he does not outline particular mechanisms. The simplest general explanation involves geographic separation of the interactors: a plant population finds itself in a situation where its former principal pollinators are rare or absent but another class of visitor is abundant. If the flowers already have some capacity to have their pollen transported by this abundant visitor, natural selection then favors characters that make the flowers more attractive to the abundant visitor and that makes the visitor a more effective pollinator. The abundant visitor becomes the new principal pollinator.

Losing mutualists: the view from PPT

Geographic displacement may not be necessary for a plant to evolve away from a formerly principal pollinator, as the results of PPT indicate. Consider a plant with various possible pollinators located in $D \bullet R$ space as in Fig. 4. Suppose first that there is only one pollinator, say a bee denoted by A. It is a beneficial mutualist and selection will act to mold the flower's morphology, pollen presentation and nectar scheduling to extract the most delivery possible from this pollinator. During this selection phase, the location of the pollinator in $D \times R$ space may change, but let us assume that it stabilizes somewhere (as in Fig. 4a). Because we are considering this pollinator to be a bee, the stable point will reflect the resolution of a conflict of interests between the bee, which is under selection to return as much pollen as possible to its larvae, and the plant, which is under selection to restrict that source of loss.

Next consider that a new pollinator, B, joins the community and visits the plant at a certain rate. PPT models can show the consequences for adding a new pollinator. For a simple case, assume that B has the same R but higher D. It is therefore a better pollinator, and on a per-visit basis, more of the grains transferred will be transferred by it. If the difference between A and B is small (Fig. 4b), both may be mutualists, but if the difference is large (Fig. 4c), A's visits may actually have a negative effect on pollen donation (context-dependent parasitism, see 'Pollen presentation theory' section). In this situation, an allele that decreases visits by A will spread. This may occur by making it harder for A to get nectar, thereby leaving more for attracting visits by B. As B becomes the dominant visitor and A becomes marginalized, selection should once again adjust visitation rate and pollen dosing

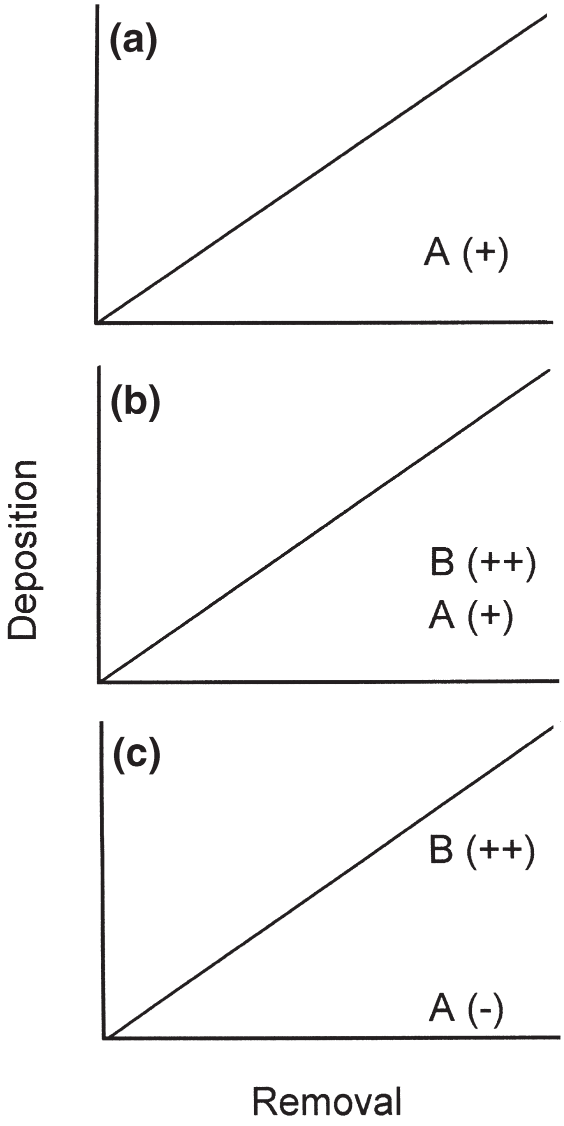

Fig. 4 (a) A single pollinator species, A, is beneficial to its host plant despite a low D-value. (b) If a higher-D pollinator species, B, becomes available, species A becomes less valuable. If the difference between the pollinators is small, A may still have a net positive effect. (c) However, if B has much higher deposition than A, A may be an effective parasite (as indicated in Fig. 2).

to a new stable point determined by the biology of species B.

We need to build more detailed and realistic models of selection to understand this process. It seems likely, however, that in the simple case where a series of pollinators are arranged one above the other in $D \bullet R$ space like rungs on a ladder, the plant can 'climb the ladder', discarding lower species and adjusting to higher species, all in sympatry and without invoking the disappearance of any of the species as a precondition for adapting away from it. The result is specialization. We can now make Stebbins's (1974) principle more specific by saying that, in such a case, the pollinator at the top of the ladder is the 'most effective.' Note that this species need not be the most abundant, nor the species that removes the most pollen grains. In more realistic cases, pollinators will not necessarily fall along vertical lines in $D \bullet R$ space, and the possibilities of transitions become more complex (see Fig. 3b).

The evolution of specialization is thought to require a trade-off (Futuyma & Moreno 1988). Such a trade-off is frequently viewed in terms of adaptation to one of two possibilities: we say that there is a trade-off if a constitutional change in the make-up of an organism that makes it better adapted to one species concomitantly renders it less adapted to another interactor. This is different from the process of climbing a ladder across $D \bullet R$ space. If we add B to the mix, the loss of A's value to the plant does not arise through any change in the constitutional ability of the plant to use A. The phenotype is unchanged, but it is no longer capable of deriving benefit from a former mutualist. The evolution of specialization by this mechanism might be better described as 'trading up' than 'trading off.'

Syndromes in adaptive landscapes

According to the principle of gradualism, shifts between pollination syndromes presumably take many generations of incremental change in the many characters involved. The best response to selection comes from variation in each character based on many genes of small additive effect. If selection is consistent, a substantial shift might occur in a few scores of generations, as is possible under artificial selection. It is more likely that hundreds of generations are involved in those pollinator shifts that amount to changes between recognized syndromes, namely dramatic changes in many characters. On the phylogenetic scale, though, such major pollinator shifts could seem rapid. They might be evident between sister species with the intermediate stages being ephemeral. If we consider this problem in terms of the classical adaptive landscape, we could expect such changes if the adaptive landscape between the two syndromes is a smooth saddle. Once a plant population crosses the low point of the saddle, selection would quickly move it to near the adjacent peak. If the adaptive landscape has well separated peaks, then we should rarely find species that are intermediate between syndromes. On the other hand, if there are ridges between, say, ornithophily and mellittophily, then we would expect to find many plants adapted to pollination by both birds and bees. Whether syndromes are discontinuous remains an open question (Armbruster 1990).

We argue, however, that the adaptive landscape is a poor metaphor for the PPT argument outlined in Fig. 4. We should not suppose that there is one peak for pollinator A and a second, higher peak elsewhere in phenotype space for pollinator B. As we set up the model, the plant was initially well adapted to pollinator A. The advent of pollinator B – with no change whatsoever in the phenotype of the plant – immediately rendered the plant less capable of deriving benefit from A. When the values of different pollinators depend on each other's presence, the addition or loss of potential mutualists will modify the landscape, perhaps radically (Wilson & Thomson 1996).

Although pollinator shifts between pollination syndromes provide the classical scenario for floral evolution (Grant & Grant 1965; Johnson *et al*. 1998), we believe it is not the only way in which flowers diverge and it is probably not even the most prevalent mode of floral evolution (Wilson & Thomson 1996). Many species of plants are distinguished by floral characters without there being any known difference in their principal pollinators. Species of *Calochortus* (Liliaceae), for example, differ primarily in floral characters, and in choice tests insect visitors distinguish between the different *Calochortus* species, but the flowers are still generalists. They attract long lists of visitors that vary greatly from site to site (Dilley *et al*. 2000). These lilies, at least the many species within the subgenus *Mariposa*, seem to have radiated without any lasting specialization or any clear pollinator shifts. It is possible that such divergence happens through what Wilson and Thomson (1996) called adaptive wandering, which fits very tidily into Thompson's (1994) 'geographic mosaic theory of coevolution'. The lineages may have adapted to disparate classes of pollinators throughout evolutionary history but did not develop exclusivity. Individual populations adapt for a time to one kind of principal pollinator but the lineages descend through an ever changing mosaic of pollinators.

Pollinator shifts can occur between broader and narrower classes of pollinators. Thus, a lineage may have flowers that are broadly adapted to many sorts of bees and then shift to being narrowly adapted to hummingbirds. Conversely, pollinator shifts may involve expansions, such as being narrowly adapted to pollination by long-tongued Bombyliidae, then shifting to being more generally adapted to pollination by a suite of longish tongued flies and bees. Shifts between comparably sized classes are also possible, of course. An example of such a shift would be between bumble bee and hummingbird pollination. Some kinds of shifts may be more frequent in evolution than are others. Perhaps birds are so reliable and effective that plant populations that are adapted to birds are almost never better pollinated by bees. Perhaps bird pollination leads to lower rates of cladogenesis and larger species ranges that result in less 'exploration' of the adaptive landscape. Perhaps bird pollination increases the probability of extinction over bee pollination. Such biases in evolutionary shifts have been studied for seed dispersal syndromes by Janson (1992), and it would be very interesting to apply Janson's methods to pollination syndromes (Armbruster 1993).

Systematic rules

The essence of pollination syndromes is the associations among floral characters and between those characters and the principal pollinators. However, the language of syndromes often takes on radical connotations. Is it meant that syndrome groups are discontinuous clusters with few plants in between? Is it meant that the floral characters involved are more strongly shaped by adaptation to their particular pollinator than by phylogenetic ancestry? Is it meant that characters predict pollinators and that pollinators predict characters, both with great accuracy? We suspect that the discrimination is not nearly so absolute, but we would welcome data that explicitly address these issues. To some, the term 'syndrome' has connotations beyond those of the term 'adaptive patterns.' We prefer to avoid these connotations by focussing on systematic rules. Familiar examples of systematic rules include Bergmann's rule ('Mammals and birds that live in cold places tend to be larger than close relatives that live in warm places.'), Gloger's rule ('Animals that live in dry places tend to be lighter in color than close relatives that live in moist climates.') and Jordan's rule ('Fishes of cold waters tend to have fewer vertebrae than relatives from warm waters.'). Rules with a similar logic are implicit in classical notions of floral evolution. Thus we could say, 'In the New World, red flowers are frequently visited and effectively pollinated by hummingbirds.' Notice that this allows red flowers in the Old World to be pollinated by beetles (Dafni *et al*. 1990), it allows hummingbirds to visit flowers that are not red (Waser 1982) and it does not preclude other visitors from also being pollinators at red New World flowers (Chittka & Waser 1997). The rules can be worded as precisely and with as many conditions as called for. In Table 1, we summarize some adaptive rules concerning bird-pollinated flowers based on pollination lore (Faegri & van der Pijl 1979; Wyatt 1983; Proctor *et al*. 1996). Similar tables could be made concerning flowers pollinated by many other classes of pollinators.

The mystery of pollination syndromes and systematic rules is why they exist. Waser *et al*. (1996) wrote, 'Actual pollination systems often are more generalized and dynamic than these traditions might suggest.' The constraints on behavior and morphology do not seem so rigid and pollinator generalization is predicted when floral rewards are similar among plant species. Flowering periods are often too short to provide food for the entire life of a pollinator. Furthermore, travel is costly and flower-foraging animals opportunistically switch between plant species. Lastly, it is not uncommon to observe a wide range of animals visiting one species of flower regardless of its supposed syndrome. Such questioning of the existence of syndromes has been based on intensive ecologic study of single plant populations. But authors who have questioned syndromes are also quick to admit that systematic patterns do exist. Ollerton (1996) expressed this tension in his title, '*Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant-pollinator systems*.' Chittka and Waser (1997) wrote:

> Assuming that the association between hummingbirds and red flowers is real, we are left with a new enigma about red coloration. Since it is not an adaptation to match an innate preference of hummingbirds, nor a means to exclude bees, red coloration might perhaps be an adaptation to enhance detectability for birds.

These authors do not dismiss the existence of a macroevolutionary pattern, even though they question the prevailing microevolutionary explanations for it.

Ornithophily versus melittophily in *Penstemon* and *Keckiella*

Considered the largest herbaceous genus endemic to North America, *Penstemon* contains some 250 species, often broken down into subgenera, sections and subsections (Bennett *et al*. 1987). *Keckiella* contains seven species. Although phylogenetic studies coordinated by Andrea Wolfe (Ohio State University) are underway, the present taxonomy is not phylogenetic (Holmgren 1979). Nevertheless, we are confident that there has been repeated evolution of hummingbird-pollinated flowers from bee-pollinated flowers. There are at least seven pairs in which an ornithophilous species is evidently more closely related to a paired melittophilous species than to any of the other six ornithophiles. We have studied seven of these pairs at various sites in western USA and Mexico. Table 2 documents the characters in which these flowers follow or do not follow eight of the systematic

Table 1 Systematic rules concerning pollination by birds. All rules are most applicable when comparing close relatives

- In the New World, red flowers are visited and effectively pollinated by hummingbirds. Ornithophilous flowers in general tend to be reddish or orangish
- Ornithophilous flowers are generally odorless, even when their moth-, fly-, bat- and bee-pollinated relatives have odors. For instance, the only odoriferous *Penstemon* is *Penstemon palmerii*, which has vestibular bee-pollinated flowers
- Ornithophilous flowers tend to have copious amounts of dilute nectar, while melittophilous flowers tend to have small amounts of viscous nectar. However, hummingbird flowers that are otherwise able to exclude bees have higher nectar concentrations (Bolten & Feinsinger 1978)
- Unlike 'insect flowers' and 'passerine flowers', 'hummingbird flowers' tend to have high sucrose:hexose ratios (Baker & Baker 1983; Freeman *et al*. 1985; Elisens & Freeman 1988)
- Hummingbird flowers have lower concentrations of amino acids than do passerine flowers (Martínez del Rio *et al*. 1992)
- Ornithophilous flowers tend not to have nectar guides. Even when their close relatives have nectar guides, ornithophilous flowers have weakened nectar guides especially in the ultraviolet
- Ornithophilous flowers tend to be robust; thick walls protect the ovaries and nectar from insect robbers
- For zygomorphic flowers, those frequented by birds tend to have less prominent lower lips than do flowers pollinated by bees who enjoy a landing platform
- Flowers that are principally pollinated by hummingbirds tend to have more inclined flowers or flowers that are on flexible pedicles compared to their relatives that are pollinated by bees and other insects that must alight on the flowers
- Passerine-pollinated flowers tend to be either near perches or parts of them function as perches
- Hummingbird flowers have narrower tubes than do bee-pollinated relatives but have broader tubes than do lepidoptera-pollinated relatives
- Hummingbird flowers tend to have more exserted anthers and stigmas than do bee pollinated relatives.
- Hummingbird-pollinated flowers have anthers that open more fully and more rapidly than do bee-pollinated flowers

Table 2 Comparisons of pollination syndrome characters of seven pairs of close relatives in *Keckiella* and *Penstemon*. Each 'Yes' is in answer to a question about whether that contrast conforms to what is expected of bird versus bee pollination syndromes. The 'No' answer means that *P. eatonii* had higher concentration nectar than *P. speciosus*, contrary to expectation. Each 'Tie' denotes that the two species do not appear to differ

	Taxon block genus *Keckiella*	subgenus *Dasanthera*	subgenus *Habroanthus*	subgenus *Saccanthera*	section *Peltanthera*	subsection *Fasciculi*	subsection *Campanulati*
Bird-visited species	*cordifolia*	*newberryi*	*labrosus*	*rostriflorus*	*centranthifolius*	*hartwegii*	*kunthii*
Insect-visited species	*rothrockii*	*davidsonii*	*speciosus*	*leatus*	*grinnellii*	*gentianoides*	*campanulatus*
Bird-visited species has:							
more red or orange coloration*	Yes	Yes	Yes	Yes	Yes	Yes	Yes
a longer or narrower tube*	Yes	Yes	Yes	Yes	Yes	Yes	Yes
more exserted anthers and stigma?	Tie	Yes	Yes	Yes	Tie	Yes	Yes
a less pronounced landing platform?	Yes	Tie	Yes	Yes	Yes	Yes	Tie
an inclined flower or flexible pedicle?*	Yes	Tie	Yes	Yes	Yes	Yes	Yes
a higher production of nectar by volume*[1]	Yes[2]	Yes	Yes[3]	Yes	Yes	Yes	Yes
nectar of a lower concentration NS[1]	Yes[2]	Tie	No[3]	Yes	Yes	Yes	Yes
less restricted pollen presentation?*	Yes	Tie	Yes	Yes	Yes	Yes	Yes

The table as a whole has a significant ratio of yes:no (48 : 1, $P \ll 0.001$ by a sign test). Asterisks denote lines with significant yes:no ratios (*$P<0.05$); NS indicates $P>0.05$; lines without an asterisk or an NS have too many ties to test.

[1] Median values of nectar measured on flowers that opened while in bridal veil bags under clear skies. [2] For nectar data, the bee-visited species was *Keckiella breviflora*. [3] For nectar data, the hummingbird-visited species was *Penstemon eatonii*.

rules concerning differences between ornithophily and mellittophily.

Comparison 1

Both ornithophilous and melittophilous flowers are found in *Keckiella*, which is probably a monophyletic group, based on several synapomorphies: dense and often stiff hairs at the bases of the filaments; nectar secreted by the hypogynous disk below the attachment of the filaments; a shrubby habit with leaves that are evenly spaced along extended stems (Straw 1966). *Keckiella cordifolia*, *K. corymbosa*, and *K. ternata* have flowers that are red and follow the hummingbird syndrome. During three 30-min censuses, and during noncensus observations, we observed hummingbirds visiting *K. cordifolia*, we also saw visits by small pollen-collecting bees. The other four species of *Keckiella* are mostly yellow or white and generally follow the bee syndrome. At these species taken as a group, we have done 30-min visitor censuses at 10 sites. Nectaring bees were abundant, including *Xylocopa*, *Bombus*, *Anthophora*, *Apis*, *Osmia*, *Centris* and *Megachile*; it was common for there to be some small pollen-collecting bees also. We have never seen a hummingbird visit one of these flowers, and once we saw hummingbirds obviously bypassing *Keckiella rothrockii* flowers to visit the ornithophilous flowers of *Penstemon labrosus*.

Comparison 2

In *Penstemon* subgenus *Dasanthera*, *P. newberryi* and *P. rupicola* have magenta flowers, whereas *P. davidsonii* has blue-violet flowers. These are evidently close relatives, given their suffrutescent wiry growth, the shape and position of leaves, and the dense hairs they have on their anthers. We have visitor censuses from nine sites of *Penstemon newberryi*. Hummingbirds foraged on them at five of the sites but this species is also visited for nectar by worker bumble bees (who can just barely fit into the flower), by *Osmia* bees and occasionally by honey bees. Some individual bumble bees actively collected pollen from *P. newberryi* and we also found the usual suite of small pollen-collecting bees. We studied the blue-flowered *Penstemon davidsonii* at one site, where it was visited by many bumble bees of several species (mostly taking nectar) as well as occasional wasps (*Pseudomasaris vespoides*).

Comparison 3

Species of *Penstemon* subgenus *Habroanthus* are united by the synapomorphy of having sagittate anthers that dehisce by slits from their distal tips toward the central connective (Crosswhite 1967). The plants are herbaceous and subsucculent, and their largest leaves tend to be basal. The red-flowered species are in section *Elmigera*, while the purple-flowered species are in section *Glabri*. We have visitor censuses on the red *P. labrosus*, *P. eatonii* and *P. barbatus*. Hummingbirds were observed at four of the five sites and we saw occasional pollen-collecting bees. For the purple *P. speciosus*, we have 30-min censuses from five sites, at which we saw no hummingbird visits, a great abundance of *Osmia* bees collecting nectar, usually a few *Anthophora* bees and *Pseudomasaris* wasps, and sometimes bumble bees and longhorn beetles. In Colorado, we have spent a great deal of time studying *P. strictus* (Thomson 1996; Thomson *et al*. 1997; Williams & Thomson 1998). Bumble bees visit throughout the day, with single flowers receiving 100–200 visits per day. *Pseudomasaris* and *Osmia* are present but are less frequent. *Selasphorus* hummingbirds occasionally make a few visits near dawn but never visit regularly.

Comparison 4

Penstemon subgenus *Saccanthera* contains the red-flowered *P. rostriflorus* as well as many purple-flowered species. These are united by having anthers that dehisce only near the connective. We have 30-min visitor censuses at *Penstemon rostriflorus* for five sites. Although hummingbirds visited vigorously during most censuses, we worked at one site near Mammoth Lakes, California, for 2 weeks without seeing any hummingbird visits. At another site only a few kilometers away, hummingbird visits were common. *Penstemon rostriflorus* flowers were also visited by many species of pollen-collecting bees, mostly small ones but also occasional bumble bees that turn upside down and buzz the anthers. For nine of the purple-flowered *Saccanthera* species, we have 16 visitor censuses. We have seen only one hummingbird visiting any of these species. *Osmia* bees of several species are the most abundant visitors. We also regularly find *Pseudomasaris* wasps, *Oligodranes* flies, *Eulonchus* flies, and the bees *Bombus*, *Anthophora*, *Ceratina* and *Apis*, as well as pollen-collecting bees such as *Lasioglossum* and small *Hoplites*.

Comparison 5

Penstemon subgenus *Penstemon* section *Peltanthera* contains both red-flowered species such as *P. centranthifolius* and many other gradations of pink to violet to purple-flowered species such as *P. grinnellii*. Although the phylogeny is not clear enough for us to establish synapomorphies, the section seems distant from most other penstemons in position, shape and texture of the leaves. *Penstemon centranthifolius* with its long narrow tube is consistently foraged on for nectar by hummingbirds in our many censuses of this species. At the other end of the spectrum, we never found *P. grinnellii* or *P. palmerii* to be visited by hummingbirds, and we suspect the nectaries must be inaccessible to them. They are visited principally by large-bodied bees such as *Xylocopa* and *Bombus*. *Penstemon spectabilis* has a morphology somewhat in-between these two extremes, and in our three 30-min censuses it was visited for nectar both by bees and by hummingbirds. It is also visited by the wasp *Pseudomasaris vespoides*, although we do not concur with Straw's (1956) characterization of it as being 'wasp pollinated'. Moreover, George (1974) presented good visitor records showing that the difference between *P. spectabilis* and *P. centranthifolius* was not strong enough to prevent hybridization. Many of the populations we have studied, including *P. centranthifolius,* were visited by an assortment of small pollen-collecting bees, regardless of floral syndrome (Mitchell 1989).

Comparison 6

Penstemon section *Fasciculus* subsection *Fasciculi* is characterized as having flowers that are remarkably large and leaves that are entire or nearly so with axillary fascicles of smaller leaves. Straw (1962) described both hummingbird and bee flowers. He wrote that *Penstemon fasciculatus* is

> visited frequently by hummingbirds, but not seen by us to be visited by insects. [*Penstemon hartwegii*] is one of the largest-flowered of the genus, with a broadly open tubular corolla that is visited regularly by both hummingbirds and bees, especially of the genus *Bombus*. Its reddish-purple color and broader shape are not typical [of mellittophily], although its general aspect and pendulous attitude are more consonant with typical bird-pollinated species.

Similar notes are made about the other red-flowered species where pollinators had been observed. In contrast, Straw wrote of the purple-flowered *P. gentianoides*,

> It is visited and apparently primarily pollinated by large bees of the genus *Bombus*, which are able completely to enter the corolla seeking the nectar that is copiously secreted on the outer bases of the upper pair of stamens. It is also visited, however, by other bees and at least occasionally by hummingbirds.

Our observations confirm Straw's statements.

Comparison 7

In *Penstemon* section *Fasciculus* subsection *Campanulati*, the leaves have axillary fascicles of smaller leaves as in the previous group but the leaves are usually sharply serrate and the flowers are generally somewhat smaller. *Penstemon kunthii* is dark red, and *P. campanulatus* is purple with a white throat. According to Straw (1963), who had spent four field seasons working on this section, the former species is typically hummingbird pollinated, whereas the latter species is bee pollinated. Again, our observations agree.

Testing the systematic rules

In Table 2, we judge each comparison and each character, whether or not a hummingbird-visited species is more like ornithophilous flowers are said to be than is a hymenopteran-visited species. We answer 'yes' 48 times and 'no' only once. There are seven 'ties', that is cases in which the species are similar and have evidently not diverged. On the null hypothesis that yes and no answers are equally probable – i.e. that bird- and bee-visited species differ from each other at random – the chances of getting our results by chance alone are vanishingly small. For lines with no more than one 'tie', we can also test particular systematic rules. The color difference, the floral-tube length difference, the inclination of the flower, the quantity of nectar produced and the pollen presentation difference are all significant in the expected direction ($P < 0.05$).

Our conclusion that the bird flowers had more restrictive pollen presentation is based mainly on the visual appearance of the fully dehisced anthers. For Comparison 1, the anthers of *K. rothrockii* are barely spreading at dehiscence, but if we had focussed on other bee-visited species such as *K. breviflora*, we would have recorded a tie, with the hummingbird-visited species. Comparison 2 does seem to be a tie, and in this case all the species have densely woolly anthers. We do not yet understand the function, if any, of the wool. For Comparison 3, Fig. 5a and b show scanning electron micrographs of anthers from the melittophilous *P. speciosus* and the ornithophilous *P. labrosus*, respectively. Other bird-visited species for this contrast, such as *P. eatonii* and *P. barbatus,* also have slightly more open anthers than other bee-visited species such as *P. strictus*. Comparison 4, shown in Fig. 5c and d, is a striking contrast between the purple *P. leatus* and the red *P. rostriflorus*. *Penstemon leatus*, like many other hymenopteran-visited species in its group, has a special mechanism by which pollen is removed: the anthers have teeth that rasp against the back and wings of the pollinator, thereby vibrating pollen out of the locules, which barely crack open (Torchio 1974). Comparisons 5, 6 and 7 all involve species in which the anthers generally are fairly open. Nevertheless, in each pair the bird-visited species appears to open more fully and faster than the bee-visited species.

Our test constitutes a block design, where the blocks are taxonomic units. It would be better if they were explicit phylogenetic units because then we could be sure they are independent and we could polarize the direction of evolution (Maddison 1990). The test as we have done it does not address whether ornithophily evolved from mellittophily or vice versa or some mixture of the two. Given that the outgroups of penstemons are all melittophilous, though, it is parsimonious to assume that some of the six cases are polarized as bird flowers evolving from bee flowers. The blocking removes much of the similarity due to relatedness. If we had not blocked but instead had pooled seven ornithophilous species and compared them to seven melittophilous species, then the syndrome difference would have been lost among taxonomic variation for many characters, including anther dehiscence. This is because the subgenera differ in how their anthers dehisce. Unfortunately, for just seven comparisons significance tests for each character are problematic. In the future, the number of comparisons could be greatly expanded by moving beyond the confines of *Penstemon* and *Keckiella*.

Refining pollen presentation and nectar characters: preliminary studies

Although the relative openness of anthers is the only aspect of presentation that we have analyzed in Table 2, it is only one component of the presentation schedule. The timing of anther openings within a flower is also important, as is the opening schedule of flowers within inflorescences. We lack data on these processes. What ultimately matters, though, is not the timing of events but how those events affect the amounts of pollen that are removable by visitors. Ideally, we would want to know how many grains are placed on each of many animals that visit a flower at brief intervals. Because of the impracticality of such studies, we have instead experimented with artificial

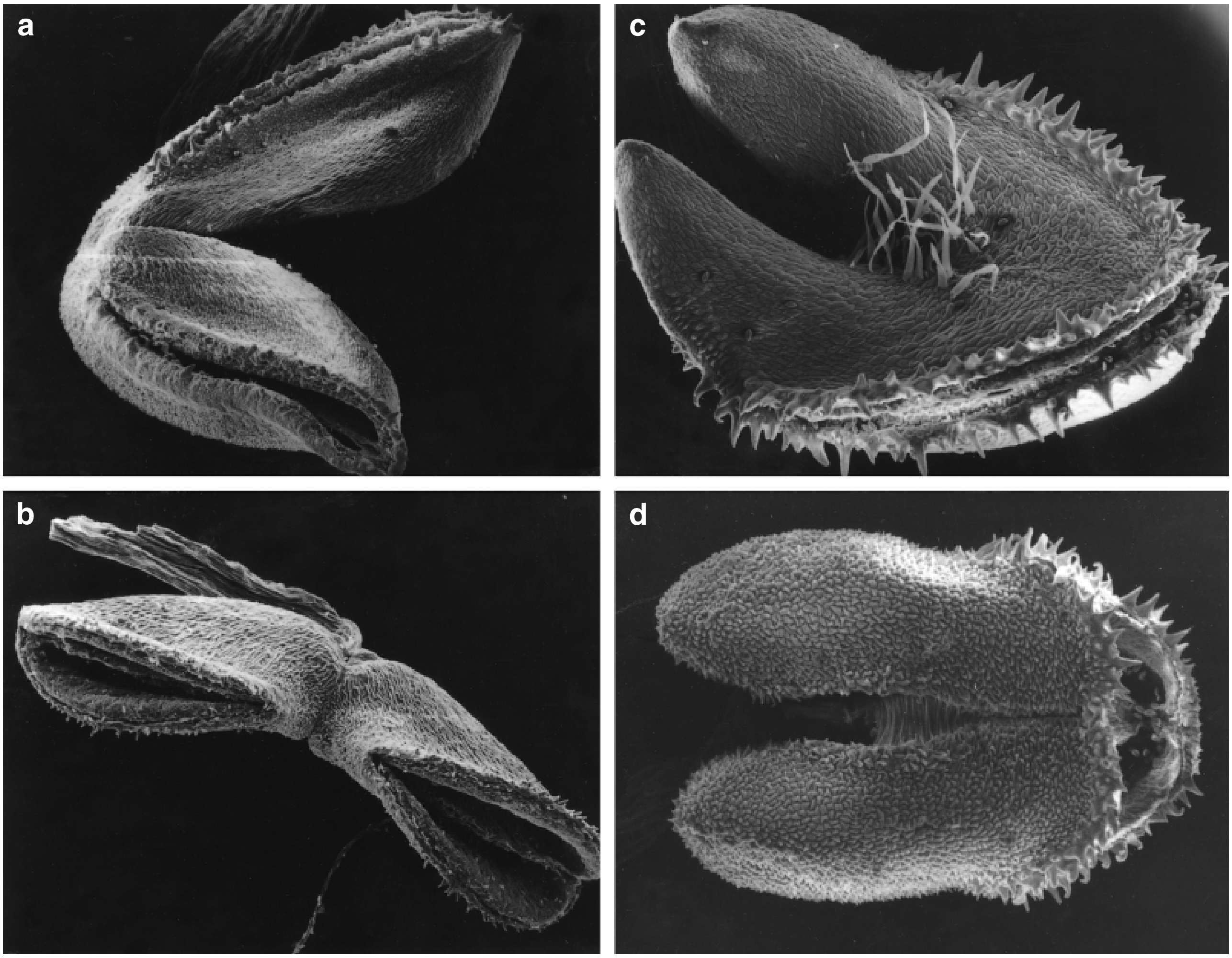

Fig. 5 Scanning electron micrographs of mature anthers of two pairs of related melittophilous (upper) and ornithophilous (lower) species of *Penstemon*. (a) *P. speciosus*; (b) *P. labrosus*; (c) *P. leatus*; (d) *P. rostriflorus*.

removal using small squares of velvet fabric to visit the flowers. After inserting and withdrawing a velvet square to simulate a flower visit, we place it on a microscope slide, add a drop of acetone to dissolve the pile of the fabric, add melted glycerin jelly tinted with basic fuchsin, and complete the mount with a cover slip. By sampling at frequent intervals, in 1998 we were able to construct pollen presentation curves for potted *P. strictus* held in controlled environmental conditions (Fig. 6). In the same species, we examined the rate of nectar refilling after drainage, by inserting precision-cut paper wicks and measuring the length that the wick moistened (Fig. 7). Clearly, new nectar is made available quickly after a visit. The rapid nectar replenishment and the gradual pollen dosing are both consistent with the high rates of bee visitation to *P. strictus*. We will extend these observations to other species.

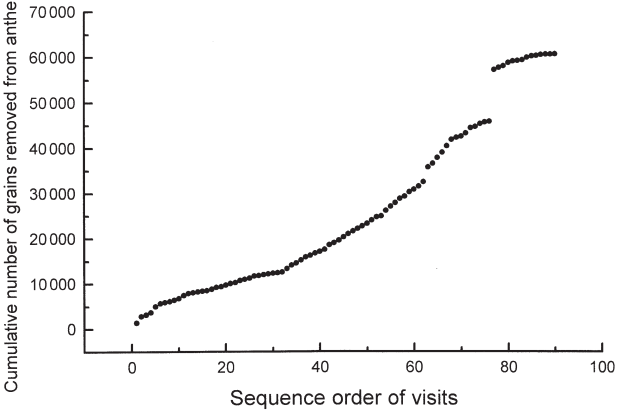

Fig. 6 Preliminary data showing extremely gradual dosing of *Penstemon strictus* pollen over many flower 'visits' with velvet squares (see text). The data come from one flower, sampled at 10-min intervals during daylight hours over 2 days.

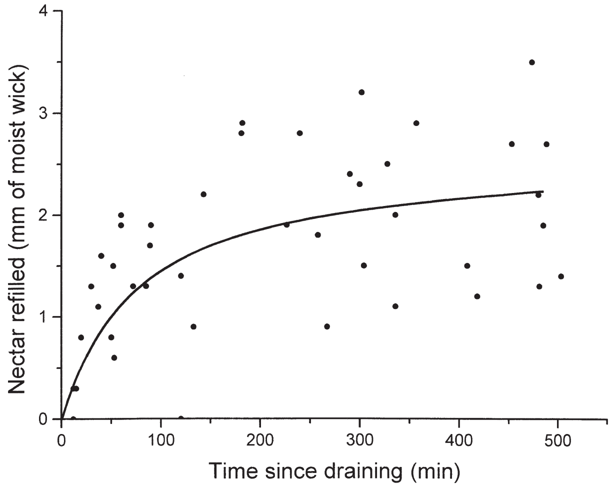

Fig. 7 Preliminary data showing the time-course of nectar refilling after *Penstemon strictus* flowers have been drained by blotting up nectar with filter paper. At various intervals after draining, new nectar was sampled by inserting narrow wicks of filter paper into the nectaries. Nectar volumes are approximated by the length of the wick that was moistened by nectar.

Pollinator shifts in Penstemon

Although penstemons conform satisfyingly well to the systematic rules that contrast ornithophily to mellittophily, we hasten to add that these plants are often visited by animals other than their designated principal pollinators (Bateman 1980; Reid *et al.* 1988; Mitchell 1989). In particular, the ornithophilous species are abundantly visited by many species of small bees and even by bumble bees. The vast majority of these are pollen collectors that are not nectaring. They seem to transfer some pollen while also consuming large quantities. In the presence of pollinators that are primarily nectaring and not actively collecting pollen, we suppose that the pollen collectors are detrimental, not beneficial, to the plants. They probably remove large quantities of pollen from the system that they never deposit on stigmas and that would have a better chance of reaching stigmas if it got onto the face of a hummingbird. In our terminology, pollen collectors are likely to be HRLD when compared to the LRHD hummingbirds. As the syndrome characters hold so well with respect to nectar collectors, this leads us to think that the characters of at least the corolla are principally adapted to those nectar collectors, and natural selection has not shaped the corolla to appeal to or to fit the pollen collectors.

Pollen-collecting bees may play similarly negative roles even in melittophilous penstemons. For example, although the great majority of visits to *P. strictus* at Irwin, Colorado, are by nectar-seeking bumble bees that receive pollen passively on their dorsa, a few visitors, usually *Bombus bifarius*, adopt a different behavior. These individuals do not probe for nectar, but turn upside down, grasp the anthers and 'buzz' the pollen out by audibly vibrating their thoracic muscles. Given that *P. strictus* has very high visitation rates and restrictive anthers, these features should interact to dispatch an extremely large number of small doses of pollen. These characters seem well suited to the nectaring bees but the pollen-collectors probably defeat the dosing mechanism and remove more pollen than is optimal for the plant. Vibrating these anthers with a musical tuning fork does remove most of the pollen.

We can now return to *D* • *R* space to reconsider the evolutionary transition from bees to birds in *Penstemon*. There are probably some intermediate morphologies, like that of *P. newberryi*, for which either bees or birds are reasonably effective pollinators, but we can envision these morphologies as unstable because a *penstemon* probably cannot be well adapted for birds and bees simultaneously. On such an intermediate plant, we might expect bees to remove more pollen per visit and to deposit less, as indicated by the 'starting points' in Fig. 8. First, consider an ecologic situation that produces low visitation rates. This would favor less restrictive anthers, to get pollen in to circulation. Open anthers, however, are subject to pollen removal by both HD visitors, like hummingbirds, and LD visitors, like bees, especially pollen-harvesting bees. Therefore, any characters that favor bird visits while reducing bee visits will be favored and anthers will evolve to be less restrictive. As this floral evolution takes place, the position of the hummingbirds in $D \bullet R$ space will follow the dashed arrow toward the upper-right vertex of the triangle in Fig. 8. Although constricted corollas, a reduced landing platform and dilute nectar may well discourage visits by nectar-seeking bees, it may be impossible for selection to produce a penstemon morphology that resists anther stripping by small pollen collectors. At least in colder habitats, however, hummingbirds will be active earlier in the day than will bees. Therefore, we predict that ornithophilous *Penstemon* species will produce nectar and present pollen early in the day, thereby reducing losses to pollen collectors. There is a positive feedback that drives this trajectory: the more successfully the plant excludes bees, the greater the value of less restricted pollen presentation. The less restricted the presentation, the greater the cost of 'improper' visits by bees. Barring a radical disruption of the pollinator fauna, this sort of ornithophily should be practically irreversible.

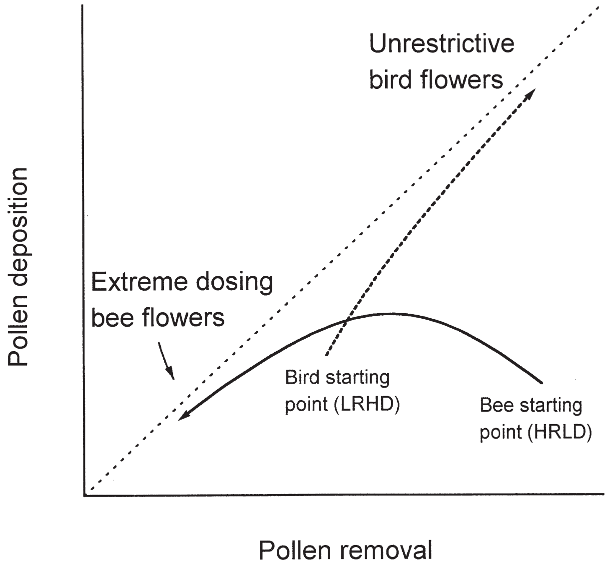

Fig. 8 Proposed evolutionary trajectories in $D \bullet R$ space for a hypothetical *penstemon*, showing alternative evolutionary pathways along which positive feedbacks push phenotypes toward ornithophilous forms with less restrictive anthers (upper right) or toward melittophilous forms with very restrictive anthers, depending on visitation rates (see text). Note that the starting points of the two trajectories represent how birds and bees might differ in removal and deposition when visiting an unspecialized flower. Bees would be expected to remove more pollen than birds but birds might deliver a considerably higher fraction of the grains they remove.

Second, suppose an intermediate, *P. newberryi*-like plant faces ecologic circumstances that produce high visitation by a mixture of many bees and just a few birds. Here, all of the pollen would go into circulation, but almost all of it would be taken by bees and delivery would be inefficient due to diminishing returns acting through grooming. Selection could then favor more restricted dosing of pollen, coupled with higher visitation rates choreographed by quickly replenished nectar. Again, positive feedback operates. The position of the dominant bees in $D \bullet R$ space would move in the direction of the solid arrow in Fig. 7, as the plants evolve a high-visitation strategy of many small doses, as exemplified by *Penstemon strictus*. As high visitation rates favor more and more restricted anthers, bird visitors would become less and less relevant because they could mobilize only small amounts of pollen. As anthers become more restricted, however, pollen-collecting bees may develop more efficient behaviors, such as buzzing, that may set up an arms race between plants and bees. We suggest that arms races of this sort may have produced, in other plant families, the 'buzz pollination' syndrome reviewed by Buchmann (1983): poricidal anther dehiscence, the loss of nectar production, and total dependence of the plant on vibratory collectors to set pollen in motion. In *Penstemon*, things have not gone so far; the nectar economy has never been abandoned. Extreme pollen dosing (the left vertex of the $D \bullet R$ triangle, Fig. 8), however, might inhibit reversions to ornithophily.

Although we have concentrated on the striking hummingbird syndrome, many species boundaries have arisen in *Penstemon* without any pollinator shift. We have collected visitors from dozens of hymenopteran-pollinated species. Some of these differ in being visited by large bees (such as *Xylocopa* and *Bombus*) versus small bees (such as *Osmia*), but the much more common situation is for there to be no evident pollinator distinction between closely related species. A great many penstemons are pollinated by a broad assemblage of bees (*Osmia*), wasps (*Pseudomasaris*) and flies (*Oligodranes*). Thus, it appears that floral divergence can happen via pollinator shifts but that very often cladogenesis and some floral divergence happens without any lasting pollinator shift. This does not necessarily mean that pollinators are not the agents of diversifying selection that were responsible for the floral divergence. Flowers may well diverge by adapting to different pollinators without any commitment to those pollinators arising, namely by adaptive wandering through a mosaic of species interactions (Thompson 1994; Wilson & Thomson 1996; Dilley *et al*. 2000).

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