

Pollination efficiency and effectiveness of bumble bees and hummingbirds visiting *Delphinium nelsonii*

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Resum

WASER, N. M. & M. V. PRICE (1990). Eficàcia i eficiència de la pol·linització d'abellots i colibrís que visiten *Delphinium nelsonii*. Collect. Bot. (Barcelona) 19: 9-20

Delphinium nelsonii Greene és una planta perenne de floració primaveral que creix a les Muntanyes Rocoses de Nordamèrica. Les seves flors blaves s'acorden a la clàssica «síndrome de pol·linització per abellots», però, a l'oest de Colorado, són visitades per colibrís (durant la primera meitat del període de floració) així com per reines d'abellots (principalment durant la segona meitat del període). Els experiments amb plantes conreades en testos mostraren que un abellot diposita unes 10 vegades més de pol·len quan visita una flor que quan ho fa un colibrí, i origina la formació d'un nombre de granes unes 10 vegades més elevat. Tanmateix, tant els abellots com els colibrís es mostren similars en la «qualitat» del pol·len lliurat, per exemple, en llurs distàncies de creuament. Al nivell de les poblacions totals de pol·linitzadors, les taxes de visita dels colibrís poden ser unes 10 vegades més altes que no pas les dels abellots, en part perquè visiten les flors més ràpidament. Les dues menes de visitants haurien de lliurar, aleshores, quantitats de pol·len similars en conjunt, cosa que es veu confirmada per les càrregues de pol·len similars a les flors al principi i al final de la floració, i haurien de contribuir aproximadament en la mateixa mesura a la producció de granes, cosa que és confirmada per diversos experiments i diverses observacions. Les contribucions relatives exactes probablement depenen de les dimensions de les poblacions de pol·linitzadors, que en el cas dels colibrís semblen haver variat en un factor de 2.5 al llarg de 14 anys. Les contribucions similars d'ocells i abellots a la producció de granes mostren que el rendiment individual de llur pol·linització s'ha de distingir de l'eficàcia a nivell de població i que la «síndrome de pol·linització» d'una flor pot no indicar l'eficàcia actual dels seus visitants.

Mots clau: Abellots, Colorado, *Delphinium nelsonii*, Colibrís, Pol·linització, Producció de granes.

Abstract

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Delphinium nelsonii Greene is a spring-flowering perennial of the Rocky Mountains of North America. Its blue flowers conform to a classical «bee pollination syndrome», but in western Colorado they are visited by hummingbirds (mostly in the first half of the flowering season) as well as bumble bee queens (mostly in the second half of the season). Experiments with potted plants showed that a bee deposits about 10 times as much pollen while visiting a flower as does a bird, and causes about 10 times as many seeds to be set. In contrast, bees and birds appear similar in the «quality» of pollen they deliver, e. g., in its outcrossing distance. At the level of entire pollinator populations, hummingbird visitation rates may be over 10 times as great as those of bumble bees, in part because birds visit flowers more quickly. Thus the two visitor classes should deliver similar pollen quantities overall, which is confirmed by similar pollen loads of flowers early and late in the season,

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and should contribute about equally to seed set, which is confirmed by several experiments and observations. Exact relative contributions probably depend on pollinator population sizes, which in the case of hummingbirds appear to have varied 2.5 fold across 14 years. The similar contributions of birds and bees to seed set shows that individual pollination efficiency must be distinguished from population-level effectiveness, and that the «pollination syndrome» of a flower may not indicate present-day effectiveness of its visitors.

Keywords: Bumble bees, Colorado, *Delphinium nelsonii*, Hummingbirds, Pollination, Seed Set.

INTRODUCTION

In dry meadows of the Rocky Mountains in the western USA, one is likely to encounter a small, attractive perennial larkspur, *Delphinium nelsonii* Greene. The species ranges north to the states of South Dakota and Idaho, and south to Colorado, Utah, and northern Arizona, at elevations roughly between 1.200 and 3.200 m (HARRINGTON, 1964; personal observation). In montane western Colorado *D. nelsonii* forms extensive populations, with densities exceeding 50 sexually mature plants per m² in some sites and years (WASER & PRICE, 1981). Flowering begins soon after snowmelt, usually between late May and early June, and lasts about one month (WASER, 1976, 1978). From 5 to 15 zygomorphic deep blue or blue-purple flowers normally are borne on one or more racemose inflorescences. The flowers conform to a classical «bee pollination syndrome» (BAKER & HURD, 1968; FAEGRI & VANDER PIJL, 1979; see also MÜLLER, 1883; KNUTH, 1906), but observations at the Rocky Mountain Biological Laboratory in Colorado (hereafter RMBL; elevation 2.900 m) show that they are visited by broad-tailed hummingbirds (*Selasphorus platycercus* Gmelin) (Figure 1) as well as queen bumble bees (mostly *Bombus flavifrons* Cresson, *B. appositus* Cresson, *B. californicus* F. Smith, and *B. nevadensis* Cresson), and less commonly by rufous hummingbirds (*S. rufus* Gmelin), white-lined sphinx moths (*Hyles lineata* «Fabricius»), and solitary bees (*Halictus* sp.) (WASER, 1978, 1982; WASER & PRICE, 1981). These visitors collect only nectar from flowers, except for the halictids, which collect only pollen.

Of the animals just listed, broad-tailed hummingbirds and bumble bees are the most regular visitors to *D. nelsonii* around the RMBL. Indeed, reproduction and nesting of the birds seems to be synchronized in time and space with *D. nelsonii* flowering (WASER, 1976; CALDER & AL., 1983). This brings up a useful feature of the system for the studies discussed below: almost all visits to *D. nelsonii* during the first half of the flowering season are by hummingbirds. Queen bumble bees emerge and begin foraging only later, roughly during the second half of the flowering season, at which time many hummingbirds have switched to other species (WASER & PRICE, 1981).

In this paper we marshal evidence on the relative contributions of hummingbirds and bumble bees to pollination and female fecundity (seed set) of *D. nelsonii*. We ask (1) whether individual visits by birds and bees differ in the quantity of pollen they deliver to flowers and thus in their effect on seed set (hereafter «efficiency» of pollinator visits); (2) whether efficiency of bird and bee visits for seed set might depend on «quality» of the pollen delivered, in addition to its quantity (see BERTIN & WILLSON, 1980; WASER & PRICE, 1983, 1991); and (3) whether pollen delivery and seed set effected by entire pollinator populations (hereafter «effectiveness» of the two visitor classes) modifies expectations derived from individual efficiency. We then discuss implications for the use of «pollination syndromes» in determining who pollinates whom.

METHODS

To assess efficiency and effectiveness of *D. nelsonii* pollinators we draw on a decade of work at the RMBL. Some results discussed below have not been reported previously; most derive from studies done for other purposes, but were not emphasized in publications from those studies or were analyzed or presented differently. In the latter case we only summarize methods and give appropriate citations where more detail may be found. We will employ 6 main lines of evidence about pollinator efficiency and effectiveness.

First, as discussed in WASER (1988), we conducted experiments on visitation and pollen deposition to individual *D. nelsonii* flowers in an aviary in 1983, 1984, and 1986, using captive hummingbirds and bumble bees. In these experiments the hermaphroditic, protandrous flowers were emasculated in bud so that stigmas (usually 3 per flower) would be free of self pollen when they opened. We recorded pollen loads deposited on such «virgin» female-phase flowers after single visits by birds or bees that first had visited several male-phase flowers.

Second, as described by WASER & PRICE (1981), we observed natural visitation to outdoor arrays of potted plants on which we counted numbers of open flowers each day. Arrays were watched continuously so that the entire visitation history was known, and seed sets were obtained subsequently. Because we watched several arrays at once, each from a distance of about 15 m, it was only possible to obtain values for mean numbers of visits per flower averaged across each plant. We observed three replicate sets of arrays beginning early in the 1979 season, at the time of first *D. nelsonii* flowering around the RMBL, and ending 4 weeks later, when flowering was nearly completed. Relative to bird visits, bee visits were very rare in the first two replicates (3.8 % of 159 foraging bouts and 3.1 % of 1137 flower visits observed over 14 days; June 11-18 & 20-25) whereas they increased substantially in the third replicate (43.1 % of 58 bouts and 39.8 % of 171 flower visits observed over 7 days; July 2-3 & 5-9).

Third, we compared pollen loads and seed sets of flowers on plants that opened either early in the 1984 flowering season, when almost all visits were by hummingbirds (see above), or late in the season, when bumble bee visits predominated. The comparison involved pairs of flowers from plants in a field population, and has not been reported previously.

Fourth, we observed birds and bees in natural populations around the RMBL between 1975 and 1979, and recorded visitation speed (previously unreported) and characteristics such as numbers of flowers visited per plant and distances flown to subsequent plants (WASER, 1982; WASER & PRICE, 1983).

Fifth, in 1976 we compared the dispersal of fluorescent dye powders from uncaged unmanipulated plants, and from neighboring plants matched for size that were caged with wire mesh to exclude hummingbirds but not bumble bees (PRICE & WASER 1979). Dyes were carefully applied to dehiscing anthers of male-phase flowers, and stigmas of female-phase flowers on surrounding plants later were scored under a dissecting microscope at 50 power for numbers of dye grains adhering to their receptive inner surfaces.

Sixth, in 1975 we compared seed sets in plants that were bagged to exclude all visitors, caged to exclude only hummingbirds, or unmanipulated (WASER 1978). Plants were matched for size and location in a meadow.

RESULTS

Pollination efficiencies of hummingbirds and bumble bees

Two lines of investigation suggest that each bumble bee visit deposits about 10 times as much pollen on a female-phase *D. nelsonii* flower as does each hummingbird visit.

First, in 15 aviary experiments with individual *B. appositus*, *B. flavifrons*, or *B. nevadensis* queens, total deposition on the first 5 flowers of a series of sequentially-visited virgin female-phase flowers averaged 341.3 pollen grains (sd = 220.6 grains), whereas in 9 experiments with individual *S. platycercus* males and *S. rufus* males and females it averaged 32.8 grains (sd = 29.4) (WASER, 1988:43). This 10.4-fold difference is significant ($t = 7.02$, $df = 22$, $P < 0.001$, two-tailed, using log-transformed data to achieve homogeneous variances).

Second, it is possible to deduce the relative contributions of birds and bees from the 1979 experiments with potted plant arrays. In the first two replicates (with most visits by hummingbirds) multiple linear regression of mean seed set per flower on mean number of bird and bee visits per flower (based on individual plants, the level at which we could score visits) indicated that only birds had a significant effect, and that each bird visit increased seed set by about 0.4 seeds (WASER & PRICE, 1981:383). In the third replicate (when both birds and bees visited) only bees had a significant effect, and each bee visit increased seed set by about 3.0 seeds. Unlike the aviary experiments above, this 7.5-fold difference incorporates all visits that a given flower received, not only the first visit. First visits need not be representative of all visits (MOTTEN & AL., 1981; SPEARS, 1983; *contra* PRIMACK & SILANDER, 1975), but in this case the results do not differ greatly among our two types of experiment.

Quality of pollen delivered

Pollinator efficiency may depend not only on the quantity of pollen delivered, but also on its quality, assessed as the probability that each pollen grain fosters a seed and as the fitness value of that seed (WASER & PRICE, 1983, 1991). Since pollen grains contribute little or nothing to embryos in the way of nutritive resources, differences in their quality imply genetic differences. These may reflect variation among pollen donors in absolute genetic quality (i.e., additive genetic variance for fitness), or variation in the value of specific maternal-paternal combinations (i.e., dominance or other forms of interaction variance; WASER & AL., 1987).

Indeed we know that one component of pollen quality is its genetic similarity to the plant being pollinated, a form of maternal-paternal interaction. In genetically-structured populations such as those of *D. nelsonii* at the RMBL (WASER & PRICE, 1983; WASER, 1987), genetic similarity corresponds on average to physical separation of mates, i.e., to outcrossing distance. Hand-pollinations (PRICE & WASER, 1979; WASER & PRICE, 1983, 1991; WASER & AL., 1987) show that pollen from an intermediate distance of about 3.30 m evokes higher seed set and higher survival of resulting offspring in nature than pollen from shorter or longer distances. Thus one way to assess whether bees and birds deliver pollen of different quality is to determine how far they move pollen among plants.

As a first attempt we measured distances between successively-visited plants in the field (PRICE & WASER, 1979; WASER, 1982). By these measures (Table 1) hummingbirds flew farther among plants than did bumble bees. Mean flight distances among flowers were more similar, because birds visited more flowers per plant than bees. Median flight distances also were similar. There is no hint that birds and bees differ measurably in their delivery of high-quality pollen from distances of 3.30 m.

Flight distances will not reflect the final destination of pollen grains if there is pollen «carryover» (sensu WASER, 1988) from flower to flower. Indeed, the similarities just noted might disappear if bees and birds cause different carryover. However, aviary experiments indicate very similar carryover by the two pollinator classes (WASER, 1988:45).

Flight distances will combine with carryover to determine distances of pollen dispersal away from and to a plant. Measurements of movement of fluorescent dye powders (whose transfer properties mimic those of *D. nelsonii* pollen transfer fairly accurately; WASER, 1988) showed that dispersal from unmanipulated plants in the field (mean = 1.57 m) and from plants caged to exclude hummingbirds (mean = 1.64 m) were statistically indistinguishable

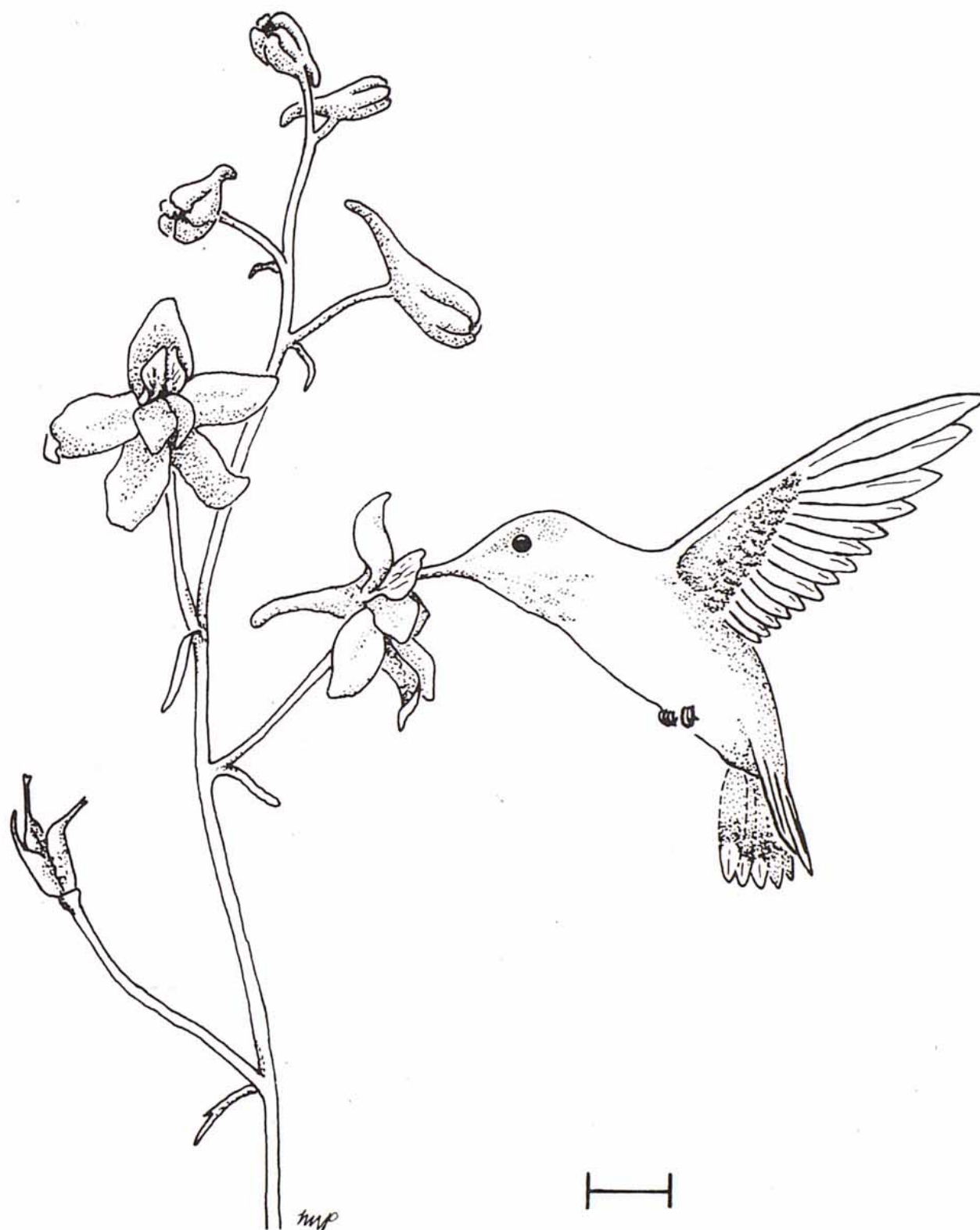


Fig. 1.— A female broad-tailed hummingbird (*Selasphorus platycercus*) visiting *Delphinium nelsonii*. The scale bar is 1 cm.

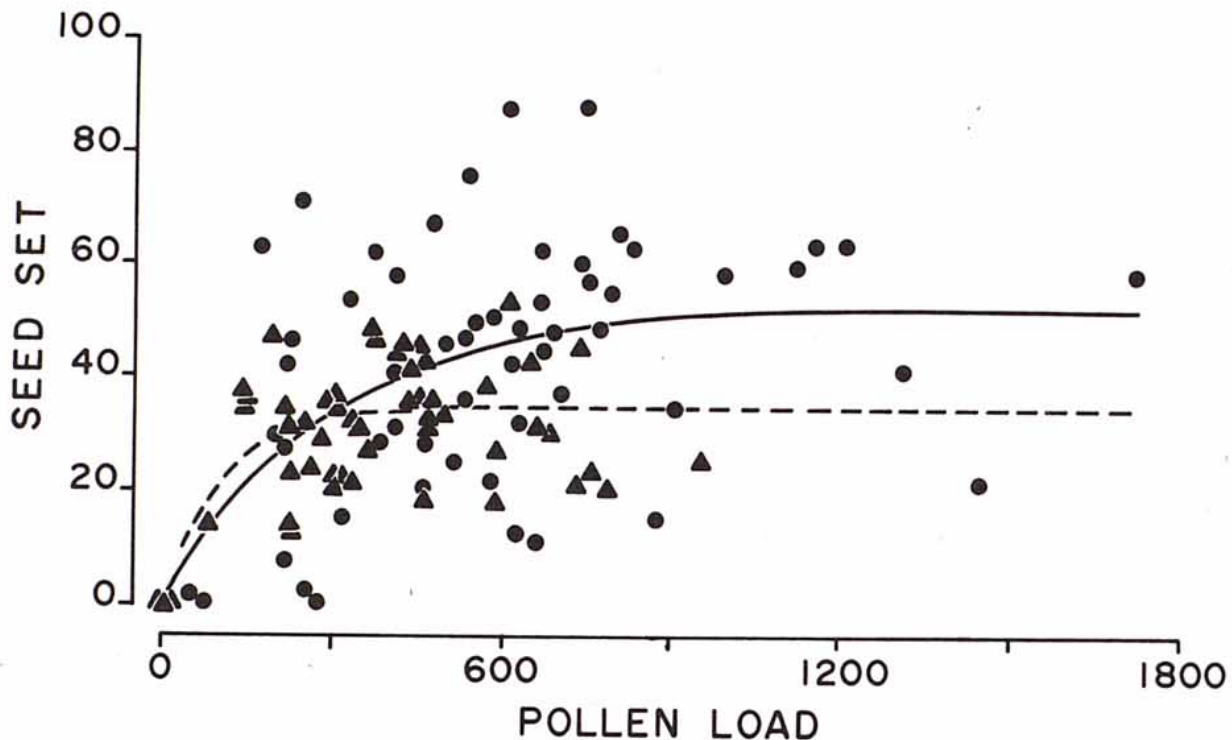


Fig. 2.— Decelerating dose-response functions relating pollen load to seed set in paired early opening flowers (filled circles, solid line) and later opening flowers (filled triangles, dotted line) of 53 plants in a natural population. Lines are best-fit negative-exponential regressions from the NLIN procedure of SAS (SAS Institute, 1985). The regression equations are $y = 53.4 (1 - \exp[-0.003x])$ for early flowers and $y = 34.6 (1 - \exp[-0.009x])$ for later flowers, where y is seed set and x is pollen load. Values of the slope parameters describing approach to the asymptotic seed set for the two types of flowers (0.003 and 0.009, respectively) do not differ significantly based on 95 % confidence limits estimated by NLIN.

(PRICE & WASER 1979:295). The dye dispersal distances measured in 1979 probably overestimated dispersal of viable pollen, since we waited 72 hours after applying dye before sampling surrounding plants. We now know that the half-life of *D. nelsonii* pollen viability is about 6 hours, and that the distance of dye dispersal increases slowly as a function of the time between dyeing and sampling. More importantly, subsequent aviary experiments show that hummingbird movement of dye underestimates movement of pollen by 1.5-1.8-fold (WASER 1988:45). Even when this correction factor is applied, however, it again seems that birds do not transfer measurably more *D. nelsonii* pollen than bees over an «optimal outcrossing distance» from the point of view of seed set and offspring fitness.

A final assessment of pollen quality is provided by comparing «dose-response» functions (WASER & FUGATE, 1986; WASER & PRICE, 1991) relating seed set to pollen load, for flowers produced at the beginning of the season and for those produced approximately 3 weeks later (Figure 2). This comparison involves pairs of flowers from 53 plants in a field population.

Early and later flowers were receptive when most visits were by hummingbirds and bumble bees, respectively (personal observations). Differences in quality should manifest themselves in the initial rate of rise of a dose-response function to its asymptote, since this reflects the expected success of each pollen grain in producing a seed when pollen loads are not saturating (WASER & FUGATE, 1986; WASER & PRICE 1991; see also BERTIN & WILLSON, 1980). By this criterion there is a suggestion that later flowers enjoy higher-quality pollen (presumably delivered mostly by bees), but the difference in initial «slopes» of the functions for early and later flowers is not pronounced or significant. Notice that the function for early flowers asymptotes at a higher maximum seed set. In part this is because earlier flowers produced more ovules than later ones, but Figure 2 also suggests that earlier flowers received somewhat higher pollen loads (see below).

Population-level effectiveness of hummingbirds and bumble bees

Although there seem to be no striking differences in the genetic quality of pollen delivered by bumble bees and hummingbirds, each bee visit is about 10 times as effective as each bird visit in the quantity delivered (see above). On the other hand, there are indications that population-level visitation rates by birds are about an order of magnitude higher than those by bees, so that the order of magnitude difference in individual efficiencies is counterbalanced and the overall contributions to pollination and seed set of *D. nelsonii* should be approximately equal.

An indirect assessment of overall contributions by bees and birds comes from experiments in which one each of a set of matched plants in the field was bagged, caged, or left unmanipulated. Seed sets increased from 1.1 per flower (sd = 2.7, N = 28) in bagged plants (no pollinator visits; this indicates that protandry effectively prevents selfing in the self-compatible flowers), to 30.8 (sd = 12.8, N = 18) in caged plants (bee but no bird visits), to 49.5 (sd = 12.4, N = 28) in unmanipulated plants (both bee and bird visits). The 1.6-fold difference between the latter values is significant ($t = 4.92$, $df = 44$, $P < 0.001$, one-tailed), suggesting that bees and birds each contribute approximately equally to seed set. There is an important caveat about such experiments, however: the results may not be «additive». In this case, for example, bumble bees might have overvisited caged plants since their nectar rewards were not being shared with hummingbirds, or undervisited them because the cage was a barrier (even though it consisted of wire mesh with an opening substantially larger than a bumble bee, and bees entered cages without apparent hesitation). Thus seed set in caged plants may not perfectly reflect the proportional contribution of bees to an unmanipulated plant.

An estimate of pollinator effectiveness that does not share this potential drawback involves comparison of paired flowers on the same plants. As noted already from Figure 2, early flowers (pollinated mostly by hummingbirds) achieved somewhat higher pollen loads and seed sets than later flowers (pollinated mostly by bumble bees). In fact, mean pollen loads were higher for early plants by 1.41-fold and mean seed sets were higher by 1.29-fold (Table 2). These differences are significant (in both cases paired-comparison $t > 3.3$, $df = 52$, $P < 0.01$, two-tailed). Thus the approximately 10-fold difference in individual efficiencies of birds and bees seems to be if anything more than offset at the level of total pollen loads and seed sets. Notice, however (Table 2) that early flowers achieved a significantly lower seed set expressed as a percentage of the maximum possible for the flower (paired-comparison $t = 2.8$, $df = 26$, $P < 0.01$, two-tailed; df are smaller than those above because unpollinated ovules were not scored in all fruits). This is because of the decline in ovule number through the season.

A direct indication of expected total visits per flower by bumble bees and hummingbirds can be derived from the arrays of potted plants placed outdoors during the first 80 % of the 1979 flowering season of *D. nelsonii* around RMBL. We recorded the entire visitation history

of each plant and the number of flowers it produced. Across replicate arrays these estimates, based on means within each array, were 0.51 visits per flower by bees (sd = 0.63, N = 12 arrays) vs. 7.93 by birds (sd = 6.09). This 15.5-fold difference is significant ($t = 5.08$, $df = 22$, $P < 0.001$, two-tailed, using log-transformed data to achieve homogeneous variances).

In part these population-level differences may reflect different foraging speeds. Field observations show that hummingbirds consistently visit flowers more quickly than bumble bees (Table 3). Combining results from the two bumble bee species for which we have estimates, and combining across years within each pollinator class, mean visitation rates are 0.72 flowers/second for birds (sd = 0.21, N = 49 foraging bouts) vs. 0.27 for bees (sd = 0.08, N = 23). This 2.7-fold difference is significant ($t = 13.3$, $df = 70$, $P < 0.001$, two-tailed, using log-transformed data).

DISCUSSION

Our observations and experiments indicate that bumble bees and hummingbirds contribute about equally to pollination and seed set of *D. nelsonii* around RMBL, in spite of bees being «more efficient» in that they deliver more pollen with each flower visit. This underscores the importance of comparing both individual efficiency and population-level visitation rates of pollinators (see also STEBBINS, 1970; PARKER, 1981; MOTTEN & AL., 1981; SCHEMSKE & HORVITZ, 1984; HERRERA, 1989), and/or of directly assessing their relative contributions to reproductive success, which integrates these two components (see BERTIN & WILLSON, 1980; MORSE & FRITZ, 1983). Furthermore, it is important to consider whether pollen quality comprises part of the differential effectiveness of flower visitors (apparently not the case in our system, but see BERTIN & WILLSON, 1980). Studies often do not extend to these additional levels of population-level effectiveness and pollen quality. We hope this paper illustrates some of the methods that can be useful in this regard.

Similar overall effectiveness of hummingbirds and bumble bees apparently involves the greater foraging speed of birds. But this seems insufficient in itself to explain similarity, suggesting that hummingbirds engage in more frequent foraging bouts than bees, and/or that the sizes of hummingbird populations foraging at *D. nelsonii* exceed those of bumble bees. Assuming that population sizes do influence the outcome, it is instructive that censuses of audible flights by male broad-tailed hummingbirds (Table 4) suggest population fluctuations of about 2.5 fold between 1975 and 1989. It is our impression that bumble bee populations also fluctuate considerably, but we have no census data. Population fluctuations mean that the result of equivalent overall bee and bird pollination, although derived from multiple years of study, is likely to vary on a longer time scale at RMBL as well as over the meso- and macrogeographic range of *D. nelsonii*.

These points raise a larger issue. Although flowers of a given larkspur species, or any other species, may conform almost exactly to a given classical «pollination syndrome», it can be misleading to infer from this what the effective pollinators are at a given time and place (see also WASER, 1983; PLEASANT & WASER, 1985). The «pollination syndrome» concept makes or implies several assertions (see e. g. VAN DER PIJL, 1961): that plants (at least «evolutionarily advanced» ones) tend to specialize on a single pollinator type; that visitors other than this type are «illegitimate», and that specialization is possible in part because of strong innate preferences that vary across pollinator types for simple floral attributes such as color. These assertions do not hold absolutely in our study system (WASER, 1983; PLEASANTS & WASER, 1985), nor necessarily in other temperate (WASER, 1979; MOTTEN & AL., 1981; DELPH & LIVELY, 1985; HERRERA, 1988; but see DUKAS & SHMIDA, 1989) or tropical systems (FEINSINGER, 1987; NILSSON & AL., 1987; WOLF & STILES, 1989). Instead, it is common for plants to have multiple visitors, several of which pollinate to some degree (see also FEINSINGER, 1983). Conversely it

is common for the animal pollinators to be plastic behaviorally, to choose flowers based on rewards, and as a consequence to visit a variety of plant species without as much regard for their «syndromes» as might be expected.

This is not to deny that there are nodes in floral «phenotype space» that lead workers repeatedly to suggest versions of «pollination syndromes». These nodes may be to some extent (perhaps a great extent) the result of evolutionary convergence due to selection imposed by pollinators and by the presence of other plants competing for pollination services (WASER, 1983). Without denying these possibilities (or the difficulty of exploring them rigorously!) we wish to urge workers not to let the appeal of orderly «pollination syndromes» obscure the richness of actual present-day relationships between plants and their floral visitors.

Acknowledgements

Thanks to W. Calder, D. Campbell, R. Mitchell, R. Patten, M. Ronsheim, and D. Samson for assistance, and to Sigma Xi, the American Ornithologists' Union, the Frank M. Chapman Memorial Fund, and the U. S. National Science Foundation (grants DEB 8102774, BSR 8313522, BSR 8905808) for support.

Table 1. Mean and median flight distances between plants and flowers for broad-tailed hummingbirds (*Selasphorus platycercus*, «S. p.» in the table) and bumble bee queens (*Bombus appositus* and *B. flavifrons*, «B. a.» and «B. f.») foraging at *D. nelsonii* in the field. Values are in m; within-plant movements are counted as zero so that a median value of 0.0 means that the median flight was within a single plant.

Visitor	Mean Distance		Median Distance	
	Plants	Flowers	Plants	Flowers
S.p.	1.6	0.8	0.3	0.0
B.a.	0.6	0.4	0.2	0.3
B.f.	0.6	0.4	0.3	0.3

Table 2. Pollen loads and seed sets of paired bottom (early opening) and middle (later opening) flowers of 53 plants in a natural population. Pollen load refers to counts summed across the (usually) 3 stigmas of each flower, seed set is absolute seed output of the flower, and % maximum refers to the percentage of all ovules maturing. Values are means followed in parentheses by standard deviations and sample sizes (numbers of flowers).

Flower Position	Pollen Load	Seed Set	% Maximum
Bottom	632.6 (336.3, 53)	42.2 (22.1, 53)	55.3 (33.0, 27)
Middle	448.6 (212.4, 53)	32.7 (10.2, 53)	76.4 (17.2, 27)

Table 3. Visitation rates of broad-tailed hummingbirds and bumble bee queens («S. p.», «B. a.» and «B. f.»; see Table 1) foraging at *D. nelsonii* in the field in different years. Values include flower-to-flower and plant-to-plant flights and are means over all foraging bouts timed in a given year. Values are flowers visited per second, followed in parentheses by numbers of bouts and total numbers of flowers visited.

Visitor	Year			
	1975	1976	1978	1979
S. p.	0.86 (9,180)	0.69 (40,1424)	—	—
B. a.	—	0.28 (3,180)	0.26 (1,46)	0.34 (6,290)
B. f.	—	0.27 (13,652)	—	—

Table 4. Activity levels of male broad-tailed hummingbirds in nature, from 10-minute censuses of the number of audible flights taken every 2-4 days at a standard time of day throughout 14 summers (see also WASER & REAL, 1979). Values are mean numbers of flights per census, followed in parentheses by standard deviations and sample sizes (numbers of censuses).

Year	Mean Activity Level
1975	10.2 (5.4, 14)
1977	8.0 (3.8, 11)
1978	5.0 (5.9, 10)
1979	8.8 (3.5, 24)
1980	5.9 (4.1, 17)
1981	7.2 (6.3, 13)
1982	6.7 (2.5, 17)
1983	5.6 (4.2, 9)
1984	9.7 (4.1, 21)
1985	8.2 (4.7, 17)
1986	4.7 (5.1, 20)
1987	4.1 (4.8, 18)
1988	8.1 (5.6, 17)
1989	6.0 (2.9, 17)

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