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# Notes and Comments

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## *RISK-AVERSE FORAGING IN BEES: A COMMENT ON THE MODEL OF HARDER AND REAL*

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Preference for rewards is said to be risk sensitive if choice depends not only on the mean reward magnitude but also on the variability in reward magnitude. In particular, when there is a choice between rewards with the same mean reward magnitude, choice is determined by the variance in reward magnitude. If a high variance is preferred, preference is said to be risk prone, whereas if low variance is preferred, preference is said to be risk averse.

Within foraging theory, it has been common to take the reward currency to be the net amount of energy that is gained. Some care is needed in defining risk-sensitive foraging in this context. Where there is only one choice between two feeding options and each option takes the same amount of time to exploit, then it is reasonable to define an animal to be risk sensitive in reward magnitude if both the mean and the variance in energy gained influence preference.

In both laboratory experiments and in the wild, animals are typically confronted with a series of foraging decisions. In such circumstances, the definition of risk sensitivity is less clear. Choices may determine not only the amount of energy that is gained, but also the amount of time that is spent. It does not seem reasonable to characterize alternatives by the mean amount of energy that a single choice yields, if exploiting one option takes much longer than exploiting the other option. It is necessary to find some way of integrating reward magnitude and time. When the foraging process stops at some fixed final time (e.g., dusk for a diurnal bird), then one can look at the total amount of energy that has been gained by this time. Again, it seems reasonable to say that the animal is risk sensitive if its choices during the foraging period depend on both the mean

of this amount and its variance. If the foraging period under consideration is long, in the sense that the animal makes many choices during the period, then the mean net gain by the end of the interval is approximately equal to the duration of the interval multiplied by the long-term mean net rate of energy gain  $\gamma$ . From this definition of risk sensitivity, it follows that animals are not risk sensitive if their foraging decisions can be understood solely in terms of differences in  $\gamma$ . If two options yield the same  $\gamma$ , then preference for the more variable option would be taken as risk-prone behavior.

If the duration of the foraging period is not fixed, or if it is not long, then the definition of risk-sensitive foraging is not so obvious.

Risk-sensitive foraging theory has been concerned with establishing the relationship between the amount of energy obtained and the animal's subsequent reproductive success. By doing so, it is possible to construct a functional account of risk-sensitive foraging behavior. For further discussion see McNamara and Houston (1986, 1987) and Real and Caraco (1986).

Real (1981) presented bees with two types of flowers. In one type of flower all flowers contained the same volume of nectar. In the other type, flowers varied in the volume of nectar that they contained. Real found that when the mean volume of nectar was the same for both types, the bees preferred the type with the constant amount. Similar results were obtained by Waddington et al. (1981) and Real et al. (1982).

This paper has the following aims:

1) We analyze the relationship between nectar volume and a bee's long-term mean net rate of energy gain.

2) Harder and Real (1987) present a model of the bees' behavior based on the maximization of the expected value of a particular currency. They refer to this currency as a rate. We point out that this rate is not the long-term rate of energy gain that is usually considered by foraging theory.

3) We outline the information that is needed to construct a functional explanation for risk-sensitive foraging in bees.

### *The Long-term Mean Net Rate of Energy Gain, $\gamma$*

We wish to find the long-term mean net rate of energy gain  $\gamma$  of a foraging bee. To do this, consider a bee between the time it leaves one flower and the time it leaves the next flower. This constitutes a cycle in terms of renewal theory. The two quantities that we require in order to calculate  $\gamma$  are the mean net energy gained during the cycle and the mean duration of the cycle. If a flower has nectar volume  $v$ , we can denote the net energy gain over the complete cycle by  $R(v)$  and denote

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the duration of the complete cycle by  $T(v)$ . When all nectar volumes are the same and equal to a constant  $\mu$ , then the net rate of energy gain obtained by the bee is

$$\gamma = R(\mu)/T(\mu). \quad (1)$$

When the volume of nectar is a random variable  $V$ , then the mean net rate of energy gain is

$$\gamma = E[R(V)]/E[T(V)], \quad (2)$$

where  $E$  denotes expectation. The mathematical derivation of this result is contained in Johns and Miller (1963) and is discussed in a biological context by Gilliam et al. (1982) and Turelli et al. (1982).

Harder and Real assume a special form for  $R(v)$  and  $T(v)$ . Let

- $e$  be the energy content per milligram of sucrose (J/mg)
- $\rho$  be the nectar density (mg/ $\mu$ L)
- $S$  be the nectar concentration (% mass of sucrose per mass of solution)
- $W$  be the bee's mass (g)
- $T_f$  be the flight time between flowers (s)
- $I$  be the ingestion rate ( $\mu$ L/s)
- $T_a$  be the time required to enter and leave the flower (s)
- $T_p$  be the duration of the flower visit (s)
- $k_p$  be the metabolic rate while on the flower ( $J \cdot g^{-1} \cdot s^{-1}$ )

and

- $k_f$  be the metabolic rate while flying ( $J \cdot g^{-1} \cdot s^{-1}$ ).

Then

$$R(v) = e\rho Sv - W(k_p T_p(v) + k_f T_f), \quad (3)$$

where

$$T_p(v) = T_a + v/I \quad (4)$$

and

$$T(v) = T_f + T_p(v). \quad (5)$$

In this case both  $R(v)$  and  $T(v)$  are linear functions of  $v$ . As a result, if nectar volume  $V$  is a random variable with mean value  $\mu$ , then

$$E[R(V)] = R(\mu)$$

and

$$E[T(V)] = T(\mu).$$

It follows from Eqs. 1 and 2 that the mean long-term net rate of energy gain depends on the mean nectar volume per flower and is not influenced by variability about this mean.

What we have considered is a special case in which  $R(v)$  and  $T(v)$  are linear functions of  $v$ . Hodges and Wolf (1981) and Harder (1985, 1986) suggest that there is a decelerating relationship between the time that the bee spends on the flower and the nectar volume of the flower. We now examine how this changes the qualitative conclusions reached above. Suppose Eq. 4 is replaced by

$$T_p(v) = T_a + \alpha(v), \quad (6)$$

where  $\alpha$  is an increasing and decelerating function of  $v$ . For a function of this form

$$E[T_p(V)] \leq T_p(\mu), \quad (7)$$

where  $\mu = E(V)$  as before. It follows from Eqs. 3 and 7 that

$$\begin{aligned} E[R(V)] &= e\rho S E(V) - W\{k_p E[T_p(V)] + k_f T_f\} \\ &\geq e\rho S \mu - W\{k_p T_p(\mu) + k_f T_f\} \\ &= R(\mu), \end{aligned} \quad (8)$$

and similarly from Eqs. 5 and 7 that

$$E[T(V)] \leq T(\mu). \quad (9)$$

Hence from Eqs. 8 and 9 we have

$$E[R(V)]/E[T(V)] \geq R(\mu)/T(\mu). \quad (10)$$

Thus when the two types of flowers have the same mean nectar volume, Eq. 10 shows that the variable flower type provides the greater long-term mean net rate of energy gain.

It follows from this analysis that the bees' empirical preference for less variable nectar volumes cannot be understood in terms of higher long-term mean net rates of energy gain. If it were reasonable to assume that bees collected nectar over an extended fixed period of time, then one could conclude that they were risk averse with respect to the total volume of nectar collected during this time.

#### *The Currency Used by Harder and Real (1987)*

In the above analysis, we have considered the currency of long-term mean net rate of energy gain  $\gamma$ , as given by Eq. 2. Harder and Real (1987) consider the currency

$$g = E[R(V)/T(V)]. \quad (11)$$

They point out that the function  $R(V)/T(V)$  is a decelerating function of  $V$ , and hence by Jensen's inequality

$$g \leq R(\mu)/T(\mu). \quad (12)$$

Thus if bees are maximizing  $g$ , they should prefer flowers with a constant nectar volume  $\mu$  rather than flowers with a variable nectar volume with mean  $\mu$ . It

appears that the currency  $g$  is able to account for the bees' preferences. But what is the biological significance of this result? Although the analysis accounts for observed behavior, there are many other functions of nectar volume and time that would produce the same qualitative results. For example, if a bee is maximizing the expected value of any decelerating function of the total nectar volume obtained over a long period, then it would show the observed preferences. One would only single out a particular currency if it provides the best fit to the data, or if it has a strong biological justification. The currency  $g$  has not been compared with other currencies. Harder and Real do not establish a relationship between their currency and fitness. We emphasize that the currency they use is not the long-term rate, i.e.,  $g \neq \gamma$  (see also Gilliam et al. 1982, Turelli et al. 1982).

#### *Functional Explanations of Bees' Foraging Behavior*

Oster and Wilson (1978) provided functional explanations of the foraging behavior of social insects by showing how this behavior contributed to the reproductive success of the colony. For example, they argued that the reproductive success of an annual species (e.g., bumble bees) was given by the number of reproductives produced by the end of the season. Functional explanations of the foraging of bumble bees must relate foraging behavior to this number. In order to do this, it is necessary to understand a lot about the biology of the colony. In particular, one must be able to quantify how energy delivered to the colony influences its growth, and how colony size affects the production of reproductives. It is important to know how much of the energy yielded by the nectar is brought to the colony as opposed to being used by the bee. One must also have an understanding of the foraging environment (e.g., spatial and temporal distribution of nectar and pollen). Given this knowledge, it might be possible to relate the distribution of available nectar volume to the number of reproductives produced by a colony, and hence provide a functional account of the bees' foraging behavior.

Although  $\gamma$  is not a perfect surrogate for fitness (see, for example, McNamara and Houston 1987), it has biological plausibility in many circumstances. It fails, however, to predict the preference of bees for constant nectar volumes. The currency used by Harder and Real (1987) gives the correct qualitative predictions but has

no obvious relationship to the colony's reproductive success.

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