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Colony energy requirements affect the foraging currency of bumble bees

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Summary. This study examines whether the foraging behavior of worker bumble bees (*Bombus*: Apidae) collecting nectar on inflorescences of seablush (*Plectritis congesta*: Valerianaceae) is affected by colony energetic requirements, which were experimentally manipulated either by adding sucrose solution to honey pots or by removing virtually all available nectar from the pots. The competing hypotheses tested were: (1) no change; energetic requirements do not affect behavior, since there is a single best way to collect food in a given environment; (2) energetic currency; the energetic currency maximized by foragers changes according to colony energetic condition, with nectar-depletion causing a shift from maximizing long-term productivity to maximizing immediate energetic gain, thereby de-emphasizing energetic costs; and (3) predation; foragers devalue risk of predation as risk of starvation increases, with colony nectar-depletion causing foragers to be less predation risk-averse in order to increase immediate energetic gain. Relative to when their colony energy reserves were enhanced, foragers from nectar-depleted colonies selected smaller inflorescences, visited fewer flowers per inflorescence, probed flowers at a higher rate while on each inflorescence, and walked between inflorescences less often, thereby spending a greater proportion of their foraging trip in flight. These behaviors increased a bee's energetic costs while foraging, and should also have increased its immediate energetic gains, allowing rejection of the no change hypothesis. Predictions of the predation hypothesis were generally not supported, and our results best support the energetic currency hypothesis. Foraging currency of bumble bees therefore appears to be a function of colony energetic state.

addressed the problem of when a bee should move from one inflorescence to the next, given that the nectar rewards on inflorescences decrease in a predictable manner. Inflorescence-departure decisions were found to be predicted by the marginal value theorem (Charnov 1976), and the currency maximized by these bees appeared to be the rate of net energy intake.

While the goal of net rate maximization is probably accurate in a general sense (i.e., over the long term), recent work suggests that it is not necessarily adequate as a short term currency for foragers (Stephens in press). The findings of risk-sensitivity (e.g. Caraco et al. 1980) and time discounting (Kagel et al. 1986) cannot be explained in terms of net rate maximizing. More recent approaches to foraging theory explicitly recognize tradeoffs between foraging and other activities, and the effects of time horizons and the forager's state on foraging behavior (e.g., McNamara and Houston 1986). Net rate maximizing, then, can be viewed as simply a special case subsumed within a general theoretical framework relating foraging to maximization of fitness (Houston and McNamara 1988).

Several aspects of the foraging behavior of bumble bees are affected by colony energetic condition. Relative to when their colony energy reserves are enhanced, foragers from nectar-depleted bumble bee colonies: (a) switch from pollen to nectar collection (Free 1955; Cartar 1989); (b) switch from in-colony to foraging tasks (Cartar 1989); (c) are less wary of a simulated vertebrate predator (Cartar 1989); and (d) choose flowers with variable over those with constant nectar rewards (given equal means; Cartar and Dill 1990; Cartar 1991). These results show that bumble bees trade-off food types, in-colony and foraging tasks, and food intake and predation risk, and that bees will forage so as to minimize their colony's probability of energetic shortfall. What is unknown, however, is whether the in-patch foraging behavior of nectar-collecting bumble bees is also a function of colony energetic condition.

This study investigates the behavior of worker bumble bees foraging for nectar on multi-flowered inflores-

Many of the early successful tests of foraging theory used nectar-collecting bumble bees (Pyke 1979, 1980; Hodges 1981; Best and Bierzychudek 1982). These tests

cences, and asks whether colony energetic condition affects foraging behavior. There are several alternative ways in which foragers might respond adaptively to variation in colony energy reserves. In addition to the tactic of switching between pollen and nectar collection (not further considered in this paper), these alternatives include: no change, a change in energetic currency, and a change in predation risk-sensitivity.

The hypotheses

The no change hypothesis requires little elaboration, and is based on the premise that bees are already foraging in the best possible way. A bee should therefore always pay the same energetic costs and extract the same nectar benefits from a given environment. While colony energetic condition may affect the trade-off between foraging and other activities, once the decision to forage has been taken, there is a single best way to collect food. This hypothesis has been implicitly assumed in past studies of bumble bee foraging behavior.

The energetic currency hypothesis recognizes that colony energetic condition may affect the short-term goals of foragers, and therefore the currency maximized. We consider 3 currencies (reviewed by Houston 1987), although others (e.g., Fagerstrom et al. 1983) may also be appropriate. The life span of honey bees (*Apis mellifera*), at least, appears to be limited by energetic expenditure (Wolf and Schmid-Hempel 1989), leading to the prediction that bees should be sensitive to the diminution in their life span caused by energetic expenditures while foraging. Such a forager may wish to maximize the ratio of energy intake to expenditure. This currency, termed "efficiency", successfully explains some aspects of honey bee foraging behavior (Schmid-Hempel et al. 1985; Schmid-Hempel 1987). A second currency – "net energy" – expresses the rate at which energy is collected, and is calculated as the amount of energy collected minus the energetic costs of obtaining it, all divided by time taken to gather it. As noted above, the inflorescence-departure decisions of bumble bees appear to be based on the currency of rate of net energy intake (e.g., Pleasants 1989). A third currency – "gross energy" – is identical to "net energy", except that it excludes foraging costs. This currency may be appropriate for a forager attempting to maximize the immediate rate of foraging gain, regardless of the (short-term) costs to itself (e.g., pied flycatchers, *Ficedula hypoleuca*, feeding hungry nestlings; Lifjeld 1988).

We can imagine the currencies described above as forming a continuum, with "efficiency" placing the greatest emphasis on energetic costs of foraging, "net-energy" being less concerned with them, and "gross energy" wholly ignoring these costs. If bumble bees have effort-limited life spans, and if workers are selected to maximize their lifetime foraging production, then we can expect foragers from healthy colonies to be efficiency maximizers. However, maximizing lifetime foraging gain is not optimal for workers whose colonies are unlikely to survive for the optimal worker life span (e.g., those under food-stress). In this case, foragers should sacrifice

a longer individual life so as to increase their immediate rate of energy intake, and should therefore adopt a currency of "net energy" or "gross energy". Where any organism is likely to lie along this currency continuum probably depends on its individual condition, but it is likely that any downward shift in colony condition will shift the currency employed in the direction of the cost-discounting end of the continuum (i.e., towards maximizing gross energy). Houston et al. (1988) also suggest that foraging currency changes with colony condition, in their case as a function of colony size.

Foraging bumble bees can walk or fly between flowers and inflorescences, with flight costing roughly 10 times more in energy per unit time than non-flight (Heinrich 1975), but generally yielding an increase in travel speed of less than 2 times. Since flight is thus relatively more expensive, foraging choices requiring flight should not be favored over those involving walking (all else being equal). An "efficiency" maximizer might therefore include fewer flowers in her diet to which she must fly, relative to a "net energy" or "gross energy" maximizer. The diet breadth resulting from these latter currencies would therefore be broader, by virtue of a greater range of locomotory options. A prediction of the energetic currency hypothesis, then, is that a downward shift in colony condition should result in an increase in the use of flight by foraging workers. This has ramifications for the size of inflorescences visited, the number of probes per inflorescence, and the frequency of walking between and within inflorescences.

The predation hypothesis recognizes that colony energetic condition may affect the degree of predation risk that foragers are willing to incur. Willingness of foragers to flee from a simulated vertebrate predator is known to be related to colony energy requirements under laboratory conditions (Cartar 1989). An increase in colony energetic requirements may therefore cause foragers to adopt risky foraging tactics which, while increasing immediate energy gain, also decrease expected life span. Hence, the predation hypothesis predicts a decrease in the predation risk-sensitivity of foragers when colony energetic condition deteriorates. For example, bees from nectar-depleted colonies may visit inflorescence sizes normally avoided because of their associated high predation risk. The predation and energetic currency hypotheses are not mutually exclusive.

Methods

In May of 1986 through 1989, wild bumble bee colonies established in domiciles on the campus of Simon Fraser University, Burnaby, B.C., Canada, were set out on Mitlenatch Island, a small 36 ha island in the Strait of Georgia (49° 56' N, 125° 00' W). Workers were marked on the thorax with unique combinations of enamel paint, or with paint and a numbered plastic disc (in 1987). 4 bumble bee species were studied: *Bombus melanopygus*, *B. occidentalis*, *B. sitkensis*, and *B. mixtus*. Since all bumble bee colonies require nectar for energy, and use it in similar ways, species differences are considered to be unimportant from the viewpoint of the questions addressed in this study.

Nectar is a critical resource for bumble bee colonies; considerable quantities are consumed to keep hive temperatures at high

levels, for larval growth, and for maintenance of adults (Heinrich 1979). It is stored in open-topped honey pots, which accumulate nectar during the day and are depleted overnight. We manipulated the energetic condition of colonies using a 1 ml pipette either to add 1 to 4 ml of 50% sucrose solution to colony honey pots ("enhanced"), or to remove all available nectar ("depleted"). Larger colonies received more sucrose solution. Treatments were assigned randomly on the first experimental day for each colony, and alternating treatments were then applied on subsequent days. Data from a given colony were collected during 2 to 6 experimental days. No observations were made on days of rain or strong winds (> 25 km/h). To compensate for lost energy, nectar-depleted colonies were given 50% sucrose solution (between 0.5 and 1.75 ml, depending on colony size, which varied from 6 to 92 workers (mean = 41, $sd = 22$, $n = 28$)) at roughly 2200 h on the day of manipulation. Manipulations were performed in the afternoon, between 1330 and 1630 h (mean = 1400 h), and observations of bee foraging made between 1600 and 2030 h (mean = 1800 h).

Bees were observed feeding on seablush (*Plectritis congesta*: Valerianaceae), which grows in dense mats on the island's NW slopes. Seablush inflorescences contain many small pink flowers (typically 10 to 60, each 3–4 mm deep) arranged on a spherical or cylindrical surface and borne at a height of 5 to 50 cm. Flowers of different age are distributed throughout the inflorescence, resulting in no systematic spatial trends in nectar volume, and adjacent flower heads are frequently closely spaced (< 1 cm).

The behavior of bumble bees foraging on seablush was recorded either by speaking into a microcassette recorder (timed later using an event recorder) or by video-tape. Workers encountered foraging on seablush were followed for several minutes or until lost from sight. To control for among-observer differences, all data used in a given analysis were collected by a single observer. Pollen-collecting bees (i.e., those with pollen in their corbiculae or exhibiting pollen-collecting behavior) were ignored. To quantify the movement patterns of foraging bees, two grids (measuring 6×11 m, and 4×17 m) were established in 1987 in patches of seablush, each divided into quadrats whose sides measured 0.5 m. The position of the bee was recorded at 10 s intervals, as signalled by a metronome. The energetic rewards offered by seablush flowers were estimated by measuring the nectar levels in the flower's spur, using an eyepiece micrometer, and converting this to an estimate of volume using a regression equation (Cartar 1989). The concentration of sugar in the nectar (mg solute/mg solution) was measured using a Kyowa hand-held refractometer. Nectar was extracted from flowers using a 2 μ l microcapillary tube. The volume of nectar in individual flowers was usually too small to allow measurement of concentration, so we used a sample pooled from several flowers.

Results

The behavior of bumble bees foraging on seablush was considered at two basic levels: traits influencing movement among inflorescences (i.e., inflorescence size visited, probes per inflorescence, frequency of walking between inflorescences, and percentage of the foraging bout spent in flight), and locomotion within inflorescences. Each will be considered separately. In all cases, comparisons are made at the level of the colony, and contrast foraging bees whose colonies were nectar-enhanced to those whose colonies were nectar-depleted.

Inflorescence size

The 3 competing hypothesis make different predictions about the effect of colony energetic condition on size of inflorescence chosen by nectar-foraging bumble bees. The no change hypothesis predicts no effect. Since bees

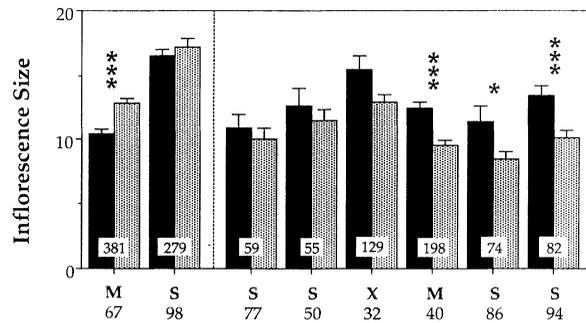


Fig. 1. Effect of colony energy stores on inflorescence size (measured as estimated number of open flowers) chosen by nectar-collecting bumble bees. Species for this and other figs. are: M, *B. melanopygus*; O, *B. occidentalis*; S, *B. sitkensis*, X, *B. mixtus*. Colony number appears beneath each species code. Means, with 1 SE, contrast enhanced (solid bars) and depleted (stippled bars) treatments for each colony. Colonies appear in ascending order according to the size of the difference between the two means (enhanced minus depleted), with the dotted vertical line separating colonies with negative from those with positive differences. Sample sizes for each paired comparison are shown within the bars. Results of a Kruskal-Wallis ANOVA are presented for each colony. Significance levels are: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Overall, bees from nectar-depleted colonies chose smaller inflorescences (Wilcoxon test, $T = 5$, $n = 8$, 1-tailed $P = 0.039$).

fly between inflorescences 86% of the time ($n = 1353$), the between-inflorescence net travel costs from visiting smaller inflorescences are relatively higher. This is because there are fewer flowers to probe on each inflorescence, causing bees to spend relatively more time in flight between them. Therefore, because the energetic currency hypothesis predicts decreased sensitivity to flight costs with poor colony condition, it predicts that bees from nectar-depleted colonies will accept a greater proportion of smaller inflorescences in their diets than will bees from nectar-enhanced colonies. Crab spiders present a major predation risk to foraging bees (Morse 1986), and the spider *Misumena vatia* Clerck (Thomisidae) is present on seablush on Mitlenatch Island. Crab spiders tend to occur more often on larger inflorescences than on small ones (mean = 31.0 flowers, $n = 6$, $SD = 16.9$; sizes of inflorescences within the 2 seablush grids: mean = 12.8 flowers, n approx. 10000). Since the predation hypothesis predicts that foragers will be less predation-averse when colony energetic condition is poor, it therefore predicts that bees from nectar-depleted colonies will choose relatively larger (and therefore riskier) inflorescences, assuming (as in the energetic currency argument) that doing so will increase intake rate.

The available evidence provides limited support for the energetic currency hypothesis. Pooled data from 8 colonies show a significant overall decline in inflorescence size for bees from nectar-depleted colonies (Fig. 1). The effect is significant for 3 colonies, but is significant in the opposite direction of one colony.

Flower visits per inflorescence

While the "no effect" hypothesis predicts no change in the number of flowers probed per inflorescence with

a change in colony energetic condition, the other hypotheses both predict the same effect: that bees from nectar-depleted colonies should probe fewer flowers per inflorescence. Both predictions are based on an information-use argument, but the nature of the information differs.

First, probing may provide information about the energetic quality of an inflorescence. In 7 of 15 2-h periods in which the nectar rewards of 9 flowers from 8 or 9 co-occurring *Plectritis congesta* inflorescences were compared, among-inflorescence differences were significantly greater than within-inflorescence differences (oneway ANOVAs, $P < 0.01$). Hence, bees may assess an inflorescence's quality by sampling several of its flowers, and leave the inflorescence once they recognize that it offers a lower-than-average expected energetic reward. According to the energetic currency hypothesis, the threshold for leaving an inflorescence changes with colony manipulation: bees from nectar-depleted colonies, for whom flight costs are relatively devalued, should have higher energetic thresholds for patch "acceptance" than should bees from nectar-enhanced colonies (even if these thresholds change with each successive flower probe, e.g., McNamara and Houston 1987). This results in a smaller average number of probes per inflorescence by bees from nectar-depleted colonies. Even if a bee's rate of gain decreases with time spent on an inflorescence, an efficiency-maximizer would probe more flowers than a gross rate maximizer, given that the energetic cost of traveling between inflorescences exceeds that of within-inflorescence travel (Houston 1990). Again, bees from nectar-depleted colonies should on average probe fewer flowers per inflorescence.

Second, information can be obtained about inflorescence safety. Bees do not appear to see crab spiders lying in ambush (Morse 1986; pers. obs.), and crab spiders will move to attack bees over an area of several adjacent flowers. Therefore, the more flowers that a bee probes on a given inflorescence without being attacked, the more confident it can be that the inflorescence is a safe, spider-free one. Hence, bees can trade-off safety and energetic gain. Bees may therefore stay longer on inflorescences of inferior energetic quality, with quality determined solely by currency-maximizing standards and recognized by sampling. This is because they have learned, through attack-free flower visits, that the inflorescence at hand has a lower-than-average associated predation risk. Although foragers have a relatively large chance of escaping from crab spider attack (82% of attacks, $n = 11$), risk of death likely increases with attack frequency, and attacks occurred in 23% of visits to inflorescences containing a crab spider. According to the predation hypothesis, then, bees from nectar-depleted colonies should increase energy gain, but also take greater risks of predation, by probing fewer flowers per inflorescence and thereby visiting more inflorescences.

The data support both the energetic currency and predation hypotheses. In 9 of 11 colonies, bees foraging under colony nectar-depletion made fewer probes (significantly so in 3 of them), and this trend was significant overall (Fig. 2). At first glance, this result may appear to be a consequence of inflorescence size, since bees will

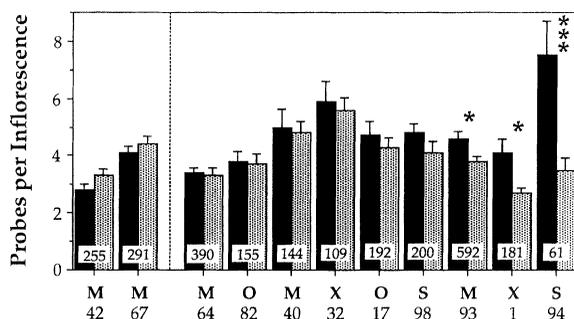


Fig. 2. Effect of colony energy stores on number of probes made on each inflorescence. Symbols and layout as in Fig. 1. Results of Kruskal-Wallis ANOVAs are presented for each colony. Overall, bees from nectar-depleted colonies probed fewer flowers on each inflorescence (Wilcoxon test, $T = 11.5$, $n = 11$, 1-tailed $P = 0.031$)

necessarily have probed fewer flowers if they visited smaller inflorescences. Two lines of evidence suggest that the trend in Fig. 2 cannot be attributed solely to a decrease in inflorescence size visited as a result of honey-pot depletion. First, to test whether the effect of treatment on number of probes was independent of inflorescence size, we performed an ANCOVA on number of probes (log-transformed to normality) for *B. sitkensis* colony 94 (the only colony which showed a significant effect of treatment on number of probes and for which number of probes and inflorescence size were collected simultaneously). After controlling for inflorescence size ($F = 5.48$, $P = 0.023$), the treatment effect remained ($F = 10.32$, $P = 0.002$; overall model $F = 12.24$, $P = 0.0001$, $n = 82$). Second, the magnitude of the treatment effect appears to be greater for probes per inflorescence (Fig. 2) than for inflorescence size (Fig. 1). These results suggest that treatment separately influenced number of probes and inflorescence size chosen.

Walking between inflorescence and time spent flying

Bumble bees usually fly between seablush inflorescences (86% of instances). The no change hypothesis predicts no change in movement patterns between inflorescences. Assuming that bees are vulnerable to predation only while on an inflorescence, and not while moving between inflorescences, then the predation hypothesis also predicts no change in between-inflorescence movement patterns. However, the energetic currency hypothesis, because of a shift in the value placed on foraging costs, predicts that bees from nectar-depleted colonies should spend a greater proportion of their foraging trip flying between inflorescences, and walk between inflorescences less frequently, and should therefore travel greater distances.

Relative to colony energy-enhancement, energy-depletion did indeed cause bees to walk less frequently between inflorescences (Fig. 3), supporting the energetic currency hypothesis. The percentage of a forager's trip that was spent in flight between inflorescences was 22.9% in enhanced colonies and 27.1% in depleted colonies. This average 4.2% increase in flying under energy-depletion is weakly significant (Fig. 4) again supporting

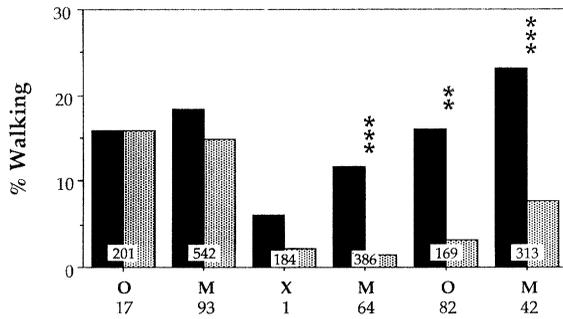


Fig. 3. The effect of colony energetic condition on frequency of walking between seablush inflorescences. Symbols and layout as in Fig. 1. Results of contingency analyses are presented for each colony. Overall, bees from nectar-depleted colonies walked between inflorescences less often (Wilcoxon test, $T=0$, $n=5$, 1-tailed $P=0.031$)

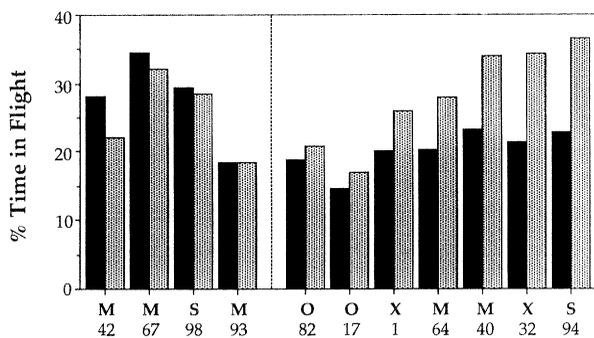


Fig. 4. The effect of colony energetic condition on mean percent time spent flying between seablush inflorescences. Symbols and layout as in Fig. 1. No within-colony tests were possible, due to a complicated error structure caused by estimating percent time flying from 2 separate variables: time in flight and time on inflorescences. Overall, bees from nectar-depleted colonies spent a marginally greater proportion of their travel time in flight (Wilcoxon test, $T=14$, $n=11$, 1-tailed $P=0.051$)

the energetic currency hypothesis. Given no differences in average among-inflorescence flight durations between treatments (Wilcoxon test, $T=22$, $n=12$, $P>0.4$), this difference in flight time presumably reflects the differences in inflorescence size, number of probes per inflorescence, and frequency of walking between inflorescences documented above.

Since bees from energy-depleted colonies visit fewer flowers (Figs. 1 and 2), and spend more of their foraging time in flight (Fig. 4), they should move through a patch of seablush more quickly (given no change in directionality). This was tested with data on timed bee movement patterns within the 2 grids of seablush (in Methods). When bee movements between quadrats were classified into 8 principal directions (a movement was considered to have occurred only if a bee moved between quadrats), there was no significant change in directionality with colony energy condition (pooling all observations; $\chi^2=2.78$, $n=345$, $P=0.91$). Hence, colony treatment did not affect the probability that a forager would move straight through a patch of seablush. However, the average distance moved by bees was affected by colony energy condition (Wilcoxon test, $T=0$, $n=5$, 1-tailed $P=0.031$).

Bees from nectar-depleted colonies moved greater distances while foraging in a patch of seablush in each of 5 colonies measured, although the trend was not significant within any given colony (Kruskal-Wallis ANOVAs). The change in proportion of time spent flying between inflorescences therefore showed up as a change in distance moved within a patch.

Flower encounter rate

A bumble bee foraging on a seablush inflorescence faces an array of flowers of differing ages scattered across a spherical surface. The no change hypothesis predicts that the rate at which bees encounter these flowers will be unaffected by colony energy status. However, the energetic currency hypothesis predicts that bees should increase their rate of encounter with flowers when their colony is energy-depleted. Bees can use at least three methods for moving between flowers – walking (mean frequency of 41.9%), buzzing (a wing-assisted walk, mean frequency of 52.3%), and flying (mean frequency of 5.8%) – which differ in their speeds and associated costs. Walking is slower and less costly than flying, and buzzing is of intermediate cost and speed. Since, under the energetic currency hypothesis, foragers from nectar-stressed colonies should devalue foraging costs and value foraging gains, such foragers should increase their use of buzzing or flying as a means of increasing immediate energy gain. Assuming that predation risk is independent of means of locomotion (crab spiders attack both walking and flying bees, pers. obs.), then the predation hypothesis (like the no change hypothesis) predicts that flower encounter rate is independent of colony energy status.

Bees from nectar-depleted colonies probed more flowers per unit time than did bees from nectar-enhanced colonies, as predicted by the energetic currency hypothesis (Fig. 5). This effect was significant for 5 of the 11 colonies. Also as predicted by the energetic currency hypothesis, bees from nectar-depleted colonies, when compared to bees from nectar-enhanced colonies, increased their use of buzzing or flying (after pooling these categories owing to the scarcity of flying) as a means of

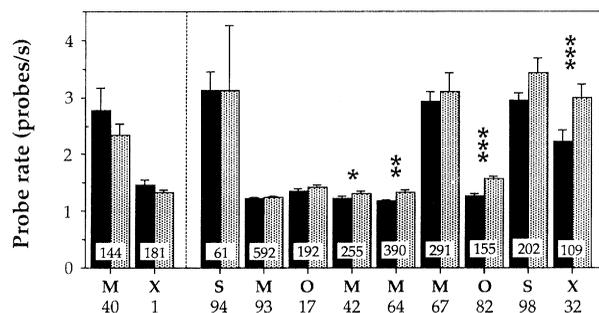


Fig. 5. Effect of colony energetic condition on speed of flower handling while on a seablush inflorescence. Symbols and layout as in Fig. 1. Results of Kruskal-Wallis ANOVAs are presented for each colony. Overall, bees from nectar-depleted colonies probed marginally more flowers per unit time (Wilcoxon test, $T=14$, $n=11$, 1-tailed $P=0.051$)

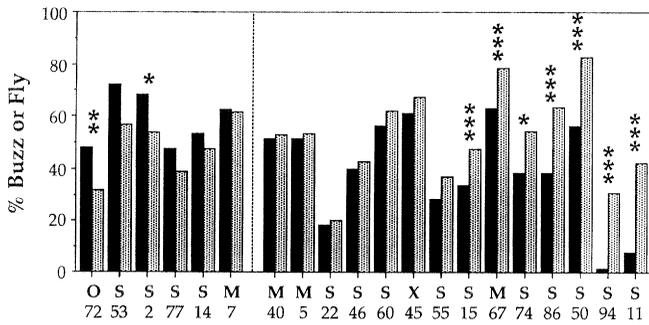


Fig. 6. Effect of colony energetic condition on method of locomotion between flowers within an inflorescence. Symbols and layout as in Fig. 1, except for sample size; sample sizes for each paired comparison varied from 259 to 1429 (mean = 573). Results of Kruskal-Willis ANOVAs are presented for each colony. Overall, bees from nectar-depleted colonies used their wings (buzz or fly) more frequently while moving between flowers (Wilcoxon test, $T=57.5$, $n=20$, 1-tailed $P=0.038$)

moving between flowers within an inflorescence (Fig. 6). Hence, the increase in flower encounter rate for bees from nectar-depleted colonies (Fig. 5) resulted at least partly from a shift in method of locomotion, with the frequency of wing-assisted movement increasing an average of 6.4%.

However, the treatment-related differences in foraging rate may also have resulted from bees from nectar-depleted colonies more often not fully draining flowers, leaving the difficult-to-reach “last dregs” (Witham 1977; Hodges and Wolf 1981). In this case, flower probing times, not between-flower travel times, could have partially caused the shift in flower encounter rate. To test this, nectar was sampled from individual flowers immediately after bees had probed them. Pooling all individuals, bees from nectar-enhanced colonies left measurable nectar on 1.1% of occasions (1 of 88 flowers) while bees from nectar-depleted colonies did so on 4.4% of occasions (4 of 92 flowers). This difference is not significant (continuity-corrected $G=0.76$, $P>0.2$). Hence, the difference in foraging rate appears to have resulted primarily from changes in between-flower travel time, and not from changes in flower probe time.

Discussion

Taken together, these results favor the energetic currency hypothesis (Table 1). It correctly, and uniquely, predicted changes in inflorescence size, flower visits (probes) per inflorescence, and frequency of walking between inflorescences, which collectively affected the proportion of the foraging trip spent in flight between inflorescences. It also correctly predicted the change in the rate at which flowers were encountered within the inflorescence. The predation hypothesis made 1 of 4 correct predictions, but it was not unique. We can safely reject the no change hypothesis, as colony energetic condition did have a significant effect on several aspects of the in-patch behavior of foraging bumble bees. It is important to note that the remaining 2 hypotheses (energetic currency and predation) are not mutually exclusive, and

that bees may have been sensitive to both factors. However, the results of this study most strongly support changes in foraging currency as the primary functional explanation for altered in-patch foraging decisions. On a cautionary note, we point out that the magnitude of the treatment effect is relatively small (Figs. 1 to 6), and much variance in bee behavior remains unexplained by shifts in energetic currency.

Relative to their enhancement, the depletion of colony energy reserves can be viewed as placing foraging bees under “time stress”, causing them to collect more energy in a shorter period of time. Other time-limited foraging animals have shown themselves to be capable of increasing their rate of intake (Robinson 1986; Swennen et al. 1989), but presumably at some cost (e.g., increasing predation risk, McNamara and Houston 1986). The cost that bumble bees probably incur by increasing foraging effort when their colony is energy-depleted is a reduced expected life span – either by senescence, predation, or starvation.

The disproportionately increased mortality in older age classes of bumble bee foragers (Rodd et al. 1980) suggests that senescence does influence worker life span. If bumble bees are typically efficiency maximizers (as honey bees appear to be: Schmid-Hempel et al. 1985; Schmid-Hempel 1987), then a downward adjustment of colony energy stores should shift foragers towards more short-term, less efficient currencies. The primary shift in behavior detected by the present study was in the method of transportation employed in moving within and among inflorescences. Bees from nectar-depleted colonies increased their use of flight, and decreased their use of walking. However, there are at least two other components of the foraging process which might also change with currency: load size (Schmid-Hempel et al. 1985), and flight speed (Welham and Ydenberg 1988). We expect both factors to be of relatively minor importance in inducing currency-related shifts in bumble bee forager behavior. This is because the time spent in transit between colony and patch is small (usually no more than 2 min of a 30 min foraging trip), and changes in load size are likely to be small at typical foraging distances. Thus, changes in load size and flight speed are probably

Table 1. An evaluation of the hypotheses tested in this study (“+” = predictions supported, “-” = predictions not supported). Percent flying is separated from the other among-inflorescence traits because it may have resulted from their combined effects, and as such is not independent

Trait	Hypothesis		
	No change	Currency	Predation
Traits reflecting travel among inflorescences:			
Inflorescence size	-	+	-
Probes per inflorescence	-	+	+
Frequency of walking	-	+	-
Percent flying	-	+	-
Traits reflecting travel within inflorescences			
Flower encounter rate	-	+	-

less important in affecting colony energy gain than are shifts in the use of flight while collecting nectar, which occur *throughout* a foraging trip.

Cartar (1989) shows that nectar-depletion of colonies causes in-colony workers to leave their colonies and forage, and that these bees make fewer foraging trips per observation period. Without showing that the responses to energetic manipulation can occur *within* individuals, all of the results reported in the present study could be attributed to a change in the *nature* of the individuals foraging. However, this was not the case. Individually-marked foragers from each of 3 colonies were observed foraging under both colony energy treatments. 2 of the 3 foragers showed the same behavior as their colonies (one with a significant treatment effect) for number of probes and probe rate, and all 3 foragers showed the same behavior as their colonies for average distance moved (2 with significant treatment effects).

Manipulation of colony energy stores is known to affect forager preference for pollen collection (Free 1955; Cartar 1989). We controlled for this factor by excluding pollen-collecting bees from the analysis. A further experiment, in which workers were followed in a patch of emasculated seablush, showed no differences in behavior on emasculated and non-emasculated inflorescences. Hence, our findings do not reflect a switch in worker preference for collection of pollen.

The shift in food-gathering technique based on energetic requirements documented in nectar-collecting bumble bees by this study lends support to the condition-dependent foraging approach embodied in the models of Houston and McNamara (1988) and Mangel and Clark (1988). It seems that how a forager behaves in a given environment is not simply a function of the food rewards present in that environment, but also depends on the forager's own condition (or, in this case, on the condition of her colony).

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