

When Is It Mutualism?

(An American Society of Naturalists Presidential Address)*

James Thomson[†]

Department of Zoology, University of Toronto, Toronto, Ontario
M5S 3G5, Canada

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Whence my possibly cryptic title? At the simplistic level that most of us first encounter plant-pollinator relations—in a basic textbook, an introductory lecture, or a television documentary—three elements tend to be stressed. First, there is a matchup between particular types of animals and particular types of flowers. Not only do animals visit plants nonrandomly within local communities, but also certain suites of floral characters seem to covary with each other and with patterns of animal visitation at regional scales and possibly global scales. These suites of covarying characters constitute “pollination syndromes” (Fægri and van der Pijl 1979). Of the relationship between plants and animals that has produced these matches, two aspects tend to be stressed: it is mutualistic, and it reflects coevolution between plant and animal. The mutualism seems comparatively obvious: visitors usually get fed; visited plants donate and receive pollen. The coevolutionary aspect is necessary to explain striking adaptive matches such as the extraordinary correspondence between extravagantly long nectar spurs and extravagantly long insect tongues. Incautious extrapolation from these three elements could lead one to think that each plant might be hooked to its own specific pollinator, that the identity of that pollinator could be inferred from the floral morphology, that the

plant and pollinator show exquisite mutual adaptations, and that they might even cospeciate.

Here, things get delicate. On the one hand, the unraveling of animal pollination as a mutualism by Sprengel (1793, 1996), the interpretation of animals as agents of natural selection on floral characters by Darwin (1862), and the recognition and compilation of syndrome-like patterns by Müller, Delpino, and others (Müller and Delpino 1869) represent a cluster of inspired triumphs of natural history. On the other hand, all three aspects of the trinity—matchup, mutualism, and coevolution—need closer and more skeptical investigation.

Many investigators have pointed out that specialized, obligate relationships between particular plant and pollinator species are rare and unusual. Therefore, these are poor exemplars of the sloppier, generalized relationships that overwhelmingly prevail in nature. Going a step farther, a recent article by Waser and colleagues not only stressed the prevalence of generalized relationships but also questioned the applicability of the “pollination syndrome” concept (Waser et al. 1996; see also Ollerton 1996). This skepticism has provoked reaction (e.g., Armbruster et al. 2000), stimulating active debate about the explanatory power of syndromes. Although syndromes will figure largely in my talk, my main concern is the essence of mutualism.

My title is a direct allusion to Daniel Janzen’s (1980) *Evolution* article titled “When Is It Coevolution?” Although Janzen’s article was aimed more at plant-herbivore interactions, it and other work from that period largely demolished two prevailing notions: first, that plant-animal coevolution betokened mutual adaptations in specific pairs of plants and animals that were locked together in a cospeciating evolutionary embrace, and second, that intimate associations of plants and animals observed in the present meant that those species had been interacting for many generations together. It became necessary to qualify terms that were formerly comfortable, to speak of diffuse coevolution, to consider vanished interactors and opportunistic replacements, and to ask focused questions about

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[†] E-mail: jthomson@zoo.utoronto.ca.

what was really coevolving with what. My essay aims to do a similar hatchet job on mutualism.

Evolved Pollinator Shifts

In particular, I want to show how a pollinating animal may function as a mutualist to a plant in some ecological circumstances but as a parasite in others. That is to say, the sign of the net interaction depends not only on the intrinsic properties of the species but also on the biotic background in which they interact. Because of this, we should not say that insect species A is a mutualist for plant species B. The furthest we can go is to say that A helps B at some particular place and time but might hurt it in some other situation. I will use this notion of conditional parasitism to ask questions about evolutionary transitions from one pollinator to another. To restrict attention to nontrivial transitions, I want to consider transitions from one pollinator syndrome to another. I think we need some special thinking about what evolutionary forces could account for a plant being well adapted for pollination by bees, for example, and then canceling that arrangement in favor of hummingbirds. Such a change poses a conundrum because it requires coordinated changes in a suite of characters—specifically, those characters that constitute floral syndromes. These typically include the nectar economy, which rewards visitors and choreographs the visitation schedule; the pollen economy, which transforms material investment into fitness; and the morphological aspects of flowers, which signal to visitors and mechanically constrain their activities.

Changing all these characters ought to be evolutionarily hard. For an analogy from human affairs, we could think of this as akin to restructuring the pollination workplace and specifying a completely new job description for the position of pollinator. For evolutionary biologists, the metaphor of adaptive landscapes may be more compelling. If pollination syndromes are real, then those phenotypes should represent adaptive peaks. If that is true, they should be separated by adaptive valleys that should, in some respects, be hard to cross. Having hung this straw man out to dry, I will next try to set fire to him by looking at models of the process of pollen transfer. These models have provided my lab's focus for some years, and for brevity I have started calling them pollen presentation theory (PPT). This theory gives us mechanistic insights into the balance between mutualism and parasitism.

To render concrete what would otherwise be an abstract discussion, I then turn to a large taxon of plants in which transitions between bee and bird pollinator syndromes seem likely to have occurred. On the basis of the early stages of ongoing collaborative work on the sister genera *Penstemon* and *Keckiella*, I ask two main questions: first,

does the syndrome concept apply with real force in this group; that is, have we a right to expect adaptive peaks? Second, does PPT seem relevant in this group; that is, are we justified in using those models and theoretical results to interpret pollinator transitions in these genera? (Sacrificing suspense for clarity, both answers will be yes.) These results help me support an explanation for pollinator transitions based on the transformation of mutualism into parasitism.

To begin, I want to consider why some classical considerations of pollinator transitions are not adequate to the task of explaining major transitions. First, since my entry into the field of pollination ecology, I have seen approving references to the most effective pollinator principle of Ledyard Stebbins (1970), generally cited in aid of various causes, including pollinator shifts, as if it were a highly explanatory concept. When I looked it up, I was surprised by the brevity of the statement.

The characteristics of the flower will be molded by those pollinators that visit it most frequently and effectively in the region where it is evolving. Hence when an evolutionist speaks of a "bee flower" or a "hummingbird flower," he refers to its relationship with the predominant and most effective vector. He does not mean that the flower is pollinated exclusively by this vector. Secondary vectors, such as *Bombus* on *Aquilegia*, may retard the process of evolutionary modification, but they are not likely to stop it or destroy the genetic integration of a floral type once it has evolved. (P. 319)

Clearly, this is not about pollinator transitions; it is about accounting for the presence of flower visitors that do not seem to be what the flower has been adapted for. In fact, this follows a section in which Stebbins defends the reality of pollinator syndromes. As I read it in context, his real purpose here is to counter claims by others that syndromes lack reality because they are not exclusive—because, say, hummingbird syndrome flowers also get visited by bees. This seems correct to me, but it certainly does not go far toward explaining evolved pollinator shifts. In fact, Stebbins explicitly indicates that a transition from a primary, adapted pollinator to a secondary one would be unlikely. Furthermore, Stebbins's view of these different pollinators is simplistic in two ways; first, he folds pollinator abundance and effectiveness together, as if these are equivalent properties or as if they must covary. Although his exact intention is unclear, he seems to treat all visitors as mutualists and the most abundant of these as the most effective pollinator, the one that drives adaptation. Second, Stebbins does not define "effective" in terms of anything that one can measure, which leaves the reader wondering if the most effective pollinator principle is anything more than a tautology. That is, floral evolution is determined by the most effective pollinator, but "most effective" seems

(by default) to be defined as the pollinator that has determined floral evolution.

Another early treatment with much more to say about evolved pollinator transitions is the masterful work by Grant and Grant (1965) on the Polemoniaceae:

A population of flowers ... becomes adapted to (a) broad range of pollinating agents in its territory. ... Now the spectrum of flower-visiting animals undergoes changes along an ecogeographical transect ... the climate of pollinators ... changes.

As a result, two populations of the same plant species may both receive effective pollinating visits from the same two classes of pollinators, say bees and beeflies, but receive the two types of visitations in different relative frequencies. If one local race receives a greater number of effective bee visits ... , natural selection will favor floral adaptations to the special characteristics of bees. ... The point of compromise will shift in correspondence with the climate of pollinators. (Pp. 162–163)

This is getting much closer to the heart of the matter: plants are seen as adapting to an overall array of pollinators in any locality. As that array—the climate of pollinators—changes over geographical space, so the plant becomes adapted to different pollinators. The Grants' metaphor of pollinator climate is a good one. Note, however, that their scenario does not really account for the most stringent case: a plant moving from one adaptive peak to another, from one well-defined syndrome of characters to another whole set, which is a fundamental change of job description. Rather, the specified starting point is a generalist floral phenotype that caters to both sorts of pollinator. I also think that the Grants, like Stebbins, stumble a bit on the question of pollinator effectiveness and abundance. By dichotomizing pollinators as effective or not, they necessarily treat relative pollinator abundance as the variable that matters. This is a misstep, I believe, that arises from acquiescing to the proposition that pollination is mutualistic. By taking a closer and more mechanistic view of pollination, we can arrive at a more critical and useful view that turns us away from that oversimplification.

In this quest, we can turn to Janzen (1986, p. 44) again, because what I have been trying to do is more or less in accordance with his prescription for studying mutualism, which is to study not mutualism but rather seed dispersal, pollen dispersal, ant defense, or whatever concrete process is distributing fitness gains and costs.

Mutualism is not a complex subject and is easily explored through the application of common sense and natural history knowledge.

Mutualism has been thought to death; what we need are solid descriptions of how organisms actually interact. (P. 44)

Pollen Transfer Dynamics

For 20 yr now, much of my lab's attention has been focused on the fates that befall pollen grains as pollinators interact with flowers. (Several other groups have been similarly occupied [e.g., Price and Waser 1982; Campbell et al. 1991; Morris et al. 1995; Rademaker et al. 1997].) Because grains are small and numerous, this is fussy work; still, we have made progress in quantifying some basic relationships involving the amount of pollen presented by a flower's anthers, the amount that an animal dislodges during a visit, and the amount of that removed pollen that gets delivered to recipient stigmas. Our early studies exploited a pollen-color dimorphism in the bumblebee-pollinated lilies *Erythronium grandiflorum* and *Erythronium americanum*. For example, we could estimate the pollen content of an unvisited red-pollen donor flower by measuring the sizes of the undehisced anthers. After pollen had been presented, we could get a bee to visit that donor and then visit a long series of yellow-pollen recipients. We could harvest the recipients' stigmas and visually count up the number of red grains delivered and then go back to the donor and count how much pollen remained in the anthers.

Through these studies and others by colleagues, we have accumulated enough data to support the collection of modeling efforts that I call PPT. Many students and colleagues have been instrumental in the design, data collection, and modeling, especially Lawrence Harder, Paul Wilson, and Will Wilson. The brilliant insights of David Lloyd (especially Lloyd 1984) were also very important in forming our approaches. Had he not become so tragically incapacitated, I am sure that pollen presentation theory would have been developed much further by now and with more power and grace.

Of the ecology of pollen transfer, one aspect leaped out from our studies of apid bees: much of the loss of pollen grains between anthers and stigma is attributable to active grooming on the part of the animal. Indeed, one can frequently see a bee leave a flower with a visible dusting of pollen, but during its flight to the next one, a variety of specialized grooming combs come into play as the bee uses all six legs to move loose pollen from exposed body surfaces into tidy, moistened corbicular pellets on the hind legs. Most of the loose grains are taken out of circulation for good, frequently within seconds of leaving the anther. In consequence, pollen carryover curves for such bees tend to fall off quickly in a decline that is steeper than exponential (Thomson 1986; Morris et al. 1995; Harder and Wilson 1998).

Furthermore, these bees usually remove a large fraction of the pollen that is freely available in a flower, frequently 70%–90%. If a flower presents all of its pollen simulta-

neously, only a handful of visits will therefore settle the fate of all of those grains. The anthers are quickly stripped clean, few of the grains are delivered, and most are wasted, at least from the plant's point of view if not from the bee's.

Another factor that frustrates the paternal aspirations of a plant is that loading up a bee with too many pollen grains only stimulates more intense bouts of grooming (Harder 1990a, 1990b). Thus, presenting more pollen produces diminishing returns in male reproductive success. Note that these results may well be specific for bees and may not hold for other pollinators.

Turned into straightforward mathematical models of pollen bookkeeping (Harder and Thomson 1989; Thomson and Thomson 1992, 2001; Harder and Wilson 1998), these relationships have several consequences, three of which are essential to my arguments concerning pollinator transitions. First, when pollen transfer follows these patterns, a plant may attain great gains in male function by restricting the amount of pollen that a bee can take in a visit, as long as visits are frequent. In the circumstances modeled by Harder and Thomson (1989, their fig. 4d), for example, a flower that will receive 25 visits will do best if it allows each visitor access to only one-tenth of its grains. If an infinite number of visitors could be attracted, the perfect flower would bestow a single grain on each of them. Pollen restriction can be achieved by both packaging and dispensing tactics, which seem almost ubiquitous in animal-pollinated plants (Harder and Thomson 1989).

The second result concerns total pollen delivery by different hypothetical pollinator species that differ in their rates of pollen removal and delivery (Thomson and Thomson 1992). The contrasts between these different visitors are sharpest when pollen is not dosed but rather is presented simultaneously. The relevant result here is that total pollen delivery quickly saturates with increasing visit number if a visitor removes a large amount of pollen. If two pollinators remove the same amount per visit, their total delivery curves will saturate equally quickly as visits increase. If they deliver different amounts, the delivery curve of the high-deposition species will be higher than that of the low-deposition species. Because of this, an infinite number of visits from a high-removal, low-delivery species will not deliver more pollen than only a few individuals of a species that removes the same amounts of pollen per visit but delivers more of it. When pollen depletion is taken into account, therefore, the relationship between pollinator abundance and effectiveness is certainly not what was envisioned by Stebbins or the Grants.

To understand why, think of pollination as a process of transferring water by bucket from a supply reservoir (i.e., pollen from a focal plant's anthers) to a receiving vessel (i.e., a set of stigmas). All pollinators are akin to leaky buckets; they vary with respect to the size of the bucket

and the number of holes through which they leak. Imagine that your job is to transfer as much water as possible into the receptacle. As you work away with your bucket, which leaks moderately, a friend comes by with a leakier bucket and offers to help. Do you want his help or not? If your supply reservoir is Lake Ontario, you should say yes; anything he transfers will be effectively added to what you transfer. However, if the supply vessel is, say, a bathtub that you will be able to empty in the time allotted, you should decline the assistance. He will spill water that you would have been able to transfer if you were working alone.

I summarize these interactions in new simulations (fig. 1) that show how many additional grains would be delivered by adding one visit from an inferior pollinator (species 2, the friend with the leakier bucket) to a situation in which a flower was already receiving some number of visits from a better pollinator (species 1, the better bucket). The main points to note are that the worse pollinators, no matter how leaky they may be, are always valuable mutualists if there is no better pollinator available. However, they can easily act as pollen-wasting parasites if the flower is successfully attracting enough visits from a better pollinator; that is, their efforts add a negative number of grains in any case where the curves fall below the horizontal line at 0. Exactly how baneful these pollen pigs can be depends on pollen removal rates; in figure 1 (*top*), both species take 70% of the remaining pollen. If both take 30%, the curves shift up (fig. 1, *middle*). If species 2 acts as a very large, very leaky bucket, the curves shift down (fig. 1, *bottom*).

Although these models are nothing more than simple-minded bookkeeping for pollen grains, my contention is that such bookkeeping exemplifies the "common sense and natural history knowledge" that Janzen (1986, p. 44) recommended for figuring out how so-called mutualisms work. Furthermore, I think that a good way to start making sense of plant-pollinator evolutionary responses is to compare the leakiness of different pollinators' buckets and explore the ecology of the region around the horizontal line where mutualists turn into parasites. With that in mind, colleagues and I proposed that hummingbirds and bees would be fundamentally different pollinators because the birds are not interested in pollen as food. Initially, I saw this as a way to test whether PPT model results were actually relevant to floral evolution: if so, bee-adapted species should have more restrictive pollen presentation than bird-adapted relatives.

The genus *Penstemon* seemed close to ideal for asking these comparative studies. First, it is large; second, some excellent colleagues were willing to join me in collaborative studies. In particular, Andrea Wolfe's fearless attack on the phylogeny of this giant genus has been essential. Third,

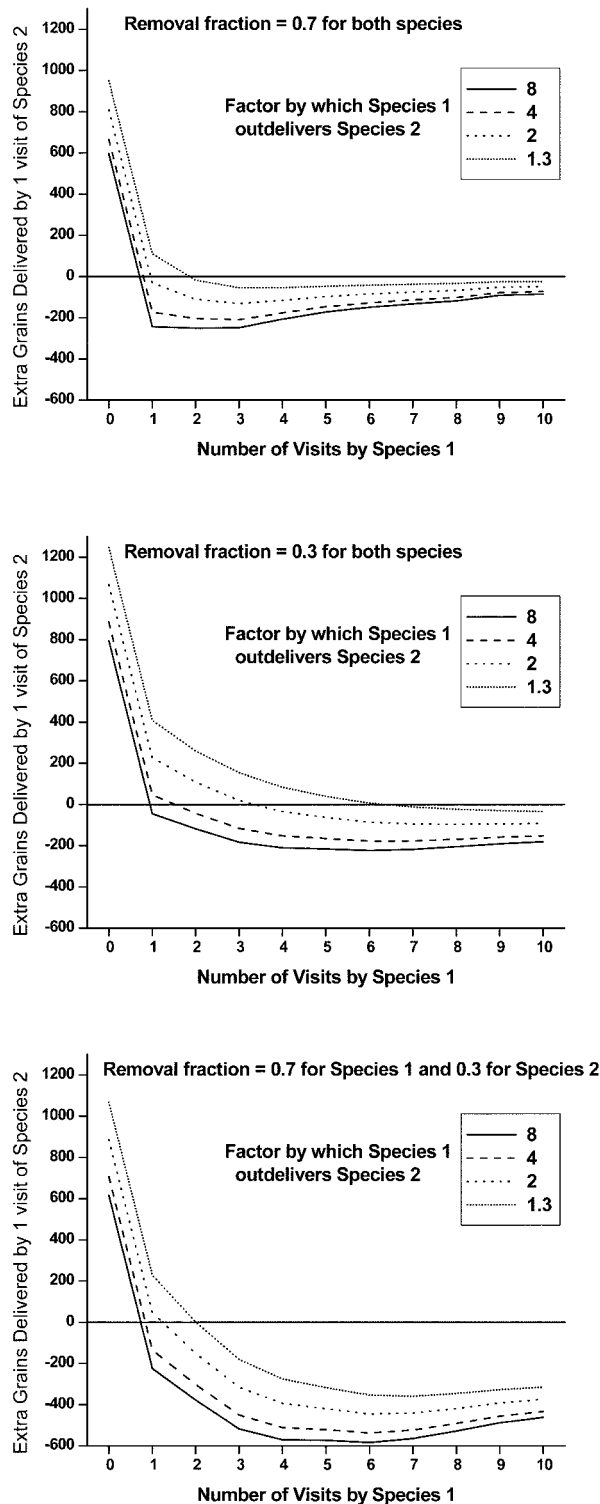


Figure 1: Results of simulation models in which a focal flower (which presents its pollen simultaneously) is visited by two species of pollinators that may differ in the fraction of pollen that they remove from the focal flower's anthers per visit or the fraction of that removed pollen that they

there is immense variation in flower shape and color, with some species that fit the classic hummingbird-adapted syndrome and some others that conform well to the bee syndrome. Fourth, *Penstemon* has access to elegant ways of restricting pollen presentation through both packaging and dispensing (Straw 1956).

To consider packaging first, some species open the four anthers in a flower sequentially, frequently over 2 d. In other species, the anthers all open within an hour or two. Turning to dispensing, some species open their anthers fully, exposing all of the pollen. Others, however, open only grudgingly. A narrow slit acts to meter out small doses of pollen to many visitors. Fifth, and most important, the red-flowered, apparently bird-adapted species are spread across the evolutionary tree, occurring in all subgenera. Although Wolfe's tree is still taking shape, it looks now as if bird-type flowers have evolved in at least 14 separate lineages.

On the pollination ecology side, Paul Wilson has led a broad survey of floral characters and quantification of visitor spectra in natural populations, with special emphasis on related pairs of putatively bee- and bird-adapted taxa. We have been careful not to classify a species as bird adapted because it is red. Instead, we identified seven species pairs where one was visited by birds and the other was not, then we compared those species to see how well their differences conformed to expectations regarding seven classic syndrome characters and one novel syndrome character (table 2 in Thomson et al. 2000). We predicted that bird-visited species would have more red or orange coloration, longer or narrower corolla tubes, more exerted sexual organs, less developed lower lips (landing platforms), floppier flower pedicels, higher nectar volumes, lower nectar concentrations, and less restricted pollen presentation. The last was the novel prediction. Character variation within each pair conforms extraordinarily well to syndrome expectations for the classic syndrome characters. For our new prediction regarding pollen presentation, anther morphology conforms to the prediction (photographs in Thomson et al. 2000). For example, in the subgenus *Habroanthus*, all species have anthers that open grudgingly, but the bee-visited *Penstemon speciosus* is more restrictive than the bird-adapted *Penstemon labrosus*.

deliver to stigmas. Both fractions are modeled as constants, given in the figures. The two types visit in random order. The vertical axis indicates how many additional grains would be delivered by a single additional visit of species 2 to a flower that is already receiving a certain number of visits by species 2. Where the curves drop below the horizontal line at 0, species 2 functions as a pollen parasite; where the curves exceed 0, it acts as a beneficial mutualist.

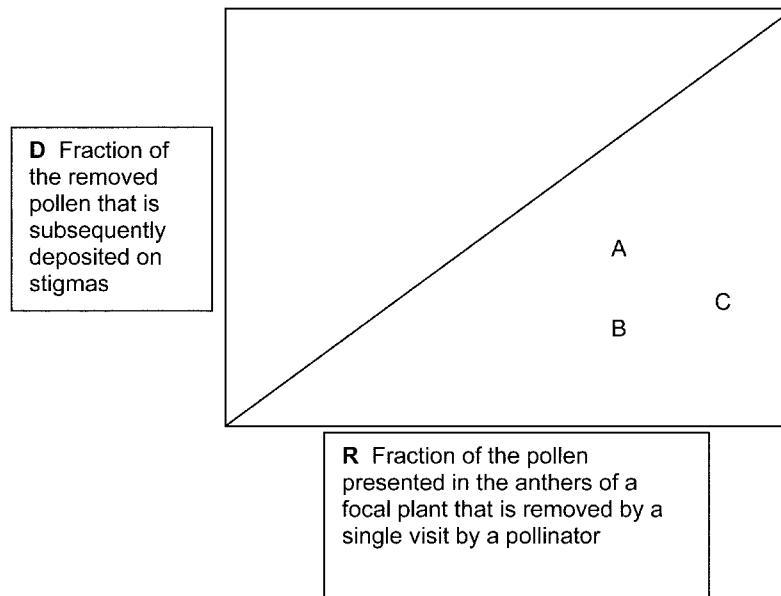


Figure 2: Variation among pollinator species in pollen removal and deposition (as in fig. 1) can be mapped in R-D space, in which each species is represented by a point. If two pollinators both remove the same fraction per visit, the most effective will simply be the one that delivers more of that pollen (e.g., species A is a more effective pollinator than species B). If two pollinators differ in both removal and deposition rates, however, (e.g., species B vs. species C), which one is more effective depends on the expected number of visits from each. Therefore, determining pollinator effectiveness requires a milieu analysis, as described in the text, to determine the marginal value of an increase in visitation by each species.

Differences in how widely anthers open need not necessarily translate to different pollen dispensing, so we are looking for the expected relationship by repeatedly visiting flowers with little squares of velvet fabric and then counting the numbers of grains extracted. These results are preliminary, but anther performance aligns well with morphology. Comparing two bee-adapted species in separate subgenera, we find that the one with patent anthers (*Penstemon whippleanus*) gets rid of its pollen in fewer visits than one with slitlike openings (*Penstemon strictus*). Comparisons of closely related bee and bird species (*P. strictus* and *Penstemon barbatus*) are also going in the right direction, so far.

The analysis of these species pairs, plus additional data from work in progress, provides affirmative answers to the two questions posed earlier. Yes, a prediction of pollen presentation theory is upheld in this taxon, indicating that floral characters have responded to selection for efficient donation of pollen. Yes, pollinator syndromes do appear to be well defined in *Penstemon/Keckiella*, at least when hummingbird flowers are considered.

Although we retain some skepticism about certain uses and interpretations of pollinator syndromes, they certainly work well in the hummingbird portions of our study clade. Steven Jay Gould has famously said that if we could rewind the tape of evolution and play it again, it would come out

differently. That is no doubt true at many levels, but *Penstemon* and *Keckiella* have played the tape of evolving hummingbird pollination at least a dozen times, and it always comes out very much the same.

I can now loop back to the main question of how penstemons are able to jump syndromes from bee to bird pollination. Penstemons served by apid bees are being served by a very leaky bucket. At least some, like *P. strictus*, have responded with the beautifully paired adaptations of a rapidly replenishing nectar flow and tight-lipped pollen dosing. The nectar flow can bring 100 bumblebee visits to a flower in a day, and the pollen dispensing ensures that each of those visitors takes away at least a little pollen (Williams and Thomson 1998; M. C. Castellanos, unpublished data). These are wonderful tactics for making the best of a pollen-consuming pollinator, but if circumstances of biogeography or community ecology bring hummingbirds into regular contact with these flowers, it is quite likely that the pollen-wasting bees could be immediately demoted from mutualists to parasites. This is easier to see if we envision different pollinators located on coordinate axes representing their pollen removal and deposition rates (fig. 2). If pollinator A removes the same amount per visit as species B and delivers more of it, A is simply a better pollinator. If the difference is marked, A's presence can turn B into a parasite. Selection should always favor up-

grading from a very leaky bucket to a less leaky one; once the conditional parasitism threshold has been crossed, any traits that favor increased visits by birds will be favored, as will any traits that discourage visits by bees.

It has been suggested before that some of the floral characters associated with the hummingbird syndrome may be best interpreted as devices to reduce bee visitation (e.g., Raven 1973). Our models reinforce this conjecture. Most likely, hummingbird plants do not have thin corolla tubes because birds find them aesthetic; they have them to protect nectar from nectar-seeking bees. Hummingbird plants do not have dilute nectar because birds like weak drinks; like any good sugar consumer, a hummingbird would probably prefer pancake syrup if it could get it. For smaller bees, though, the costs of carrying water around are more prohibitive. It is important to note that getting rid of bees is seldom completely successful. Starting with the basic penstemon flower, although nectar-collecting bees can be eliminated, it does not seem possible to completely eliminate pollen collectors. In a hummingbird-adapted system, these pollen collectors probably have strong negative effects. These are the sorts of secondary visitors that Stebbins disparaged as not being important in shaping floral adaptations. However, it may be more accurate to say that they have contributed to floral evolution but in a negative way. (And still, if the hummingbirds disappeared, these bees might well become the most effective pollinator.)

I conclude with some miscellaneous reflections. The first is a fairly obvious caveat: this pollen-centric perspective of floral evolution is clearly a pet idea. My colleagues and I tend to see how many aspects of flowers we might possibly be able to explain with reference to pollen presentation tactics. This is heady but dangerous: there is grandiosity in this view of life. As the more mature results of the *Penstemon* project emerge over the next few years and receive a proper critique, we should get a better idea of the validity of this enterprise.

Second, we can remove that whiff of tautology from Stebbins's most effective pollinator principle by allowing an operational definition of effectiveness. If life were simple and all pollinators removed the same amount of pollen per visit (species A and B, fig. 2), the most effective pollinator would simply be the one with the greatest delivery fraction. But things are not that simple, and if pollinators do not line up vertically (species A and C, fig. 2), which one is more effective depends on the expected numbers of visits. Therefore, any measurement of a pollinator's effectiveness depends on the ecological milieu. If we know the visitation rates, the pollen presentation schedules of the plants, and the removal and deposition characteristics of the pollinators, we can construct a "milieu analysis" that can calculate how many additional grains, ΔG_i , would

be delivered by a single additional visit of each species i of pollinator. The pollinator with the highest ΔG_i is the most effective. This pollinator need not be more abundant than a less effective pollinator, so we can improve on both the Stebbins and the Grant formulations by throwing out the misleading inferences that a pollinator must be abundant to catch the eye of natural selection. Indeed, the most effective pollinator can be quite rare, as long as it is especially potent in getting grains to stigmas. Viewing pollination effectiveness as milieu dependent is a particular case of Thompson's (1994) "geographical mosaic" model of species interactions (also see Thompson and Pellmyr 1992).

Third, it is important to consider the contrast between conditional parasites, as defined here, and the animals that are commonly called cheaters in mutualisms. There is a burgeoning literature on cheaters, who usually circumvent floral mechanisms by robbing nectar without pollinating (Maloof and Inouye 2000; Irwin and Maloof 2002) or by preying on ovules without pollinating (Herre and West 1997). These situations are not the same as conditional parasitism in the sense that I have used it. All of these situations do involve what Janzen would call "parasitism of the mutualism," and to some extent these other cheating situations may grade into conditional parasitism, but the parasites I have been considering are completely legitimate pollinators; they are just not very good at it from the plant's point of view. An aside here is that people have tended to assume that host-specialized oligolectic bees are especially superior pollinators of the plants that they are specialized for visiting. This need not be true; indeed, such bees are very effective at harvesting pollen, but they may be comparatively poor at delivering it.

Fourth, it should be clear that the metaphor of an adaptive landscape—with one phenotypic peak representing bee-adapted flowers and another representing bird-adapted flowers, with a valley of poor phenotypes in between—is not really useful for describing bee to bird shifts in *Penstemon*. If we must stick with a topographic model, a better metaphor might be that a particular phenotype has evolved to get the maximum pollination efficiency possible from bees. It has thus climbed to the top of a fitness peak, but this peak is something like an old cinder cone of a dormant volcano. A change in community ecology that brings in hummingbirds is akin to a new eruption that punches up a new cone from a lateral vent. Our plant, without changing its phenotype or losing fitness by descending into a valley, now finds itself on the flank of a higher mountain, whose peak represents adaptation to birds (and away from bees). Under the influence of natural selection, it begins to climb the new peak. It is clear that mutations of large effect can be potent forces in the evolution of pollinator shifts (Schemske and Bradshaw 1999).

Nevertheless, milieu analysis suggests that shifts could also arise by gradual accumulation of small effects, following a sustained, quantitative change in the spectrum of flower visitors.

Fifth, the phenomenon of conditional parasitism—which basically means that the services of different pollinators are not additive but can interfere with each other—ultimately depends on the supply of pollen being finite and depletable: a bathtub rather than a Great Lake. Is this a peculiarity of pollination systems, or does it occur in other mutualisms? I believe that this sort of nonadditivity probably occurs in most but not necessarily all mutualisms. In fruit dispersal interactions, for example, frugivores use up fruits just as pollinators use up pollen. In ant-guarded plants, extrafloral nectar can be depleted. Space in domatia may be somewhat less depletable in practice, but it certainly is depletable in principle. Gut symbionts also may be limited by depletable space. The least depletable example I could think of would be the recruitment of parasitoids by volatile chemicals released by plants that are being eaten by folivores. Here, I can see little cost of recruiting some weaker parasitoids along with better ones; it is harder to envision conditional parasitism here. In any case, I think that people who are trying to categorize and compare mutualisms would do well to consider this point, because I think it is relevant to how shifts could evolve.

Finally, with some reluctance, I raise the question whether we should continue to describe pollination as being a mutualism. When a bee can visit a plant, disperse some of its pollen grains to other stigmas, and still have a negative effect on the plant's fitness, can we justify using a term that implies by definition that the plant has benefited from the relationship? If we consider plant-pollinator relationships to be members of the set of mutualisms, along with other set members such as gut symbioses, we have inverted the real hierarchical structure; we have drawn the wrong Venn diagram. In fact, mutualistic plant-pollinator relationships constitute a subset of all plant-pollinator relationships. I am not someone who goes on semantic crusades, but in my own work, I have begun to speak more often about plant-pollinator relationships and much less often about mutualism.

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