

- Purnell, D. J. & Thompson, J. N. Jr. 1973. Selection for asymmetrical bias in a behavioural character of *Drosophila melanogaster*. *Heredity*, **31**, 401-405.
- Reeve, E. C. R. 1960. Some genetic tests on asymmetry of sternopleural chaeta number in *Drosophila*. *Genet. Res., Camb.*, **1**, 151-172.

(Received 10 November 1980; MS. number: sc-90)

### The Logic of Risk-Sensitive Foraging Preferences

It has recently been shown that the foraging preferences of animals are sensitive to variance in the probability distribution of a food reward (Caraco et al. 1980). This is an important result for optimal foraging models, because they often assume that the expected value of the food reward distribution is the quantity that should be maximized and that variance may be safely ignored (see Pyke et al. 1977 for a review). Caraco (1980) has suggested that some aspects of risk sensitivity may be explained by minimization of the probability of starvation, where starvation is defined as falling short of some threshold food requirement at the end of the day. In this note I formalize this alternative optimality hypothesis and show analytically that it accounts for the existence and some aspects of the nature of the risk sensitivity reported by Caraco et al. (1980).

Caraco et al. (1980) offered yellow-eyed juncos (*Junco phaeotus*) a choice between two feeding stations. One station always provided a constant number of seeds, while the alternative station provided a variable number determined by a probability distribution. The number of seeds at the constant station was equal to the expected number provided at the variable station. Caraco et al. (1980) demonstrated that juncos preferred the constant station (or were risk-averse) when their expected daily energy intake exceeded their expected daily energy expenditure. More surprisingly, they also demonstrated that juncos preferred the variable station (or were risk-prone) when their expected daily energy expenditure exceeded their expected daily intake. Juncos show preferences which are consistent with a simple rule: be risk-averse if your expected 24-h energy budget is positive, be risk-prone if your expected 24-h energy budget is negative. This rule has been suggested, on intuitive grounds, by Caraco (1980). In this note I show that the expected energy budget rule follows directly from minimization of the probability of starvation.

Consider a small bird foraging in winter. Imagine that at least  $R$  units of food reserve are required to survive the night. Let  $S_0$  be the random variable that describes the bird's food reserve when it becomes too dark to forage. The probability of starvation is equivalent to  $P(S_0 < R)$ . (This assumes that starvation only occurs at night, which may not be true; however the results are not affected as long as food reserves are unlikely to become dangerously low during the day.) Assume that the day's foraging is divided into  $n$  intervals. At the beginning of the  $i$ th interval the forager makes some decision about how to forage and receives  $X_i$  units of food. The  $X_i$ 's are random variables and are assumed to be independently distributed with  $E(X_i) = \mu_i$  and  $\text{Var}(X_i) = \sigma_i^2$ . Assume that exactly  $r$  units of food are expended during each interval (this assumes that  $r$  is independent of the foraging decision, which cannot be strictly true). Let  $S_n$  be the bird's internal food supply when there are  $n$  decisions left before night-fall. We can express the reserves at the end of the day as

$$S_0 = S_n + \sum_{i=1}^n X_i - nr.$$

The probability of starvation is

$$P(S_0 < R) = P\left(\sum_{i=1}^n X_i < R - S_n + nr\right). \quad (2)$$

The central limit theorem for independent random variables states that for  $n$  sufficiently large, the random variable

$$Z = \frac{\sum_{i=1}^n X_i - \sum_{i=1}^n \mu_i}{\sqrt{\sum_{i=1}^n \sigma_i^2}}$$

has a normal distribution with a mean of zero and a variance of one. For convenience we define the following

variables: the mean expected value  $\bar{\mu} = \frac{1}{n} \sum_{i=1}^n \mu_i$ ,

the mean variance

$$\bar{\sigma}^2 = \frac{1}{n} \sum_{i=1}^n \sigma_i^2, \text{ and } \bar{\sigma} = \sqrt{\bar{\sigma}^2}.$$

Also let

$$t = \frac{1}{\bar{\sigma}} \left[ \frac{(R - S_n) + n(\bar{\mu} - r)}{\sqrt{n}} \right].$$

It follows from the central limit theorem and appropriate substitutions into equation (2) that

$P(\text{starving}) = P(S_0 < R) = P(Z < t) = \Phi(t)$ , (3) where  $\Phi(t)$  is the cumulative distribution function (cdf) of the standard normal distribution,  $N(0, 1)$ . By definition of the cdf of an absolutely continuous random variable,  $\Phi(t)$  increases in a strictly monotonic way with  $t$ . This means that as  $t$  increases, the probability of starvation increases. Therefore, we can restrict our attention to effects on  $t$ .

Consider the partial derivative of  $t$  with respect to  $\bar{\sigma}$ ,

$$\frac{\partial t}{\partial \bar{\sigma}} = \frac{1}{\bar{\sigma}^2} \left[ \frac{(S_n - R) + n(\bar{\mu} - r)}{\sqrt{n}} \right]. \quad (4)$$

The sign of  $\partial t / \partial \bar{\sigma}$  is the same as the sign of the term  $(S_n - R) + n(\bar{\mu} - r)$ .

Therefore

$$\partial t / \partial \bar{\sigma} > 0 \text{ where } \bar{\mu} - r > (R - S_n)/n, \quad (5a)$$

$$\partial t / \partial \bar{\sigma} < 0 \text{ where } \bar{\mu} - r < (R - S_n)/n. \quad (5b)$$

These are the asymptotic (large  $n$ ) conditions for risk sensitivity. Expression (5a) is the condition for risk aversion, because the probability of starvation increases with increasing variance. Expression (5b) is the condition for risk proneness, because the probability of starvation decreases with increasing variance. This is an analytical derivation of the 24-h expected energy budget rule of Caraco (1980). This result also shows the following. (a) Indifference to risk is unlikely, because it should only occur in the unlikely situation where expression (5) becomes an exact equality. (b) The direction of the change in the probability of starvation with increasing variance is independent of the magnitude of the variance. Figure 1

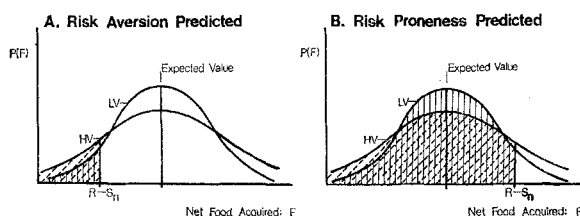


Fig. 1. The figure shows two normal probability distributions of the net amount of food acquired during the day. They have equal expected values but different variances. The area under the curves to the left of  $R - S_n$  is the probability of starvation, because  $R - S_n$  is the amount of food required to survive. The area marked with sloping dashed lines represents the probability of starvation if high variance (HV) is chosen; vertical solid lines are for the low variance (LV) choice. The rule derived in the text is simply the observation that: (Case A) when the expectation is greater than the requirement, the probability of starvation is smaller for low variance; and (Case B) when the expectation is less than the requirement, the probability of starvation is less for high variance.

presents a graphical argument which illustrates this derivation.

Expression (5) may be unnecessarily strict. If  $n$  is large,  $\lim (R - S_n)/n = 0$ , and these conditions become:

$$\begin{aligned} &\text{be risk-averse if } \bar{\mu} > r, \\ &\text{and be risk-prone if } r > \bar{\mu}. \end{aligned} \quad (6)$$

When many decisions are left to make, the forager may base its risk-sensitivity on a simpler rule of thumb. Expression (6) states that if environmental conditions are such that the forager's reserves are expected to increase, the forager should be risk-averse. If reserves are expected to decrease, the forager should be risk-prone.

The 24-h expected energy budget rule holds because the total energy acquired,  $T = \sum_{i=1}^n X_i$ , is normally distributed.  $T$  will probably be normal, because it will be the sum of many independent random variables and should approach normality according to the central limit theorem. If  $n$  is not large enough, or if  $T$  is non-normal for other reasons, the rule may not hold. In cases where the mean and variance are closely related, the 24-h expected energy budget rule will be too simplistic.

A forager's risk-sensitivity may also be influenced by the number of decisions left to make,  $n$ . Expression (5) suggests that a forager with only a few decisions left will become risk-prone at a higher reserve level than will a forager with many decisions left to make. Risk sensitivity should have a sequential component. This is a characteristic of many procedures in statistical decision theory (DeGroot 1970).

The results presented show that an hypothesis based on the minimization of the probability of starvation explains both risk-averse and risk-prone foraging preferences. It is not generally true that 'a risk-prone forager accepts a greater probability of starvation in attempting to acquire a greater net energetic intake' (Caraco 1980). The model shows that there are situations, i.e. (5b), where the forager may decrease its probability of starvation by risk-prone behaviour.

I am grateful to Tom Caraco for helpful discussions, stimulating manuscripts, and lunch. A. I. Houston, J. R. Krebs, R. C. Ydenberg and the referees provided needed criticism. E. L. Charnov pointed out the importance of mean/variance relationships. A manuscript by J. McNamara and A. I. Houston has helped shape my ideas.

D. W. STEPHENS

Edward Grey Institute,  
Department of Zoology,  
South Parks Road  
Oxford OX1 3PS.

## References

- Caraco, T. 1980. On foraging time allocation in a stochastic environment. *Ecology*, **61**, 119–128.
- Caraco, T., Martindale, S. & Whitham, T. S. 1980. An empirical demonstration of risk-sensitive foraging preferences. *Anim. Behav.*, **28**, 820–830.
- DeGroot, M. H. 1970. *Optimal Statistical Decisions*. New York: McGraw-Hill.
- Pyke, G. H., Pulliam, H. R. & Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.*, **52**, 137–154.

(Received 3 September 1980; revised 19 November 1980;  
MS. number: sc-82)

## Giving-Up as a Poisson Process: The Departure Decision of the Green Lacewing

Predators that forage for aggregated prey appear to require a decision rule for determining the point at which to discontinue their search in a given prey patch and move on to another. Although the optimum rule depends heavily on features of the searching behaviour of the predator and the distribution of the prey (Oaten 1977), most previous authors have assumed that the decision must involve an assessment of the capture rate within a patch and a comparison with the mean capture rate in the environment as a whole (Krebs 1978). When the perceived quality of the given patch becomes significantly less than the expected quality of the next one, the predator should leave. Because the time interval since the last prey capture is the most readily available measure of the instantaneous capture rate, it has been suggested that foraging animals may monitor this interval and leave the patch when it exceeds some critical value (Krebs 1978). The 'giving-up time', by this argument, should be uniform across patches within a habitat and inversely proportional, across habitats, to the mean prey availability. Although this inference has been supported by empirical studies, Cowie & Krebs (1979) have recently suggested that the correlation could be a sampling artifact. Even if departure from a patch were independent of the interval between prey encounters, the mean giving-up time would still be shorter, on the average, in a rich environment than in a poor one. A re-analysis of several experiments on patch foraging by predatory insects, described in detail elsewhere (Bond 1980), can be used to test Cowie & Krebs' independence hypothesis.

The predatory larva of the green lacewing, *Chrysopa carnea* Stephens, responds to an encounter with either a prey item or a branch terminus with a transient increase in searching intensity and thoroughness. Under the assumption that an animal's hunger level is its simplest accessible indicator of mean prey abundance, differences in prey availability were simulated by