

ON THE TRADEOFF BETWEEN THE MEAN AND THE VARIANCE IN FORAGING: EFFECT OF SPATIAL DISTRIBUTION AND COLOR PREFERENCE¹

LESLIE REAL, JAMES OTT, AND EVA SILVERFINE
Department of Zoology, North Carolina State University,
Raleigh, North Carolina 27650 USA

Abstract. An enclosed colony of bumblebees (*Bombus pennsylvanicus*) was restricted to foraging on two artificial flower types. The means and variances were adjusted in the two flower types in order to detect risk sensitivity. Both the mean and the variance contributed to the bees' foraging decisions. A series of experiments was designed to construct the bees' indifference curve under a variety of ecological conditions. The indifference curve represents combinations of mean and variance in nectar reward for which bees showed no preference. In three of the four experiments there was a positive tradeoff between the mean and the variance, i.e., a relatively more variable flower type could be compensated for by increasing its expected reward. The quantitative nature of the tradeoff is shown to be sensitive to ecological parameters (e.g., spatial distribution of flowers) and independent behavioral parameters (e.g., intrinsic color preference).

Key words: *Bombus pennsylvanicus*; bumblebees; gene flow; optimal foraging; pollination; pollinator-plant interactions; risk-sensitive foraging; risk-sensitive foraging in bumblebees; uncertainty; variable environments.

The role of variation in nectar reward in determining the floral preferences of pollinators remains a new and relatively unexplored facet of foraging behavior. Most models of foraging assume that pollinators choose flowers so as to increase their expected energetic reward (Pyke 1978, 1980, Waddington and Holden 1979). However, net energetic gain may not completely characterize the organism's choices. A pollinator faced with variability in nectar reward per flower may select flowers that reduce the uncertainty of the results of its foraging. Such risk-sensitive foraging has been suggested on theoretical grounds (Oster and Wilson 1978, Caraco 1980, Real 1980a, b), and there is some empirical evidence suggesting that foragers do assess the variance in reward while foraging (Caraco 1980, Caraco et al. 1980, Real 1981, Waddington et al. 1981).

The logic behind the argument is simple. While maximizing the expected reward from foraging may prove advantageous, so may minimizing the uncertainty that a particular behavior will actually generate a given reward. Minimization of the uncertainty minimizes the probability that the organism will actually fare very poorly in its foraging. Two behaviors may generate the same ultimate value, though they differ in their expected values so long as the behavior with the lower expectation is compensated for by a higher degree of certainty. Consequently, there may be a tradeoff between the expected value of a behavior and its certainty.

Real (1981) chose to depict such a relationship as the expected reward discounted by a function of the variance in reward, i.e.,

$$F(x) = E(x) - AV(x) \quad (1)$$

where $E(x)$ = expected reward from flowers of type X , $V(x)$ = variance in the reward between flowers, A is the "coefficient of risk aversion" (a measure of the degree to which increasing variance is undesirable), and $F(x)$ = the perceived value to the pollinator of flowers of type X .

This relationship assumes that, given a choice between two floral types with equal expected rewards, the pollinator will choose the type with the lower variance. Using artificial flowers on a Plexiglas® grid and an enclosed colony of bumblebees (*Bombus sandersonii*), Real (1981) tested this assumption. Under controlled manipulations in which the two artificial flower types had equal mean rewards, the foragers chose the floral type with the least variance. This corroborates the minus sign in Eq. 1.

However, more is needed than simply to show risk aversion. If the model is correct, the perceived value of the variable floral type can be enhanced by increasing its mean reward. When the variance is fixed, the expected reward can be increased until the foragers show equal preference (or "indifference") between constant and variable floral types. For the two floral types to be of equal perceived value, $F(x)$ for the two types must be equal. We designate this indifference value as $F_0(x)$. The set of means and variances that will be of equal preference is then given by the equation:

$$V(x) = \frac{E(x)}{A} - \frac{F_0(x)}{A} \quad (2)$$

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The model predicts that the tradeoff between variance and expectation will be linear and that a plot of

all such indifference points will generate a straight line on an $[E(x), V(x)]$ -coordinate system. A demonstration that the tradeoff between expectation and variance is linear would further corroborate the model. It would also yield the coefficient of risk aversion since the slope of Eq. 2 is $1/A$. If the tradeoff is nonlinear, then the model must be modified accordingly.

In the experiments reported here we determined the shape of the indifference curve and the coefficient of risk aversion for two spatial distributions and two flower types. The methods we used are identical to those used by Real (1981) and are only briefly described here.

METHODS

During summer 1981 we established a colony of bumblebees (*Bombus pennsylvanicus*) inside a 2.5 m \times 1.5 m \times 2 m enclosure. The enclosure was located in a second-growth woods at Yates Pond Research Lab operated by the Department of Zoology, North Carolina State University, \approx 11 km from Raleigh, North Carolina.

We used a technique initially described by Waddington (1979) and further modified by Real (1981). Wells 3 mm deep and 2.54 cm apart were drilled into a 1.2 m \times 1.2 m \times 6 mm Plexiglas sheet (or "bee-board"), generating a uniform distribution of 2304 wells. From these possible positions random coordinates for 200 artificial flowers (squares of blue and yellow cardboard centered and fixed under the appropriate wells) were assigned. Floral color was assigned alternately, producing a mixed patch of 100 blue and 100 yellow flowers distributed randomly over the bee-board. The board was placed over a plywood sheet painted green. For each trial known quantities of diluted honey were dispensed into the appropriate wells. The diluted honey was adjusted to 30% sucrose equivalents measured by a hand refractometer and dispensed using either a Gillson variable-volume or Hamilton fixed-volume microdispenser. The bee-board was then slipped into the enclosure and the foraging sequence of individual bees was monitored. Each trial consisted of a known distribution being inserted into the enclosure and a single forager's choices of flowers to visit. After a bee finished foraging, or after she had visited \approx 40 flowers, the board was removed and washed.

The data presented are the pooled responses of many individual bees to a given distribution of nectar rewards. No single individual bee was subjected to the entire range of means and variances, and no doubt pooling the data obscures some of the natural variation in individual response that has been observed elsewhere (Waddington et al. 1981). Ideally one should obtain sufficient data to assess individual differences in risk sensitivity. We hope to carry out these fine-tuned experiments in the future. For these data, however, we collected (and pooled) the responses from

eight foragers. Most of the data were collected from three bees. Each distribution was tested three times. In all but one case, when different bees were subjected to the same distribution they responded similarly, i.e., when one bee was indifferent so were the others. Consequently, we feel that the qualitative response to variance is similar among bees, while quantitative responses may vary. Since our analysis is ordinal, i.e., the magnitude of preference is not considered, pooling the data seems justifiable.

Using these techniques we determined the tradeoff relationship between mean and variance in reward per flower for the colony. One floral type on the bee-board was kept constant with a known reward expectation. The other floral type had a fixed variance, but the expectation was increased or decreased until the individual bees showed no preference for either type (measured as no significant deviation from random foraging by a chi-square test). This gave us one pair of points for the indifference curve. Next, the variance in the variable-type flower was increased, and again, the point of indifference between it and the constant-type flower was determined by adjusting its expectation until foragers exhibited random foraging. This yielded another indifference point. The process was continued until the relationship was established over a range of variances. For a given constant type we have then the combinations of means and variances in the variable type that generate (1) preference for the constant type, (2) indifference between constant and variable types, and (3) preference for the variable type. Regression of the indifference points then reveals the curvature and the slope of the tradeoff. We performed four experimental series to arrive at four indifference curves under different ecological conditions.

Experimental series number 1.—In this first series nectar content of blue flowers was kept constant, with 2 μ L/flower. The nectar content of the yellow flowers was variable, with means and variances generated from the distributions listed in Table 1.

Experimental series number 2.—Once again the nectar content of blue flowers was constant with 2 μ L of nectar in each; that of yellow flowers was variable. However in this series, the yellow were clumped rather than randomly mixed over the board. We adjusted the positions so there were 10 clumps of 10 flowers each more or less uniformly spaced over the board. Our hypothesis was that clumping the flowers should reduce risk aversion, i.e., pollinators should be more willing to accept uncertainty when the flowers are clumped. Means and variances for the variable yellow flowers were generated from the distributions listed in Table 2.

Experimental series number 3.—From previous experiments by Real (1981) and repeated experiments during the early part of the summer we know that bumblebees (under these conditions) show a yellow color preference, i.e., when all the flowers have the

TABLE 1. Distribution of nectar quantities per flower used to generate the means variances of the variable-reward color for series number 1. Nectar content of blue was held constant at 2 $\mu\text{L}/\text{flower}$, while that of yellow was variable; both blue and yellow were distributed randomly in space. Pooled qualitative preferences of the bees are indicated in column P, with B = blue, Y = yellow, and I = indifferent.

Nectar reward (μL)			
μ	σ^2	Distribution	P
0	0	all empty	B
1	0	1.0 in all	I
2	0	2.0 in all	Y
2.5	2.25	1/2 1.0, 1/2 4.0	I
4	2.25	1/2 2.5, 1/2 5.5	Y
2	4	1/2 0, 1/2 4.0	B
3	4	1/2 1.0, 1/2 5.0	I
4	4	1/2 2.0, 1/2 6.0	Y
3.5	6.25	1/2 1.0, 1/2 6.0	I
5	6.25	1/2 2.5, 1/2 7.5	I
3	9	1/2 0, 1/2 6.0	B
4	9	1/2 1.0, 1/2 7.0	I
5	9	1/2 2.0, 1/2 8.0	I
6	9	1/2 3.0, 1/2 9.0	Y
3.5	12.25	1/2 0, 1/2 7.0	B
4	12.25	1/2 0.5, 1/2 7.5	I
5	12.25	1/2 1.5, 1/2 8.5	I
4	16	1/2 0, 1/2 8.0	I
5	16	1/2 1.0, 1/2 9.0	I
6	16	1/2 2.0, 1/2 10.0	Y
3	21.5	1/2 0, 1/4 1.0, 1/4 11.0	B
4.5	20.25	1/2 0, 1/2 9.0	I
6	20.25	1/2 1.5, 1/2 10.5	Y
3.25	25	1/2 0, 1/4 1.0, 1/4 12.0	B
5	25	1/2 0, 1/2 10.0	I
6	25	1/2 1, 1/2 11	Y

same reward the bees prefer yellow to blue. To test for the effects of color preference on risk sensitivity we switched the constant and variable types. Now yellow nectar content was constant, with 2 $\mu\text{L}/\text{flower}$,

TABLE 2. Distribution of nectar and associated means and variances of the variable-reward color used in series number 2. The nectar content of blue was constant with 2 $\mu\text{L}/\text{flower}$, while that of yellow was variable. Blue was distributed randomly in space, while yellow was clumped. Preferences (P) are as in Table 1.

Nectar reward (μL)			
μ	σ^2	Distribution	P
0	0	all empty	B
1	0	1.0 in all	Y
1.5	4.25	1/2 0, 1/4 1.0, 1/4 5.0	Y
2	4	1/2 0, 1/2 4.0	Y
1	9	9/10 0, 1/10 10.0	I
2	8.5	1/2 0, 1/4 1.0, 1/4 7.0	Y
3	9	1/2 0, 1/2 9.0	Y
2	12	3/4 0, 1/4 8.0	I
4	16	1/2 0, 1/2 8.0	I
6	16	1/2 2.0, 1/2 10.0	Y
1	17	17/18 0, 1/18 18.0	B
3	18	2/3 0, 1/3 9.0	I
5	25	1/2 0, 1/2 10.0	I
6	25	1/2 1.0, 1/2 11.0	I
7	25	1/2 2.0, 1/2 12.0	Y
3.5	26.5	2/3 0, 1/3 11.0	B

TABLE 3. Series number 3's nectar distribution, with associated means and variances of the variable-reward color. In this series, the nectar content of yellow was held constant at 2 $\mu\text{L}/\text{flower}$, while that of blue was variable. Both blue and yellow flower types were distributed randomly in space. Preferences (P) are as in Table 1.

Nectar reward (μL)			
μ	σ^2	Distribution	P
1	0	1.0 in all	Y
3	0	3.0 in all	I
4	0	4.0 in all	I
5	0	5.0 in all	I
6	0	6.0 in all	B
2	4	1/2 0, 1/2 4.0	Y
4	4	1/2 2.0, 1/2 6.0	I
5	4	1/2 3.0, 1/2 7.0	I
6	4	1/2 4.0, 1/2 8.0	I
7	4	1/2 5.0, 1/2 9.0	B
3	9	1/2 0, 1/2 6.0	Y
5	9	1/2 2.0, 1/2 8.0	I
6	9	1/2 3.0, 1/2 9.0	I
7	9	1/2 4.0, 1/2 10.0	B
4	16	1/2 0, 1/2 8.0	I
6	16	1/2 2.0, 1/2 10.0	I
7	16	1/2 3.0, 1/2 11.0	B
2	20	5/6 0, 1/6 12.0	Y
3	21.25	1/2 0, 1/4 1.0, 1/4 11.0	I
4.5	20.25	1/2 0, 1/2 9.0	I
5.5	20.25	1/2 1.0, 1/2 10.0	I
6.5	20.25	1/2 2.0, 1/2 11.0	B
3.25	25	1/2 0, 1/4 1.0, 1/4 12.0	Y
5	25	1/2 0, 1/2 10.0	I
6	25	1/2 1.0, 1/2 11.0	I
7	25	1/2 2.0, 1/2 12.0	B

and blue was variable. Yellow and blue were both randomly mixed over the bee-board. Distributions for the variable blue type are listed in Table 3.

Experimental series number 4.—This final series tested the effects of reducing the quality of the preferred floral type. Nectar content in yellow flowers was held constant but this time with only 0.5 $\mu\text{L}/\text{flower}$. Blue was variable, and the two flower types were randomly mixed. Distributions for the variable type are listed in Table 4.

The series numbers do not correspond to the chronology of the experiments. Rather, series 2 was performed last, following 1, 3, and 4. For pedagogical reasons we list them in numerical order.

RESULTS AND DISCUSSION

Series number 1.—Regression analysis of the indifference points (Fig. 1: closed circles) reveals a significant positive relation between the mean and the variance in nectar reward. It appears that increasing uncertainty can be compensated for by increasing mean reward, or conversely, as the expected reward increases, greater degrees of uncertainty are accepted. At first glance these data appear nonlinear, which would indicate a violation of the basic model. However, moving from a linear model to a quadratic model is not justified statistically as an insignificant amount of

TABLE 4. Reward distributions of the variable-reward color for series number 4, in nectar content in yellow was constant with 0.5 $\mu\text{L}/\text{flower}$, and that in blue was variable. Each flower type was distributed randomly in space. Preferences (P) are as in Table 1.

Nectar reward (μL)			
μ	σ^2	Distribution	P
0	0	0 in all	Y
1	0	1.0 in all	I
2	0	2.0 in all	B
2	1	1/2 1.0, 1/2 3.0	I
6	2.6	3/4 0, 1/4 3.0	Y
1.5	2.25	1/2 0, 1/2 3.0	I
2.5	2.25	1/2 1.0, 1/2 4.0	B
1.5	4.25	1/2 0, 1/4 1.0, 1/4 5.0	I
2	4	1/2 0, 1/2 4.0	B
1	9	9/10 0, 1/10 10.0	Y
2	8.5	1/2 0, 1/4 1.0, 1/4 7.0	I
3	9	1/2 0, 1/2 6.0	I
4	9	1/2 1.0, 1/2 7.0	B
2	12	3/4 0, 1/4 8.0	I
1.5	15.75	7/8 0, 1/8 12.0	Y
4	16	1/2 0, 1/2 8.0	B
3	18	2/3 0, 1/3 9.0	I
4.5	20.25	1/2 0, 1/2 9.0	B
2	24	6/7 0, 1/7 14.0	Y
3.5	26.5	2/3 0, 1/3 11.0	I
5	25	1/2 0, 1/2 10.0	I
6	25	1/2 1.0, 1/2 11.0	B

additional variance is accounted for by moving from the linear to the quadratic. The best-fit linear equation is given by $\sigma^2 = -5.76 + 4.14 \mu$ ($r^2 = .48$, $P < .01$), and the coefficient of risk aversion is 0.24 (the reciprocal of the slope of the regression).

There is reason to expect a quadratic relation if the organism's preferences are ordered according to the geometric mean of the nectar distribution. There is a simple relationship between the geometric mean and a generalized version of the variance-discount model. One approximation for the geometric mean (G) is given by Markowitz (1959) as

$$G \cong \mu - \frac{\sigma^2}{2\mu}, \quad (3)$$

where μ is the arithmetic mean. A geometric mean decision criterion indicates that the organism's risk aversion decreases as the arithmetic mean of the distribution increases, i.e., as the expected reward increases the organism is less sensitive to increasing variance in reward. Such diminishing risk aversion would give rise to an upwardly curving indifference relation similar to that suggested by the data in Fig. 1. If we compare Eq. 3 with Eq. 1 we see that they are equivalent if the coefficient of risk aversion is half the reciprocal of the arithmetic mean. For a constant geometric mean (G_0) the indifference curve is defined by

$$\sigma^2 = 2 \mu^2 - 2 \mu G_0, \quad (4)$$

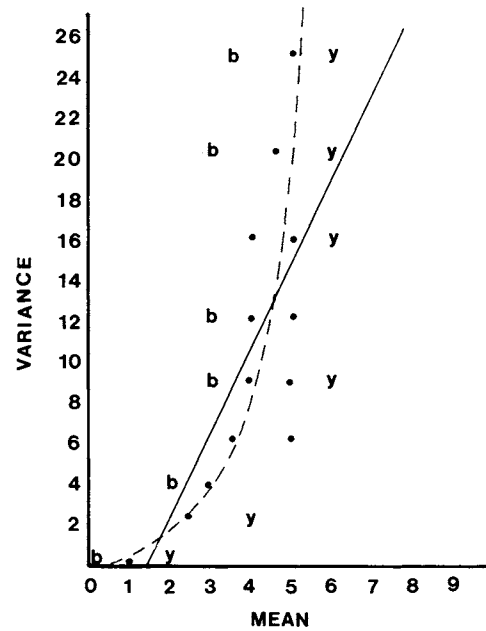


FIG. 1. Plot of combinations of means and variances for yellow that generated yellow preference (Y), indifference (\bullet), and blue preference (B), when nectar content of blue flowers was held constant, with 2 $\mu\text{L}/\text{flower}$, and that of yellow was variable. Both blue and yellow were randomly distributed in space. Linear regression yields the relation $\sigma^2 = -5.76 + 4.14 \mu$ ($r^2 = .48$, $P < .01$). The coefficient of risk aversion is 0.24. The dashed line is the fitted exponential curve $\sigma^2 = 0.11 e^{1.04\mu}$ ($r^2 = .78$, $P < .01$).

and consequently we might expect a quadratic relationship between the mean and variance for the indifference points. However, no such relationship seems justified statistically. It appears that the geometric mean is not a better descriptor of the organism's decision criterion.

Significant nonlinear effects are revealed if we fit either an exponential curve ($\sigma^2 = 0.11 e^{1.04\mu}$, $r^2 = .78$, $P < .01$) or a power function ($\sigma^2 = 0.08 \mu^{3.39}$, $r^2 = .90$, $P < .01$). The relationships do account for a significant amount of additional variance and suggest that there is diminishing risk aversion. Still, since there is no prior reason to expect either an exponential or a power relationship and since no other experiments indicate a nonlinear component, we will hold to the linear model when comparing this series with subsequent experiments.

Series number 2.—Having accepted a significant positive linear relationship for the indifference points, we can now determine how this relationship varies under different ecological conditions. One question of particular interest to the pollination biologist and population geneticist is: what are the consequences of a species having clumped rather than random or hyperdispersed flowers through the habitat? Even on the small scale of our experiments, clumping significantly

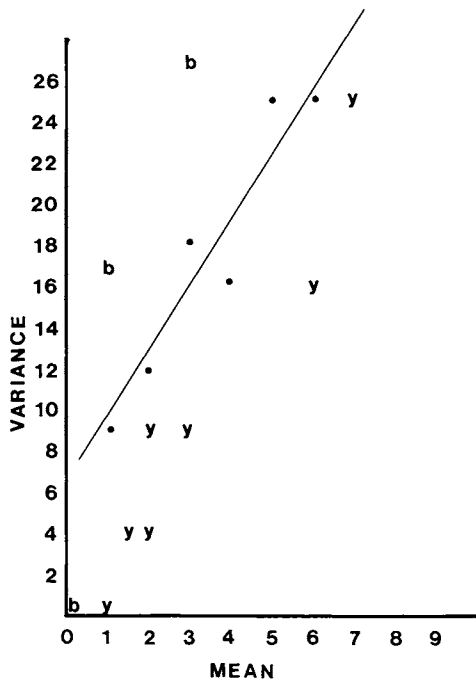


FIG. 2. Plot of combinations of means and variances for yellow when nectar content of blue was constant ($2 \mu\text{L}/\text{flower}$) and that of yellow was variable (Symbols as in Fig. 1.). Blue was distributed randomly in space, while yellow was clumped. Linear regression yields the relation $\sigma^2 = 5.8 + 3.34\mu$ ($r^2 = .89$, $P < .01$). The coefficient of risk aversion is 0.30, which is not significantly different from that of series number 1.

affected risk taking (Fig. 2). The linear regression for the clumped series is $\sigma^2 = 5.8 + 3.34\mu$ ($r^2 = .89$, $P < .01$), and the coefficient of risk aversion is 0.30. Statistical analysis of the regression lines for Figs. 1 and 2 indicates no difference in slope but a significant difference in intercept ($P < .05$). This means that for a given expected reward the bees are accepting more variance in reward with clumping, but the tradeoff between mean and variance (the coefficient of risk aversion) remains the same. This can only occur when $F_0(x)$, the initial perceived value of a flower, is greater when clumped than when randomly dispersed through the habitat.

If the propensity to attract pollinators influences plant fitness, then these results have obvious consequences for the evolution of inflorescence size, patch size, and the timing of flower presentation. The clumping of flowers makes them more desirable for bee visitation, and consequently, selection for reduced variation in reward would be relaxed in these species. In comparison with other flowers in the habitat, clumped individuals may experience an energetic advantage in one of two ways. (1) For a given level of variance in reward, clumped individuals may be as attractive to pollinators as other plants in the habitat while providing a lower expected reward. Consequently, the plants save

energy by not having to produce as much nectar on average. (2) Alternatively, clumped individuals may produce the same expected reward as other plants in the habitat but with greater variance and still be attractive. The energy saved in this case corresponds to energy that would be allocated to mechanisms that reduce the variance in nectar reward. These could be biochemical or morphological mechanisms. For example, certain flowering plants may possess nectar production mechanisms that are sensitive to visitation frequency and rate of nectar removal. This machinery would help stabilize the amount of nectar per flower, thereby reducing the variance. This sort of mechanism has been found by comparing standing crops of bagged and unbagged tropical passion flowers (F. Gill, *personal communication*). The maintenance of such machinery must incur some cost to the plant, a cost not shared by plants that lack such an insurance mechanism. These two energetic advantages are different in that we expect the costs of nectar production to be different from the costs of maintaining a certain level of variability. If either of these energetic benefits surpasses the energetic cost of clumping, then we expect clumping to be energetically advantageous.

However, the energetic advantage may be reduced by the depressing effects of increased inbreeding. The genetic disadvantage in producing clumped flowers or being an individual within a clump may far outweigh any energetic advantage, and there will probably be some form of tradeoff between the energetic benefits and the genetic costs of clumping. At least one difficulty in assessing the benefits and costs is apparent: the currencies of benefits and of costs are different. The genetic costs are measured directly in fitness components, while energy is assumed to correlate indirectly with fitness components. Unless we can arrive at the direct translation of energy into fitness components, the resolution of the tradeoff will be difficult to establish empirically.

Series number 3.—From previous experiments under identical experimental design, we know that bumblebees prefer yellow flowers to blue flowers when the flowers are of equal quality (Real 1981). These results were confirmed with our bumblebee colony earlier in the summer. What are the consequences of making the preferred flower constant and the less-preferred flower variable? In series number 1 the nectar content of blue flowers was constant, with $2 \mu\text{L}/\text{flower}$, and that of yellow flowers was variable. For this series the roles of the flowers were reversed; nectar content of yellow was constant with $2 \mu\text{L}/\text{flower}$, and that of blue was variable.

The consequences of such a simple change are quite dramatic. There is no longer any tradeoff between the mean and the variance in determining preference (Fig. 3). Linear regression reveals no significant relation ($r^2 = .02$, $P > .60$). The bees do switch from the constant yellow to the variable blue, but only after the

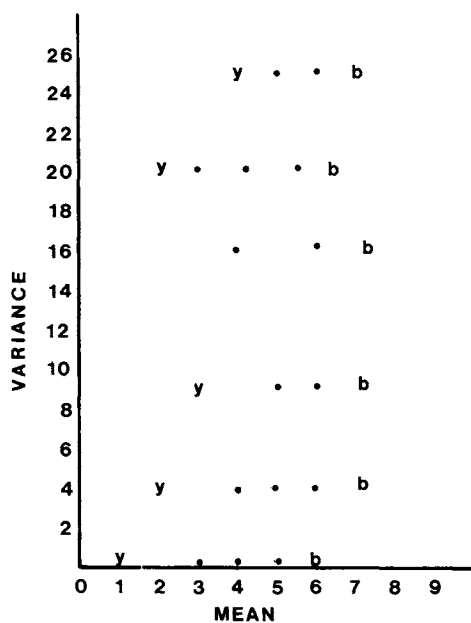


FIG. 3. Plot of combinations of means and variances for blue when nectar content of yellow was held constant ($2 \mu\text{L}/\text{flower}$) and that of blue was variable; both blue and yellow were distributed randomly in space. (Symbols as in Fig. 1.) There is no significant linear relationship ($r^2 = .02$, $P > .60$).

mean nectar content for the blue flowers increases above a certain critical level ($\approx 6 \mu\text{L}/\text{flower}$), and this critical level is independent of the variance in the distribution.

This indicates that when the preferred flower is providing a sufficiently high reward the bees track only the mean. When the mean of the less-preferred flower increases to a threshold level the bees will switch.

It appears that there is no intrinsic tradeoff between mean and variance in reward. Whether or not the bees consider the variance in their floral choices depends then upon complex ecological conditions relating to the relative rewards offered by flowers of different intrinsic preferences, for instance, the preference for yellow over blue. Can the bees be induced to resume tracking the variance if the quality of the preferred floral type is reduced? They can, and the next series was designed to show this.

Series number 4.—When the constant nectar content of the yellow flowers is reduced to $0.5 \mu\text{L}/\text{flower}$ and nectar content of blue flowers is kept variable, the bees start tracking the variance (Fig. 4). The linear relation is given by $\sigma^2 = -5.0 + 6.7 \mu$ ($r^2 = .76$, $P < .001$), and the coefficient of risk aversion is then 0.15. There is no significant nonlinearity. The slope is significantly different from those of Figs. 1 and 2 ($P < .05$). When the yellow flower is providing a constant but low reward, the bees not only resume tracking the variance but are less averse to risk than

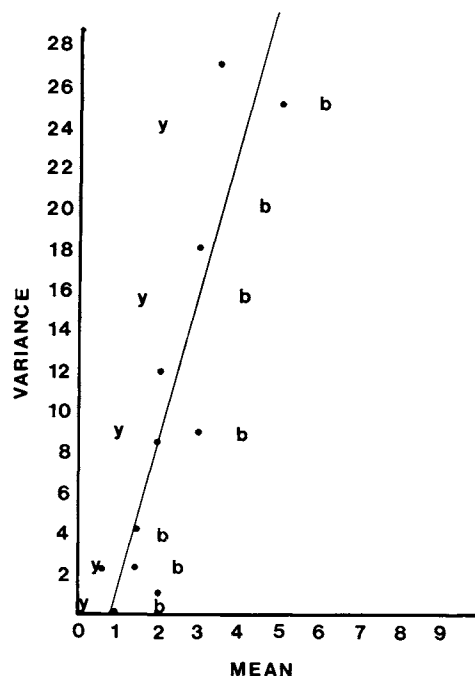


FIG. 4. Plot of combinations of mean and variance for blue when yellow nectar content was constant ($0.5 \mu\text{L}/\text{flower}$) and that of blue varied; both blue and yellow were randomly distributed. (Symbols as in Fig. 1.) Linear regression yields the relation $\sigma^2 = -5.0 + 6.7 \mu$ ($r^2 = .76$, $P < .001$). The coefficient of risk aversion is 0.15 and is significantly different from those of series number 1 and 2.

when nectar content of blue flowers was constant at $2 \mu\text{L}/\text{flower}$. For a unit increase in the mean, the bees are now willing to accept twice as much variance. It is presumed that the constant reward level of the preferred yellow could be adjusted to generate the same slope as that obtained when blue was held constant. At that reward level the energetic difference between the constant yellow and the constant blue would indicate the energetic "premium" associated with the yellow preference (Caraco et al. 1980).

The intercepts of the linear relations in Figs. 1 and 4 are not significantly different. Since the intercept is defined by $F_0(x)/A$, and since the A 's are different, $F_0(x)$ must be proportionately different. In general, we do not suspect a relationship between the initial perceived value $F_0(x)$ and the coefficient of risk aversion, A , i.e., the ratio of $F_0(x)$ to A is constant, even though a relationship is suggested by comparing Figs. 1 and 4.

Remarks

Two important conclusions derive from these experiments. First, there can be a tradeoff between the mean and the variance in reward for pollinators choosing flowers, and that tradeoff is predicted by the variance-discount model of decision making. Second, whether there will or will not be a tradeoff and the

quantitative nature of the tradeoff depends upon complicated ecological and behavioral preconditions that impinge upon the decision process.

These two results can be combined to foster a single question of paramount importance to the pollination biologist: what is the relationship between the quantifiable parameters of the habitat (or the organism's behavior) and the parameters determining the mean-variance tradeoff? We can determine these relationships either by carrying out comparative empirical studies over a graduated scale of ecological parameters or by searching for the underlying behavioral mechanisms that will generate the different responses as special cases. The latter approach, though sounder since based on first principles, seems an enormous task with little chance of success. Consequently, we opt for the less sound but more practical comparative approach.

We are continuing to test the model with bumblebees, but the questions raised here are applicable to many other organisms and biological interactions. The model should apply to nectarivorous birds and bats as well as frugivores. In fact, any sort of diet selection should incorporate some measure of uncertainty. The model may be equally well suited to other sorts of decisions where there are uncertain outcomes, such as mate selection, habitat selection, breeding time, etc. We hope that the examination of the role of uncertainty in decision making will be extended to other systems.

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