Behav Ecol Sociobiol (1990) 26:121–127

Behavioral Ecology and Sociobiology

Why are bumble bees risk-sensitive foragers?

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Received December 12, 1988 / Accepted June 5, 1989

Summary. In a controlled laboratory experiment, we re-examined the question of bumble bee risk-sensitivity. Harder and Real's (1987) analysis of previous work on bumble bee risk aversion suggests that risk-sensitivity in these organisms is a result of their maximizing the net rate of energy return (calculated as the average of expected per flower rates). Whether bees are risk-sensitive foragers with respect to minimizing the probability of energetic shortfall is therefore still an open question. We examined how the foraging preferences of bumble bees for nectar reward variation were affected by colony energy reserves, which we manipulated by draining or adding sucrose solution to colony honey pots. Nine workers from four confined colonies of *Bombus occidentalis* foraged for sucrose solution in two patches of artificial flowers. These patches yielded the same expected rate of net energy intake, but floral volumes were variable in one patch and constant in the other. Our results show that bumble bees can be both risk-averse (preferring constant flowers) and risk-prone (preferring variable flowers), depending on the status of their colony energy reserves. Diet choice in bumble bees appears to be sensitive to the "target value" of a colony-level energetic requirement.

Introduction

Risk-sensitive foraging is a topic of considerable current interest (Real and Caraco 1986). Its importance stems from its explicit consideration of how resource variability affects foraging decisions. In the special case where rewards are identical for all options, risk-sensitive foragers are said to be risk-prone if they prefer variability in their food rewards, and risk-averse if they avoid such variability.

Some of the earliest studies of risk-sensitive foraging used bumble bees (Real 1981; Real et al. 1982). In these studies, bees were given a choice between two floral types: constant and variable. Bees were found to be always risk-averse (i.e., avoiding variable flowers when mean nectar volume was the same for the two alternatives) and would only feed on variable flowers if their mean volumes were increased, relative to the constant type. Indeed, attempts to induce risk-prone behavior in bumble bees (i.e., preferring variable flowers when mean volumes are the same) have thus far met with failure (Real and Caraco 1986:384).

Harder and Real (1987) recently re-analyzed these experiments, focusing on the effect of reward size on flower handling time. Given a linear relationship between floral volume and time taken for full nectar extraction and given that all flowers require a finite time to travel between and to handle before extracting nectar, there is a non-linear relationship between rate of net energy return and floral volume. This means that bees that are offered a choice between a constant and a variable reward (but with the same mean volumes) are actually offered a choice between patches that differ in their profitabilities (as measured by expected rate of net energy intake). Harder and Real (1987) found that in all previous experiments (Real 1981; Real et al. 1982), bees chose the most rewarding flowers, i.e., those that yielded the highest expected rate of net energy intake. This result does not preclude risk-sensitivity, since bees were sensitive to reward variance when faced with distributions of equal mean *volumes*.

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There is a problem with the Harder and Real (1987) calculation of expected rate of net energy intake for variable flowers (Possingham et al. MS). Harder and Real calculated this value as the average of the expected rates associated with each flower volume, weighted by their frequencies, rather than as the net energetic expectation (for all volumes) divided by the total time expectation, thereby committing the "fallacy of averages" (Templeton and Lawlor 1981).

Remarkably, however, bees actually seem to commit such a fallacy in their estimation of flower profitabilities. Harder and Real (1987), using their method of calculating expected rate of net energy intake, showed that bees preferred the constant flower type when it offered the higher rate, were indifferent when the two flower types offered equivalent rates, and preferred the variable flower type when it offered the higher rate (their Figs. 2, 3). Further, in both experimental series for which Harder and Real produced computer simulations, the "fallacious" per flower average rate model correctly and *uniquely* predicted floral preference on 11 occasions (of 51), while the "theoretically correct" rate model made no uniquely correct predictions. The difference is significant (sign test, 1-tailed $P < 0.001$). Both models correctly predicted the bees' behavior in 13 additional cases. We therefore conclude that bees determine profitability as described by Harder and Real, and hereafter use their measure of expected rate of net energy intake (i.e., the average of the per flower rates) in our treatment of this variable.

The Harder and Real model argues that risk-sensitivity in bumble bees functions to maximize expected net rate of energy intake. An alternative functional model of risk-sensitivity (characterized at its simplest by the *z*-score model of Stephens and Charnov 1982), argues that risk-sensitivity functions to minimize the probability of not meeting some energetic requirement. Energetic needs are known to underlie risk-sensitive decisions in many foraging situations. For example, the sensitivity to variance in food reward of small seed-eating birds (Caraco et al. 1980; Caraco 1981, 1982, 1983; Caraco and Chasin 1984; Caraco and Lima 1985), shrews (Barnard and Brown 1985), warblers (Moore and Simm 1986), and hummingbirds (Stephens and Paton 1986) is apparently affected by the probability of meeting daily energetic requirements. Since stored reserves affect an organism's expectation of meeting its food requirement, reserves should be a determinant of foraging risk-sensitivity.

Before accepting the idea that bumble bee risk-sensitivity is simply related to maximizing rate of net energy intake, we should first attempt to do the critical experiment in which expected rate of net energy intake is the same among alternatives. This experiment will allow us to discriminate between the two models: the Harder and Real model predicts indifference, while the energetic shortfall model predicts risk-sensitivity based on expected net energy gain. In this paper, we report findings which suggest that bumble bees can show either risk-prone or risk-averse behavior in such a situation, depending on colony energetic needs.

Nectar is the energy source for a bumble bee colony and is stored in a few open-topped pots in the nest. We therefore manipulated these honey pot levels to test for changes in risk-sensitivity. Bees were given a choice between two nectar distributions of the same expected rate of net energy intake but different variance. If bee risk-sensitivity is based on variability in expected rate of net energy intake and is an adaptation for minimizing the probability of energetic shortfall, then foragers should prefer the variable distribution when colony energy reserves are lowered, relative to when their colony energy reserves are increased.

Methods

In June through August of 1986 and 1987, we worked with nine workers from four *Bombus occidentalis* colonies that were established in field domiciles in April and brought into the laboratory. Each had produced at least two worker broods (which me marked individually with numbered plastic discs or unique patterns of Testor's enamel paints), and each contained broods of both larvae and pupae. We confined the colonies singly outdoors in screen tents ($4 \times 4 \times 2$ m) in a semi-shaded area at Simon Fraser University in Burnaby, B.C. Bees were trained over several days to collect 40.0% (mg solute/mg solution) sucrose solution from "flowers" (shallow wells, measuring 3.0 mm in diameter and 2.5 mm in depth, drilled into a 6.5 mm plexiglass board) arranged to form a square grid with flowers 4.5 cm apart. We filled flowers with a Hamilton syringe mounted in a repeating dispenser. Boards were washed with a jet of hot water and blow- or heat-dried between each use.

The flowers in each patch were marked with a circle or star placed under the plexiglass board, which lay on a table top at a 43 deg angle to the horizontal (to discourage bees from walking between flowers). The flowers in each patch were arranged in three adjacent rows of seven, and patches were separated by a 1 cm high cardboard barrier (to minimize "unintended" forager movement between them). The habitat containing both patches formed a square. To control for the attractiveness of each floral type, all flowers were blue and the pigmented areas of both types were equal. Preliminary trials showed that bees left no measurable nectar behind in the flowers.

The experimental procedure was as follows. Bees were presented with a choice between a "constant" patch (all flowers contained the same volume) and a "variable" patch (half the flowers contained one volume, and the other half another volume), both of which yielded identical mean rates of net energy return. Patches were side-by-side and equidistant from the hive entrance, with the position (north or south) and flower type (circle or star) of the variable patch being determined by two coin tosses before each trial. The variable patch was north and (independently) composed of stars for five of nine bees. Each trial was run in the afternoon. Since bees slowed down at lower temperatures, we performed trials only on days when ambient temperatures exceeded 15° C. After experiments, and up to 3 h before them, bees had unlimited access to sucrose solution in gravity feeder tubes. Pollen was provided in excess by adding it directly to the colony. Before each foraging bout, all foragers were returned to the colony and prevented from leaving.

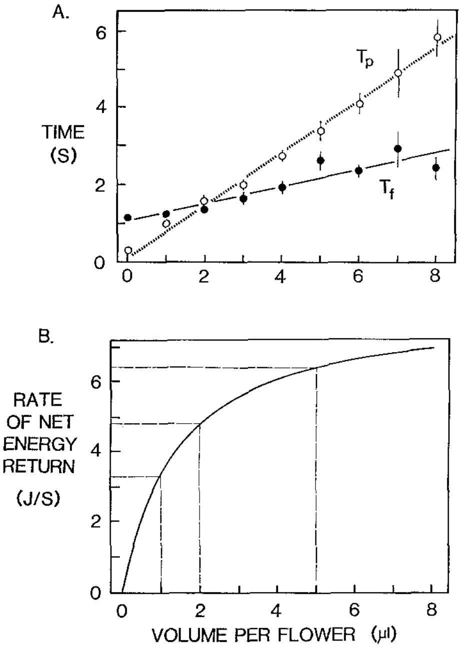

Fig. 1 A. Relationship between nectar volume per flower and the two components of handling time: probe time (T_p, open circles) and inter-floral travel time (T_f, closed circles). Plotted are overall means (±1 SE) based on mean values for each bee. Each bee ($n = 7$) was timed 6 to 15 times at each nectar volume. Regressions, fitted to overall means only, are: $T_p = 0.174 + 0.673\ V$ ($R^2 = 0.99$, $P < 0.001$, dashed line); $T_f = 1.075 + 0.220\ V$ ($R^2 = 0.85$, $P < 0.001$, solid line). **B** Relationship between nectar volume in each flower and rate of net energy return, based on the regressions from panel A. Note that equivalent rates are achieved by offering 2 µl in each flower or 1 µl in half of the flowers and 5 µl in the other half (as shown by dashed lines), but that offering 2 µl in each flower or 1 µl in half of the flowers and 3 µl in the other half (the approach of Real (1981) and Real et al. (1982)) would not result in equal rates (as calculated by the per flower rate averaging method, see text) for these bees

Using a 1 ml plastic disposable micropipet, we either entirely drained ("depleted") or added ("enhanced") 2–4 ml of 40% sucrose solution to the honey pots. The feeder tubes were then removed for 3 h to ensure that the bees had an opportunity to thoroughly assess their new honey pot levels. Six to 20 foraging bouts were then run, depending on time remaining in the afternoon. All trials were finished by 1800 h. On the next day (weather permitting), or as soon as possible thereafter, the same experiment was performed on the same bee, but with the reverse manipulation. This pairwise experiment was done twice for two bees (bees 2 & 5), but in the reverse order, and the results pooled for each bee. Colony treatment was decided by a coin toss; five of the nine bees had their colonies depleted as the first treatment.

In a foraging bout (= trip), the focal bee (and no other) left the colony, foraged on flowers injected with nectar no more than 10 min earlier, and returned to the colony. On days when colony stores were depleted, we emptied honey pots after each foraging bout, in order to maintain a depleted condition. The variable flower patch contained 10 flowers of one volume and 11 of the other, the volume of the 21st flower alternating between bouts. Unique and randomly-chosen nectar distributions were used in each bout. While injecting new boards and between foraging bouts, we kept the bee in the colony for at least 5 min. Preliminary results (and those of Real 1981) showed that bees learned the rewards associated with each patch within roughly three bouts. Therefore the first three bouts were discarded from analysis and treated as a learning period. A tenth forager (from colony 1) was not included in the analysis because it developed a complete preference for one patch, and this preference was unaffected by honey-pot manipulation. The other bees almost always visited both patches, and often visited most flowers within each patch during a single foraging bout.

A "wild type" analog of our feeding scenario would have the two flower types present in abundance, such that specialization on one type is possible. The logistical problems of injecting flowers forced us to offer both flower types in reduced abundance, making the bees visit both types (but not necessarily all flowers) to gain a full nectar load. We reason that any "wild type" preference for flower type would manifest itself in our system as an initial patch preference. Over the course of the experiment, bees did not appear to learn that both patches had to be visited during a single foraging trip, which would have rendered initial preference unimportant.

In 1986, we used a slightly different experimental procedure from that in 1987. Bees 8 and 9 were given a series of foraging bouts both before and after the manipulation of their colony's honey pots. This ensured a within-day "control" against which to contrast post-manipulation behavior. Honey pots were 1/3 to 1/2 full in all pre-manipulation bouts. Flower patches were placed flat on the table. Bees were held in the colony for 30 min after the manipulation. In the 2 µl versus 1 and 4 µl trials (see below), bee 8 was presented with two square patches (49 flowers in each) separated by 15 cm. Bee 8 was also tested in a second experimental series using a higher mean and variance, but again with equal expected rate of net energy intake.

Calculations

The experimental protocol required that we offer the bees two reward distributions with equal mean rates of net energy return, but different variances. To specify the appropriate distributions, we required measures of the time-related costs of foraging. We therefore used an event recorder to measure probe times (T_p: time a bee spent with its tongue in a flower) and inter-floral travel times (T_f: time between probes of adjacent flowers, mostly in flight) for a series of trials within which all flowers contained the same nectar volumes (V; ranging from 0 to 8 µl). We timed bees 5, 6, 8, 9, and three others that were not used in subsequent experiments. Both probe time and inter-floral travel time were affected by nectar volume per flower (Fig. 1 A). Note that this previously unreported travel time effect is small in comparison to that of probe time.

With these statistics, we calculated rate of net energy return (E) achieved at each nectar volume from the equation (modified from equation 4 of Harder 1986):

$$E = (epSV - M(c_p T_p + c_f T_f))/(T_p + T_f)$$

where: e is the energy contained in 1 mg of sucrose (15.48 J); p is the nectar density (1.177 mg/µl at 20° C); S is the nectar concentration (40%); V is the nectar volume (µl); M is the bee's mass (0.15 g); c_p is the energetic cost of probing (0.034 J/gs, Heinrich 1975); and c_f is the energetic cost of flight (0.436 J/gs, Heinrich 1975). Figure 1 B shows how rate of net energy return changed with nectar volume per flower. Using this relationship, we decided to offer most bees a constant patch containing 2 µl in each flower, and a variable patch in which half the flowers contained 5 µl and the other half contained

1 µl. One exception was bee 8, which foraged particularly quickly (average handling time of 3.9 sec, compared to 4.7 sec for the other bees pooled) and was therefore offered a variable array whose flowers contained 1 and 4 µl. As can be seen from Fig. 1 B, the constant and variable patch offer the bees the same expected mean rate of net energy intake.

Table 1. Preference for the variable patch, as measured by the patch first visited. Number of foraging bouts is shown in parentheses. Each bee is represented equally in the calculated means, i.e., averages are unweighted by the number of bouts

Bee	Colony	% First visits to the variable side		Difference in predicted direction?
		Enhanced	Depleted	
1	1	38.5 (11)	94.1 (17)	+
2	1	25.9 (27)	38.5 (26)	+
3	2	14.3 (13)	21.4 (14)	+
4	2	35.7 (14)	75.0 (11)	+
5	3	38.1 (20)	41.7 (25)	+
6	3	50.0 (10)	83.3 (12)	+
7	3	40.0 (5)	40.0 (10)	−
8	4	0.0 (3)	50.0 (4)	+
9	4	33.3 (6)	66.7 (6)	+
averages		30.6	56.7	(43.6 overall)

Table 2. Average preferences for the variable patch, as measured by the percentage of visits to flowers in the variable patch in the first 30% of all visits in each bout. Sample sizes are as in Table 1. Standard error of the mean is shown in parentheses

Bee	Colony	% of early visits to the variable side		Difference in predicted direction?
		Enhanced	Depleted	
1	1	48.2 (11.6)	72.4 (5.6)	+
2	1	33.5 (5.4)	28.8 (6.0)	−
3	2	44.6 (8.8)	48.5 (8.1)	+
4	2	41.9 (7.4)	57.3 (11.7)	+
5	3	45.1 (8.7)	47.4 (7.5)	+
6	3	44.7 (11.9)	56.5 (7.8)	+
7	3	47.2 (21.0)	48.6 (13.4)	+
8	4	0 (0)	46.2 (26.8)	+
9	4	37.8 (19.9)	79.4 (16.1)	+

Results

If bees were risk-sensitive and behaved in a manner consistent with minimizing the probability of energetic shortfall, they should have preferred the variable patch after honey pot depletion and the constant patch after honey pot supplementation. Using the patch first visited in the foraging bout as the criterion of preference, the foragers behaved in such a manner. Relative to their behavior when their colony was fed, all bees but one increased their percentage of first visits to the variable patch when their colony nectar stores were depleted (Table 1; Wilcoxon matched-pairs test, $T=1$, 1-tailed $P<0.004$). Note, however, the considerable among-bee variation in response, even under these controlled circumstances.

To reaffirm the conclusion of this first analysis, we calculated another measure of patch preference: the percentage of visits to flowers in the variable patch in the first 30% of visits in each bout (Table 2).

The value of 30% was chosen arbitrarily to represent behavior early in the foraging bout. A 2-way ANOVA (GLM procedure of SAS Institute Inc, 1985) using arcsin transformed data yielded results that paralleled those for patch first visited (using type III sums of squares, since the design was unbalanced). Despite significant among-bee differences ($F=2.56$, $P=0.011$), there was a significant treatment effect ($F=8.04$, $P=0.005$) when these among-bee differences were statistically controlled (overall model $R^2=0.136$, $n=241$). Furthermore, there was no bee-by-treatment interaction ($F=1.09$, $P=0.368$). Hence, not only did bees from depleted colonies more often fly to the variable side first, but they also spent a greater proportion of their early foraging bout there than did bees from nectar-enhanced colonies.

The preceding analyses clearly show an effect of colony energy reserves on risk-sensitivity. However, without reference to foraging under some normal "unmanipulated" condition, *both* risk-aversion and risk-proneness have not been demonstrated. To do this, we tested the foraging preferences of two bees (8 & 9) both before and after the manipulation of their colony energy supplies. In all six cases (Table 3), bee behavior was consistent with that predicted by risk-sensitivity based on minimizing the probability of energetic shortfall ($P=0.016$, 1-tailed sign test). Furthermore, if we suppose that 43% preference for the variable patch represents indifference [the average preference for the variable patch across all trials was 43.6% (Table 1), similar to that for the 1986 control (pre-manipulation) situation of 43.7% (Table 3), perhaps because expected foraging gain was not precisely equal between the patches], then we again have support for both risk-averse and risk-prone behavior. In both tables, the average preference for the variable patch was >43% in the depleted condition and <43% in the enhanced condition. Finally, we get a similar result using the other measure of preference: the percentage of visits to flowers in the variable patch in the first 30% of all

Table 3. A comparison of risk-sensitivity before and after manipulation of colony nectar stores. Number of foraging bouts is shown in brackets. Six of six of pre- vs postmanipulation contrasts are in the predicted direction ($P=0.016$, one-tailed sign test). Averages are calculated as in Table 1

Bee	Manipulation	Reward volume (μl)	% First visits to variable side		Difference in predicted direction?
			Pre-manip.	Post-manip.	
8	depletion	2 vs 1 or 4	40.0 (5)	50.0 (4)	+
8	enhancement	2 vs 1 or 4	40.0 (5)	0.0 (3)	+
8	depletion	4 vs 2 or 10	20.0 (5)	100.0 (4)	+
8	enhancement	4 vs 2 or 10	80.0 (5)	50.0 (4)	+
9	depletion	2 vs 1 or 5	16.7 (6)	66.7 (6)	+
9	enhancement	2 vs 1 or 5	66.7 (6)	33.3 (6)	+
		averages	43.7	72.2 (depleted) 27.8 (enhanced)	

visits in each bout. Pre-manipulation (mean = 31%) and post-manipulation (mean = 75%) groups differed significantly for the depleted treatment (Mann-Whitney $U=165.5$, $P<0.025$), but pre-manipulation (mean = 60%) and post-manipulation (mean = 32%) groups did not differ significantly for the enhanced treatment (Mann-Whitney $U=137$, $P=0.07$). This latter result is presumably because colony honey pots were well-stocked to begin with, making their enhancement less of a change than their depletion.

Discussion

Our results provide evidence that bees exhibit risk-sensitive foraging when the reward rates of alternative flower types are equivalent. The foraging process seems to be sensitive to an energetic "target value" (or requirement), such that response to variance in food reward depends on the colony's present position with respect to this value. Bees show both risk-averse and risk-prone behavior, depending on colony energy reserves. When their honey pots were drained, bees preferred the "risky" patch. When their honey pots were supplemented, bees preferred the "constant" patch. This result refutes the suggestion that all risk-averse foraging by bees is no more than an artifact of a simple behavioral rule: minimize the revisiting of previously-emptied flowers (Plowright and Laverty 1984). Empty flowers were not included in our experimental design and were no more common in one patch than the other.

Harder and Real (1987) suggest that the functional explanation for bumble bee risk-aversion results from a lowering of the expected rate of net energy intake in the variable patch, brought about by increased variance in floral handling time. They conclude that "risk sensitivity requires a no more proximate mechanism than an animal simply assessing its rate of energetic return". We believe this conclusion to be incomplete, since it does not consider the more commonly addressed issue of risk-sensitivity as an adaptation for minimizing the probability of energetic shortfall (reviewed by Real and Caraco 1986). Nevertheless, if bees calculate expected rate of net energy intake on a per flower basis (as suggested by Harder and Real 1987), and they appear to do so, then we can successfully explain risk-sensitivity in bumble bees as a phenomenon related to colony energy requirements.

There is a possible alternative explanation for our results. Manipulating colony energy stores may cause bees to alter their foraging rates such that the relationships depicted in Fig. 1 are dependent on colony condition. If this were the case, then the risk-sensitivity that we found may simply be of the sort postulated by Harder and Real (1987). Foragers may have responded to variance in volume solely to maximize expected rate of net energy intake, and our finding of a treatment effect would simply result from a change in the shape of the fitness function (Fig. 1B) between the two treatments. To evaluate this hypothesis, we performed an analysis of covariance on the time taken to probe 15 flowers early in the foraging bout (flower visits 5 to 20; bees 1, 4, 5, 7, and 10). Controlling for the number of revisited flowers, we found no effect of treatment ($F=0.30$, $P=0.586$, $n=235$). Hence, manipulation of colony energy reserves did not affect the relationship between volume and the rate of net energy intake and therefore cannot explain our results.

What is the functional basis for our finding of apparent risk-sensitivity? It is unlikely that short-term energetic shortfall in colonies will lead to death by starvation; workers simply become torpid and allow brood temperatures to drop, resuming normal activities when more energy is received (Sladen 1912:123). For bumble bees, the costs of energetic shortfall are more likely to be an inability to repel predators and social parasites, and a longer period of brood development (Cartar, unpublished data). Risk-sensitivity in bees might therefore be similar to that postulated for spiders by Gillespie and Caraco (1987): selection would favor minimization of the probability of reproductive failure. Oster and Wilson (1978) present another model for risk-sensitive foraging, based on nonlinear returns to scale at different stages of colony development, but this model does not predict the changes in risk-sensitivity based on colony energetic requirements observed in the present study.

Most models of risk-sensitivity that minimize the likelihood of energetic shortfall consider that an animal's accumulated food stores at the end of a foraging day determine its present foraging behavior. One misconception is that by visiting many flowers, bees should experience a reduction in the variance of their accumulated intake simply by the law of large numbers, "so that the total volume of nectar ingested by a bee visiting 50 variable flowers during a foraging trip should approach the volume consumed by visiting only constant flowers" (Harder and Real 1987:1104). If this were true, bees would have little reason to be risk-sensitive. One way to resolve this dilemma is to consider two levels of variance: (1) the variance associated with estimating a population's true mean from a sample (a sampling distribution), which is equivalent to the standard error of the mean and which decreases exponentially with increased sampling (Fig. 2A) and (2) the variance in foraging gain, which reflects the spread in individual observations (a population distribution) and which actually increases with increased sampling (Fig. 2B). It is the former variance to which Harder and Real apparently refer. It is the latter variance, characterizing the expected distribution of accumulated intake after some foraging period in the variable patch, to which a forager should be sensitive. Therefore, there remains some scope for risk-sensitive diet choice, even when many prey items are accumulated.

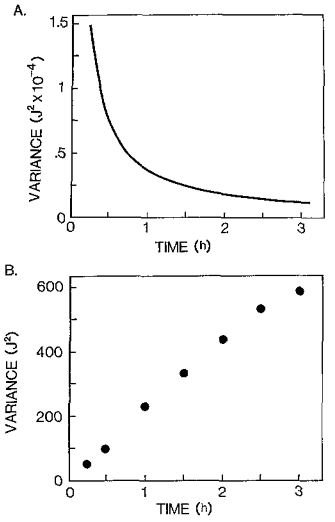

Fig. 2A. How prolonged foraging decreases the variance in the distribution of expected mean accumulated nectar gain. The plotted curve is based on a forager sampling entirely from the variable patch under conditions used in this experiment. To calculate the population variance, we began with a two-flower population (one flower of each type) and used a handling plus travel time that averaged the times associated with the two nectar volumes (average of 3.93 s). The population contained flowers offering 1.33 J/s and 2.50 J/s, which yielded a variance of 0.3417. The number of samples (n) at any time (t) equals $t/3.93$, and the variance equals $0.3417/n$. Note that the variance in expected mean reward associated with feeding in the variable patch diminishes rapidly. **B** How variance in actual accumulated energy gain changes with time foraging continuously in the variable patch, under the conditions used in this experiment (based on a computer simulation of 1000 foraging trips). Flower types were randomly encountered in each foraging trip, and each trip was uninterrupted (e.g., by returning to the colony, by grooming, etc.). Note that the variance associated with small differences between individual flowers is amplified (in absolute terms) as foraging continues

It is worth considering why bees made only qualitative shifts in their patch preferences when theory predicts total shifts: bees from enhanced colonies should always have preferred the constant patch, and bees from depleted colonies the variable patch. The answer remains speculative, but several possibilities exist. First, the experimental design may not have controlled all factors important to the bees, so that risk was not their sole consideration in patch choice. Second, bees may continuously monitor their environment to track changes in flower profitability and should therefore never exhibit total preferences. Third, partial preferences may result from pooling a sequence of risk-sensitive decisions, during which a bee switched between the two risk-sensitive states (see Houston and McNamara 1982), although visual inspection of our data suggests that this was not the case. Finally, bees may have learned that it was possible to empty all flowers in both patches during a single foraging bout, such that the cost of visiting the "wrong" patch first vanishes upon completion of the foraging trip.

One distinction between the present study and past studies on risk-sensitive foraging is that bumble bees appear to base their decisions on energetic shortfalls at the colony, not individual, level. Foraging individuals themselves were never in danger of starvation, as they could easily gain enough energy for self-maintenance after the first few flower visits. This may explain the previous failure to induce risk-prone behavior in bumble bees (cited in Real and Caraco 1986). Clearly, an appropriate focus for studying risk-sensitive foraging in bees is the condition of the colony, the entity on whose behalf the forager labors.

Acknowledgements. We thank Lawrence Harder for valuable correspondence, and Mark Abrahams, Tom Caraco, Lawrence Harder, John McNamara, Peter Nonacs, Graham Pyke, Les Real, Mary Reid, and Ron Ydenberg for comments which improved the manuscript. Discussions with Steve Lima proved especially helpful, and a conversation with Chris Barken led to the model in Fig. 2B. Dave Inglis and Andrew Mencarelli assisted with the experiments, and Alex Fraser helped with beekeeping. This work was supported by a grant-in-aid of research from Sigma Xi the Scientific Research Society to RVC, and an NSERC of Canada operating grant A6869 to LMD.

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