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Partial preference of insects for the male flowers of an annual herb

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Summary. The flowers of the annual herb *Impatiens capensis* have distinct male and female phases. The male phase lasts four times as long as the female phase, and male flowers contain about 50% more nectar than female flowers. This suggests that the bulk of allocation to the flower is designed to ensure the dispersal of pollen rather than the fertilization of ovules. Honeybees, wasps and bumble bees all land on male flowers more often than would be expected by chance, and, having landed, wasps and bumble bees are more likely to enter a male flower than a female flower. The frequency of male flowers in the diet therefore exceeds their frequency in the population. This preference, although strong and consistent, is only partial, since some female flowers are included in the diet. We propose two hypotheses to account for the observed partial preference, the first based on competition between bees for flowers, and the second asserting that the bees detect nectar levels directly without using floral gender as a cue. The results of an experiment in which the most obvious gender cue, the androecium, was removed are consistent with the second hypothesis.

Jewelweed (*Impatiens capensis* Meerburgh, Balsaminaceae) is a common annual herb growing in wet terrestrial habitats throughout eastern North America. It bears large, brightly-coloured, zygomorphic flowers whose nectar is taken by a wide variety of insects (Robertson 1928, Heinrich 1972, Rust 1977) and by humming-birds (Josselyn 1672, Martin et al. 1951). Bisexual (perfect) flowers such as those of *Impatiens* have two functions: the reception of pollen (female function) and the dispersal of pollen (male function). In general these functions cannot be separated, since both are served by the same set of secondary structures. In the case of *Impatiens*, however, they are separate in time; the flowers are strongly protandrous, with an initial male phase and a subsequent female phase. The petals persist more or less unchanged through both phases, but in principle the flower could emphasize either male or female function by altering the rate of nectar secretion. This would create differences in nectar standing crop, which, if perceived by insects, would lead them to visit male and female flowers at different rates.

The purpose of this paper is then to ask whether there is any difference in the quantity or quality of nectar borne by male and female flowers, and, if such a difference exists, whether the insects will prefer to visit those flowers offering the greater reward. Further, we can ask whether any difference in reward offered by the flowers or any preference shown by the insects can be interpreted satisfactorily by current theory.

The nectar content of flowers

Our work was done at the McGill University Field Station at Mont St-Hilaire, Québec (see Maycock 1961). This is an almost undisturbed section of eastern deciduous forest, where jewelweed is very widely distributed in wet hollows and along streams. Nectar samples were taken at two sites about 400 m apart: the Forest patch, a partly shaded area in regenerating beech-maple woodland, and the Charbonneau patch, an exposed area at the forest edge where a small seasonal seep escapes from a wooded slope. We measured the nectar volume of individual flowers by cutting off the distal end of the spur and expressing the nectar manually into 5 μl microcapillary tubes, measuring the height of the column to ±0.5 mm and later converting this measurement into microlitres. Sugar concentration was measured in pooled samples of ten or more flowers, using a handheld refractometer calibrated against standard sucrose solutions.

The nectar samples are summarized in Table 1. Both volume and concentration varied between sites and with time of day, but male flowers held consistently more nectar than female flowers. From a total of 20 samples (22 for nectar volume) involving 1689 flowers in all and taken throughout the day between 0920 h and 1930 h, male flowers had a greater average nectar volume in 19 cases ($P < 0.001$, two-tailed binomial test with H_0: male = female), a greater sugar concentration in 15 cases ($P = 0.02$) and a greater total sugar content in 18 cases ($P < 0.001$). When all samples are pooled the average difference between male and female flowers is highly significant for volume and for total sugar, although not for concentration (t-test, details in legend to Table 1). The factor by which the total available reward offered by male flowers exceeds that offered by female flowers (as mean male/female sugar content, taken over all samples) is 1.43 for the Forest patch and 1.60 for the Charbonneau patch. In short, male flowers consistently contain about 50% more sugar than do female flowers. This is not due to the depletion of an initially large volume of nectar. Male flowers of known age, tagged on

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Table 1. Nectar quantity and quality in male- and female-phase flowers of jewelweed. Units of volume are μl/flower; concentration is percent sucrose equivalent; total sugar is mg/flower; sample size is number of flowers sampled. The five samples for 1030 h on 2 September in the Charbonneau patch were taken at different stations within the patch. Comparisons of male and female flowers yields

		Volume	Concentration	Sugar
Forest:	*t*	2.07	1.79	2.72
	p	0.05	0.10	0.02
Charbonneu:	*t*	2.60	0.76	2.78
	p	0.02	0.45	0.02
Pooled:	X^2_4	13.8	6.2	15.6
	p	0.01	0.18	0.01

The nonparametric two-sample Kolmogorov-Smirnov test yields more highly significant results in all cases, although the pooled data for concentration still does not quite yield a two-tailed $P < 0.05$

Date	Time	Volume		Concentration		Total sugar		Sample size	
		M	F	M	F	M	F	M	F
Forest patch									
29/8	1100	1.199	1.047	–	–	–	–	47	47
	1700	1.523	1.112	–	–	–	–	56	56
31/8	0940	2.03	1.75	25.2	22.9	0.511	0.400	10	11
	1005	1.05	1.50	38.2	17.4	0.401	0.261	10	11
	1100	2.20	1.42	31.8	23.3	0.698	0.330	20	20
	1130	1.59	1.50	30.6	25.2	0.514	0.394	20	20
	1230	1.76	1.68	27.3	26.3	0.481	0.441	20	20
	1300	1.47	2.09	40.2	35.4	0.593	0.738	20	20
	1415	1.94	1.57	42.7	32.9	0.830	0.518	20	20
	1500	1.97	1.71	39.3	32.6	0.857	0.556	15	20
	1530	1.59	1.26	39.7	33.9	0.630	0.426	18	19
	1630	1.88	1.10	38.0	37.1	0.714	0.409	16	20
	1700	1.55	0.70	38.8	29.2	0.602	0.203	20	18
	1730	1.51	0.99	33.4	40.6	0.503	0.403	19	20
	1930	1.78	1.74	43.7	47.6	0.778	0.827	19	20
unweighted mean:		1.669	1.411	36.1	31.1	0.624	0.454	330	342
sd:		0.311	0.369	5.8	8.2	0.143	0.174		
Charbonneau patch									
29/8	1400	0.514	0.454	49.0	44.4	0.252	0.202	146	141
30/8	1000	0.966	0.811	30.1	29.7	0.291	0.241	165	165
2/9	1030	1.00	0.55	32.5	44.5	0.324	0.244	20	20
	1030	1.26	0.81	37.4	39.5	0.473	0.320	20	20
	1030	0.88	0.80	45.9	23.2	0.352	0.186	20	20
	1030	0.79	0.66	37.3	41.4	0.295	0.275	20	20
	1030	1.33	0.37	45.5	33.7	0.567	0.126	20	20
unweighted mean:		0.963	0.636	39.7	36.6	0.365	0.228	511	506
sd:		0.278	0.182	7.2	8.1	0.114	0.063		

the evening before anthesis, each contained 0.854±0.128 (s.e.) μl of nectar on the first day, 0.959±0.133 μl on the second day, and 0.957±0.275 μl on the third day. Most flowers had become female on the third day; these contained 0.577±0.252 μl of nectar each. These results suggest that it is male function which is emphasized by jewelweed flowers. Moreover, the duration of the male phase greatly exceeds that of the female phase. Of the tagged flowers referred to above, all remained male for two days (43/43 male after one day; 35/35 male after two days), changing sex on the third day (4/14 male after three days, excluding 5 flowers which had already fallen) and falling before the fourth day. The male phase therefore lasts about 2.2 days, and since male flowers are about four times as frequent as females (see next section) the female phase must last about 0.5 days. Rust (1977) found rather shorter lifespans but a greater disparity between male and female (male lifespan 1.4 days, female lifespan 0.2 days) in a Delaware population. Because the nectar taken by insects during the life of the flower is continually replenished, the longer life of the male flowers, together with their standing crop of nectar, implies that about six times as much nectar is secreted during the male phase than during the female phase, even if insects visit male flowers no more frequently than they visit female flowers. If male flowers are visited more often, the disparity in nectar production must be even greater than the disparity in standing crop would lead us to suppose.

Table 2. Duration of behaviours. 'Travel' is time between leaving one flower and initiation of hovering before the next flower visited; 'hover' is time between initiation of stationary flight and contact with flower; 'land' is time between contact with flower and initiation of crawling into corolla; 'discriminate' is total time available for discrimination between encounter with flower and entry = 'hover' + 'land'; 'enter' is time spent in corolla until flight from flower, excluding insects which groomed pollen before flight. All durations are in s. No value of *t* for comparisons between male and female flowers is individually significant at $P<0.05$ and nonsignificant differences have no consistent direction

		Travel	Hover			Land			Discriminate	Enter		
			M	F	mean	M	F	mean		M	F	mean
Wasps	mean	9.68	1.62	2.27	1.67	2.89	2.20	2.80	4.47	11.57	15.66	11.83
	sd	8.90	1.30	1.41		2.70	1.50			7.88	10.64	
	N	64	44	4	48	54	8	62		73	5	78
	t		−0.96			+0.70				−1.10		
Honey bees	mean	6.45	1.94	1.38	1.81	4.40	4.97	4.58	6.39	9.09	7.10	8.71
	sd	4.12	1.47	0.71		3.20	3.13			10.01	3.07	
	N	90	58	17	75	46	22	68		60	14	74
	t		+1.52			−0.69				+0.73		
Bumble Bees	mean	3.22	0.96	–	0.96	1.69	1.78	1.71	2.67	4.58	3.42	4.44
	sd	2.44	0.42	–		0.91	0.94			2.32	1.27	
	N	137	10	0	10	36	12	48		59	8	67
	t			–		−0.29				+1.38		

The behaviour of insects

Insects visiting jewelweed flowers alight on the lamina of the two lower petals before crawling beneath the androecium into the saccate sepal; before alighting they may or may not be seen to hover for a short time in front of the flower. We were thus able to distinguish three categories of behaviour with measureable durations: "hover", "land" and "enter". Insects which hover do not always land; those which land do not always enter. There are therefore two ways in which the insects may discriminate between male and female flowers: by landing disproportionately more often on one sex, or, having landed, to enter more often. The specialist native pollinators are hummingbirds, which were only rarely seen at our sites, and bumble bees (mostly *Bombus vagans*, with occasional *B. terricola* – often collecting nectar from cut spurs and thus not scored – and *B. perplexus*) which were very common and whose long proboscis enables them to exploit the flowers efficiently. Honeybees (*Apis mellifera*) also visit the flowers but must crawl further down the corolla; wasps (*Vespula acutifrons*) must crawl right down to the throat of the spur to lap nectar. Other insects (syrphids and ichneumonids) were negligibly rare. Honeybees were often seen collecting pollen from the anthers; bumble bees accumulate pollen dorsally and remove it by grooming, but are said (by Heinrich 1978) to find jewelweed pollen distasteful. At two sites nectar was gathered by perforating the spur from the rear of the flower without entering the flower, or by feeding at old perforations. Only legitimate frontal nectar-collecting visits are used in this study.

The mean durations of the three categories of behaviour in the three categories of visitors are given in Table 2, together with the time spent in travelling between visits to flowers in the same patch. Three features of these data deserve special comment. First, the time spent for any behaviour is the same for male and female flowers for all three categories of visitor. Secondly, bumble bees spend less time for any behaviour, reflecting their specialization to flowers with deeply concealed nectar. The total time required to exploit a flower, including the travel time between flowers, is 10.3 s for bumble bees, as compared with 21.6 s for honeybees and 26.0 s for wasps. These estimates agree fairly well with those published by Rust (1977), who found that *Bombus vagans* visited 8.4 flowers per min (7.1 s per visit), *Apis* 4.0 flowers (15.0 s per visit) and *Vespula maculifrons* 2.8 flowers (21.4 s per visit). Thirdly, the travel time between flowers, the "discrimination time" (time between start of hovering and start of feeding or departure if the flower is rejected) and the "handling time" (time between start of feeding and departure from flower) are all roughly equal in duration for bumble bees.

To detect any discrimination between male and female flowers shown by the insects, observations were made in the Forest patch, at five different stations within the Charbonneau patch, and in 15 other sites scattered throughout the field station. In general, each patch was watched by two observers for 30 min, whilst a third person recorded the data. When a visitor was seen, it was followed from flower to flower until it left the patch or was lost. For each visit, the sex of the flower and the behaviour of the insect was recorded. In total, 4965 visits were recorded, of which 3394 involved entry to the flower. Population sex ratio was estimated in each patch by scoring a random sample of about 250 flowers per patch (range 126–608; total 5234 flowers).

The data for the 22 sites are given in Table 3. Their chief feature is a strong and consistent preference by insects for male flowers. Honeybees land more often than expected on male flowers but after landing reject males and females with equal probability. Wasps show a significant discrimination in favour of males whether judged in terms of landings or of entries after landing, but this result is based on observations at only four sites. The clearest preferences are shown by bumble bees, the specialist native pollinator, which are most efficient in exploiting the flowers (Table 2). Besides the very highly significant discrimination exercised in favour of males both before and after entering the flowers evident from pooled data (legend to Table 3), the table shows that these effects are consistent across sites: the pro-

Table 3. The behaviour of visitors towards male and female flowers. 'Entries' are visits which terminated in entering the flower to feed; other visits terminated when the insect left the flower before feeding, the fraction of such visits being given under 'rejection rates'. The third pair of columns gives the results of random counts of flowers in patches where the insects were observed, at the time of observation. The final pair of columns compares the proportion of males in the population (=males/total in 'population' columns) with that in the diet of the insects (=male/total in 'entries' columns).

Discrimination between male and female flowers may occur either before landing (disparity between number of male flowers receiving landings and number of male flowers in population), or after landing and before entry (disparity between number of male and female flowers rejected and accepted), giving rise to an overall discrimination (disparity between proportion of male flowers in diet and that in population). The hypothesis that in each case for each category of pollinator there is no discrimination was tested by goodness-of-fit chi-square with one degree of freedom, to give these values of X_1^2:

	Before landing	Before entering	Overall
Bumble bees:	47.7***	17.8***	101.3***
Honeybees:	10.9**	0.01	5.43*
Wasps:	28.7***	7.49**	37.9***

No asterisk, $P>0.05$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$

Site	Entries		Rejection rates		Population		Male fraction	
	males	total	males	females	males	total	popn	diet
Bumble bees								
1. G7	137	154	0.074	0.261	193	217	0.889	0.890
2. V7	40	47	0.111	0.222	96	126	0.762	0.851
3. F31	216	244	0.212	0.489	161	200	0.806	0.885
4. CMJ2	19	21	0.269	0.333	145	200	0.725	0.905
5. CDJ2	2	2	0.600	1	140	200	0.700	1
6. CLB2	40	51	0.024	0.313	133	200	0.665	0.784
7. CM2	20	20	0.091	–	136	200	0.680	1
8. SW8	44	49	0.200	0.500	151	171	0.883	0.898
9. BBB8	106	113	0.248	0.364	200	222	0.902	0.938
10. BBNS8	168	186	0.067	0.379	214	244	0.877	0.903
11. BBLN8	310	355	0.081	0.167	279	338	0.825	0.873
12. NCDEF8	45	48	0.151	0.250	141	148	0.953	0.938
13. NCDS8	8	10	0.000	0.333	166	195	0.851	0.800
14. WCVS9	39	48	0.093	0.357	215	299	0.719	0.813
15. GTW9	16	17	0.333	0.800	216	284	0.761	0.941
16. NCC9	110	135	0.167	0.432	224	308	0.727	0.815
17. NCV9	107	128	0.201	0.364	248	327	0.758	0.836
18. OET8	114	116	0.123	0.500	126	135	0.933	0.983
19. MIX30	294	345	0.228	0.358	148	200	0.740	0.852
20. MIX1	58	66	–	–	478	608	0.786	0.879
pooled	1893	2155	0.1313	0.3417	3810	4822	0.7901	0.8784
Honeybees								
9 sites pooled	581	760	0.456	0.451	1450	1995	0.727	0.764
Wasps								
4 sites pooled	411	479	0.489	0.642	587	800	0.734	0.858
All visitors								
22 sites pooled	2885	3394	0.2878	0.4431	4127	5234	0.7885	0.8500

portion of males was greater in the diet than in the population at 18/20 sites ($P<0.001$, binomial test with H_0:diet= population) and the rejection rate (proportion of visits in which landing was not followed by entry) was lower for males than for females in 18/18 cases ($P<<0.001$). The rest of this paper will be concerned exclusively with the relationship between bumble bees and the flowers.

The relationship between the proportion of male flowers in the population and in the diet of the bumble bees, which will be important in evaluating the predictions of rival theories of foraging behaviour, is shown in Fig. 1.

This overall preference for male flowers is the result of a discrimination exercised by all individual bumble bees, and does not result either from the existence of specialization on male or female flowers among the insects or from a clumped distribution of male and female flowers among the plants. From the data collected to construct Table 3, we know the frequency of female flowers amongst runs of visits made by insects followed from flower to flower. If some individuals visit only males and others only female flowers then the frequency distribution of the frequency of female flowers per run will be bimodal at 0 and 1, where-

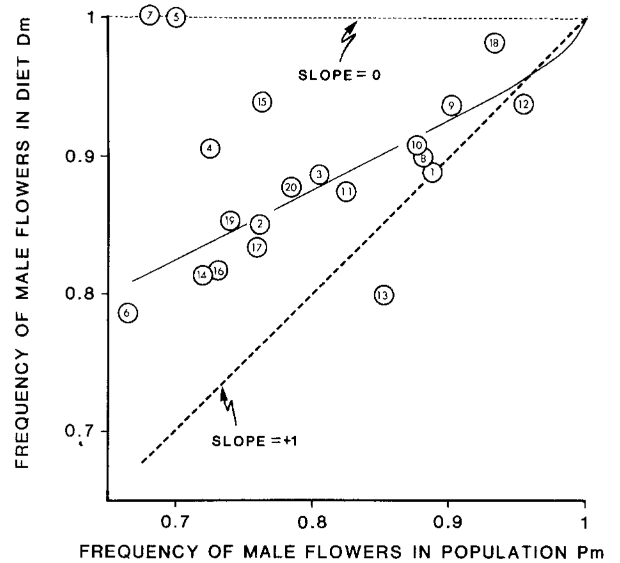

Fig. 1. The relationship between the frequency of male flowers in the population and their frequency in the diet of bumble bees. See Table 3. For regression analysis the data were first transformed as arcsin square-root into radians, and then weighted by the sample size of the Y-variate (i.e. by number of visits observed; sample sizes of the X-variate are large and do not vary sufficiently to use them as additional weights). The regression equation is then $D_m = 31.37 + 0.598\ P_m$. The standard error of the slope is 0.175 and it therefore differs significantly both from zero and from unity. The linear model has $r^2 = 0.393$; a quadratic model did not explain a significantly greater proportion of the variance of the data. Numbers inside the plotted points identify the sites listed in Table 3

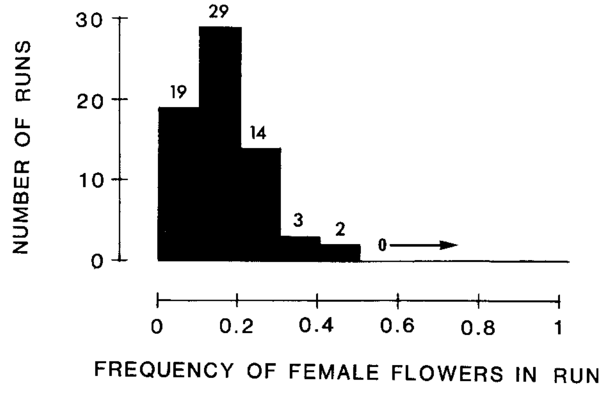

Fig. 2. The proportion of female flowers in runs of visits by bumble bees. The data used comprised 1609 visits from 67 runs; all runs of seven flowers or more were included in the analysis. A comparison of the data with a Poisson distribution having the observed mean value gives $X_3^2 = 1.81$ with associated $P > 0.50$

as if males and females are taken with equal probability by all individuals the frequency distribution will be Poisson. Figure 2 shows that a Poisson distribution provides a good description of the data, and the hypothesis of specialization is rejected. Moreover, the flowers are encountered randomly. Observers traced paths through several patches, imitating as closely as possible the flight paths of bumble bees, and recording the sex of each flower encountered. If the flowers are distributed at random with respect to sex along these paths, then the frequencies of runs of successive female flowers should follow a geometric distribution; encounters with 80 female flowers (of a total of 336 flowers scored) were compared with the fitted geometric distribution and yielded $X^2 = 0.003$ ($P > 0.90$). The same procedure, but using the data of Fig. 2 to examine runs of female flowers in the flight paths of the bees themselves (97 female flowers from a total of 859 landings) gave $X^2 = 0.014$ ($P > 0.90$). We conclude that female flowers are distributed randomly with respect to males and are visited with the same probability by all individual bumble bees.

Optimal pollination and optimal foraging

Flowers and insects are antagonists who have certain interests in common. The flower offers to hire the services of the insect, and should attempt to do so as cheaply as possible; the insect in turn should try to exact as large a wage as possible for the least amount of labour. Although the flower-insect relationship is mutualistic at the level of population dynamics, it is essentially competitive at the level of individuals. Each should attempt to maximize reproduction without direct regard for the interests of the other.

Plant strategy. Despite the voluminous literature devoted to the qualitative description of floral architecture in relation to pollination, the quantitative aspects of the plant's strategy seem scarcely to have been studied. Indeed, we have been unable to find any explicit reference to the criterion that should direct the quantity of energy and materials allocated to secondary structures such as petals and nectar. Our work suggests that the appropriate criterion, at least for *Impatiens*, should concern the dispersal rather than the reception of pollen. Many insect visits are necessary to remove most of the pollen from the anthers, whilst a single visit may suffice to fertilize all the ovules, and the greater longevity and nectar content of male flowers ensures that they will be visited much more frequently. To assess the average rate of visits to flowers, a team of observers watched large numbers of flowers for set periods of time at a site (V7 of Table 3) about halfway between the Forest and Charbonneau patches. Two series of observations were made, each over a period of 5000 s, with students rotating from station to station within the patch every 500 s. In the first series, 451 visits were recorded from a total of 939 flowers observed; in the second series 1117 visits were recorded from a total of 2090 flowers. The total number of visits expected by a flower during its female phase is then the product of the number of visits per flower per h, the lifetime of the flower in daylight h (assuming that visits occur during the ten h between 0800 h and 1800 h) and the proportion of female flowers in the diet of the insects, or $(1568/3029) \times (3600/5000) \times 27 \times (509/3394) = 1.5$ for our data. The corresponding estimate for male flowers is 8.6 visits. Thus, female flowers are visited only once or twice, while males are visited repeatedly.

Insect strategy. Our analysis of insect visits shows that pollinators exhibited partial preference for the male flowers of *Impatiens capensis*. Conventional optimal diet theory predicts either complete specialization on the more profitable food type or consumption of all types in proportion to their frequencies in the population (Charnov 1973). Despite this prediction, partial preference has often been described; the recent review by Krebs et al. (1983) lists six such reports. In addition, Waser and Price (1983) found

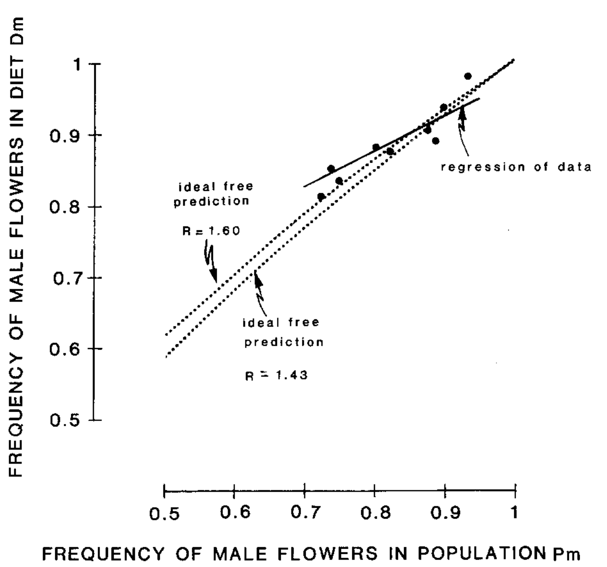

Fig. 3. The partial preference of bumble bees for male flowers predicted by a simple competitive model based on the ideal free distribution. The broken lines refer to the reward ratios found in the Forest and Charbonneau patches (1.43 and 1.60 respectively), with the largest samples (N>100) from Fig. 1 plotted to illustrate the fit of the model to the data

that both bumble bees and hummingbirds exhibited partial preference for the more profitable blue flowers of *Delphinium nelsonii.*

Partial preference can be accomodated by current optimal diet theory only if we assume that the different food types contain different nutrients (Pyke et al. 1977), or that foragers often make mistakes. Neither represents a satisfactory explanation of our data: it seems very unlikely that the nectar of male and female phase flowers differs except in quantity, while the inclusion of an arbitrary error rate would make the model unfalsifiable. We have instead developed two simple alternative models that could account for our results.

Competition. The first model is based on the idea that pollinators may compete with one another for nectar. If predators are sufficiently numerous or active to deplete the prey population, a population of specialist predators will quickly reduce their encounter rate with the preferred food item and thus create conditions in which feeding on a lower-quality food item becomes profitable. The nectar produced by flowers is generally depleted by insect visits (review by Cruden et al. 1983) and in particular is depleted in jewelweed: published estimates of the quantity of nectar secreted per flower per day are 2.8 μl (Rust 1977; morning samples in Delaware) and 5.2 μl (Heinrich 1972; evening samples in Maine), whilst very few of our samples gave a mean content of more than 2 μl in unbagged flowers (see Table 1). Heinrich (1976) estimates that insect visits remove 94% of available nectar in the closely related *Impatiens biflora.* It follows that the average reward obtained from male flowers will be a function of the number of insects which prefer to visit males, and therefore that the reward obtained by such specialists will be a decreasing function of their frequency. If all individuals display partial preferences by accepting male flowers when encountered with probability p and female flowers with probability q then the net reward obtained through the mixed strategy (p, q) will depend on the extent to which the nectar of male and female flowers has been depleted by the average strategy ($\bar{p}$, $\bar{q}$) of the population. The problem is similar to the Ideal Free Distribution model of Fretwell (1972), which is essentially a spatial ESS. Pleasants (1981) shows how this model can apply to insects foraging on flowers which offer different rewards.

Suppose that the frequency of male flowers in the population is P_m, whilst their frequency in the diet of the insects is I_m. The average reward offered by male flowers is then proportional to $P_m R_m / I_m$, varying universely with the degree of specialization shown by the insects. Conversely, the average reward offered by females will be proportional to $(1-P_m)R_f/(1-I_m)$. If the male flowers are the more rewarding then I_m should increase, and vice versa; insect diet will then change until the two items are equally rewarding, i.e. $P_m R_m / I_m = (1-P_m)R_f/(1-I_m)$, or $I_m/(1-I_m) = [P_m/(1-P_m)]\,(R_m/R_f)$, defining the predicted diet in terms of the population sex ratio and the relative sugar content of male and female flower, both of which can be estimated with confidence from our data. The prediction is shown in Fig. 3, which can be compared with the observations described in Fig. 1 and Table 3. Clearly the model provides a reasonably good description of the data: the slope of the observed regression is intermediate between zero and unity but significantly different from both. The model also predicts that a quadratic equation fitted to the data should have a positive second-order coefficient; the estimated value of this coefficient is $+0.026 \pm 0.028$ with one-tailed $P = 0.19$.

Direct resource perception. Since male flowers offer a greater reward we have assumed that the insects forage by using the presence of an androecium as a cue to indicate the likelihood of finding large quantities of nectar. It is at least conceivable, however, that the insects are capable of perceiving directly the quantity of nectar held by a flower. Let us suppose that a quantity y of nectar represents a threshold, below which it is more profitable to reject the flower and search for another. What is then the expected proportion of male flowers in the diet?

Let the frequency of male flowers whose nectar volume is x be $g(\mathrm{m}, \mathrm{x})$. The proportion of male flowers whose volume exceeds y is thus $\Sigma g(\mathrm{m}, \mathrm{x}) = G(\mathrm{m}, \mathrm{y})$, with this and subsequent summations taken over $\mathrm{x} > \mathrm{y}$, and we can define $G(\mathrm{f}, \mathrm{y})$ similarly as the proportion of female flowers whose nectar volume exceeds y. The proportion of male flowers in the diet is then $D(\mathrm{m}, \mathrm{y}) = P_m G(\mathrm{m}, \mathrm{y})/[P_m G(\mathrm{m}, \mathrm{y}) + (1-P_m)\, G(\mathrm{f}, \mathrm{y})]$. From our observations of the frequency distributions of nectar volume and the population sex ratio we can calculate $D(\mathrm{m}, \mathrm{y})$ and plot it as a function of the threshold value y (Fig. 4).

To predict the diet, we next need to calculate the optimal value of the threshold. This should be set so that insects reject flowers whose nectar volume would yield a net rate of energy uptake less than the average rate available in the patch, taking into account the time required to travel to the next flower encountered. The overall frequency distribution of nectar volume is $V(\mathrm{x}) = P_m\, g(\mathrm{m}, \mathrm{x}) + (1-P_m) g(\mathrm{f}, \mathrm{x})$. The net rate of energy uptake given by accepting a flower with nectar volume y is $\mathrm{y}/(T_h + T_d)$, whilst the rate associated with rejecting such a flower is $\Sigma\, \mathrm{x}V(\mathrm{x})/(T_h + T_d + T_t)$. Since our data show that $T_h = T_d = T_t$ is roughly correct, the threshold value should be set at about $\mathrm{y} = (2/3)\, \Sigma\, \mathrm{x}V(\mathrm{x})$. This yields threshold values of 0.55 μl for

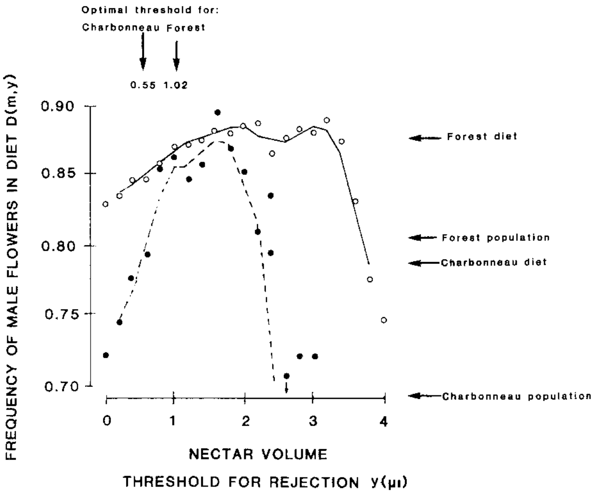

Fig. 4. The fraction of male flowers in the diet as a function of the threshold value of nectar volume below which flowers will not be visited. Calculated from the frequency distributions of nectar volume in the Forest and Charbonneau patches. For the threshold y = 0 diet and population coincide; for y > 0 diet exceeds threshold, except that in both populations nectar volume is more variable in females, the few flowers with very large nectar volumes being predominantly female, so that for y large the curves move downwards. Hollow circles are data for the Forest patch and solid circles for the Charbonneau patch; the lines are three-point moving averages to show the trend of the data

Table 4. Results of the emasculation experiment. A. *Nectar content.* The values of *t* for the pooled data refer to the (upper figures) male-emasculate and emasculate-female comparisons respectively and (lower figure) to the male-female comparison. No asterisk signifies $P > 0.05$; * $P < 0.05$; ** $P < 0.01$. Note that the flowers held smaller volumes of more highly concentrated nectar than in previous samples (cf Table 1). B. *Visits.* Format of test statistics is the same as in part A; they are goodness-of-fit Chi-square

		Volume			Concentration		
		male	emas-culate	fe-male	male	emas-culate	fe-male
A. Nectar content							
8 Sept.	mean:	0.476	0.508	0.244	59.2	58.4	44.9
	sd:	0.546	0.528	0.373			
9 Sept.	mean:	0.360	0.396	0.124	65.5	61.2	48.5
	sd:	0.440	0.412	0.220			
pooled	mean:	0.418	0.452	0.184	62.4	59.8	46.7
	sd:	0.494	0.470	0.297	4.45	1.98	2.55
	N:	50	50	50	2	2	2
	t:		−0.35	+3.41**		+0.74	+5.74*
			+2.87**			+4.32*	

		male	emasculate	female
B. Visits				
	visits:	505	296	100
	population:	281	154	76
	X^2_2:		0.84	10.9**
			8.18**	

the Charbonneau patch and 1.02 μl for the Forest patch. Substituting these values into Fig. 4, we predict that the proportion of males in the diet should be 0.870 for the Forest patch and 0.805 for the Charbonneau patch, which conform reasonably well with the observed values (for all pollinators) of 0.879 for the Forest patch (N = 601 visits) and 0.788 for the Charbonneau patch (N = 609 visits). The hypothesis of direct perception therefore provides adequate qualitative and quantitative explanations of the observed partial preference.

The response to emasculation. The rival hypotheses of competition and direct perception both lead to simple models competent to explain the main features of the data. We next conducted an experiment to test the hypothesis that the presence or absence of the androecium has a direct effect on the frequency of insect visits. Male flowers can be emasculated by removing the androecium, to create patches in which male, female and emasculate flowers occur at random. We performed this manipulation in 3 m × 3 m stations within the Forest patch on two successive days. On each day insect visits were scored between 1000 h and 1300 h and between 1400 h and 1700 h, and nectar volumes from 25 flowers of each type were measured between 1700 h and 1800 h. We then used the results of the experiment to evaluate two hypotheses: first, that the nectar volume of emasculate flowers is equal to that of male flowers and that both exceed female flowers; and secondly, that the number of visits to emasculate flowers is equal to that for male flowers and that both exceed the number of visits to female flowers. If both hypotheses are false, so that the effect of the manipulations is to reduce nectar to female levels and the manipulated flowers receive only as many visits as female, we have got no new information. If the first hypothesis is false and the second true, then insects must discriminate between male and female flowers using some cue other than the presence or absence of the androecium or the quantity of nectar present. If the first hypothesis is true and the second false, then insects must use the presence of the androecium rather than the quantity of nectar to recognize male flowers. If neither hypothesis is false then direct perception of nectar levels is a parsimonious explanation of the data, the two rival interpretations given above being falsified.

The results of the experiment are given in Table 4. The manipulation has no effect on nectar levels: emasculate flowers contained as much sugar as males, and both contained more than females. Moreover, the manipulation had no effect on insect preference: emasculate flowers were visited as frequently as males, and both were visited disproportionately more frequently than females. The presence or absence of the androecium can thus be firmly rejected as a potential cue for the observed discrimination between male and female flowers. It is possible that more subtle cues may be used to recognise floral gender, but their utility is questionable – the androecium is a very obvious structure – and we have no evidence that they exist. Male and female flowers do not differ to human observers either in the visible or the ultraviolet spectra (personal observations); moreover, even signs of extreme age in female flowers do not prohibit insect visits, since we have often seen insects land on senescent flowers and fall with the corolla to the ground. Other than the presence of the androecium, nectar volume is the only character known to differ systematically between male and female flowers, and the direct perception of nectar volume is therefore the most parsimonious explanation of our result.

Future work will involve the direct manipulation of nectar content. If this supports the hypothesis of direct resource perception, it will carry an interesting implication of general relevance to foraging studies. To human eyes, the flowers fall into two distinct categories, for each of which the bees display a partial preference or avoidance. To insect senses, however, the flowers seem continuously distributed along a single axis, and a total preference or avoidance for flowers above or below a certain threshold could be the true foraging rule. We must be careful to avoid constructing theories whose categories are irrelevant to the organisms they are designed to help us to understand.

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