THE USE OF INFORMATION BY RISK-SENSITIVE FORAGERS

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Caraco and Gillespie (1986) present a model which illustrates the ideas of risk-sensitive foraging behavior. A female orb-web spider can remain at one site for many days or may build its web in different sites each day. Caraco and Gillespie assume that the animal can choose one of two strategies: remain in one site until she reproduces, or choose a new site every day. Each of these strategies leads to the same expected number of prey caught during the foraging period, but staying in one site leads to a larger variance in the number of prey caught. The suggestion is that spiders that need more than the expected number of prey in order to survive and reproduce should be "risk-prone" and should remain in one site to increase the variance in the number of prey caught and thus maximize the chance of catching sufficient prey. Spiders that require fewer than the expected number of prey should be "risk-averse." They should reduce the variance in the number of prey caught and increase the probability of catching the required number of prey by moving from one site to another each day.

Using the same model as Caraco and Gillespie (1986), I consider a different strategy—one that takes account of a spider's success at a site. In my simple assessment strategy, a spider is assumed to leave a site if no prey are caught during the first day there. If one or more prey are caught at a particular site on the first day, then the spider remains at that site for the rest of its time until reproduction. This strategy is not optimal (it would be better, for example, to leave a site in which some, but very few, prey have been caught after some time), but it is probably simple enough for a spider to use, and it is generally better than both of the strategies considered by Caraco and Gillespie (1986). What I show is that Caraco and Gillespie's model permits the simultaneous treatment of the ideas of "risk" and "information."

Stephens and Charnov (1982) introduced the terms "risk" and "information" to refer to two different kinds of uncertainty that an animal might face. These words point to the same distinction as the economists' terms "risk" and "uncertainty." The distinction is illustrated by a gambler playing craps. He knows what his chances are if the dice are fair, but he does not know whether he will win or not. This is referred to as "risk." If the gambler is unsure whether or not the dice are fair, this may be referred to as "uncertainty." The gambler may be able to do something about "uncertainty," but he can do nothing about "risk," unless he decides to avoid it by refusing to play.

Krebs, Stephens and Sutherland (1983) divide stochastic foraging models into "information" models and "risk" models. This division is not very useful, however, because it is neither exclusive nor exhaustive. Typical information and risk models differ in several ways, including what goal the animal is assumed to have, whether information about prey distribution and patch quality can be used, and where uncertainty occurs in the environment. For any particular problem, a more general approach would be to consider a number of different foraging strategies, including ones that permit the use of information obtained while foraging, and a number of different goals that a forager might have, including the maximization of the long-term average rate of finding prey and the maximization of the probability of finding some critical number of prey.

Caraco and Gillespie's model

Caraco and Gillespie (1986) assume that their foragers have a choice of sites, at each of which prey are caught at random, according to a Poisson process with rate λ . The rate λ is constant within a site, but varies from site to site, having a gamma distribution. For convenience, I use parameters α and β for the gamma distribution (in place of θ and $1/\alpha$, respectively, in Caraco and Gillespie (1986), see DeGroot (1970)). The probability density of λ is

$$f(\lambda) = \frac{\beta^{\alpha}\lambda^{\alpha-1}e^{-\beta\lambda}}{\Gamma(\alpha)}. \tag{1}$$

The number of prey, x, found at a site in one day will have a negative binomial distribution with probability function

$$p(x|\alpha,\beta) = \binom{\alpha+x-1}{x}\left(\frac{\beta}{1+\beta}\right)^{\alpha}\left(\frac{1}{1+\beta}\right)^{x}. \tag{2}$$

Caraco and Gillespie (1986) consider two strategies an animal might use: a *mobile* strategy, in which a spider changes its web site every day, choosing its new site at random; and a *sit-and-wait* strategy, in which a spider remains in one randomly chosen site. The total numbers of prey caught by animals using these strategies will be random variables, denoted by Y_m and Y_s , respectively. It is assumed that the costs of these two strategies are equal.

I consider a simple *assessment* strategy: remain in each site for only one day until at least one prey is caught; then remain for the rest of time in the site where prey were caught. The total number of prey caught using this stategy is denoted by Y_a .

Caraco and Gillespie (1986) calculate the probabilities that foragers using their two strategies will catch no more than some critical number of prey, R, within n days, and thus be unable to survive and reproduce. They compare these probabilities of failing to survive and reproduce, $P\{Y_m \leq R\}$ and $P\{Y_s \leq R\}$, for various values of R. I will compare my simple assessment strategy with the mobile strategy and the sit-and-wait strategy by calculating $P\{Y_a \leq R\}$.

There are several mathematical advantages in assuming, as Caraco and Gillespie do, that prey are caught according to a Poisson process in which parameter λ is a random variable having a gamma distribution with parameters α and β.

a) In n days at a randomly chosen site the number of prey caught will have a negative binomial distribution with parameters α and β/n. This is the distribution of Y_s.

b) In n visits to randomly chosen sites the number of prey caught will have a negative binomial distribution with parameters $n\alpha$ and β. This is the distribution of Y_m.

c) If x prey are caught in the first day at a randomly chosen site, the number of prey found on the next day, or on any particular subsequent day, will have a negative binomial distribution with parameters $\alpha + x$ and $\beta + 1$. If a forager using my simple assessment strategy finds prey for the first time on the tth day, and the number of prey found is x, then the total number of prey found in the remaining $n - t$ days at that site will have a negative binomial distribution with parameters $\alpha + x$ and $(\beta + 1)/(n - t)$.

The distribution of Y_a can be found using the fact that the probability of finding no prey during one day in a randomly chosen patch is

$$q = p(0|\alpha, \beta) = \left[\frac{\beta}{1+\beta}\right]^{\alpha}. \tag{3}$$

Then we have

$$\begin{aligned} &P\{Y_a = 0\} = q^n, \\ &\text{and} \\ &P\{Y_a = k\} = q^{n-1}p(k|\alpha, \beta) \\ &\qquad + \sum_{i=1}^{n-1}\sum_{j=1}^{k} q^{i-1}p(j|\alpha, \beta)\, p\left[k - j|\alpha + j, \frac{\beta + 1}{n - i}\right], \qquad \text{for } k \geq 1 \end{aligned} \tag{4}$$

We can use (4) to calculate $P\{Y_a \leq R\}$ and compare the simple assessment strategy with the two strategies considered by Caraco and Gillespie, who compare their strategies for two sets of parameters. All three strategies are compared in Figures 1 and 2 for the two sets of parameters considered by Caraco and Gillespie. It is seen that except for very low values of R, that is, very low food requirements in order to survive and reproduce, the simple assessment strategy is better than both strategies considered by Caraco and Gillespie.

One way to understand the advantage of the assessment strategy is to compare the expected number of prey caught using this strategy with the expected numbers caught by animals using the other two rules. The expected numbers of prey caught by the two strategies considered by Caraco and Gillespie are the same. That is,

$$E[Y_m] = E[Y_s] = n\frac{\alpha}{\beta}. \tag{5}$$

An animal using my simple assessment rule might not catch any prey at all. However, if prey are caught, the first must be caught on some day. Let T indicate the day on which the first prey are caught. X_1 indicates the number of prey caught on the first day on which prey are caught, X_2 indicates the number of prey caught on any particular subsequent day, and Z indicates the total number of prey caught on the $n - T$ days remaining after the day on which the first prey are caught. The total number of prey caught is then $Y_a = X_1 + Z$. If prey are caught we have

$$E[X_1] = \frac{\alpha/\beta}{1-q}, \tag{6}$$

$$E[X_2|X_1] = \frac{\alpha + X_1}{\beta + 1}, \tag{7}$$

$$E[X_2] = E\{E[X_2|X_1]\} = \frac{\alpha + \frac{\alpha/\beta}{1-q}}{\beta + 1}, \tag{8}$$

and

$$E[T] = \frac{1}{1-q^n}\left\{1/(1-q) - q^n\left[n + \frac{1}{(1-q)}\right]\right\}. \tag{9}$$

The probability that some prey are found is $1 - q^n$, and we have

$$E[Y_a] = (1-q^n)\{E[X_1] + E[X_2]\,(n - E[T])\}. \tag{10}$$

Calculations show that for the parameters considered by Caraco and Gillespie, $E[Y_a] = 92$ in Case 1 ($\alpha = .1, \beta = .2, n = 40$), and $E[Y_a] = 28.16$ in Case 2 ($\alpha = 2, \beta = 10, n = 100$), while $E[Y_m] = E[Y_s] = 20$ in each case. Thus, the assessment strategy has a higher expected number of prey caught in both cases and has a substantially higher number in Case 1, in which variability in site quality is great.

Discussion

Models of risk-sensitive foraging usually assume that:

a) Different foraging strategies available to animals result in the same average number of prey being captured, but different variances.

b) Foragers cannot, or do not, use information obtained while foraging to increase the rate of finding prey, and

c) The goal of the forager is to obtain some fixed amount of food; there is no advantage in finding more food than this; and the cost of finding less is the same, no matter how much less.

Caraco and Gillespie (1986) make all these assumptions, but, using the same model, I propose a simple alternative foraging strategy that uses information about the environment to achieve a much higher rate of catching prey than the strategies considered by Caraco and Gillespie. This is important theoretically because it suggests that it may be difficult to think of natural situations in which the usual assumptions of risk-sensitive foraging apply. It is certainly important to check whether the assumptions made in a model hold true in the natural situation being modelled.

Caraco and Gillespie assume that they can safely ignore strategies that use information about differences in site quality, because temporal variability in foraging success effectively masks the spatial variability for animals, such as spiders, that catch few prey each day. This may be true in nature; however, as I show, in the model that they present, spatial variability is large enough, relative to temporal variability, to permit the profitable use of information. It is important that the intuitive interpretation of biological assumptions be checked against the mathematical consequences of the model in which they are embodied. It may be that, as my calculations suggest, the intuitive idea that temporal varibility masks spatial variability is incorrect. It is also possible that the natural relationship between temporal and spatial variability is not reflected in the model, and that more attention should be paid to the pattern of variability in nature.

Caraco and Gillespie (1986) suggest that the problem of discriminating among local rates of prey capture might be beyond the "cognitive ability" of a spider. The strategy which I suggest—to leave sites in which no prey are found—does not require much cognitive ability. If all the assumptions of their model hold—if there is no cost of movement, and if a spider could roughly double its chance of surviving and reproducing by using a simple assessment strategy—it is likely that the ability to use some simple strategy would have evolved. (Other simple strategies, for example—leave each site at which no prey is caught after one day; leave any site at which no prey has been caught for two days—may be better than the one I suggest. The effectiveness of such strategies is difficult to determine, but a rough assessment could be done quite easily using Monte Carlo simulation.)

Caraco and Gillespie (1986) make a number of biologically questionable assumptions. They first assume that changing sites costs a spider nothing. Then they relax this assumption and interpret this change in assumptions in terms of risk-sensitive foraging. It is possible that there is a cost of movement, and that this cost is greatest relative to available energy when few prey are available. If few prey are available overall, spiders might stand to increase the number of prey caught by moving, but the gain might be small compared to the cost of moving. If this is true, spiders that are catching few prey might be reluctant to move, not because they are "risk-prone," but because the cost of moving is relatively large. When many prey are available there would be little advantage in changing sites if, as Caraco and Gillespie assume, a spider's only goal is to catch some relatively small critical number of prey. On the other hand, if spiders profit by catching more than some fixed number of prey, perhaps by increasing their reproductive output, then it might pay to move among sites and use information available about site quality to increase the expected number of prey caught.

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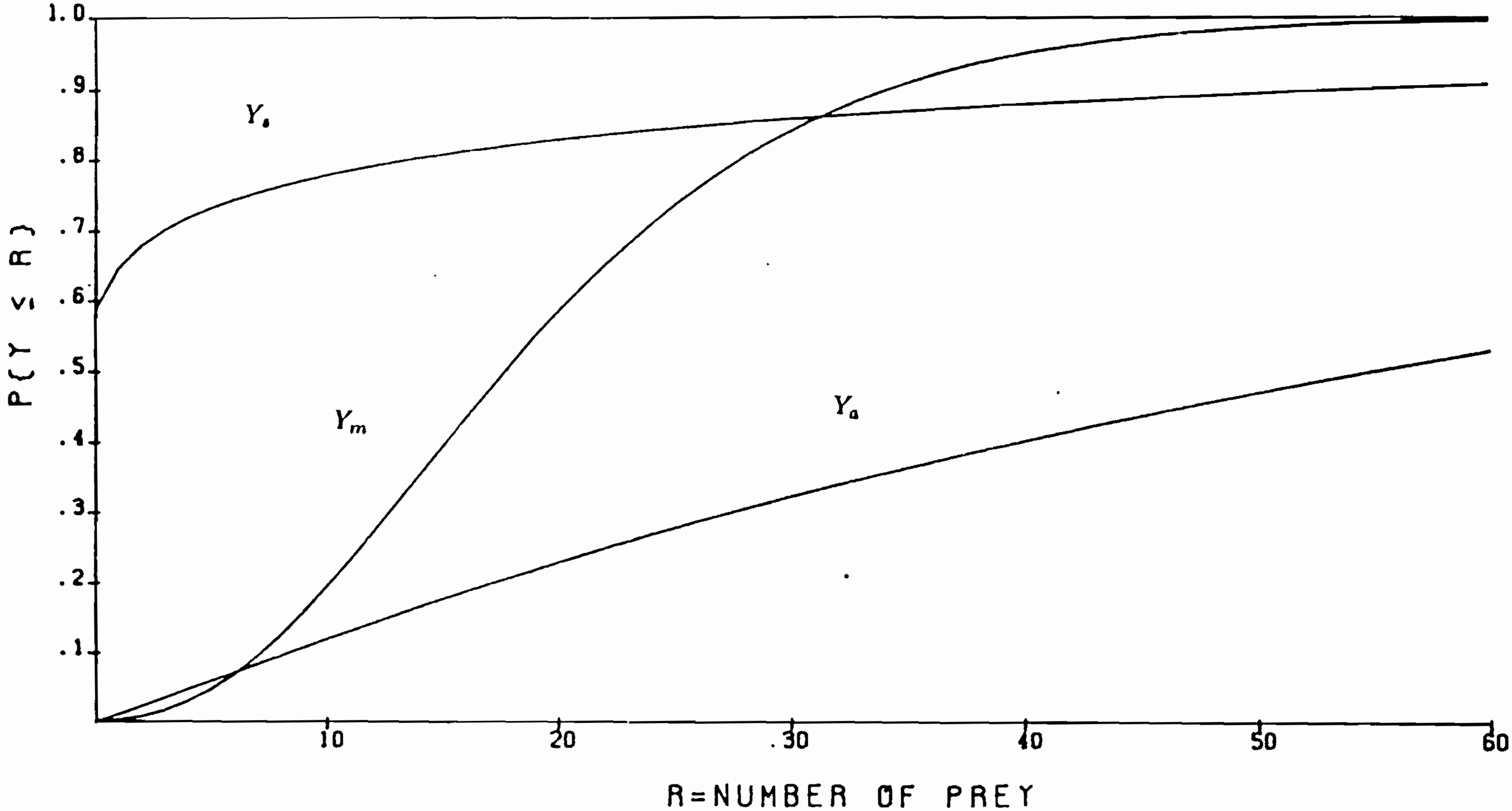

FIG. 1. Probability of a shortfall in the number of prey caught, $P\{Y \leq R\}$, where Y_s, Y_m, and Y_a are the numbers of prey caught by animals using the sit-and-wait, the mobile, and the assessment strategies, respectively. The animal is unable to survive and reproduce if no more than R prey are found during an n-day foraging period. Lower values of $P\{Y \leq R\}$ indicate a better strategy. Notice that the assessment strategy is substantially better than the other strategies, except for very low food requirements. The parameters for Case 1 are $\alpha = 0.1$, $\beta = 0.2$, and $n = 40$. The parameters of site quality (α and β) indicate substantial spatial varability in patch quality.

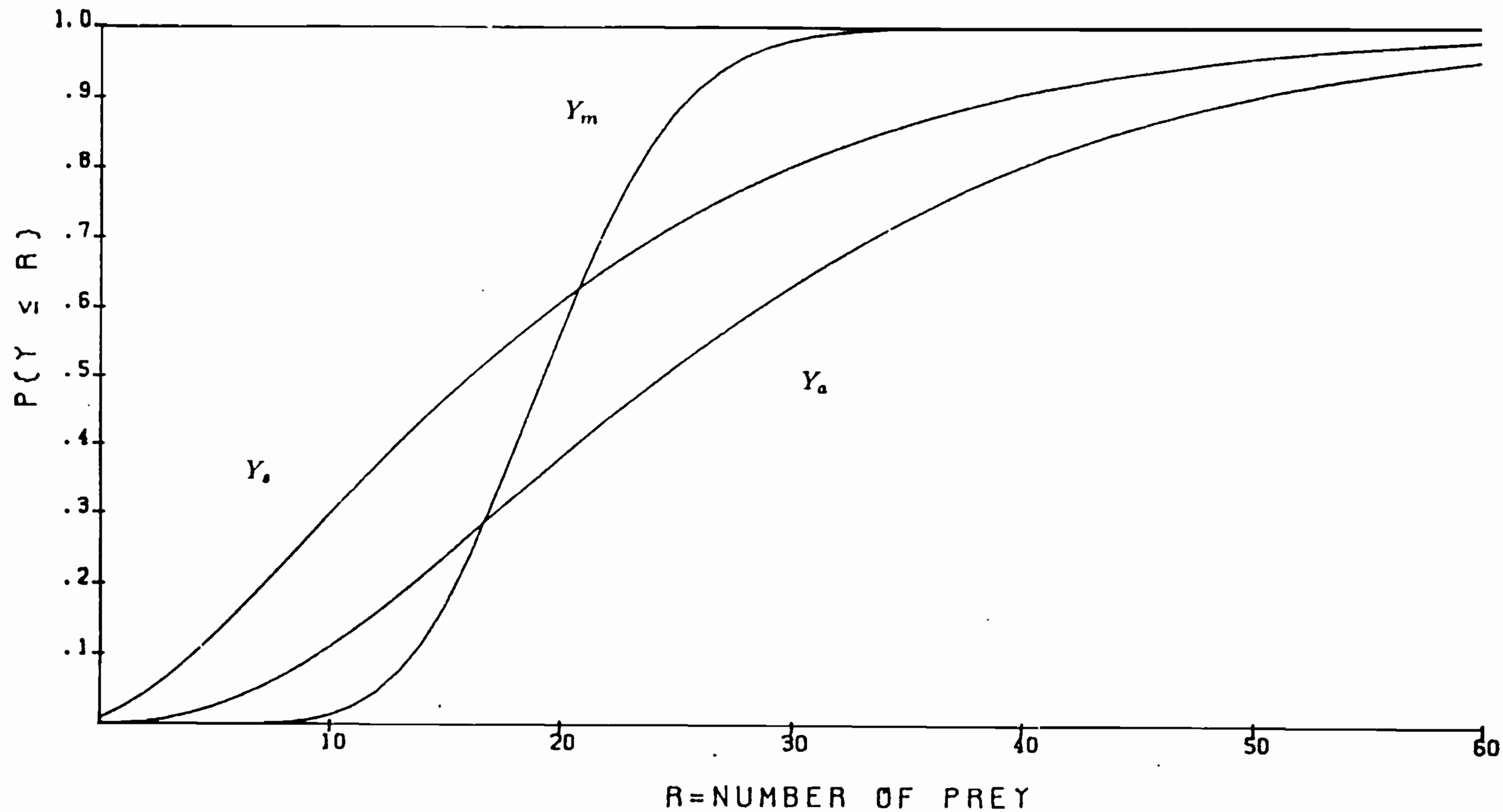

FIG. 2. Probability of a shortfall, $P\{Y \leq R\}$, plotted against prey requirement, R. In Case 2 the parameters are $\alpha = 2$, $\beta = 10$, and $n = 100$. There is much less spatial variability in Case 2 than in Case 1. My Figs. 1 and 2 are the same as Figs. 1 and 2 in Caraco and Gillespie (1986), except that I have also included the assessment strategy.