

## **Vigilance and Diet Selection: The Classical Diet Model Reconsidered**

STEVEN L. LIMA†

*Department of Biological Sciences, Simon Fraser University, Burnaby, B.C.,  
Canada V5A 1S6*

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A simple diet model is developed that explicitly considers an animal's need to be vigilant for predators while foraging. The currency of fitness is survival over some time period rather than energy intake rate *per se*. The model considers vigilance both while searching for and consuming prey items. When vigilance and prey consumption are mutually exclusive activities (i.e., vigilance interrupts consumption), the "classical" diet model yields the diet maximizing survival, even though the forager is by no means an energy maximizer. However, the classical diet model will fail if, for any available prey types, vigilance and prey consumption can be accomplished simultaneously. Since several animals are vigilant while consuming prey items, the classical model may have been improperly applied in some of its empirical tests.

### **Introduction**

Most foraging animals may themselves become prey for others. Perhaps unsurprisingly, there is a growing body of literature demonstrating that decision-making in feeding animals is not only strongly dependent upon the risk of predation, but represents an adaptive trade-off between the needs to avoid predation and obtain adequate food (Milinski, 1986; Dill, 1987). The analysis of such behavioral trade-offs has also yielded insights into similar trade-offs in life-history evolution (e.g., Werner, 1986).

A very active area of research on behavioral trade-offs under the risk of predation is that of vigilance for predators. Many animals regularly interrupt feeding to scan the environment for potential predators, and since vigilance often conflicts with energy intake, observed levels of vigilance should represent a trade-off sensitive to determinants of predation risk (see Lima, 1987). One such determinant receiving much attention is group size. Prompted by the seminal work of Pulliam (1973, 1976), several studies have demonstrated that individual group members become less vigilant as group size increases (e.g., Sullivan, 1984), presumably because risk is diluted and predator detection is more certain as group size increases. This trend in vigilance with group size is probably the most-studied behavioral trade-off under the risk of predation.

The need to be vigilant for predators may have ramifications extending beyond the organization of social behavior to the "standard" foraging decisions often

† Present address: Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A.

addressed by behavioral ecologists. However, few attempts have been made to integrate vigilance into standard foraging theory. Here, vigilance for predators will be incorporated into the now familiar "classical", or sequential-encounter contingency model of diet selection (Stephens & Krebs, 1986). As will be shown, the need to be vigilant while feeding may fundamentally alter the predictions of this and other models of diet selection. In some circumstances, however, the classical model may indeed yield the diet which maximizes fitness, even though the forager is by no means an "energy maximizer."

### Model

In the classical model of diet selection developed independently by Schoener (1971), Pulliam (1974), Werner & Hall (1974), and Charnov (1976), an animal maximizes its fitness by choosing which encountered items to accept or reject such that its rate of energy intake is maximized; vigilance was not a consideration. On the other hand, current models of vigilance behavior treat energy intake and its relationship to vigilance as an entity independent of the diet. The present task is therefore clear: combine models of diet and vigilance in a manner yielding predictions about diet selection *per se*. Pulliam's (1974) version of the diet model, and Lima's (1987) model of vigilance, will serve as the basis for the "hybrid" model. The assumptions in these two models hold throughout, and they will be elaborated on below, where appropriate. Note that symbols frequently used below are summarized in the Appendix for the reader's convenience.

An animal foraging through its environment makes repeated prey captures. The period from one capture to the next forms a convenient renewal cycle upon which to derive the expected rate of energy intake. A renewal cycle can be divided into the two mutually exclusive activities of searching for and handling prey items. Both search and handling may be periodically interrupted to scan the environment for predators.

First, consider the search component of a renewal cycle. Let  $t$  be a random variable denoting the time actually spent searching, exclusive of scanning, and let  $n$  be a discrete random variable denoting the number of scanning events during search ( $n \geq 0$ ). Assume scanning and search are mutually exclusive. If  $p(n, t)$  denotes the joint probability distribution that  $n$  and  $t$  are realized during a given renewal cycle, the expected time engaged in search (including time spent scanning) is

$$E(S) = \int_{t=0}^{\infty} \sum_{n=0}^{\infty} p(n, t)[ns + t] dt \quad (1)$$

where  $s$  is the time per scan. With the standard relationship  $p(n, t) = p(n|t)p(t)$ , (1) can be expressed as

$$E(S) = \int_{t=0}^{\infty} p(t) \left\{ \sum_{n=0}^{\infty} p(n|t)[ns + t] \right\} dt$$

which is further reduced to

$$E(S) = \int_{t=0}^{\infty} p(t) \left\{ t + s \sum_{n=0}^{\infty} p(n|t)n \right\} dt. \quad (2)$$

As in most models of vigilance, scanning is treated as a Poisson process with rate  $\lambda_s$  (Pulliam, 1973; Lima, 1987). Thus, the factor  $\sum_{n=0}^{\infty} p(n|t)n$  in (2), the expected number of scans during the interval of time necessary to complete  $t$ , is simply  $\lambda_s t$ . Substituting this into (2) and rearranging yields

$$E(S) = (1 + s\lambda_s) \int_{t=0}^{\infty} p(t)t \, dt. \quad (3)$$

Let  $\rho_i$ ,  $i = 1, 2, \dots$  be the proportion of the encountered items of type  $i$  that are accepted (attacked) and consumed. Furthermore, assume that prey items are randomly and independently distributed in the environment, and let  $\varepsilon_i$  be the forager's encounter rate with the  $i$ th prey type. Prey capture is therefore a Poisson process with rate  $\sum_i \rho_i \varepsilon_i$ . Accordingly, the integral in (3), which is simply the mean time actually spent searching (exclusive of scanning), is given by  $1/\sum_i \rho_i \varepsilon_i$ . Thus, (3) reduces to

$$E(S) = (1 + s\lambda_s) / \sum_i \rho_i \varepsilon_i. \quad (4)$$

Next, consider that segment of a renewal cycle concerned with handling. Let  $h_i$  be the time necessary to handle the  $i$ th prey type in the *absence* of scanning. Let  $\delta_i$  be a parameter indicating whether scanning is possible while handling the  $i$ th prey type;  $\delta_i = 0$  when scanning and handling are mutually exclusive, and  $\delta_i = 1$  indicates that scanning and handling can be done simultaneously. If  $\delta_i = 0$ , then handling is interrupted to scan at rate  $\lambda_h$ , and thus the expected number of scans during handling is  $\lambda_h h_i$ . Accordingly, the expected effective handling time for the  $i$ th item (the handling time including time scanning) is  $h_i + (1 - \delta_i)s\lambda_h h_i$ . Noting that  $\rho_i \varepsilon_i / \sum_i \rho_i \varepsilon_i$  represents the proportion of the diet consisting of the  $i$ th type, the expected time engaged in handling per renewal cycle (including scanning time) is

$$E(H) = \frac{\sum_i \rho_i \varepsilon_i h_i + s\lambda_h \sum_i (1 - \delta_i) \rho_i \varepsilon_i h_i}{\sum_i \rho_i \varepsilon_i}. \quad (5)$$

Therefore, combining (4) and (5), the expected time per renewal cycle is

$$E(T) = E(S) + E(H)$$

or

$$E(T) = \frac{1 + s\lambda_s + \sum_i \rho_i \varepsilon_i h_i + s\lambda_h \sum_i (1 - \delta_i) \rho_i \varepsilon_i h_i}{\sum_i \rho_i \varepsilon_i}. \quad (6)$$

The expected gain per renewal cycle is determined in a manner similar to (5):

$$E(G) = \sum_i \rho_i \varepsilon_i e_i / \sum_i \rho_i \varepsilon_i$$

where  $e_i$  is the net energy content of the  $i$ th prey type. With both  $E(G)$  and  $E(T)$  determined, the long-term rate of energy intake ( $R$ ) is  $E(G)/E(T)$  or

$$R = \frac{\sum_i \rho_i \epsilon_i e_i}{1 + s\lambda_s + \sum_i \rho_i \epsilon_i h_i + s\lambda_h \sum_i (1 - \delta_i) \rho_i \epsilon_i h_i}. \quad (7)$$

Consider next the relationship between vigilance and the risk of predation. Assume that predator detection and escape are certain if attack occurs while the forager is vigilant (scanning). However, if attack occurs when the forager is not scanning, survival requires that a scan be initiated before the predator gets so close that escape is impossible, even if the predator is eventually detected. Following the reasoning in Lima (1987), there is a time period  $\tau$  during which a scan must be initiated if escape is to be successful. The probability of initiating a scan during  $\tau$  is directly related to the scanning rate. As seen earlier,  $\lambda_h$  is the scanning rate while handling prey items for whom  $\delta_i = 0$ , and  $\lambda_s$  is the scanning rate while searching. Note, however, that the effective scanning rate while searching ( $\lambda_{s,\text{eff}}$ ) may be diet-dependent. This follows because a scan is effectively initiated every time the forager encounters and consumes a prey item for whom scanning and handling can be done simultaneously (i.e.,  $\delta_i = 1$ ). Thus,  $\lambda_{s,\text{eff}}$  will exceed  $\lambda_s$  according to the encounter rate with items for whom  $\delta_i = 1$ . Since scanning and prey encounter are independent Poisson processes,

$$\lambda_{s,\text{eff}} = \lambda_s + \sum_i \delta_i \rho_i \epsilon_i. \quad (8)$$

In any case, recalling that non-vigilant time is time spent actually handling items for whom  $\delta_i = 0$ , or time spent actually engaged in search, the probability of *not* detecting an attack with sufficient time to escape ( $P_{ND}$ ) is

$$P_{ND} = \omega \exp(-\lambda_{s,\text{eff}}\tau) + (1 - \omega) \exp(-\lambda_h\tau) \quad (9)$$

where  $\omega$  is the proportion of non-vigilant time per renewal cycle actively engaged in search. From (6), it can be shown that

$$\omega = \frac{1}{1 + \sum_i (1 - \delta_i) \rho_i \epsilon_i h_i}.$$

Following Lima (1987), in addition to (9), two more factors must be derived before determining the probability of being killed: the proportion of time spent scanning ( $p$ ) and the probability of attack ( $P_A$ ). A useful formulation for the probability of attack is

$$P_A = 1 - \exp(-\alpha T_F) \quad (10)$$

where  $\alpha$  is the attack rate and  $T_F$  is the total foraging time (including scanning) needed to satisfy a given metabolic requirement  $M$  (see Lima, 1987);  $T_F = M/R$ .

The proportion of time spent scanning can easily be determined from (6):

$$p = \frac{s\lambda_s + s\lambda_h \sum_i (1 - \delta_i) \rho_i \varepsilon_i h_i + \sum_i \delta_i \rho_i \varepsilon_i h_i}{1 + s\lambda_s + \sum_i \rho_i \varepsilon_i h_i + s\lambda_h \sum_i (1 - \delta_i) \rho_i \varepsilon_i h_i} \quad (11)$$

where the first, second, and third terms in the numerator represent time spent scanning while searching, handling items for whom  $\delta_i = 0$ , and handling items for whom  $\delta_i = 1$ , respectively. With (9), (10) and (11), the overall probability of being killed while foraging during a given day [ $P(K)$ ] can now be determined as in Lima (1987):

$$P(K) = (1 - p) \cdot P_{ND} \cdot P_A$$

or

$$P(K) = (1 - p)[\omega \exp(-\lambda_{s, \text{eff}} \tau) + (1 - \omega) \exp(-\lambda_h \tau)][1 - \exp(-\alpha T_F)]. \quad (12)$$

Assume that the forager in question is a non-breeding individual for whom maximizing fitness is equivalent to maximizing the probability of surviving until the next breeding season. This is equivalent to maximizing daily survival if all days are roughly equivalent during the non-breeding season. In any case, survival entails avoiding both predation and starvation. Thus

$$P(\text{survival}) = [1 - P(K)] \cdot [1 - P(S)] \quad (13)$$

where  $P(S)$  = the daily probability of starvation. A reasonable form for  $P(S)$  is

$$P(S) = 1 - \exp(-\gamma T_F) \quad (14)$$

where  $\gamma$  is a positive constant (see Lima, 1987). Since  $T_F = M/R$ , minimizing  $P(S)$  is equivalent to minimizing  $T_F$ , which, in turn, is equivalent to maximizing  $R$ . Note, however, that (14) shows diminishing returns in  $R$ .

In maximizing (13), the forager has control over  $\lambda_s$ ,  $\lambda_h$ , and the value of  $\rho_i$ ; optimal values are indicated by a “\*”. The  $\rho_i^*$  values reveal the nature of the optimal diet.

## Results

A series of special cases will be considered in examining diet selection under the risk of predation. Throughout, for simplicity, the foraging environment contains two prey types where  $e_1/h_1 > e_2/h_2$ ; the inherent profitability of prey (type) 1 exceeds that of prey (type) 2. The first set of analyses will be done numerically relative to a set of baseline parameters (Table 1) common to all cases unless otherwise specified. These baseline parameters are chosen to be representative for a small bird in winter, for whom the currency of survival is particularly relevant (e.g., Caraco, 1979). The qualitative conclusions reached below, however, are independent of the exact values chosen.

TABLE 1

*Baseline parameter values. These values are used for all numerical analyses unless otherwise noted*

$\tau = 1.5 \text{ sec}$	$e_1 = 0.25 \text{ units}$
$M = 1000 \text{ units}$	$e_2 = 0.25 \text{ units}$
$s = 1.0 \text{ sec}$	$h_1 = 1 \text{ sec}$
$\gamma = 1 \times 10^{-6} \text{ sec}^{-1}$	$h_2 = 5 \text{ sec}$
$\alpha = 1 \times 10^{-5} \text{ sec}^{-1}$	$\varepsilon_2 = 1 \text{ sec}^{-1}$

An important entity in the following analysis is  $\hat{\varepsilon}_1$ , the critical encounter rate with prey 1 above which the diet consists solely of prey 1 (i.e.,  $\rho_1^* = 1$ ,  $\rho_2^* = 0$ ). In particular, the numerical results are expressed as plots of  $\hat{\varepsilon}_i$  vs. the attack rate ( $\alpha$ ) for various values of the energy content of prey 2 ( $e_2$ );  $\alpha$  serves as the primary index of predation risk, and  $e_2$  serves as an index of the profitability of prey 2. Note that  $\hat{\varepsilon}_1$  represents the condition of equal fitness (survival) for diets consisting of both prey types or prey 1 alone, not necessarily equal rates of energy intake.

#### CASE 1: $\delta_1 = \delta_2 = 0$

Handling and scanning are mutually exclusive activities for both prey types in this case, and from Fig. 1a, it is clear that diet selection is independent of the risk of predation. However, an increase in the profitability of prey 2 leads to an increase in  $\hat{\varepsilon}_1$ . Although not shown,  $\hat{\varepsilon}_1$  is also independent of  $\varepsilon_2$ , and  $\rho_1^* = 1$  throughout (i.e., all prey 1 encountered are consumed). The "zero-one" rule of diet selection (see Stephens & Krebs, 1986) also holds as  $\rho_2^*$  assumes only two values: 0 or 1.

Figure 1b shows a plot of the optimal scanning rates while searching ( $\lambda_s^*$ ) and handling ( $\lambda_h^*$ ) vs.  $\varepsilon_1$  for various attack rates ( $\alpha$ ). First note that  $\lambda_h^* = \lambda_s^*$ . The equivalence of optimal scanning rates follows directly from assuming that attack occurs without regard to the activity of the forager; there is no point in scanning more while searching vs. handling. In fact, this result generalizes in the following analyses to  $\lambda_{s,\text{eff}}^* = \lambda_h^*$ . In any case, scanning rates increase with  $\alpha$  (Fig. 1b). Thus the effective handling times [ $h_i(1 + s\lambda_h)$ ] and the effective encounter rate [ $\varepsilon_i/(1 + s\lambda_s)$ , which is the inverse of (4)] increase and decrease with  $\alpha$ , respectively. However, despite these dependencies,  $\hat{\varepsilon}_1$  is independent of  $\alpha$ , and a key to understanding this independence is the fact that the optimal scanning rates show no discontinuity at  $\hat{\varepsilon}_1$  in Fig. 1b (see below). In fact it will be shown that  $\hat{\varepsilon}_1$  is given by the classical diet model.

#### CASE 2: $\delta_1 = 1$ , $\delta_2 = 0$

In Case 2, scanning and handling can be done simultaneously for prey 1 but not for prey 2. Here, as in Fig. 1a, the diet is dependent upon the profitability of prey 2 (i.e.,  $e_2$ , Fig. 2a). The diet is also independent of all but the smallest attack rates

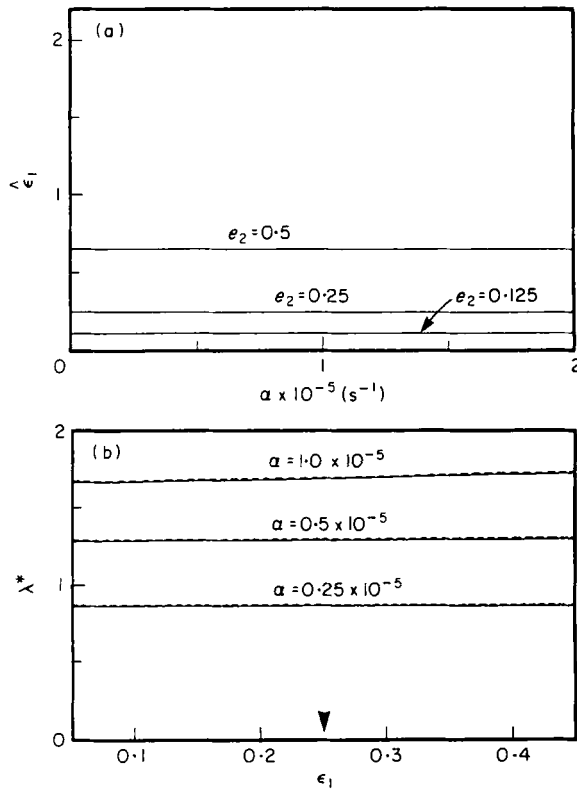


FIG. 1. For Case 1: (a) relationship between  $\hat{\epsilon}_1$  and attack rate ( $\alpha$ ) for levels of the energy content of prey 2 ( $e_2$ ) as shown; (b) scanning rates as a function of  $\epsilon_1$  for values of  $\alpha$  as shown; the arrow indicates  $\hat{\epsilon}_1$ . - - - -  $\lambda_{h_1}^*$ ; —  $\lambda_s^*$ . For this and all other figures, values for parameters not shown are as in Table 1.

( $\alpha$ , Fig. 2a). Note that the  $\hat{\epsilon}_1$  values at  $\alpha = 0$  are identical to corresponding values in Fig. 1a. In addition, as before,  $\rho_1^* = 1$ ,  $\hat{\epsilon}_1$  is independent of  $e_2$ , and the zero-one rule holds for prey 2.

Figure 2b shows that the optimal scanning rate while handling prey is identical to the optimal effective scanning rate while searching ( $\lambda_{s,\text{eff}}^*$ ) for the reasons outlined earlier. However, note from (8) that for Case 2,  $\lambda_{s,\text{eff}}^* = \lambda_s^* + \epsilon_1$ , hence  $\lambda_s^* = \lambda_{s,\text{eff}}^* - \epsilon_1$  and the negative relationship between  $\lambda_s^*$  and  $\epsilon_1$  evident in Fig. 2b. In addition, note that  $\lambda_s^*$  is continuous across the  $\hat{\epsilon}_1$  threshold. For clarity, only one value of  $\alpha$  is considered in Fig. 2b (the baseline value) but all optimal scanning rates increase with  $\alpha$  as seen in Fig. 1b.

The lack of a predation-risk effect for larger attack rates in Fig. 2a is not a general result; it reflects the fact that  $h_1 = s$  in the baseline parameters (Table 1). As Fig. 3 shows, the diet is generally predation-risk-dependent with  $h_1 \neq s$ , although weakly so. Notice that  $\hat{\epsilon}_1$  converges to 0.2 (the value of  $\hat{\epsilon}_1$  when  $h_1 = s = 1$ ) as  $\alpha$  increases, regardless of the value of  $h_1$ .

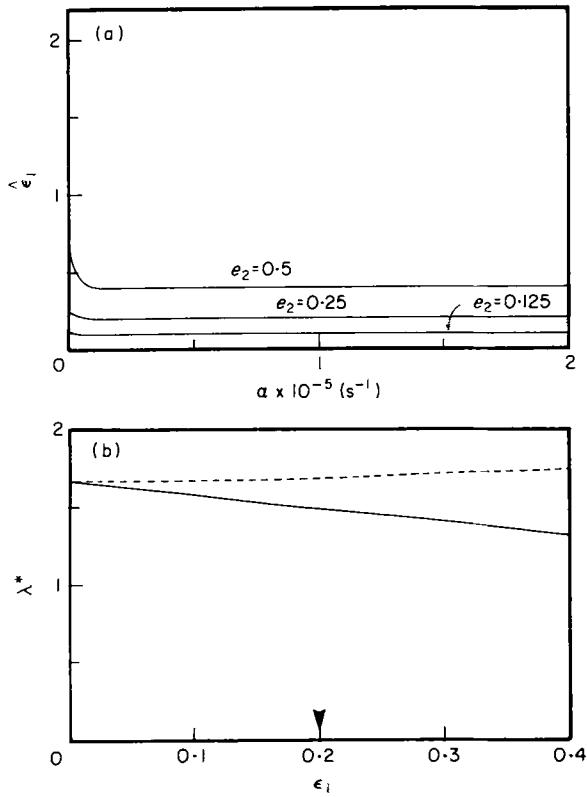


FIG. 2. For Case 2: (a) relationship between  $\hat{\epsilon}_1$  and  $\alpha$  for values of  $e_2$  as shown; (b) scanning rates as a function of  $\epsilon_1$ ; the arrow indicates  $\hat{\epsilon}_1$ . - - - -  $\lambda_h^* = \lambda_{s,\text{eff}}^*$ ; —  $\lambda_s^*$ .

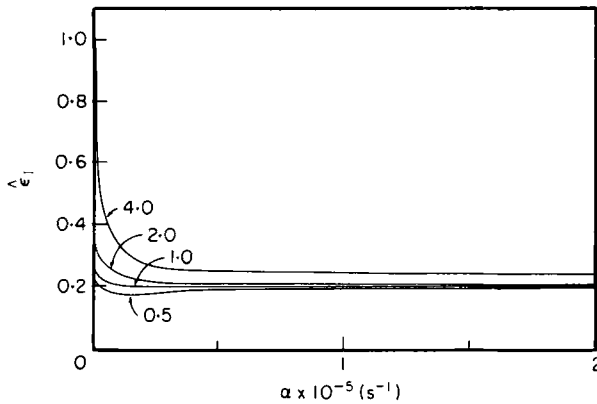


FIG. 3. For Case 2: relationship between  $\hat{\epsilon}_1$  and  $\alpha$  when  $h_1 \neq s$ . The numbers refer to values of  $h_1$ .



CASE 3:  $\delta_1 = \delta_2 = 1$ 

Figure 4a depicts the nature of the diet when handling and scanning are simultaneous for both prey items. Unlike Cases 1 and 2, the critical encounter rate  $\hat{\epsilon}_1$  is clearly influenced by the risk of predation; the monotonic increase in  $\hat{\epsilon}_1$  means that, as  $\alpha$  increases, prey 1 must be increasingly more abundant before the forager will specialize on prey 1 only. As before,  $\rho_1^* = 1$  throughout.

A plot of scanning rates vs.  $\epsilon_1$  for Case 3 (Fig. 4b) exhibits more complexity than in those examined earlier. For Case 3,  $\delta_1 = \delta_2 = 1$ , thus  $\lambda_h$  is irrelevant. As in Figs. 1b and 2b, the optimal effective scanning rate while searching ( $\lambda_{s,\text{eff}}^*$ ) is insensitive to  $\epsilon_1$ . However, for Case 3,  $\lambda_s^*$  is influenced by both  $\epsilon_1$  and  $\epsilon_2$ , and shows a marked discontinuity at  $\hat{\epsilon}_1$ .

The complexity in  $\lambda_s^*$  follows from the fact that  $\delta_1 = \delta_2 = 1$ . In fact, since  $\rho_1^* = 1$ ,  $\lambda_s^*$  is given by (see (8))

$$\lambda_s^* = \lambda_{s,\text{eff}}^* - \epsilon_1 - \rho_2^* \epsilon_2. \quad (15)$$

Recall that  $\rho_2^* = 0$  when  $\epsilon_1 > \hat{\epsilon}_1$ . Thus, from (15),  $\lambda_s^*$  is negatively dependent upon  $\epsilon_2$  for  $\epsilon_1 < \hat{\epsilon}_1$  and independent otherwise (Fig. 4b); this also explains the discontinuity

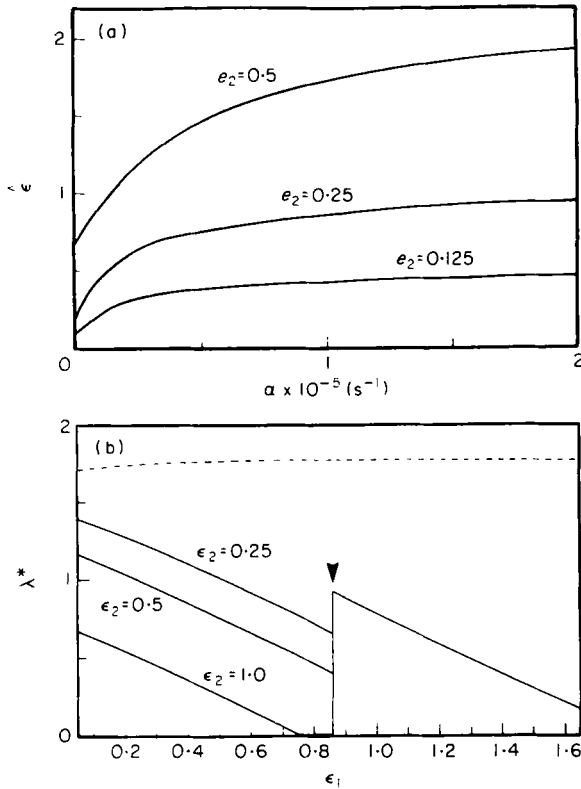


FIG. 4. For Case 3: (a) relationship between  $\hat{\epsilon}_1$  and  $\alpha$  for the values of  $\epsilon_2$  indicated; (b) scanning rates as a function of  $\epsilon_1$  for the given values of  $\epsilon_2$ ; the arrow indicates  $\hat{\epsilon}_1$ . - - - -  $\lambda_{s,\text{eff}}^*$ ; —  $\lambda_s^*$ .

at  $\hat{\varepsilon}_1$ . The negative relationship between  $\lambda_x^*$  and  $\varepsilon_1$  evident throughout Fig. 4b is also readily understood with reference to (15).

The dependency of  $\lambda_x^*$  on  $\varepsilon_2$  (15) leads to the possibility of "partial preferences," or  $0 \leq \rho_2^* \leq 1$  (see Stephens & Krebs, 1986). Figure 5 shows some examples of this phenomenon for two different attack rates ( $\alpha$ ). For small values of  $\varepsilon_1$ ,  $\rho_2^* = 1$ . The value of  $\rho_2^*$  then drops until  $\varepsilon_1 = \hat{\varepsilon}_1$ , where  $\rho_2^*$  equals zero. The drop in  $\rho_2^*$  begins earlier as  $\varepsilon_2$  increases. Note that  $\rho_2^* = 0$  when  $\varepsilon_1 > \hat{\varepsilon}_1$ , thus preserving the meaning of  $\hat{\varepsilon}_1$  as previously defined. In any case, this phenomenon of partial preferences follows from (8) and (15); when  $\varepsilon_2$  is large enough,  $\lambda_{x,\text{eff}}$  is "regulated" at its optimal level by altering the diet (i.e.,  $\rho_2^*$ ) rather than  $\lambda_x$ .

#### CASE 4: $\delta_1 = 0$ , $\delta_2 = 1$

Here, scanning and handling are mutually exclusive only in the prey type that is inherently more profitable (prey 1). This situation leads to much more complex

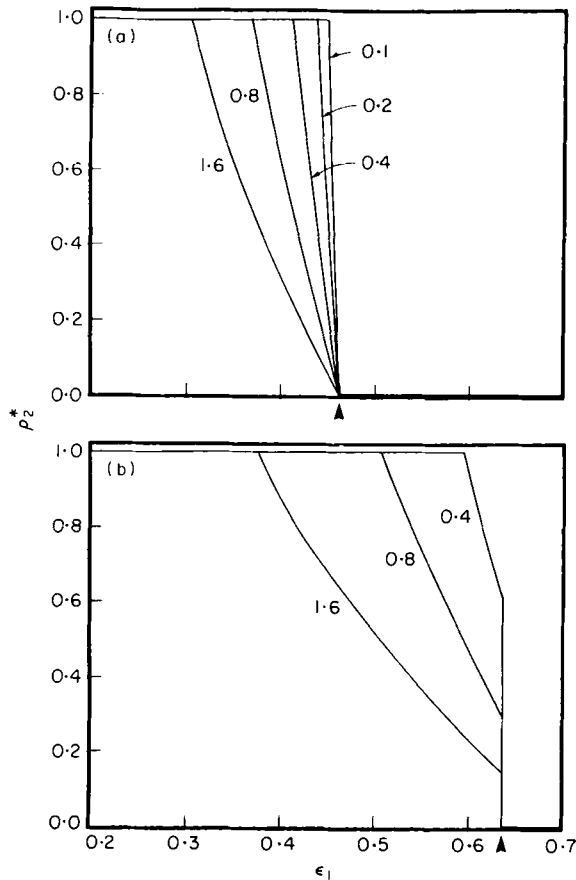


FIG. 5. For Case 3: relationship between  $\rho_2^*$  and  $\varepsilon_1$  for  $\alpha = 0.1 \times 10^{-5}$  (a) and  $0.25 \times 10^{-5}$  (b). Numbers represent values of  $\varepsilon_2$ . Arrows indicate  $\hat{\varepsilon}_1$  values.

behavior than seen thus far. As seen in Fig. 6a,  $\hat{\epsilon}_1$  may be strongly dependent upon  $\alpha$ , especially as  $e_2$  increases; as  $e_2$  increases, a diet consisting solely of prey 1 may be unattainable regardless of  $\epsilon_1$ . As before,  $\hat{\epsilon}_1$  is independent of  $\epsilon_2$  and  $\rho_1^* = 1$  throughout.

The various optimal scanning rates are given in Fig. 6b. Throughout the figure,  $\lambda_h^* = \lambda_{s,\text{eff}}^*$ . For  $\epsilon_1 > \hat{\epsilon}_1$ ,  $\lambda_s^* = \lambda_{s,\text{eff}}^*$ . The discontinuity in  $\lambda_s^*$  (Fig. 6b), as before, reflects the relation in (8), which for Case 4 is  $\lambda_{s,\text{eff}}^* = \lambda_s^* + \rho_2^* \epsilon_2$ . Since  $\rho_2^* = 0$  for  $\epsilon_1 > \hat{\epsilon}_1$ ,  $\lambda_s^*$  is dependent upon  $\epsilon_2$  for  $\epsilon_1 < \hat{\epsilon}_1$  (Fig. 6b); this dependence may lead to partial preferences ( $0 \leq \rho_2^* \leq 1$ ) but they are not as marked as those seen in Fig. 5.

The optimal diet for Case 4 is not as simple as it appears so far. Consider the following. Figure 7a shows that  $\lambda_h^*$  increases (at a decreasing rate) with  $\alpha$ . This dictates that the effective profitability of prey 1,  $e_1/h_1(1 + s\lambda_h)$ , decreases with  $\alpha$  (Fig. 7b). Since the difference in the profitabilities of the two items decreases as  $\alpha$  increases (Fig. 7b), ever increasingly higher values of  $\epsilon_1$  are needed to effect a diet consisting solely of prey 1 as  $\alpha$  increases, hence the concave-upwards relationships in Fig. 6a that become more marked as  $e_2$  increases.

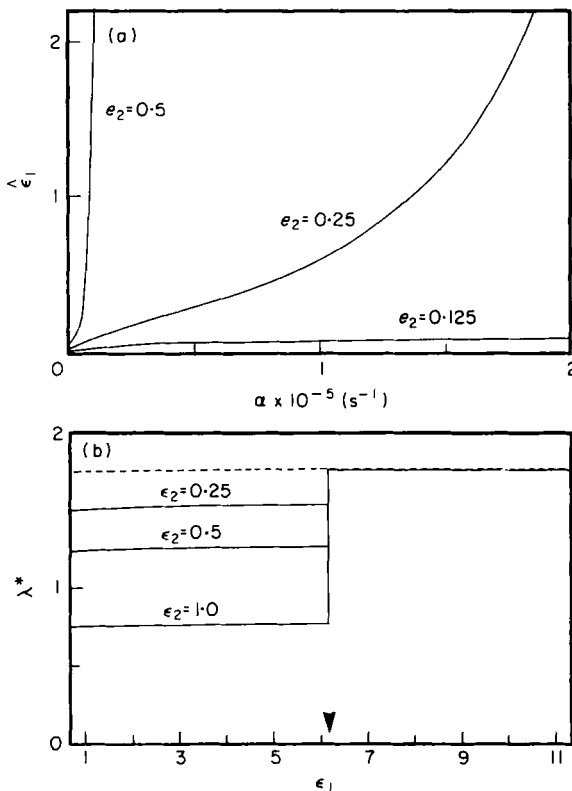


FIG. 6. For Case 4: (a) relationship between  $\hat{\epsilon}_1$  and  $\alpha$  for the values of  $e_2$  indicated; (b) scanning rates as a function of  $\epsilon_1$  for the given values of  $e_2$ ; the arrow indicates  $\hat{\epsilon}_1$ . - - - -  $\lambda_h^* = \lambda_{s,\text{eff}}^*$ ; —  $\lambda_s^*$ .

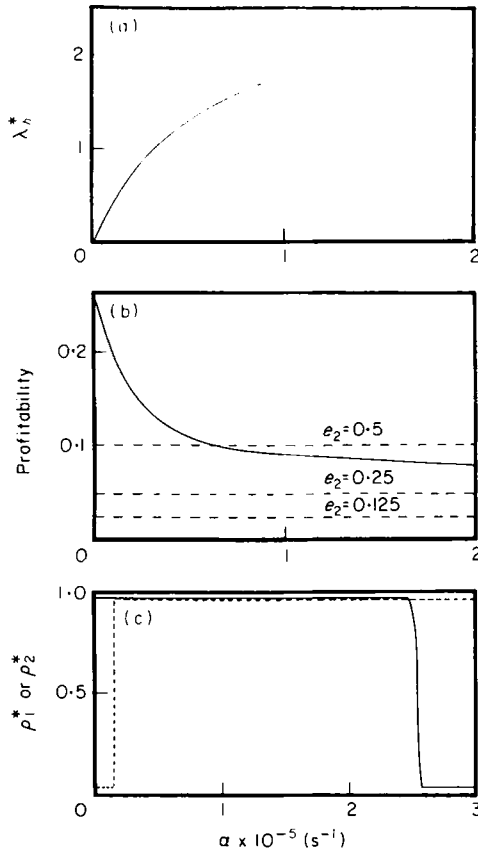


FIG. 7. For Case 4: (a) scanning rate ( $\lambda_s^*$ ) as a function of attack rate ( $\alpha$ ); (b) effective profitability of prey 1 (—) and prey 2 (---) as a function of  $\alpha$ . The profitability of prey 2 is constant with  $\alpha$ , and is given for the values of  $e_2$  indicated; (c)  $\rho_1^*$  (—) and  $\rho_2^*$  (---) as a function of  $\alpha$ ;  $\varepsilon_1 = 5$ ,  $\varepsilon_2 = 1$  and  $e_2 = 0.5$ .

Diet selection for Case 4 is still more complex, because at some  $\alpha$  the effective profitability of prey 1 may drop below that of prey 2 (e.g., Fig. 7b), leading to the possibility that *prey 1* may be dropped from the diet. Fig. 7c shows an example of this phenomenon. At low  $\alpha$ , the diet consists solely of prey 1 ( $\rho_1^* = 1, \rho_2^* = 0$ ). As  $\alpha$  increases, item 2 is added to the diet ( $\rho_1^* = \rho_2^* = 1$ ), and prey 1 is dropped as  $\alpha$  increases still further ( $\rho_1^* = 0, \rho_2^* = 1$ ).

In summary, diet selection for Cases 1 and 2 is independent of, or relatively weakly influenced by, the risk of predation, whereas the opposite holds for Cases 3 and 4. Given the dependence of (13) on various aspects of diet and vigilance, it is not surprising that diet selection may be predation-risk-dependent. What needs explaining is the *lack* of a predation-risk-dependency in Case 1 (and 2).

As mentioned earlier, the key to understanding Cases 1 and 2 is the continuity of  $\lambda_s^*$  across  $\hat{e}_1$  (see Figs 1b and 2b). This continuity implies that  $\lambda_s^*$  is independent

of the diet at  $\hat{\varepsilon}_1$ . This, in turn, implies that  $\lambda_h^*$  and the proportion of time spent scanning ( $p$ , see equation (11)) are independent of the diet at  $\hat{\varepsilon}_1$ . In addition, since  $\lambda_{s,\text{eff}}^* = \lambda_h^*$  for Cases 1 and 2, the above implies that the probability of not detecting an attack ( $P_{\text{ND}}$ , see equation (9)) is also independent of the diet at  $\hat{\varepsilon}_1$ . Thus, the first two factors of  $P(K)$  (the probability of being killed, see equation (12)) are independent of the exact diet at  $\hat{\varepsilon}_1$ , thus minimizing  $P(K)$  is equivalent to minimizing the probability of attack ( $P_A$ ). Since  $P_A = 1 - \exp(-\alpha T_F)$ , and  $T_F = M/R$ , minimizing  $P_A$  is equivalent to maximizing  $R$ . Maximizing  $R$  also minimizes the probability of starvation ( $P(S)$ , see equation (14)), hence the diet maximizing  $R$  given  $\lambda_{s,\text{eff}}^* = \lambda_h^* > 0$  is the optimal diet. Let  $R(1)$  and  $R(1, 2)$  represent the energy intake rate from a diet consisting of prey 1 only or both prey types, respectively. The above discussion implies that the criterion of diet selection for Case 1 can be found by setting  $R(1) = R(1, 2)$ . Doing so yields

$$\frac{\varepsilon_1}{1 + s\lambda_s} \leq \frac{e_2}{e_1 h_2 [1 + s\lambda_h (1 - \delta_2)] - e_2 h_1 [1 + s\lambda_h (1 - \delta_1)]} \quad (16)$$

as the criterion for the inclusion of prey 2 in the diet for Cases 1 and 2. The LHS of (16) is the effective encounter rate with item 1 (the encounter rate including scanning time). In the RHS of (16),  $h_i [1 + s\lambda_h^* (1 - \delta_i)]$  represents the effective handling time for prey  $i$ .

For Case 1 ( $\delta_1 = \delta_2 = 0$ ),  $\lambda_h^* = \lambda_s^*$  (see Fig. 1b), and thus (16) reduces to

$$\varepsilon_1 \leq \frac{e_2}{e_1 h_2 - e_2 h_1} \quad (17)$$

which is independent of  $\varepsilon_2$ ,  $\lambda_h$  and, in fact, is the criterion for the inclusion of prey 2 for the classical diet model. For Case 2 ( $\delta_1 = 1$ ,  $\delta_2 = 0$ ), (8) implies that (since  $\lambda_h^* = \lambda_{s,\text{eff}}^*$ , see Fig. 2b)  $\lambda_s^* = \lambda_h^* - \varepsilon_1$  and thus (16) reduces to

$$\frac{\varepsilon_1}{1 + s(\lambda_h^* - \varepsilon_1)} \leq \frac{e_2}{e_1 h_2 [1 + s\lambda_h^*] - e_2 h_1}$$

which can be rearranged to

$$\varepsilon_1 \leq \frac{e_2}{e_1 h_2 - e_2 k} \quad (18)$$

where  $k = (h_1 - s)/(1 + s\lambda_h^*)$ . Thus, when  $h_1 = s$ ,  $\hat{\varepsilon}_1$  is independent of  $\lambda_h^*$  and thus the attack rate  $\alpha$ . However, note that (18) holds only when  $\lambda_s = \lambda_h - \varepsilon_1 > 0$ ; i.e., (18) holds for higher attack rates (cf. Fig. 2a). Equation (18) also explains the general effect of  $\alpha$  or  $\hat{\varepsilon}_1$  when  $h_1 \neq s$  (Fig. 3), and the fact that  $\hat{\varepsilon}_1$  approaches  $e_2/e_1 h_2$  as  $\alpha$  (or  $\lambda_h^*$ ) increases (i.e., as  $k$  approaches zero) (Fig. 3).

The crux of all this is simple: the classical model's criterion for the inclusion of prey 2 in the diet holds only when scanning and handling are mutually exclusive

for both prey types. It must be stressed, however, that the validity of (17) when  $\delta_1 = \delta_2 = 0$ , does not imply that the forager is an energy maximizer. Strictly speaking, energy maximizers do not scan for predators since this always detracts from the rate of energy intake.

Before proceeding it will be instructive to consider diet selection as a function of predation-risk-determinants other than attack rate. One such determinant in (12) is  $\tau$ , the time period after attack initiation during which the forager must initiate a scan for successful escape. As outlined in Lima (1987),  $\tau$  is determined by factors such as the distance to cover (e.g., safety); an increase in this factor decreases  $\tau$ . Only Cases 3 and 4 will be examined with respect to  $\tau$  since diet selection in these cases is strongly predation-risk dependent.

Figure 8a shows the relationship between  $\hat{e}_1$  and  $\tau$  for Case 3 given various values of  $e_2$ . The general trend is for  $\hat{e}_1$  to increase with decreasing  $\tau$  to the point where  $\tau = 0$ , whereupon  $\hat{e}_1$  drops to a low, constant value given by (17) (not shown);  $\hat{e}_1$  is generally greater as  $e_2$  increases for  $\tau > 0$ . The basic shape of these curves reflects the fact that a decrease in  $\tau$  puts a premium on increasing the proportion of time spent scanning, particularly for small values of  $\tau$ . Since  $\delta_2 = 1$  for Case 3 (scanning and handling are simultaneous for prey 2) the forager becomes increasingly "reluctant" to drop prey 2 from the diet with decreasing  $\tau$ , and this reluctance is greater for higher values of  $e_2$ . However, with  $\tau < 0$ , escape is not possible given any level of vigilance and the optimal diet is that which maximizes energy intake in the classical sense (because this minimizes time exposed to attack);  $\hat{e}_1$  is given by (17)

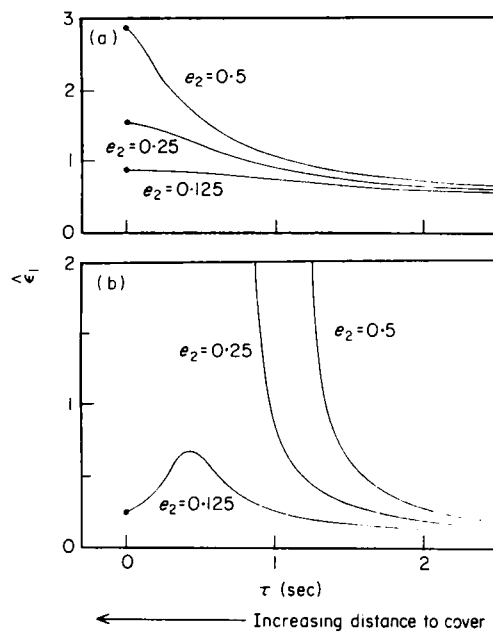


FIG. 8. Relationship between  $\hat{e}_1$  and  $\tau$  for (a) Case 3, and (b) Case 4, for various values of  $e_2$ .

for  $\tau \leq 0$ . Note that  $\tau$  in (12) is actually defined only for attack perpendicular to cover (see Lima, 1987); a consideration of all possible directions of attack would lead to a statistical view of  $\tau$  that transforms the step-functions in Fig. 8a to a continuous one with a maximum at some  $\tau$ .

Figure 8b shows the relationship between  $\hat{e}_1$  and  $\tau$  for Case 4, and it is immediately apparent that  $\hat{e}_1$  is more sensitive to  $\tau$  than in Case 3 (note the differences in scale of the ordinate). This follows from the fact that  $\delta_1 = 0$  and  $\delta_2 = 1$ . In other words, the forager is more reluctant to drop prey 2 from the diet because only this prey allows for simultaneous scanning and handling; prey 2 is virtually never dropped from the diet for small  $\tau$  and large  $e_2$ . For small  $e_2$ , however, the relationship between  $\hat{e}_1$  and  $\tau$  reveals a maximum. In any case,  $\hat{e}_1$  is given by (17) for  $\tau \leq 0$  for the reasons outlined above.

### Discussion

The classical model of diet selection was among the first developed by evolutionary and behavioral ecologists in an attempt to both understand and predict the behavior of feeding animals, and many variations of this model have been developed over the last 15 years (see Stephens & Krebs (1986) for a cogent review). However, despite the growing awareness that the risk of predation is indeed an important determinant of behavior (e.g., Dill, 1987), virtually no theoretical consideration of diet selection under the risk of predation has previously been put forward. This is perhaps traceable to Schoener's (1971) view that an animal feeding under the risk of predation would maximize its rate of energy intake and thereby minimize its time spent exposed to predators—they are time minimizers following the classical model's decision criteria. It is a trite, but nonetheless important, point that a vigilant animal cannot be an energy maximizer. The fact that vigilance detracts from energy intake is the cornerstone of both empirical and theoretical studies of vigilance, but its significance for "standard" foraging decisions (*sensu* Stephens & Krebs, 1986) is still largely unrecognized. Here, a case is made for the importance of vigilance in diet selection, and several quantitative and qualitative predictions are readily apparent from the foregoing discussion. Further work integrating vigilance into other aspects of feeding behavior will likely lead to a new view of some other, old questions.

Stephens & Krebs (1986) provide an extensive review of the empirical work on diet selection (their table 9.1) which shows good qualitative support for several aspects of the classical diet model, although there is considerable lack of support. Can the model herein shed any light on this review? The short answer is "not yet," because the necessary information on vigilance is rarely reported (if even considered). Interestingly, those few studies rigorously supporting the classical model, such as those with great tits (*Parus major*; Krebs *et al.*, 1977; Rechten *et al.*, 1983; Getty & Krebs, 1985) and redshanks (*Tringa totanus*; Goss-Custard, 1977), probably dealt with Case 1 where handling and scanning are mutually exclusive for all prey types. In addition the rigorous work of Stephens *et al.* (1986) in support of a variant

of the classical model examined foragers (bumblebees, *Bombus* sp.) which may actually not respond to a risk of predation (see Morse, 1986).

In general, however, most foragers are themselves foraged-upon by others, and in higher vertebrates there are myriad studies documenting a general tendency to scan for predators while foraging (Lima, 1987). In the author's experience, many (if not all) animals will simultaneously scan while handling prey items if their physical abilities and the nature of the prey item allows for this. For instance, the squirrels in Lima *et al.* (1985) would invariably scan while handling food items. Several recent studies have noted such behavior and its potential importance in patch selection (Glück, 1986) and the organization of vigilance (Metcalf, 1984; Glück, 1987). Many granivorous birds also simultaneously scan while consuming seeds with long husking times. In fact, Lima (1988) provides evidence that the granivorous dark-eyed junco (*Junco hyemalis*) exhibits markedly non-classical diet selection when potential prey items differ in the exclusivity of handling and scanning (in a special case of Case 4). The juncos also showed flock-size-dependent diet selection, reflecting the decreased need to be vigilant as flock size increases. A flock-size effect is beyond the scope of this paper, but it could be incorporated into the current framework with relative ease. Overall, it seems likely that a consideration of vigilance may lead to greater insight into the organization of, and the evolutionary pressures shaping, the behavior of feeding animals.

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## APPENDIX

**Frequently Used Symbols**

$\lambda_s$	scanning rate while searching.
$\lambda_{s,\text{eff}}$	effective rate of scanning while searching (diet-dependent).
$\lambda_h$	scanning rate while handling prey for whom $\delta_i = 0$ .
$s$	time per scan.
$\varepsilon_i$	encounter rate with prey type $i$ .
$\hat{\varepsilon}_1$	critical encounter rate with prey type 1 above which the diet consists solely of prey 1.
$\rho_i$	proportion of encountered items of type $i$ that are accepted and consumed.
$\delta_i$	$\delta_i = 0$ if handling and scanning are mutually exclusive, $\delta_i = 1$ if handling and scanning can be done simultaneously.
$e_i$	net energy content of prey type $i$ .
$h_i$	handling time of prey type $i$ exclusive of any time spent scanning.
$R$	energy intake rate.
$M$	daily metabolic requirement.
$T_F$	daily time spent feeding (including scanning) to meet $M$ .
$p$	proportion of time spent scanning.
$\tau$	time period after attack initiation during which the forager must initiate a scan in order to escape successfully.
$\alpha$	attack rate.
$P(K)$	daily probability of being killed.
$P(S)$	daily probability of starvation.