An experimental study of the effect of colony resource level manipulation on foraging for pollen by worker bumble bees (Hymenoptera: Apidae)

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Two free-foraging colonies of *Bombus terricola* Kirby were stressed, on alternate days, by removing either their honey or their pollen stores. The amount of pollen taken into the colonies by foragers was significantly greater under pollen stress than under honey stress. This effect was not due to an increase in the number of foraging trips but rather to an elevated rate of pollen acquisition per foraging trip.

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Deux colonies de *Bombus terricola* Kirby libres de leurs mouvements ont été soumises à deux formes de stress, suppression du miel ou du pollen, imposées en alternance. L'apport du pollen aux colonies par les ouvrières était significativement plus important les jours de suppression de pollen que les jours de suppression de miel. Cet effet n'est pas attribuable à l'augmentation du nombre de sorties, mais à l'amélioration du rendement à chaque sortie.

Introduction

Bumble bees require two food resources for growth and reproduction: nectar and pollen. Although a great deal of attention has been paid to the nectar component of the diet of *Bombus*, pollen collection has received only scant treatment in the literature (for a discussion of this point, and references, see Plowright and Laverty 1984). Whereas optimality considerations relating to foraging for nectar have been extensively examined (references in Plowright and Laverty 1984), prior to the work of Zimmerman (1982) on *Potentilla gracilis* and Galen and Plowright (1985) on *Epilobium* (=*Chamaenerion*) *angustifolium*, very little attention was paid to comparable optimality considerations governing pollen collection by foraging bumble bees.

At least in the earlier part of the bumble bee colony cycle, pollen may indeed be the dominant limiting resource (Pendrel 1977). Moreover, Pendrel found an association between the amount of pollen brought in by the worker force and the size of the colony's larval population. This result, being only correlational, cannot by itself be taken as evidence that pollen collection is regulated by demand for it from within the colony. It might equally be argued that since the demands for pollen and for honey generally march hand in hand, the relationship between colony pollen intake and larval biomass in Pendrel's data is merely a by-product of an even stronger relationship between larval biomass and the intenity of nectar foraging.

This issue can only be settled by experimental manipulation. The present paper reports the results of such experimentation on colonies of a common North American bumble bee.

Materials and methods

Two laboratory-reared colonies of *Bombus terricola* Kirby, at approximately the same stage of their development cycle, were set up on 21 June 1983 to forage freely through tubes from upstairs windows at our field site at Bell Rapids, Hastings County, Ontario. On 2 July the colonies, hereafter referred to as A and B, contained 29 and 32 adult workers, respectively. These were marked with individually numbered tags glued to the thorax when the experiment was begun on the morning of 3 July. As the experiment proceeded, newly emerged workers were also marked until, at the conclusion of the study on 8 July, 55 workers had been marked in colony A and 54 in colony B.

The experimental procedure was to remove from each colony, alternately, its stores of either honey or pollen at the start of a 6-h period (beginning between 06:00 and 07:30, depending upon weather conditions) on each of 6 consecutive mornings. Thus, colony A was deprived of pollen on 4, 6, and 8 July and of honey on 3, 5, and 7 July, whereas colony B was deprived of pollen on 3, 5, and 7 July and of honey on 4, 6, and 8 July.

Honey deprivation was effected by carefully dissecting the comb, prior to the start of the experiment, and removing all empty cocoons. This ensured that at the beginning of each deprivation period it was necessary only to empty the wax honey pots, and any newly emerged cocoons, to create a complete deficit of stored honey. Deprivation of pollen was achieved by scraping all pollen from the pollen storage cylinders which, in *B. terricola* as in other members of the subgenus *Bombus* sensu stricto, are positioned in the centre of the comb.

Deprivation of one resource was always accompanied by augmentation of the other: a generous surplus of pollen was placed in the pollen cylinders of the honey-deprived colony, and the honey pots of the pollen-deprived colony were kept filled with 2:1 honey–water solution.

TABLE 1. Statistics for samples of pollen load size categories

Size category	*n*	Mass (mg) Mean	Mass (mg) SE
Very large	10	27.33	1.08
Large	19	18.28	0.73
Medium	26	11.05	0.46
Small	28	4.68	0.26
Trace	30	1.44	0.09

TABLE 2. Summary statistics for estimated total mass of pollen brought in by each bee on each day

	Total mass (mg) Days with pollen	Total mass (mg) Days without pollen
Colony A	14.69 (2.39)	38.16 (3.86)
Colony B	15.75 (3.49)	23.37 (2.96)
Colonies combined	15.25 (2.17)	30.86 (2.60)

NOTE: Values in parentheses show standard error.

Observations were begun 2 h after each act of deprivation and were continued for 4 h. The time of arrival and identification code of each returning forager were recorded together with an assessment of the size of its pollen loads. Loads were classified as very large, large, medium, small, trace, or zero. Samples representing each category were removed each day and weighed at the end of the observation period. The status of the honey and pollen stores in each colony was monitored throughout the observation period; to maintain the deprivation, accumulated honey or pollen was removed when necessary.

Results

Overall pollen intake per colony

Over all 6 days of the experiment, 353 incoming foraging trips to colony A and 304 to colony B were recorded. The mean estimated amount of pollen per trip was greater for A (14.1 mg) than for B (10.4 mg). Since, on the last day of the experiment, colony A contained more than twice as many last-instar larvae as colony B (25 vs. 10), this difference in the means may reflect different larval food demands in the two colonies (see Pendrel 1977).

In all, 35 bees from A and 47 from B were observed to have made at least one flight during the six observation periods. Many of these flights were short orientation flights made by recently emerged individuals. To confine our attention to foragers that were both experienced and active, we have restricted analysis to those bees (14 in A and 13 in B) which flew on at least 4 out of the 6 days and were recorded to have made nine or more trips. These individuals accounted for 429 (65.5%) of the total of 657 returns recorded during the entire experiment.

Table 1 contains statistics for the samples taken to characterize pollen load size categories. For each bee on each day the total amount of pollen brought back to the colony over the 4-h observation period was estimated using the mean masses in Table 1. The totals, averaged over bees and days, are reported for each colony and treatment in Table 2. More pollen was brought into both colonies on pollen-deprived days than on honey-deprived days, though the difference was greater in colony A than in colony B.

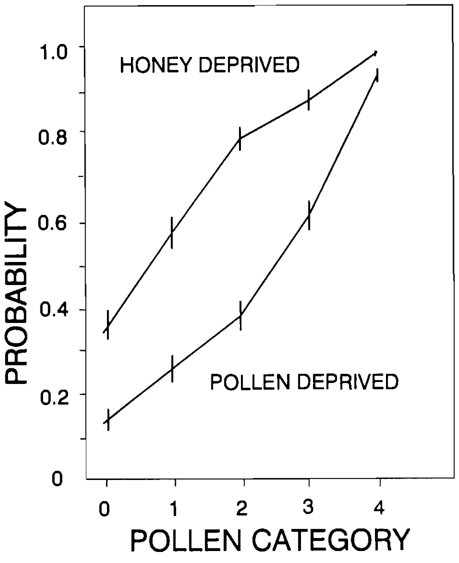

FIG. 1. Cumulative probability of pollen loads of a particular category or less for each treatment. Categories 0–4 correspond to pollen categories of zero to large, respectively. Vertical bars indicate standard errors.

Rate of pollen intake

Since the size of pollen load returned to the colony was classified into six categories (ranging from zero to very large), the data are ordinal. Logistic models for polytomous data on ordinal scales of measurement (McCullagh, 1980; see also McCullagh and Nelder 1989) were fitted using GENSTAT (Lawes Agricultural Trust 1987, Release 5.1). The factors were colony (A or B), treatment (pollen or honey deprived), bee, and day. The dependent variable was the proportion of flights with pollen loads less than or equal to each pollen category ranging from zero to large. Figure 1 shows the fitted proportions of flights for each treatment for the five pollen categories. For each category, the probability of a flight with a pollen load of that amount or less was smaller for the pollen-deprivation treatment. Although the pollen load sizes seemed to be easily discriminable (see Table 1), discrimination may not have been perfect. Using the rationale that the experimenters likely could accurately distinguish at least between small and not small loads, the statistics reported in Table 3 are for the third analysis (i.e., for the midpoint on the pollen load scale in Fig. 1, the fitted proportion of flights with small or less than small pollen loads), for which the effect of treatment was significant. The interaction of colony × treatment was also significant, the effect of treatment being more pronounced for colony A than for colony B: the fitted proportions for colony A were 0.824 (SE = 0.028) when honey deprived versus 0.206 (SE = 0.032) when pollen deprived, and for colony B were 0.636 (SE = 0.042) versus 0.500 (SE = 0.048). In summary, the pollen-deprivation treatment led to an increase in the proportion of flights with comparatively large pollen loads.

Trip frequency

A log-linear model was fitted to the trip frequencies for individual bees shown in Table 4. No effect of treatment was found ($\chi^2_{(1)} = 0.06$, $p \approx 0.81$), nor were there significantly different frequencies for colony A than for colony B ($\chi^2_{(1)} = 3.36$, $p \approx 0.072$), nor was there an interaction of treatment

TABLE 3. χ^2 table for logistic model on proportion of flights with small or less than small pollen loads, and fitted proportions for individual bees

	df	χ^2	p
Colony	1	0.11	ns
Treatment	1	83.13	<0.0001
Colony × treatment	1	20.96	<0.0001
Day	4	7.45	ns
Colony × day	4	29.31	<0.0001
Colony × treatment × bee	50	175.56	<0.0001
Residual	79	95.90	
Total	140	412.411	

	Fitted proportion	
Bee No.	Pollen deprived	Honey deprived
Colony A		
1	0.49 (0.30)	1.00 (0.00)
2	0.00 (0.00)	1.00 (0.00)
3	0.00 (0.00)	0.91 (0.08)
4	0.00 (0.00)	0.91 (0.06)
5	0.39 (0.12)	1.00 (0.00)
6	0.16 (0.14)	0.50 (0.25)
7	0.20 (0.10)	1.00 (0.00)
8	0.23 (0.19)	0.50 (0.17)
9	0.00 (0.00)	0.45 (0.15)
10	0.15 (0.13)	0.50 (0.25)
11	0.10 (0.10)	0.83 (0.15)
12	0.39 (0.18)	0.00 (0.00)
13	0.00 (0.00)	1.00 (0.00)
14	0.74 (0.09)	1.00 (0.00)
Colony B		
1	0.26 (0.16)	0.00 (0.00)
2	0.68 (0.26)	0.76 (0.19)
3	0.42 (0.18)	0.14 (0.12)
4	0.43 (0.18)	0.59 (0.22)
5	0.65 (0.16)	0.52 (0.16)
6	0.25 (0.15)	0.77 (0.10)
7	0.60 (0.21)	0.79 (0.16)
8	0.20 (0.12)	0.40 (0.15)
9	0.60 (0.18)	0.79 (0.12)
10	0.26 (0.16)	0.75 (0.19)
11	1.00 (0.00)	1.00 (0.00)
12	0.83 (0.15)	1.00 (0.00)
13	0.66 (0.17)	1.00 (0.00)

NOTE: Numbers in parentheses show standard error. ns, not significant.

TABLE 4. Number of trips for each bee in each treatment

	Number of trips	
Bee	Pollen deprived	Honey deprived
Colony A		
1	2	16
2	4	22
3	8	8
4	8	15
5	13	12
6	8	2
7	14	13
8	4	4
9	5	6
10	7	2
11	8	6
12	8	3
13	7	3
14	22	11
Total	118	123
Colony B		
1	8	5
2	3	4
3	7	6
4	8	4
5	9	8
6	8	14
7	5	8
8	9	8
9	7	10
10	8	5
11	9	8
12	6	9
13	7	5
Total	94	94

by colony ($\chi^2_{(1)} = 0.045$, $p \approx 0.83$). However, the bees within the colonies differed significantly ($\chi^2_{(25)} = 60.154$, $p < 0.001$) in the number of trips made and also ($\chi^2_{(25)} = 50.149$, $p < 0.002$) in their behaviour with respect to the treatment, probably because of differences in maturity among bees.

Individual differences

Table 3 shows the fitted proportions of flights with small or less than small loads for individual bees. In colony A the fitted proportion is smaller in the pollen-deprived condition for all except one bee (No. 12). Hence, the overall increases reported above could not be attributed to the behaviour of a select few individuals. For colony B all bees except for three (Nos. 1, 3, and 5) showed a smaller proportion in the pollen-deprived condition. For bee 11 the proportions were equal.

Discussion

While the results of this study seem to demonstrate that foraging effort for pollen on the part of *Bombus* workers is influenced by the level of pollen reserves within the colony, one alternative explanation is not altogether excluded: it is just possible that the difference in pollen collection rates between the honey-deprivation and the pollen-deprivation days is not so much a result of elevation in the rate of pollen collection rate as a consequence of pollen shortage as it is depression of that rate under conditions of honey shortage (see Cartar 1992). This possibility, however, in no ways affects our major conclusion: the relative allocation of effort that bumble bees put into collecting their two types of food is evidently controlled by changing levels of stored resources within the colony.

In both experimental colonies, the foragers greatly increased the amount of pollen collected per unit foraging time under conditions of pollen stress. The question of how, in general, bumble bees are able to vary the proportions of nectar and pollen that they bring back to the colony deserves discussion. Three alternative mechanisms would probably repay investigation: (1) The insects may select different plant species on which they forage: some flowers (e.g., *Solanum* and *Hypericum* spp.) offer only pollen, others only nectar (e.g., the female flowers of dioecious species). Possibly an individual forager that kept track of several "minor" species (in the sense of Heinrich 1976) could change, from one foraging trip to the next, the relative proportions of flowers of different species that she visited. This may involve going to different places to forage: for example, Brian (1952) recorded changes in the departure directions of bees leaving a *Bombus pascuorum* colony. (2) The forager may not select different plant species but instead change the way in which she visits her major speciality. The work of Galen and Plowright (1985) on *E. angustifolium* provides a model for this possibility: pollen-collecting bees foraged higher up on the inflorescence, i.e., on male-phase flowers, than nectar-collecting bees, which tended to visit the lower, female-phase, flowers preferentially. Alternatively, foragers could forage more heavily at times of day corresponding to maximum nectar or pollen availability. (3) Bees may change neither their preferred flower species, nor the way in which they visit them, but may simply choose whether or not to pack the pollen deposited on their bodies. Several cases of differences in the rate of pollen collection among bees simultaneously working on the same stand of flowers appear to support this latter possibility: for example, Laverty and Plowright (1985) noted that whereas neither *Bombus fervidus* nor *Bombus vagans* were observed to collect pollen from a population of *Impatiens biflora* on Amherst Island, Ontario, in the late summer of 1983, workers of *Bombus impatiens* foraging from the same stand at the same time were often seen with large loads of *I. biflora* pollen. Similarly, Thomson et al. (1987) observed that individually marked workers of *Bombus affinis*, foraging on *Aralia hispida*, began collecting just nectar after several days of collecting both nectar and pollen. In the most closely observed case, the bee appeared to have sustained a leg injury that may have prompted the change in behaviour, but there may also have been a ''voluntary'' component to this and other such switches.

Which, if any, of these three mechanisms is dominant among foraging bumble bees remains to be determined. At the level of the colony, the majority of our *B. terricola* workers did, as expected, bring back more pollen under conditions of pollen deprivation than under nectar shortage. Furthermore, they did so not by increasing the frequency of their foraging trips, but rather by increasing their rate of pollen collection per foraging trip.

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