

Risk-Sensitive Foraging in a Patch Departure Context: A Test with Worker Bumble Bees¹

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SYNOPSIS. Typically, tests of risk-sensitive foraging involve observing a subject's choices of alternative prey types differing in some combination of mean and variance of expected foraging gain. Here, we consider the problem of risk-sensitive foraging when there is a single prey type. We observed worker bumble bees (*Bombus occidentalis*) foraging in an array of artificial 2-flower inflorescences. After visiting the bottom flower in an inflorescence and obtaining a reward of some size, the bee decides whether to visit the top flower or to move to a new inflorescence (a patch departure). Here, risk-sensitive behavior is expressed as the forager's choice of patch departure threshold (PDT) of reward obtained in the bottom flower. We measured the PDTs of bees whose colony energy stores (and therefore energy requirements) had been manipulated (Enhanced or Depleted). Simulations led us to predict that shortfall-minimizing bees should decrease their PDTs when their colony energy reserves were depleted, relative to when the reserves were enhanced. Bees did not use a strict patch departure threshold, but instead the probability of departure varied with nectar volume in the bottom flower. Colony energy stores *did* affect patch departure behavior, but this effect was confounded by the order in which manipulation of colony reserves was applied. Further, simulations of observed bee patch departure decisions did not produce behavior expected if the decisions were based on shortfall-minimization. We conclude that a bee's decision of when to leave an inflorescence is not predicted by a static shortfall-minimizing model. Our results also implicate an important interaction between learning and foraging requirements. We review risk-sensitivity in bees, and discuss why risk-sensitive foraging may be adaptive for bumble bees.

INTRODUCTION

Food items frequently occur in patches that differ in quality. The question of how foragers should efficiently move between such patches has been the focus of a large body of theory and experiments (reviewed in Pyke, 1984; Stephens and Krebs, 1986). In most of these tests of the "patch departure paradigm", foragers appear to maximize their net rate of energy gain. In

a separate body of theory and experiments, usually dealing with the question of what food types to include in the optimal diet, both mean and variability in foraging gain have been shown to be important in determining foraging behavior (*e.g.*, Caraco *et al.*, 1990; Reboresda and Kacelnik, 1991; Barnard, 1990; Schmitz, 1992). Foraging decisions that are sensitive to the variance, in addition to the mean, of foraging alternatives are termed risk-sensitive foraging (Real and Caraco, 1986; McNamara and Houston, 1992). We expect to see risk-sensitive foraging when there is a non-linear relationship between foraging gain (*e.g.*, the amount of food acquired in a foraging bout) and its fitness consequences (*e.g.*, growth rate, probab-

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ity of starvation, probability of breeding, etc.). The most commonly considered basis for risk-sensitive foraging has been foragers that minimize their probability of energy shortfall.

We have a growing body of work on risk-sensitive foraging with respect to diet choice, but almost no experimental tests of risk-sensitive patch departure (but see Smallwood 1993). In contrast to the problem of what items to include in the optimal diet, the problem of when to leave a patch involves a continuum of choices of behavior. For example, if the forager is using a threshold departure rule (*i.e.*, continue foraging in a patch if the last n items exceed some threshold, leave otherwise), it must choose one of a large range of potential values for its patch departure threshold. Risk-sensitive foraging is clearly a possibility in the patch departure paradigm, but in this case risk is generated by the forager's choice of patch departure rule. That is, different patch departure thresholds will not only result in different expected mean foraging gains, but (as we demonstrate in this paper) will also produce different variances in foraging gain. For example, Stephens and Charnov (1982) show how, in a world of single-item patches and unpredictable travel times between patches, different patch residence times can produce a range of means and variances in foraging gain. A similar result applies to the problem of diet breadth when there is a large range of prey sizes to potentially include in the diet (Weissburg, 1991). While a rate-maximizing forager will always select the policy that yields the highest expected rate of energy gain, a risk-sensitive forager will not necessarily do so.

Bumble bees are well studied from both risk-sensitive and rate maximization perspectives. The flower choice of foraging bumble bees has frequently been found to be risk-sensitive, at least when the choice is reduced to two alternative flower types and the bee must decide whether to choose one, or the other, or both types, in its diet (Waddington *et al.*, 1981; Real, 1981; Real *et al.*, 1982; Cartar and Dill, 1990; Cartar, 1991; but see Waddington 1995 for contrary results). However, the patch departure

decisions of bumble bees are clearly consistent with maximization of net rate of energy gain (Pyke, 1982; Hodges and Wolf, 1981; Hodges, 1985; Pleasants, 1989). Bumble bees appear to use a patch departure threshold (PDT) while foraging on inflorescences (Hodges and Wolf, 1981; Hodges, 1985). That is, if the rewards obtained from the last n flowers on an inflorescence (weighted appropriately) are less than the patch departure threshold, the bee moves to another inflorescence. Otherwise, it continues visiting flowers on the same inflorescence. An inflorescence is a spatially discrete collection of flowers growing on a shared stalk, a collection that we view as a patch. Leaving an inflorescence then becomes a problem of patch departure. We therefore assume that PDTs guide the bee's decision of when to depart from an inflorescence.

In this paper, we construct a laboratory experiment that captures key elements of a bee's natural foraging environment, and use simulations based on empirical observations of bees foraging within the experimental setup to predict the consequences of adopting different PDTs. Bumble bees are social, and combine their foraging gains in their colony's honey pots. Like Cartar and Dill (1990) and Cartar (1991), we propose that risk-sensitive foraging in bumble bees is based on minimizing the colony's probability of exhausting its energy reserves overnight (the consequences of such a shortfall are considered in Cartar and Dill 1991). The probability that a colony will experience an energetic shortfall will depend on its present energy reserves, which should therefore influence the foraging behavior of its workers. We therefore use manipulations of colony energy reserves to determine whether foraging worker bumble bees show risk-sensitive PDTs. In so doing, we test for risk-sensitive foraging in patch departure decisions. Most previous treatments of patch departure decisions have not considered risk (but see Barnard and Brown, 1987; Alonso *et al.*, 1995).

METHODS

The experimental setup consisted of bees foraging on artificial inflorescences that

varied in their nectar rewards. Two wild-established colonies of *Bombus occidentalis* from SW Alberta were moved inside a $4 \times 4 \times 2$ m screen tent, and their foragers were marked on the thorax with unique combinations of enamel paint. The colonies were small, each containing a queen and between 6 and 10 workers, in addition to brood in all stages of development. Bees were trained to collect nectar from artificial flowers formed from yellow push pins with a well (2.5 mm in diameter and 4 mm deep) drilled centrally in the top and set into a 2 cm square of blue polystyrene foam. To form inflorescences, a flower was positioned at heights of 15 cm and 20 cm, facing up at a 45° angle, along the same side of a vertical wooden dowel. Inflorescences were arranged in two parallel rows of 10, with flowers facing the adjacent row. The rows were 60 cm apart, and inflorescences within a row were spaced 20 cm apart. Flowers were filled with nectar ($50 \pm 0.5\%$ weight/vol. sucrose solution) injected into the base of the well with a blunt tipped 50 μ l Hamilton microsyringe mounted on a repeating dispenser.

An important feature of this experiment is that bees encountered nectar volumes in a pattern that is similar to that normally experienced in the wild. That is, nectar volumes follow a negative exponential pattern (Fig. 1; see Zimmerman, 1988). The distributions we used were generated with a beta random variate algorithm (Deák, 1990), with shape parameters 1, 20 (Fig. 1, lower left). Ten unique patterns of $n = 20$ were generated (Fig. 1, upper right), each with a mean of 2.5 μ l. Also, we incorporate positive within-inflorescence autocorrelation, another common pattern observed in the field (*e.g.*, Best and Bierzychudek, 1982; Hodges, 1985), although in this case the autocorrelation was extreme ($r = 1$). That is, both flowers on an inflorescence contained the same volume of nectar. Hence, foragers did not face a situation of diminishing returns (as they often do in the field). Nor did they face a problem of information; after sampling one flower, the volume in the other flower was the same. Finally, there was no spatial autocorrelation among inflorescences (*e.g.*, Waser and Mitchell, 1990); the

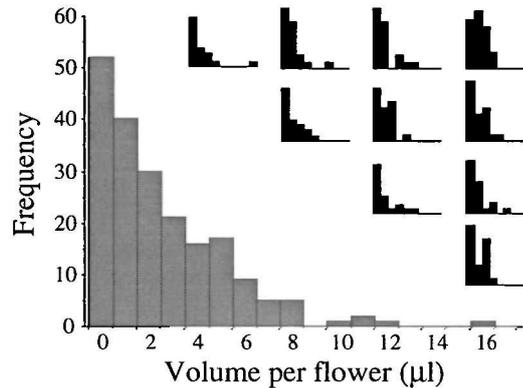


FIG. 1. Distribution of inflorescence qualities used in this study, where both flowers on each inflorescence contained the same volume. The distribution was generated by random draws from a beta distribution ($\beta_{1,20}$) with mean 2.5 and SD 2.7. The shapes of the 10 replicates (all on the same scale) are shown in the upper right of the figure.

nectar in a given inflorescence was independent of the nectar in its neighbor. Within-trial revisitation of flowers changed these conditions somewhat, which can account for bees moving to the top flower even after receiving no reward in the bottom flower (demonstrated and discussed later).

Simulations

To make predictions about the consequences of using a particular patch departure threshold, we used observed handling and flight times in a simulation of forager behavior. We assumed that a bee foraged continually in an infinite array of 2-flower inflorescences (whose nectar levels were determined in the same manner as those in Figure 1, but where nectar volumes varied continuously between 0 to 20 μ l), where it always first visited the bottom flower, and moved to the next flower on the same inflorescence (=top flower) if the volume that it received was greater than or equal to the PDT, and moved to the bottom flower on the adjacent inflorescence if that volume was less. If the forager visited the top flower on an inflorescence, it always went first to the bottom flower on the adjacent inflorescence. The foraging trip ended when the bee had accumulated 80 μ l of nectar, and there was no revisitation of flowers. Observed flight times in our setup were: bot-

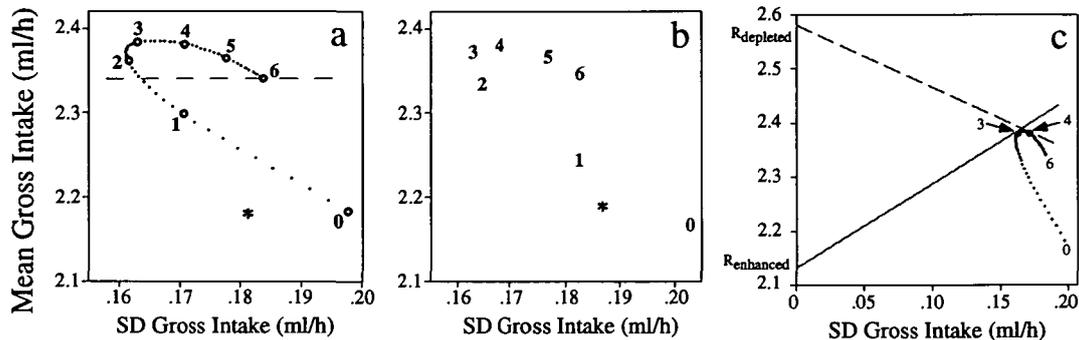


FIG. 2. The consequences of adopting different bottom-flower thresholds while foraging under conditions used in the experiment, as determined by simulation. Each point indicates a different PDT, varying between 0 and 6 μ l and incremented by 0.1 μ l. Integer thresholds are numbered to indicate their actual value. a. the general case, which allows for continuous variation in nectar amounts in flowers. The dashed horizontal line indicates an example of two PDTs that have the same mean intake, but different SDs. b. the specific case, which more closely approximates conditions used in the experiment; *i.e.*, nectar integer μ l volumes of nectar were used. To indicate the consequence of foraging randomly in this setup, the asterisk shows the expected outcome of a bee moving to the top flower with a constant probability of 0.5. See text for details of the model. c. the expected effect of changes in colony energy reserves on the patch departure threshold that minimizes the probability of energetic shortfall in the static z-score model. The points are the same as in a, but the x-axis now begins at zero. Colony mean requirements in the two experimental conditions are represented at entirely hypothetical positions along the Y axis as $R_{depleted}$ and $R_{enhanced}$. Note that the optimal patch departure threshold (large dot) increases at the higher level of colony requirement.

tom flower to top flower, 0.71 s; bottom flower to bottom flower, 0.82 s; top flower to top flower, 1.06 s. Flights between top flowers were rare (less than 2% in the analyzed experimental data), and not allowed in the simulation. To calculate the probe time associated with a given nectar volume, we used a linear regression of probe times vs nectar volume using the equation fit to observed bee times: Probe Time = 0.740 + 1.009 · Volume, where probe time is in s, and volume in μ l ($R^2 = 0.95$). The simulation was repeated 1,000 times for each level of bottom flower threshold between 0 μ l and 6 μ l, incremented by 0.1 μ l, and the mean and standard deviation of the rate of gross nectar gain (J/h) calculated for each threshold (Fig. 2a). Since we used integer nectar volumes in our experiment, we also performed a simulation examining the consequences of foraging in an integer reward environment (Fig. 2b). Finally, to contrast use of a PDT with random foraging, we calculated the mean and standard deviation of foraging gain for a bee that moves to the top flower with a constant probability of 0.5 (Fig. 2). We use gross, rather than net, rate of energy intake because these currencies are virtually identical in the energy-rich cir-

cumstances of this experiment (*i.e.*, energetic costs associated with foraging (roughly 2.6 to 2.8 KJ/h) are dwarfed by energy gains from foraging (roughly 960 KJ/h)). We simulated 30,000 runs for each threshold.

The simulations reveal that, under the conditions of this experiment, bees using different threshold departure rules will experience different combinations of mean and standard deviation of expected foraging gain (Fig. 2). For example, a bee who almost always moves to the top flower (as will happen with a PDT of 6) will have a much higher SD of intake, but the same mean, as a bee with a PDT of 1.6 μ l who frequently moves between inflorescences (dashed horizontal line in Fig. 2a). Note that the threshold associated with the highest mean rate (≈ 3.5 μ l) does not minimize SD, and that a randomly foraging bee (asterisks in Fig. 2) experiences a generally lower mean and higher SD foraging gain than does a bee foraging using a PDT. Finally, the range of means and SDs in Figure 2 is relatively narrow, suggesting that the consequences of adopting any PDT might be similar, such that selection for the optimal behavior in this system may be weak.

For this reason, we may not expect to see risk-sensitive behavior in this system.

We can now use these simulation results to predict the effect of a manipulation of colony energy stores on the shortfall-minimizing PDT. For the static (*i.e.*, the forager is not permitted to change its behavior while foraging) shortfall-minimizing z-score model of risk sensitivity (Stephens and Charnov, 1982), the optimal behavior is found by constructing a line of highest slope rooted on the Y axis at the colony requirement (R), and tangent to the "feasible set" of PDTs (Fig. 2c). Unfortunately, we do not know enough about the physiology of bumble bee colonies to quantitatively predict the position of R. However, we can make a qualitative prediction about the relative effect of colony state on PDT: because R_{depleted} will be higher on the Y axis than R_{enhanced} , the shortfall-minimizing PDT will be relatively higher for a bee whose colony was energy-depleted (Fig. 2c). In other words, colonies with well-stocked honey pots have a lower R (required foraging intake); the z-score model then predicts a lower PDT would minimize the risk of shortfall. We therefore predict that if bees have risk-sensitive PDTs, a downward shift in colony energy state (and therefore and upward shift in colony energy requirement) will result in an upward shift in PDT (causing bees to visit more inflorescences).

Experiment

During a trial, a single bee was allowed to leave her colony, forage in the patch, and return to the colony. Bees were videotaped during the trials, to obtain information on the timing and pattern of flower visitation. Eight individual bees (four from each colony) were observed over three (not necessarily contiguous) days. On the first day, during which bees were allowed to learn the setup, each flower contained 2 μl . On each of the next two days, bees experienced 12 trials of the distributions shown in Figure 1, in a random order and sampling without replacement (for trials 1 to 10), or sampling with replacement (for trials 11 and 12). Bees returned to their colony with a mean crop load of 79 μl (range 49 to 92), and an

average of 32% of flower visits within a trip were revisitations.

To test for risk-sensitive behavior, we compare behavior of workers whose colony energy requirements were manipulated by increasing or decreasing energy state (see Cartar and Dill, 1990). We used two treatments: Enhanced (1 ml of nectar added to colony honey pots), and Depleted (all nectar, usually about 1 ml, removed from colony honey pots). These manipulations occurred at roughly 1000 h, and bee behavior was observed between 1300 h and 1900 h (with most observations occurring between 1500 to 1800 h). During the experiment, the Depleted condition was maintained by removing a forager's contribution immediately after she deposited it into a honey pot. Experiments occurred between 20 July and 21 August 1994. In each colony, 2 foragers (chosen randomly) experienced the Enhanced treatment first, while the other 2 received the Depleted treatment first. Our experiments were not of the "closed economy" variety (Houston and McNamara, 1989), and colonies experiencing the Depleted treatment were supplemented with nectar before nightfall to prevent energy shortfall (Cartar and Dill, 1990). In our analyses, we considered only those cases where: 1. the first visit to an inflorescence was to the bottom flower (99.3% of cases), 2. a flower was visited for the first time in a particular trial, and 3. fewer than 30 flower visits had occurred within a trial (during which there was little revisitation of flowers). Throughout the paper, unless otherwise noted we report means \pm one standard deviation.

RESULTS

Before testing for a risk-sensitive shift in PDT based on colony energy stores, we need to ensure that manipulating colony energy reserves did not concomitantly change other aspects of foraging behavior. In particular, a forager faced with a food deficit might alter foraging speed so as to increase her rate of intake. However, we found no detectable changes in the timing of bee behavior: regardless of colony energy state, bees took the same amount of time to remove a given volume of nectar from a flow-

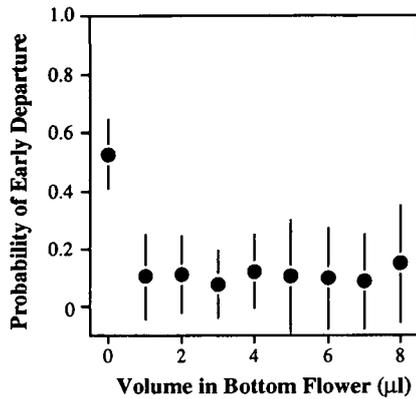


FIG. 3. The relationship between volume of nectar in the bottom flower and the probability (mean \pm SD) that the bee leaves the inflorescence early (based on means for each bee for all treatments).

er (univariate repeated-measures ANCOVA on probe time (ln-transformed) with bee as a random effect; treatment $F_{6,69} = 0.33$, $P = 0.92$; volume $F_{6,69} = 13.62$, $P < 0.0001$; treatment-volume $F_{6,69} = 0.21$, $P = 0.97$) and to fly a given distance between flowers (univariate repeated-measures ANCOVA on flight time (ln-transformed) with bee as a random effect; treatment $F_{6,80} = 1.04$, $P = 0.41$; distance $F_{6,80} = 13.62$, $P < 0.0001$; treatment-distance $F_{6,80} = 0.56$, $P = 0.76$). Alternatively, the distance that a forager moves between resource points may change with state. Again, there were no detectable effects of colony energy state on between-inflorescence flight distance (Enhanced: 16.3 ± 3.4 cm; Depleted 17.1 ± 3.4 cm; Paired $t_7 = 1.22$, $P = 0.26$). Hence, treatment affected neither foraging speed nor flight distance.

The model tested requires that bumble bees use a patch departure threshold, for which we have some evidence in the present experiment (Fig. 3). However, bees would move to the top flower on the same inflorescence roughly 50% of the time even with no nectar in the bottom flower. When there was some nectar in a bottom flower, bees proceeded to the top flower on roughly 90% of occasions (Fig. 3). So rather than having an all-or-none PDT, bumble bees appeared to shift their already high probability of moving to the next flower by about 40%, depending on whether or not the bottom flower contained nectar. Because bees adjust their probability of switching inflorescences instead of applying an all-or-none threshold rule (Fig. 3), we refer to a probability of early departure (PED) rather than a PDT. Given that there was no relationship between nectar volume and inflorescence departure for nectar volumes equal to or exceeding 1 μ l, in subsequent analyses we collapsed nectar volume into a simpler 2-state character: nectar present, or nectar absent.

Recall that if patch departure decisions are risk-sensitive, we predict that bees from energy-Depleted colonies will be more likely to leave an inflorescence without visiting the top flower than bees from energy-Enhanced colonies. Our experiment provides no support for this prediction (Table 1): treatment significantly interacted with the order in which the treatment was applied, such that bees from Enhanced-first colonies increased their probability of early departure when their colony was Depleted (consistent with the prediction), while bees from

TABLE 1. Results of a mixed-model ANOVA predicting the probability that a bee leaves an inflorescence after visiting the bottom flower.†

Source	F	df	P	Least square means	
Treatment	0.1	1	0.75	E: 0.518	D: 0.507
Order	1.3	1	0.29	E \rightarrow D: 0.548	D \rightarrow E: 0.478
Treatment*order	7.8	1	0.011	E*(E \rightarrow D): 0.504 ^{ab}	E*(D \rightarrow E): 0.534 ^{bc}
				D*(E \rightarrow D): 0.592 ^c	D*(D \rightarrow E): 0.423 ^a
Nectar volume	128.9	1	<0.0001	none: 0.513	some: 0.110
Bee (order) (error)	2.9	6	0.033		

† Data are means for each bee. Order (enhanced or depleted first), Treatment (enhanced [E] or depleted [D]), and Volume (nectar in bottom flower present or absent) are fixed effects; Bee (1 to 8) is a random effect. Model $R^2 = 0.88$ ($F_{10,21} = 15.8$, $P < 0.0001$). Lowercase letters indicate statistically similar ($P > 0.05$) Treatment*Order group means.

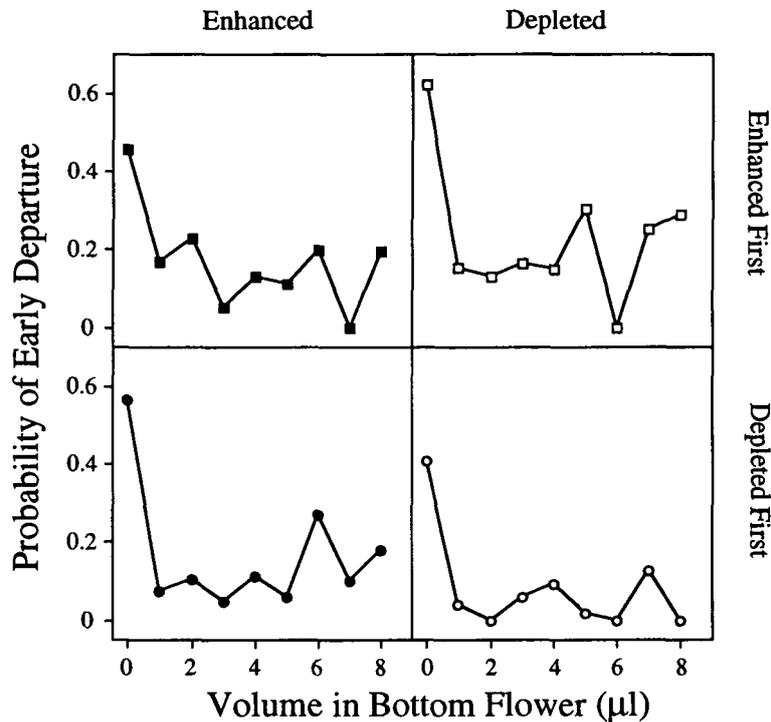


FIG. 4. The relationship between volume of nectar in the bottom flower and the probability that the bee leaves the inflorescence early (based on means for each of 4 bees), plotted separately for each treatment and treatment order.

Depleted-first colonies did the opposite when their colony was Depleted (opposing the prediction). In other words, treatment *did* affect patch departure, but not in a straightforward manner. Comparing the two Enhanced groups across days, whose means are similar (Table 1), suggests that the main effect of colony energy manipulation occurred in the Depleted treatment.

Instead of two treatments, we appear to have four, formed by combinations of energy-manipulation and order (Table 1). To consider the treatment-related variation that Figure 3 masks, we plotted the relation between nectar volume and the probability of early departure from a patch for each treatment-order combination (Fig. 4). As in Figure 3, there is no significant (*i.e.*, $P < 0.05$) relationship between nectar volume and probability of departure for nectar volumes equal to and exceeding 1 μl (Fig. 4).

Inspection of Figure 4 shows that although there are treatment-related differences in probability of early departure, the

patch departure threshold does not vary: in all cases, bees usually stayed on inflorescences whose bottom flower contained any non-zero volume of nectar. Because bees adjusted their probability of switching inflorescences instead of applying an all-or-none threshold rule (Fig. 4), the assumptions of the PDT model (Fig. 2) are potentially invalid in this context. It is tempting to suggest that probability of early departure (PED) is analogous to PDT, but in a more probabilistic way. A high PDT implies a high PED. But it is not clear whether different PEDs would produce mean-SD patterns similar to those generated by PDTs (Fig. 2). The case of PEDs is slightly more complex than that for PDTs; bees in our experimental setup have two PEDs to independently decide: one for empty flowers, and one for flowers with nectar (Figs. 3 and 4).

To test whether bees using observed PEDs would at least produce shifts in mean-SD outcomes consistent with the stat-

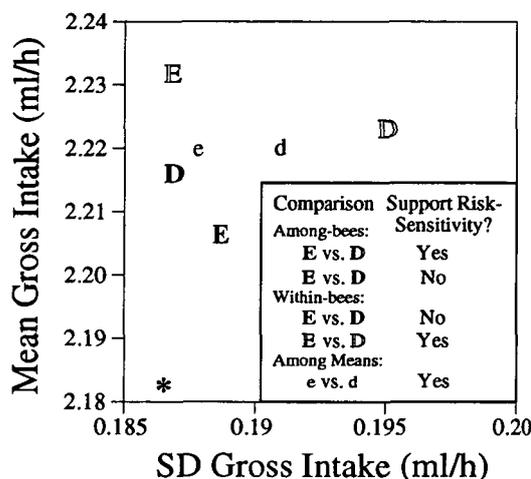


FIG. 5. The consequences of adopting different bottom-flower probabilities of early departure (PED) while foraging under conditions used in the experiment, as determined by simulations. Each point indicates an observed relationship between PED and nectar volume (shown in Fig. 4). Letters indicate treatment: E for Enhanced, and D for Depleted. Type face indicates treatment order: bold face for Enhanced-first, shadow for Depleted-first, lower case for treatment means. The inset shows the comparisons relevant to risk sensitivity; Yes indicates support, and No rejection. To indicate the consequence of foraging randomly in this setup, the asterisk shows the expected outcome of a bee moving to the top flower with a constant probability of 0.5.

ic shortfall-minimizing model of risk-sensitivity (like those for PDTs shown in Fig. 2), we simulated bees continuously foraging in the experimental setup (as described in Methods). However, unlike in the previous simulation, the simulated bees now used observed PEDs (using means for nectar volumes $\geq 1 \mu\text{l}$, and for each of the 4 treatment-order groups) rather than PDTs. All four treatment groups had higher, and more variable, intake rates than a bee using no PED rule (“*”, Fig. 5). However, we found little correspondence between observed inflorescence-departure behavior and treatment-related shifts predicted by the z-score model (Fig. 5). Five pairwise treatment group comparisons are relevant to address the question of risk sensitivity (Fig. 5, inset): comparing the same bees on the 2 different experimental days (*i.e.*, day 1 vs. day 2 for each treatment order), different bees on the same day (*i.e.*, Enhanced vs.

Depleted for each day (1 or 2)), and treatment means (ignoring Order). Recall that the relative effect of energy depletion is to shift the Y-intercept upwards (Fig. 2c). With this in mind, support for a risk-sensitive shift in behavior induced by colony energy budget is equivocal (summarized in the Fig. 5 inset). For example, in no case will a tangent from the Y-axis to the bold-face “E” (enhanced-first treatment) ever have a higher slope than a tangent to the bold-face “D” (enhanced-first treatment). However, a shift from the bold-face “E” to the shadowed “D” (depleted-first treatment) is potentially consistent with the risk-sensitive model. Most importantly, the treatment order that supported the interpretation of risk-sensitive patch departure (*i.e.*, Enhanced first, Table 1) does *not* support a risk-sensitive interpretation in this analysis. That is, the behavior employed by bees would not have resulted in a detectable lowering of their colony’s probability of energy shortfall.

DISCUSSION

To summarize, we found no consistent effect of colony energy reserves on a bee’s patch departure. If observed shifts in patch departure have an adaptive basis, they cannot be adequately accounted for by a static shortfall minimizing model (the z score model of Stephens and Charnov, 1982). Only one treatment order produced behavior consistent with the predictions of the risk-sensitive model (Table 1), but this treatment order did not result in any admissible change in the predicted probability of energy shortfall (Fig. 5). We conclude that risk sensitivity cannot account for the patch-departure decisions of bees in our experimental setup.

Our failure to find risk sensitivity may relate to the selective advantage of adopting risk-sensitive behaviors in a patch departure context. Because of the restricted range of SDs associated with adopting different PDTs (Fig. 2; a SD range of 2 ml for mean intakes of 235 ml), being risk-sensitive may have no biologically significant fitness consequences. That is, the range of possible outcomes from adopting different risk-sensitive patch departure behaviors may be se-

lectively equivalent in their consequences for colony fitness, such that selection does not favor risk sensitivity. We cannot eliminate rate-maximization as an appropriate currency, though, since bees probably obtained higher rates of foraging gain than would a random forager (Fig. 5, “*”).

According to Fig. 2, the PDT that maximizes the rate of energy gain (maximum observed Y value) is roughly $3.5 \mu\text{l}$. The PDT that minimizes the probability of energy shortfall depends on the colony requirement (which was undefined), but should be greater than $2.5 \mu\text{l}$ (Fig. 2). The observed mean PDT (Fig. 3) is not predicted either as a potentially shortfall minimizing PDT, or as a gross rate maximizing PDT. Instead, it is considerably lower (about $1 \mu\text{l}$). Does this imply that either currency is irrelevant in the case of the bees used in this study? We think not. Our simulation did not allow for revisitation, or for moves of greater than one inflorescence distant. In reality, bees did revisit flowers (mean frequency of 32%), particularly later in their foraging trips, and they did fly to non-adjacent inflorescences (mean frequency of 1.1%). Including more empty flowers in the simulation would lower the optimal PDT, but the dynamics of depletion would be considerably more difficult to simulate and probably not worthwhile given the mostly heuristic value of the exercise. We therefore hesitate to use the observed PDT to reject the hypothesis of rate maximization.

The strongest effect of our experiment was the difference in behavior between the Depleted treatment of the two treatment orders (Table 1). Behavior in the Enhanced treatment did not differ detectably with Order. Behavior in the Depleted treatment for the Depleted-first group of bees is particularly difficult to explain from a risk-sensitive, or an energy-maximization, perspective. We now develop an argument to explain how this result may have obtained. As bees forage, they learn about the pattern of nectar distribution; the more inflorescences they sample, the better their estimate of habitat quality. Bees were trained on inflorescences where all flowers contained $2 \mu\text{l}$ of reward. On the first day of the experi-

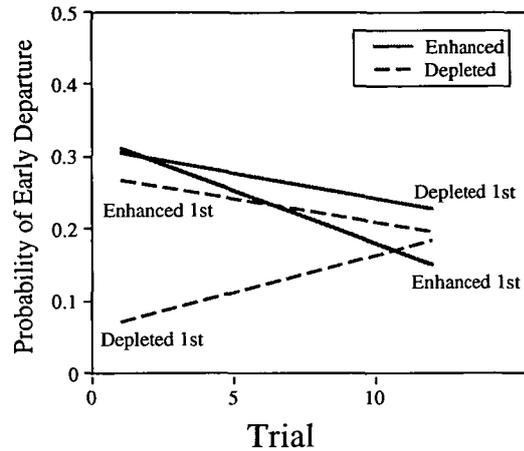


FIG. 6. Support for an effect of learning on the behavior of bees who experienced the colony-depleted treatment first. Note that the behavior of this group of bees converges on that of the others with time. Data used in the regressions are means for each bee and trial. Only the regression line for the Depleted First group is significant ($F_{1,11} = 6.17$, $P = 0.032$, $R^2 = 0.38$).

ment, they therefore had to learn a new pattern (*i.e.*, that shown in Fig. 1). We hypothesize that bees foraged in a different manner when their colony was energy-depleted first. Presumably, they perceived their colony's need for immediate nectar return to be so great that they did not have the luxury of sampling the environment to arrive at a PED that would have been more appropriate in the long term. Instead, they visited virtually every flower that they encountered. Only after several trials in this environment would they acquire enough information about the pattern of nectar distribution to adopt a more appropriate PDT. Bees whose colony experienced the Enhanced treatment first did not have the same pressing short-term need for nectar, and could therefore sample longer to more quickly arrive at a more appropriate characterization of the pattern of nectar distribution in their environment. Support for this “luxury of sampling” hypothesis is provided in Figure 6. Whereas the probability of moving to the top flower did not change with trial for 3 of the 4 treatment-order groups, it decreased significantly for Depleted bees who received the Depleted condition first. Only later in the for-

aging day, after which bees had ample opportunity to learn their environment, did the PDTs of this group of bees converge on those of the other three groups.

We designed this study to represent the simplest possible case of patch departure: 1. there was no within-patch diminishing rate of foraging return (so that the marginal value theorem was not relevant), 2. the nectar reward in the top flower was identical to that in the bottom flower (so that the problem of patch assessment was trivial), and 3. the location of flowers and travel time between flowers was unambiguous (the bee could easily see the whole foraging patch). Essentially, the choice facing a forager after having visited the bottom flower was whether to accept the same reward again on the next flower visit, or to try again with a random draw from a new inflorescence. The relevance of our experiment to the wild is strengthened by our use of a "typical" pattern of nectar standing crop (Fig. 1), and a within-patch correlation of nectar volumes. Further, the patch departure decision modeled here is one made countless times every day by a foraging bee, so its potential for influencing the fitness of social insect colonies is obvious. However, at least two elements of the natural situation were not successfully captured: the nectar standing crops are up to an order of magnitude higher than those normally encountered by bumble bees (*e.g.*, Zimmerman, 1988; but see Hodges and Wolf, 1981), and nectar standing crops did not change within the day (due to visitation and secretion) as they do in nature (*e.g.*, Stucky, 1984; Gyan and Woodell, 1987). The importance of these two elements remains undetermined. Overall, we conclude that if there is no detectable risk-sensitive patch departure under the controlled conditions of our experiment, risk-sensitive patch departure is improbable in wild-foraging bumble bees.

This paper adds to a number of studies of risk-sensitive foraging in bees, most of which have detected some form of risk sensitivity (Waddington *et al.*, 1981; Real, 1981; Real *et al.*, 1982; Cartar and Dill, 1990; Cartar, 1991; but see Waddington, 1995; Perez and Waddington, 1996; this

study). Despite this body of work, we lack a general consensus on how risk might influence foraging behavior of bees, because each study approaches risk sensitivity in a different manner. Variance is generated by differences in: 1. time to reward (Waddington *et al.*, 1981), 2. nectar volume (Real 1981; Real *et al.*, 1982; Cartar and Dill 1990), 3. nectar concentration (Waddington 1995, Perez and Waddington 1996), 4. a combination of nectar volume and encounter rate (Cartar 1991), or 5. choice of patch departure threshold (present study). Prior to the present study, all tests of risk sensitivity have involved a choice between two alternative food types (but see Smallwood (1993) for risk-sensitive patch choice), and risk-sensitive behaviors, when detected, are usually subtle. The proposed function of risk sensitivity in bumble bees has varied from maximization of short-term rate of energy gain (Real *et al.*, 1990), to minimization of colony energy shortfall (Cartar and Dill 1990, Cartar 1991, present study), or has remained unspecified (Waddington *et al.*, 1981, Waddington 1995). Clearly, a means of integrating the results of these disparate studies awaits, perhaps based on mechanisms of how bees acquire information and make decisions (Waddington 1995), as does the need to confirm their results. More importantly, we need to explicitly link risk-sensitive models to relevant aspects of the biology of the organisms under study.

Why should bumble bees ever be risk-sensitive foragers? This question has two elements: one theoretical, and one empirical. First we consider the theoretical. Some authors (*e.g.*, Real *et al.*, 1990) suggest that since bees visit many flowers, and pool their combined intake, there will be little variance in accumulated reward on which selection can act. While intuitively appealing, this argument focuses on the wrong trait: estimation of the mean. The law of large numbers ensures that we get a better estimate of the mean with increased sampling. It does *not* ensure that the variance of a sum (in this case, the sum of flower rewards pooled across bees) will go down. It is this variance in combined group intake that should be relevant to risk sensitivity in

bumble bees, if risk sensitivity is based on shortfall minimization. As Cartar and Dill (1990) showed, variance in accumulated foraging gain continues to increase with continued foraging. This point is developed by Stephens (1990), who perceptively noted that "foragers do not eat means, they eat sums." Hence, there is no theoretical reason to suppose that visiting many flowers eliminates the need for risk sensitivity.

The empirical answer to why bumble bees might be risk-sensitive foragers is less certain. As noted in the introduction, for risk sensitivity to be of selective importance, there must be a nonlinear relationship between food gain and fitness (reviewed by Smallwood 1996). We hypothesize that bees forage so that their colony does not run out of nectar overnight, a time of no foraging but high nectar use; bumble bees use nectar to warm their colonies with metabolic heat, in addition to feeding adults and growing brood. Hence, the relationship between overnight colony nectar stores and fitness should be non-linear to elicit risk-sensitive behavior; *e.g.*, a colony with 2 ml of nectar at nightfall will experience consequences that are more (or less) than 2 times the significance of those endured by the same colony with 4 ml of nectar. Some of these potential non-linearities, identified by Cartar and Dill (1991) are susceptibility to predators, usurpation, and length of brood development. The relative importance of these, or other, factors remains unresolved. The functional basis for risk-sensitive foraging also needs to be identified in other social insects for whom shortfall-minimization has been tested (*e.g.*, honey bees, Banschbach and Waddington, 1994; bumble bees, Waddington 1995).

Models of risk-sensitive foraging assume that foragers have perfect knowledge of their foraging environment, particularly of the probabilities associated with alternative choices. This is an obvious, but pragmatic, oversimplification. The results of the present study highlight an interesting apparent interaction between the need to acquire information, the value of that information, and the need to use it optimally (*e.g.*, Stephens, 1989). While we did not set out to test this dynamic, our results showing the

non-discriminating behavior of Depleted bees whose colonies were Depleted first, strongly suggest that state dependent behavior extends to the process of acquiring information. In our case, the value of information appears to have been diminished by a more compelling short-term requirement of the colony. In contrast, having adequately characterized their foraging environment, bees foraging for colonies with high short-term energy requirements (*i.e.*, Depleted treatment) may actually do a *better* job of tracking changes in their environment. This is because bees are more likely to leave each inflorescence early, causing them to visit more inflorescences per unit time, and allowing them to obtain a better estimate of mean inflorescence quality. The model of Houston and McNamara (1985) also predicts non-discriminating behavior for certain conditions of high food requirement, without invoking learning. However, it cannot explain the Order-related differences in the behavior of Depleted bees, an effect we attribute to learning. State, then, may influence the way that organisms learn about their environment. This problem merits further attention.

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