

Optimal Diet Selection with Variable Nutrient Intake: Balancing Reproduction with Risk of Starvation

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We develop a model to predict optimal diet selection when energy intake varies over consecutive foraging periods. The model assumes that fitness is maximized when the forager maximizes its net reproduction (survivorship \times reproduction) over some specified time period. This goal differs from earlier risk-sensitive foraging models which assume that the forager minimizes the risk of failing to satisfy minimum requirements for survivorship or reproduction. In our model, the net number of offspring produced per reproductive bout is expressed as an explicit function of fitness gained from reproduction and fitness lost due to starvation risk for different potential diets. Potential model solutions are explored graphically and are compared with solutions for previous foraging models. In general, the model predicts that foragers with a goal of maximizing net reproduction should accept greater risks of starvation than foragers with a goal of minimizing the risk of failing to satisfy minimum energy requirements. © 1991 Academic Press, Inc.

INTRODUCTION

Optimal foraging theory (Schoener 1971, Stephens and Krebs 1986) is based on the premise that a forager's nutrient intake is related to its fitness (survival and reproduction). Traditional foraging models, which predict the range of food types a forager should include in its diet (i.e., "contingency" (Schoener, 1974) or "classical" (Krebs *et al.*, 1983) models), are based on the assumption that fitness increases simply with the forager's mean net energy intake, although other currencies are possible (Pyke *et al.*, 1977; Pyke, 1984).

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Several recent studies (Oaten, 1977; Caraco, 1980; Stephens and Charnov, 1982; Houston and McNamara, 1985), however, have argued that food characteristics of real foraging environments exhibit random variation. Foragers selecting diets in such environments will accordingly have variable energy intakes.

If animals select diets to maximize only the mean energy intake in any foraging period, and the variation in energy intake over several time periods is large, there is a probability that the forager will fail to satisfy its energy requirements in a given foraging period (Caraco, 1980; Stephens and Charnov, 1982). Consequently, variability may lead to a risk of starvation; a forager will not necessarily maximize its fitness by selecting a diet which maximizes its mean energy intake. Both mean and variance in energy intake become important determinants of fitness.

A body of theory (Caraco, 1980; Real, 1981; Stephens, 1981; Stephens and Charnov, 1982; Houston and McNamara, 1985) conventionally known as "risk-sensitive" foraging (Stephens, 1981; Regelman, 1984; Weissburg, 1986; Real and Caraco, 1986; Stephens and Krebs, 1986) has been developed recently to predict how a forager should select its diet when energy intake varies. Each of these models is basically a special case of a general expected fitness model (Real and Caraco, 1986; Ellner and Real, 1989) where it is assumed that expected fitness is maximized if the forager minimizes its risk of starvation (Caraco, 1980; Real, 1981; Stephens, 1981; Stephens and Charnov, 1982; Houston and McNamara, 1985) or minimizes its chance of failing to satisfy some threshold requirement for reproduction (Caraco and Gillespie, 1986; Gillespie and Caraco, 1987).

While a goal of minimizing risk of failure may be appropriate under certain conditions or for a period of time (e.g., small birds in winter), it is not necessarily the goal during all stages of a forager's life history. For instance, it may be more important to gain as much energy as possible for growth, reproduction, or periods of energy shortage (McNamara and Houston, 1982, 1986; Rubenstein, 1982; Stephens and Charnov, 1982; Mangel and Clark, 1986). Consequently, minimizing risk may not always be appropriate since natural selection should favor individuals with the greatest net lifetime reproduction.

Foragers with a goal of maximizing net reproduction may be faced with conflicting demands. For example, diets which provide the greatest mean nutrient intake may also have high associated variances and correspondingly high starvation risks (Houston and McNamara, 1985). Thus foragers may have to select diets that balance a trade-off between maximizing mean energy intake (to maximize offspring production) and minimizing starvation risk.

Although the variance discounting model of risk-sensitive foraging (Real and Caraco, 1986; Ellner and Real, 1989) also can be used to examine

effects of variation on reproduction (Powell, 1989), it cannot be used to examine a potential trade-off because both reproduction and survival components must be subsumed in a single fitness function. To examine the potential trade-off, we construct a model in which the risk of starvation and potential offspring production associated with different diets are expressed as explicit functions that contribute to the forager's fitness. The model assumes that a forager's goal is to maximize its net reproduction over time.

THE MODEL

Consistent with the classical foraging model, we assume the forager includes food items in its diet on the basis of food profitability, measured as energy per unit handling time, regardless of the prey species (types). We assume food items are continuously distributed in the environment and that this distribution remains constant during the period foraging behavior is examined. We further assume the forager randomly encounters food items (i.e., food items are randomly or uniformly distributed in the environment).

Let m be the rank of the lowest profitability category the forager includes in its diet such that food items are accepted if their profitability is greater than or equal to m . In other words, m defines the forager's "diet breadth."

We assume the forager feeds for a fixed amount of time T within some time period T_f (e.g., time feeding per day) and there are k such time periods such that $[T_1, T_k]$ represents the interval over which variation in energy intake, reproduction, and survival will be considered. If food items are ranked from highest (h) to lowest profitability, then the forager's energy intake per period T_f for a given diet breadth $\varepsilon(m)$ is (Schoener, 1974)

$$\varepsilon(m) = \frac{\int_{i=h}^m e(i) n(i)/n di}{T_s + \int_{i=h}^m t(i) n(i)/n di} \quad (1)$$

where $e(i)$ (energy/item) is the energy content for food category i , $n(i)$ is the number of food items from category i that were encountered and consumed during T , T_s (time/item) is the search time for all food items in the diet, and $t(i)$ is the handling time (time/item) for items from category i . T_s and $t(i)$ are expressed in the same time units as T . Search costs are ignored. The total number of food items n eaten in T is assumed to be constant. This is done for mathematical simplicity but the general conclusions will not change if n is variable.

Each $n(i)$ will vary among the k time periods and will depend on (1) the

number of items from each food category encountered, (2) the relative frequency of profitability i in the environment, and (3) m , the diet breadth. The value $n(i)$ will vary because of the assumption that food items are randomly encountered (distributed) in an environment. This implies that over the interval $[T_1, T_k]$, the energy intake for a given diet breadth becomes a random variable with expected value $E[\varepsilon(m)]$ and variance $V[\varepsilon(m)]$.

The magnitude of $E[\varepsilon(m)]$ and $V[\varepsilon(m)]$ will, in turn, determine the forager's level of offspring production. We assume offspring production is an increasing function of energy intake, $f\{\varepsilon(m)\}$ (Schaffer and Rosenzweig, 1977; Rubenstein, 1982; Ellner and Real, 1989). If there is variation in $\varepsilon(m)$, then this results in variation in accrued offspring production in each time period. To account for this variation, offspring production is expressed as the expectation of the function describing offspring production in relation to energy intake, $E[f\{\varepsilon(m)\}]$ (Rubenstein, 1982; Powell, 1989). This expected value will vary with the distribution of $\varepsilon(m)$ (i.e., whether it is normal or skewed) and the shape of the offspring production function (see later).

In addition to influencing offspring production, $E[\varepsilon(m)]$ and $V[\varepsilon(m)]$ also influence the forager's potential risk of starvation (Caraco, 1980; Real, 1981; Stephens and Charnov, 1982). This risk can be estimated as the probability of failing to meet the maintenance energy requirement R within time T , where R is defined over time T_f . The risk of starvation for a given diet breadth ($D(m)$) is estimated as

$$D(m) = 1 - \left[\int_R^H q(\varepsilon(m), j) dj \right], \quad (2)$$

where q is the probability density function for the distribution of energy intakes for a diet breadth and H is the highest energy intake for the diet breadth.

The expected offspring production and starvation risk can now be combined to estimate fitness $W(m)$ for different potential diet breadths. Let $S(m) = 1 - D(m)$, the probability of survival. Fitness at the end of the interval $[T_1, T_k]$ is then determined by

$$W(m) = E[f\{\varepsilon(m)\}] S(m). \quad (3)$$

The diet breadth that maximizes fitness is provided by \hat{m} such that $dW/dm = 0$. This gives the condition for the optimum

$$\frac{E[df\{\varepsilon(m)\}/dm]}{E[f\{\varepsilon(m)\}]} = \frac{-dS(m)/dm}{S(m)}, \quad (4)$$

where

$$\begin{aligned}
 E[df\{\varepsilon(m)\}/dm] &= \int_L^H f\{\varepsilon(m, j)\} \frac{dq}{dm}(\varepsilon(m, j)) dj \\
 &\quad + \frac{df}{dm}\{\varepsilon(m, j)\} q(\varepsilon(m, j)) dj, \\
 E[f\{\varepsilon(m)\}] &= \int_L^H f\{\varepsilon(m, j)\} q(\varepsilon(m, j)) dj
 \end{aligned}$$

and L is the lowest $\varepsilon(m)$ value for a diet breadth.

Equation (4) is the standard form when fitness is a product of two variables (Charnov, 1982). The optimal diet breadth occurs when any further change in diet breadth results in decreased fitness through either lower expected reproduction or increased mortality.

MODEL SOLUTIONS

The solution to this model depends on the probability density function of ranked item profitabilities in the environment and the shape of the offspring production function. A general explicit solution is not possible without specification of these functions. However, the qualitative behavior of the model can be understood if $V[\varepsilon(m)]$ changes predictably with increasing m for all profitability distributions.

Equation (1) shows that variation in $\varepsilon(m)$ is proportional to variation in the number of items of each profitability ranking ($n(i)$) eaten in a foraging period. Therefore, to determine how $V[\varepsilon(m)]$ changes with increasing diet breadth, we need only determine how the variance of the sampling distribution of food items included in the diet changes with increasing m . Appendix 1 shows that the variance will increase when incrementing from $m-1$ to m categories if

$$(m^2 - 2m) \int_{i=1}^m g(i) di > \int_{i=1}^m i^2 g(i) di - \left[\int_{i=1}^m ig(i) \right]^2 di, \quad (5)$$

where $g(i)$ is the probability density function for the distribution of all i profitability rankings.

This condition is not satisfied when $m \leq 2$ (i.e., when the diet contains the highest or the highest and second highest profitabilities). However, for $m > 2$, we explored when $V[\varepsilon(m)]$ can be expected to increase with diet breadth. We examined distributions that were skewed right, normal, and

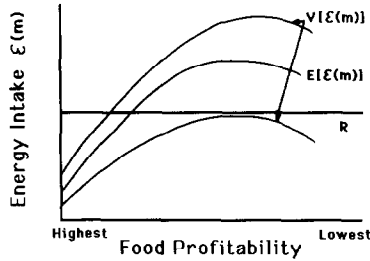


FIG. 1. Mean $E[\varepsilon(m)]$ and variance $V[\varepsilon(m)]$ in energy intake as a function of the range of food profitabilities included in the diet (diet breadth). Here the diet breadth contains food profitabilities at a given point on the x -axis and left of that point (higher profitabilities). Horizontal line R is the energy requirement for survival.

highly skewed left. These reflect distributions likely to be encountered under natural conditions (Schoener and Janzen, 1968; Werner, 1977; Belovsky, 1981; Richardson and Verbeek, 1986; Dickman, 1988). The condition was satisfied for all increments in all distributions, including the case when 99% of the distribution was assigned to the last category. Therefore, $V[\varepsilon(m)]$ should increase with increasing diet breadth when $m > 2$ (Fig. 1) for most naturally occurring distributions.

1. Influence of Variation on Offspring Production

We begin examining the influence of variation in energy intake on the qualitative behavior of the model by considering three shapes of offspring production functions $f\{\varepsilon(m)\}$: linear, concave upward, and concave downward (Fig. 2). Biologically, linear functions occur if energy is converted to offspring production at a constant rate (Schaffer and Rosenzweig, 1977). Concave upward functions occur if foragers must make some initial investment before offspring production is realized (Schaffer and Rosenzweig, 1977). Finally, concave downward functions occur when there are upper constraints on offspring production (Schaffer and Rosenzweig, 1977).

For the following analysis we assume $\varepsilon(m)$ is normally distributed and $m \geq 3$ (we address the case for $m \leq 2$ in the Discussion). Stephens and Charnov (1982) demonstrate that according to the central limit theorem the distribution of $\varepsilon(m)$ will tend to be normal when the number of foraging periods is large ($k \rightarrow \infty$). Therefore, for any diet breadth m , $V[\varepsilon(m)]$ will be symmetrical about $E[\varepsilon(m)]$ for any range of $\varepsilon(m)$ values. This range defines the potential range of offspring production values resulting from variation in energy intake. The range of offspring production values, in turn, determines the forager's expected offspring production $E[f\{\varepsilon(m)\}]$ for a given diet breadth.

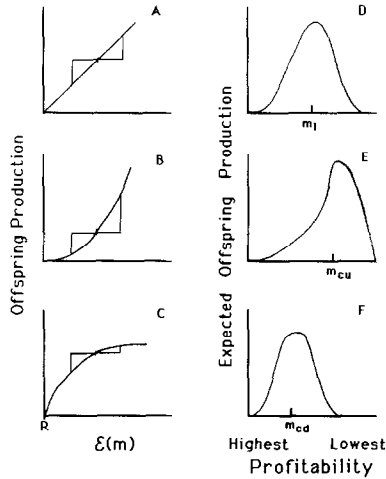


FIG. 2. Offspring production as a function of energy intake $\varepsilon(m)$ (Figs. 2A–2C) and expected offspring production as a function of the range of food profitabilities in the diet (diet breadth) (Figs. 2D–2F). Offspring production is presented for linear (Fig. 2A), concave upward (Fig. 2B), and concave downward functions (Fig. 2C). Horizontal lines in each curve represent the range of possible energy intakes for a diet breadth, defined by the variance $V[\varepsilon(m)]$. Figs. 2A, 2B, and 2C show relative loss and gain in offspring production for the same mean and variance in energy intake. The diet breadth that maximizes expected offspring production for the linear function m_l will be intermediate between diet breadths maximizing expected offspring production for a concave upward, m_{cu} , and a concave downward function m_{cd} (Figs. 2D, 2E, and 2F).

If $f\{\varepsilon(m)\}$ is linear, then offspring production varies symmetrically about $f\{E[\varepsilon(m)]\}$. Thus, $E[f\{\varepsilon(m)\}] = f\{E[\varepsilon(m)]\}$ (Fig. 2A). If the offspring production function is concave upward, then a given deviation in energy intake above $E[\varepsilon(m)]$ increases production more than the same deviation below the mean will decrease it (Fig. 2B). Consequently, $E[f\{\varepsilon(m)\}] > f\{E[\varepsilon(m)]\}$. If the production function is concave downward, then the opposite is true. Thus $E[f\{\varepsilon(m)\}] < f\{E[\varepsilon(m)]\}$ (Fig. 2C).

As diet breadth increases (i.e., m increases), $E[\varepsilon(m)]$ and $V[\varepsilon(m)]$ will change predictably because prey are ranked from highest to lowest profitability and because $V[\varepsilon(m)]$ increases with m . This predictability allows us to compare how $E[f\{\varepsilon(m)\}]$ changes with diet breadth for different shapes of production functions.

When f is linear, expected offspring production will be maximized when expected energy intake is maximized (i.e., when the forager selects the optimal diet predicted by the classical model) (McNamara and Houston, 1982; Pyke, 1984; Ellner and Real, 1989).

To examine effect of nonlinear functions on diet breadth let μ and σ^2 represent $E[\varepsilon(m)]$ and $V[\varepsilon(m)]$, respectively. Because $\varepsilon(m)$ is assumed to be normally distributed, the effect of mean and variance can be approximated using a Taylor expansion in the deviations from the expected energy intake which, after expected value operators are applied, gives the variance discounting formula (Real and Caraco, 1986; Powell, 1989; Ellner and Real, 1989)

$$E[f\{\varepsilon(m)\}] = f(\mu) + \frac{1}{2}f''(\mu)\sigma^2,$$

where $f'' = d^2f(\mu)/d\mu^2$.

Let μ_1 and σ_1^2 be the mean and variance in energy intake for the classical optimal diet breadth and μ_2 and σ_2^2 be the mean and variance for an alternative diet breadth. The alternative diet breadth will give higher expected offspring production if

$$f(\mu_2) + \frac{1}{2}f''(\mu_2)\sigma_2^2 > f(\mu_1) + \frac{1}{2}f''(\mu_1)\sigma_1^2.$$

When f is concave upward, $f''(\mu) > 0$ and

$$f(\mu_2) - f(\mu_1) > \frac{1}{2}[f''(\mu_1)\sigma_1^2 - f''(\mu_2)\sigma_2^2]. \quad (6)$$

However, $\mu_1 > \mu_2$, by definition. Thus $f(\mu_2) - f(\mu_1) < 0$ and $f''(\mu_1) > f''(\mu_2)$ (whenever $f''(\mu)$ is nonconstant). Condition (6) will not be satisfied when $\sigma_1^2 > \sigma_2^2$ (i.e., when diet breadth is narrower than the classical diet breadth). Therefore, when f is concave up, a forager will never maximize expected offspring production with a diet breadth narrower than the classical diet breadth.

When f is concave downward, $f'' < 0$ and

$$f(\mu_2) - f(\mu_1) > \frac{1}{2}[f''(\mu_2)\sigma_2^2 - f''(\mu_1)\sigma_1^2]. \quad (7)$$

Because $|f''(\mu_2)| > |f''(\mu_1)|$, condition (7) will never be satisfied when $\sigma_2^2 > \sigma_1^2$. Thus, a forager will never maximize expected offspring production with a broader diet breadth than the classical optimal diet breadth.

These results are presented graphically in Figs. 2D–F.

2. Influence of Variation on Starvation Risk

When $\varepsilon(m)$ is normally distributed, Eq. (2) will be equivalent to (Stephens and Charnov, 1982; Ellner and Real, 1989)

$$\Phi[z(m)] = \Phi\left[\frac{R - \mu}{\sigma}\right],$$

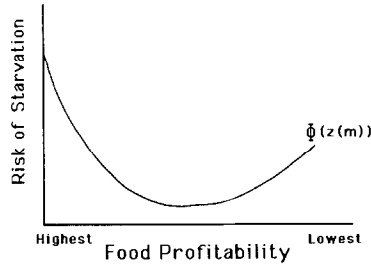


FIG. 3. Starvation risk as a function of the range of food profitabilities in the diet (diet breadth).

where $\Phi[]$ is the cumulative standard normal distribution function. Since Φ is an increasing function, the diet breadth minimizing starvation risk is the one which gives the smallest value of $(R - \mu)/\sigma$ (Stephens and Charnov, 1982; Ellner and Real, 1989).

When $\mu_1 > \mu_2 > R$, $(R - \mu_1)/\sigma_1$ will always be smaller than $(R - \mu_2)/\sigma_2$ when $\sigma_2 > \sigma_1$. Therefore, a forager with a positive energy budget (i.e., expected energy intake exceeds requirements) should never select a diet breadth broader than the classical diet breadth to minimize starvation risk. Whether or not it should select a narrower diet breadth will depend on the magnitude of the μ 's and σ 's (see also Stephens and Charnov, 1982).

When $R > \mu_1 > \mu_2$, $(R - \mu_1)/\sigma_1$ will always be smaller than $(R - \mu_2)/\sigma_2$ when $\sigma_1 > \sigma_2$. Consequently, a diet breadth narrower than the classical diet breadth can never minimize starvation risk when the forager has a negative energy budget. Again, whether a broader diet breadth minimizes risk will depend on the magnitude of μ 's and σ 's (Stephens and Charnov, 1982).

Qualitatively, starvation risk will decrease to some minimum and then increase with increasing diet breadth (Fig. 3) because the mean energy intake increases to some maximum and decreases with increasing diet breadth whereas the variance continually increases (Fig. 1).

3. Qualitative Outcomes

Functions for expected offspring production and starvation risk in relation to diet breadth can be substituted into Eq. (4) to determine the optimal diet. The explicit solution will depend on the exact parameter values that determine the various functions. The model solutions, however, can be examined graphically. Solutions in Fig. 4 are presented for a linear offspring production function.

The diet that maximizes expected offspring production is defined when $(E[df\{\varepsilon(m)\}/dm])/E[f\{\varepsilon(m)\}] = 0$ (Fig. 4). When $f\{\varepsilon(m)\}$ is linear, this

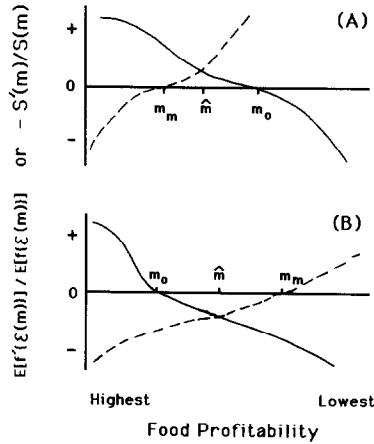


FIG. 4. Graphical solutions to the optimization model for a linear offspring production function. Solid lines represent $E[f'\{\varepsilon(m)\}]/E[f\{\varepsilon(m)\}]$ and dashed lines represent $-S'(m)/S(m)$, where f' and S' are df/dm and dS/dm , respectively. Diets balancing expected offspring production with risk of starvation occur at \hat{m} . Diet breadths maximizing mean energy intake, m_o , (i.e., classical model optimum diet breadth) and minimizing starvation risk, m_m , are present for comparison. Solutions are presented for positive (A) and negative (B) expected energy budgets.

will be the diet predicted by the classical foraging model (i.e., the diet that maximizes mean energy intake). The diet that minimizes the risk of starvation (risk-sensitive diet) occurs when $(-dS(m)/dm)/S(m) = 0$ (Fig. 4).

In the first example, we present the case when the forager can expect a positive energy budget but there will be a risk of starvation associated with the diet that maximizes mean energy intake (Fig. 4A). Relative to simply maximizing expected offspring production, the optimal strategy is to select a more narrow diet breadth and accept a lower expected offspring production to decrease the risk of starvation. However, the forager must accept a nonminimal risk of starvation to maximize fitness.

We also show the solution when a forager incurs a negative energy budget (i.e., expected energy intake is less than average energy requirements) (Fig. 4B). In this case, variation in energy intake may contribute to offspring production because the shape of the expected offspring production function $E[f\{\varepsilon(m)\}]$ will remain the same. However, the forager will incur greater risks of starvation for different potential diet breadths causing the function $(-dS(m)/dm)/S(m)$ to shift to the right. Here, the optimal strategy is to select a diet broader than the contingency diet to maximize fitness. However, the forager should still select a diet with greater than minimal starvation risk.

There is also the trivial special case where the risk of starvation is minimized and expected offspring production is maximized by the same diet.

DISCUSSION

Most previous studies of risk-sensitive foraging have focused on predicting behavior when foragers must choose among prey or patches with the same mean rewards but different variances and when starvation risk is the only component of fitness (Real and Caraco, 1986). In this case, there are two optimal strategies: risk prone and risk averse (Real and Caraco, 1986).

A risk prone forager should select the more variable reward while a risk averse forager should select the less variable reward over the variable one (Caraco, 1980). Risk prone behavior is optimal when the forager has a negative energy budget, on average. By selecting a more variable reward, a risk prone forager maximizes its probability of obtaining sufficient energy intake to meet requirements. Risk averse behavior is optimal when the forager has a positive energy budget, on average, but the risk of starvation with the variable rewards is nonzero. A risk averse forager selects a less variable reward to reduce the risk of obtaining a reward that falls below requirements.

When foragers must choose among prey or patches with differing means and variances these simple predictions break down. The optimal strategy depends on the magnitude of means and variances (Stephens and Charnov, 1982; Houston and McNamara, 1985).

In this paper, we examine diet selection when the forager must choose among combinations of $E[\epsilon(m)]$ and $V[\epsilon(m)]$ represented by different potential diet breadths. Consequently, there is a different level of risk associated with each potential diet breadth. We assume the forager identifies prey items simply on the basis of their individual profitability values and the forager accepts items of profitability rank m or better whenever they are encountered.

Previous risk-sensitive models (e.g., Stephens and Charnov, 1982; Houston and McNamara, 1985) assume that foragers select prey on the basis of mean and variance in profitability for each prey type (species). Energy gain for a diet (i.e., prey type 1, 2 or both) is estimated using both the means and variances of each prey type and the encounter with each prey type. Our approach reduces this level of complexity by subsuming the variability in profitability, for each prey type, into a single distribution. Energy gain for a diet then depends only on encounter with different profitability prey items.

In our model the condition provided by Eq. (5) suggests that including lower profitability items in the diet increases variance in energy intake

except when the diet contains fewer than 3 different profitabilities (i.e., $m < 3$). When $m \leq 2$, the general predictions of our model do not hold because the variance could increase or decrease with diet breadth. Houston and McNamara (1985) arrive at the same result in their examination of diet selection for two different prey types.

Applying the concepts of risk prone vs. risk averse strategies to the foraging situation presented here, a risk averse forager should select a more narrow diet breadth than the one which maximizes mean energy intake (classical optimal diet, Fig. 4). A risk prone forager should select a broader diet than the contingency diet. However, such a simple "rule of thumb" does not yield unique predictions.

First, when the forager has a positive energy budget and is reproductive the optimal diet breadth may also be more narrow than the classical optimal diet breadth but it usually will be intermediate between the classical diet and one which minimizes starvation risk. The exact optimal diet will depend on the degree to which reproductive output changes relative to the risk of starvation. This will depend not only on the mean and variance in energy intake relative to requirements but also on the shape of the offspring production function in relation to energy intake.

We also obtain opposite predictions than provided by the "rule of thumb" when considering the effect of variation in energy intake on both reproduction and starvation risk. For example, if a forager has a positive expected energy budget, starvation risk, and a concave upward offspring production function, its fitness maximizing diet may be broader than the diet predicted by the classical optimal foraging model. This shows that we cannot use observations of shifts in diet breadth or support for "rules of thumb" as evidence that foragers are behaving in accordance with an optimal diet selection model.

In our model, the objective function (Eq. (3)) is the static analog of McNamara and Houston's (1986, e.g., Eq. (10)) dynamic optimization model. When foraging behavior is considered over several intervals, the foraging decisions may involve sequences of choices which depend on the forager's energy budget in previous time intervals. In this case, a dynamic optimization approach may be most appropriate.

However, Ellner and Real (1989) have shown that if net energy intake for a foraging strategy (analogous to diet breadth) is independent of strategies and energy budgets in previous time periods, the dynamic approach becomes equivalent to a sequence of static expected fitness maximizations. Our model provides a means of determining the static optimal diet within an interval. We predict the *average* diet selection strategy for average conditions during the time interval $[T_1, T_k]$ given the expected fitness for different potential diet breadths at the end of this time interval (i.e., short-term fitness *sensu* McNamara and Houston, 1982).

Overall, foragers which are reproductive should always select diets with some intermediate risk of starvation, so risk averse and risk prone strategies represent endpoints of a continuum of possible optimal diets. Consequently, the description of foraging behavior using these two alternatives becomes relative. For example, with a positive energy budget, a forager will be risk averse relative to a forager maximizing its expected offspring production but it will be risk prone relative to a forager minimizing its starvation risk. Consequently, the terms risk prone and risk averse only provide limited information about the exact optimal diet. Instead, the optimal diet might be better described as that which balances relative gains in reproduction with relative losses in survivorship.

APPENDIX 1

For any random variable x with probability density g , we can define the variance of x ($V[x]$) as

$$V[x] = E[x^2] - E[x]^2, \quad (\text{A1})$$

where $E[\]$ is an expected value. For any finite range $[A, B]$ within the domain of x , let

$$E[x] = \int_A^B xg(x) dx \quad (\text{A2})$$

and

$$E[x^2] = \int_A^B x^2g(x) dx, \quad (\text{A3})$$

where A remains constant and B increases. Then substituting Eqs. (A2) and (A3) into (A1) we obtain

$$V[x] = \int_A^B x^2g(x) dx - \left[\int_A^B xg(x) dx \right]^2. \quad (\text{A4})$$

However, when sampling from a finite portion of a distribution, the variance must be standardized by the factor $1/(\int_A^B g(x) dx)$. Thus, the variance for the portion being sampled becomes

$$V(x) = \frac{\int_A^B x^2g(x) dx - \left[\int_A^B xg(x) dx \right]^2}{\int_A^B g(x) dx}. \quad (\text{A5})$$

The variance will increase as the range $B - A$ increases when $dV(x)/dx > 0$. Upon obtaining $dV(x)/dx$ and ignoring the denominator, since it will always be positive, we obtain the condition when the variance increases as

$$(B^2 - 2B) \int_A^B g(x) dx > \int_A^B x^2 g(x) dx - \left[\int_A^B xg(x) dx \right]^2. \quad (\text{A6})$$

Equation (A6) states that the variance will increase with increasing range of the sampling distribution if the product of the proportion of the distribution being sampled and a function of the number of classes being sampled is greater than the variance of the sampling distribution.

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