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Predator Errors, Foraging in Unpredictable Environments and Risk: The Consequences of Prey Variation in Handling Time Versus Net Energy

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PREDATOR ERRORS, FORAGING IN UNPREDICTABLE  
ENVIRONMENTS AND RISK: THE CONSEQUENCES OF PREY  
VARIATION IN HANDLING TIME VERSUS NET ENERGY

Although fine-grained foraging models (Charnov 1976; Pulliam 1974; Schoener 1971) are used primarily to predict the range of prey items to be included in the diet by an optimally foraging predator, the algebra of these models may also be used to generate a "harvesting curve." Such curves (fig. 1) describe the average yield (energy per unit foraging time) a predator achieves as it adds successively poorer value prey types (energy per unit handling time) to the diet, and they span the entire array of ranked prey (Charnov 1976). Each solid symbol on the curve (fig. 1) corresponds to the average net energy intake rate (average yield) if all items of equivalent or higher rank are consumed when encountered. With such a descriptive curve, it is thus possible to assess the consequences of predator decisions at any point along the resource spectrum including: (1) adding additional 'appropriate' prey (prey in the optimal set, fig. 1), (2) adding additional 'inappropriate' prey (prey not in the optimal set), (3) rejecting otherwise 'appropriate' prey, or (4) rejecting 'inappropriate' prey. Decisions 2 and 3 would be considered errors in that either adding inappropriate prey or rejecting otherwise appropriate prey will result in a decrease in the average yield.

Previous considerations of foraging models (Charnov 1976; Estabrook and Dunham 1976; Hughes 1979; Pulliam 1974; Schoener 1971) have assumed that prey that vary in handling time are functionally equivalent to those that vary in net energy. I will demonstrate here that this is not in fact true and that while the location of the optima and the conclusions of previous models are not affected, the energetic consequences of both correct and incorrect prey-choice decisions are different depending on the mode of variation of prey value.

VERBAL ARGUMENT

Charnov (1976, eq. [1]) presents an equation describing the average energy intake for a predator as progressively lower value prey are added to the diet:

$$\frac{E_N}{T} = \frac{\sum \lambda_i E_i^*}{1 + \sum \lambda_i h_i^*}$$

where  $E_N$  = total net energy,  $T$  = total foraging time,  $\lambda_i$  = encounter rate of the  $i$ th prey type,  $E_i^*$  = expected net energy of one item of type  $i$  and  $h_i^*$  = the expected handling time for an item of type  $i$ . The value of any prey ( $i$ ) is thus  $E_i^*/h_i^*$ , the expected net energy per unit handling time (X in fig. 1). However, when considering a hypothetical array of ranked prey, there is no a priori reason for assuming that prey value decreases because of a decrease in expected net energy ( $E^*$ ) or an increase in expected handling time ( $h^*$ ). A change in either can result in an identical decrease in prey value.

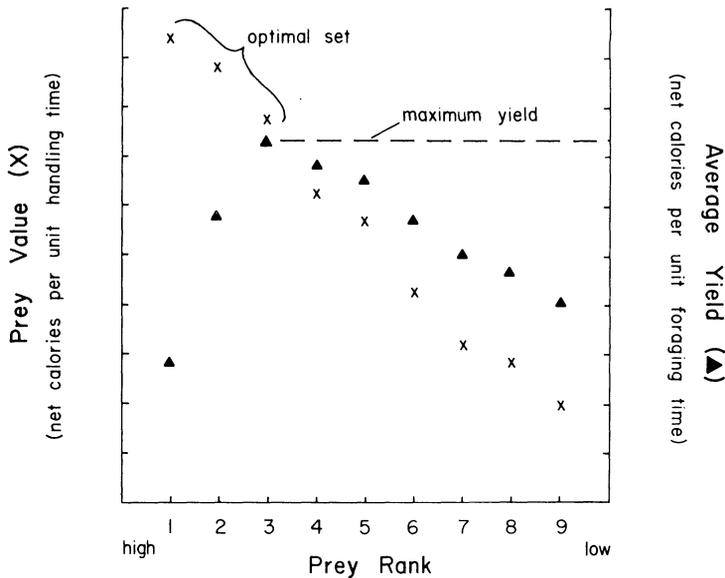


FIG. 1.—Graphical representation of the fine-grained foraging model's mechanics. Modified from Charnov (1976). The solid symbols describe a "harvesting curve" which indicates average energy intake for both optimal and nonoptimal combinations of prey types.

Figure 2 illustrates several harvesting curve pairs for arbitrarily chosen values of  $\lambda$ ,  $E^*$ , and  $h^*$ . For all curves, the average yield increases more rapidly to the optimum and then declines more rapidly beyond it where prey differ in handling time (dashed lines) rather than net energy (solid lines). This occurs even though the numerical values of the ratio  $E^*/h^*$  are the same for each pair of solid and dashed lines.

The implications of these curves are as follows for prey of identical values which may have different handling times ( $h^*$ ) or net energy ( $E^*$ ). (1) Adding prey types to the diet that are in the optimal set (a correct decision) results in a greater increase in the average yield ( $E_N/T$ ) if the added prey have a longer handling time than if the added prey have a lower net energy. (2) Adding prey types to the diet that are not in the optimal set (an incorrect decision) results in a greater decrease in the average yield or greater cost if the added prey have a longer handling time than if they have a lower net energy. (3) Rejecting prey types that are in the optimal set (an incorrect decision) results in a greater decrease in the average yield or greater cost if the rejected prey have a shorter handling time than if they have a higher net energy.

The explanation for the harvesting curve differences lies in the nature of how prey are ranked and how average yield is computed. Using figure 1 as an example, consider a predator who at the moment is only including the highest ranked prey in its diet (rank 1). What are the consequences of adding the next lowest ranked prey (rank 2)? If the next lowest ranked prey has only a lower net energy ( $E_2^* < E_1^*$ ) but the same handling time ( $h_2^* = h_1^*$ ), and for the sake of argument has the same

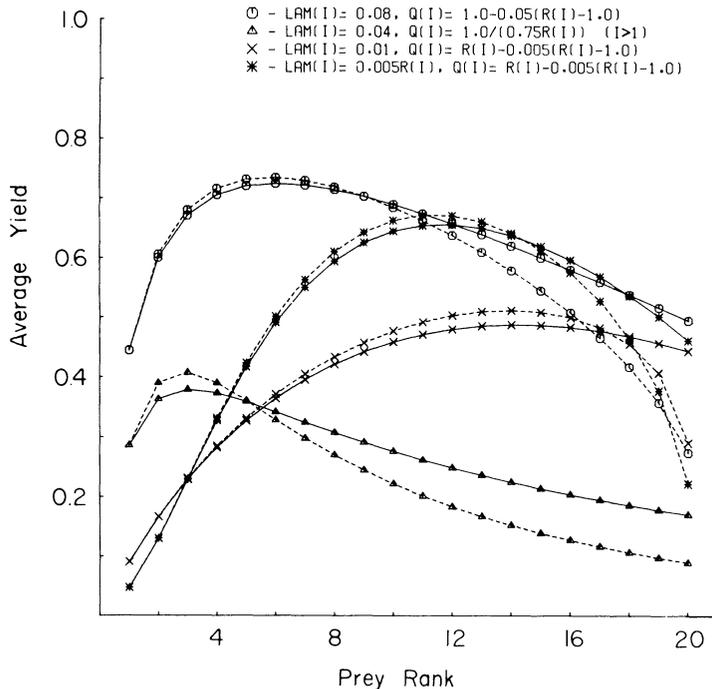


FIG. 2.—Selected harvesting curves illustrating the shape change when prey vary in handling time (dashed lines) versus net energy (solid lines). The value of the highest ranked prey is 1.0 (net energy = 10, handling time = 10) for all curves. LAM-encounter rate,  $Q(I)$  = value of the  $I$ th ranked prey type,  $R(I)$  = rank of  $I$ th ranked prey. The equation used to generate these curves is Charnov's (1976) equation (1). Equations in the figure describe the parameter values used to generate the curves.

encounter rate as prey 1 ( $\lambda_1 = \lambda_2$ ), then the predator will be consuming twice as many total prey items per unit foraging time as it was when it was only consuming prey of rank 1. It will also be spending twice as much time in the act of feeding as it was before. While actually in the process of feeding it is obtaining  $E_2^*/h_2^*$  calories per unit time (the expected value of prey 2) and because the net energy per unit time gained while in the process of feeding is greater than the average energy per unit time ( $E_N/T$ ) when it was only including prey 1, its average energy intake increases.

If, however, the next lowest ranked prey (rank 2) has only a longer handling time ( $h_2^* > h_1^*$ ) but the same net energy ( $E_2^* = E_1^*$ ), and as before it has the same encounter rate as prey 1 ( $\lambda_2 = \lambda_1$ ), the result of adding it to the diet is somewhat different. As in the first example, while in the process of feeding the predator is obtaining  $E_2^*/h_2^*$  calories per unit time, which is greater than the average when including only prey 1, but in this instance it is spending even more time actually in the act of feeding. The encounter rates are still the same, but, because of the longer handling time of prey 2, fewer total prey items are consumed per unit foraging time. Therefore a greater proportion of the total foraging time (searching

plus handling time) is now directly involved with feeding. In other words, a greater proportion of total foraging time spent feeding (an energy gaining activity) is equivalent to a lower proportion of time spent searching (an energy expending activity) and consequently the average yield increases more than it would if the next lowest prey was only of lower net energy.

This reasoning may also be applied when adding prey whose value is less than the average yield (an incorrect decision). As described above, if an inappropriate prey has a longer handling time ( $h^*$ ) rather than a lower net energy ( $E^*$ ), the predator will be spending a greater proportion of its time actually in the act of feeding. In this instance, however, the energy per unit time obtained while in the act of feeding is less than the average, hence the average will drop more.

ALGEBRAIC ARGUMENT

The question posed above may be expressed algebraically as follows: What is the relation between  $Y_e$  (the new average yield when a prey type of different net energy [ $E^*$ ] is added to [+ ] or rejected from [- ] the diet) and  $Y_h$  (the new average yield when a prey type of different handling time [ $h^*$ ] is added to [+ ] or rejected from [- ] the diet)?  $Y_e$  and  $Y_h$  are defined as:

$$Y_e = \frac{\sum_{i=1}^n \lambda_i E_i^* \pm \lambda_k (1/s) E_n^*}{1 + \sum_{i=1}^n \lambda_i h_i^* \pm \lambda_k h_n^*}, \tag{1}$$

and

$$Y_h = \frac{\sum_{i=1}^n \lambda_i E_i^* \pm \lambda_k E_n^*}{1 + \sum_{i=1}^n \lambda_i h_i^* + \lambda_k s h_n^*}. \tag{2}$$

As before  $\lambda_i$  = encounter rate of  $i$ th prey type,  $E_i^*$  = expected net energy of an item of prey type  $i$ , and  $h_i^*$  = expected handling time of an item of prey type  $i$ .  $\lambda_k$  = encounter rate of the prey type in question and  $s$  = the proportional difference between the value of the lowest ranked prey type presently included in the diet (where  $i=n$ ) and the value of the prey type in question ( $s > 1$  when lower value prey are added,  $0 < s < 1$  when prey of higher value are rejected). This permits prey of identical value to be added to or rejected from the diet [ $(1/s)E_n^*/h_n^* = E_n^*/s h_n^*$ ] but in one case vary net energy and in the other case handling time.

Inspection of the harvesting curve pairs in figure 2 reveals that the handling-time dependent curves (dashed lines) rise more rapidly to the optimum (have a greater slope) than net-energy dependent curves, but that beyond the optimum they also drop more rapidly (handling-time dependent slope less than net-energy dependent slope). Hence the relation between  $Y_e$  and  $Y_h$  after the prey type in question has been included in or rejected from the diet will depend on which side of the

optimum is being considered, and an additional parameter  $r$  must be introduced.  $r$  indicates the proportional difference between the value of the last prey type included in the diet and the average yield with that prey type included:

$$\frac{E_n^*}{h_n^*} = r \frac{\sum_{i=1}^n \lambda_i E_i^*}{1 + \sum_{i=1}^n \lambda_i h_i^*}. \quad (3)$$

If  $r$  is greater than one, the value of the last prey type is greater than the present average yield and we are still on the rising portion of a harvesting curve (to the left of the optimum, fig. 1); if  $r$  is less than one the value of the last prey type added is less than the present average yield and we are on the declining portion of a harvesting curve (to the right of the optimum, fig. 1). Although the value of  $r$  determines the present position on the harvesting curve, it is not sufficient to determine if the optimum will be passed on addition of the next lower value prey type, as will be shown below. First, however, it is possible to investigate the relationship between  $Y_e$  and  $Y_h$  for various combinations of  $r$  (present position on the harvesting curve) and  $s$  (relative value of the prey being added or rejected).

Consider initially the situation where prey are added to the diet in equations (1) and (2). Under what conditions is the inequality

$$Y_e > Y_h \quad (4)$$

true? To simplify notation, let  $A = \sum_{i=1}^n \lambda_i E_i^*$ ,  $B = 1 + \sum_{i=1}^n \lambda_i h_i^*$ ,  $C = \lambda_n E_n^*$  and  $D = \lambda_n h_n^*$ . Inequality (4) thus becomes:

$$\frac{A + (1/s)C}{B + D} > \frac{A + C}{B + sD}. \quad (5)$$

Substituting as above in equation (3) yields:

$$\frac{C}{D} = r \frac{A}{B},$$

or alternatively,

$$BC = rAD. \quad (6)$$

Cross multiplying and canceling like terms in inequality (5) results in:

$$sAD + (1/s)BC > AD + BC. \quad (7)$$

Substituting  $rAD$  for  $BC$  (from eq. [6]) in inequality (7) and canceling  $AD$  we obtain:

$$s + r/s > 1 + r,$$

which upon multiplying through by  $s$  ( $s$  is always positive) and consolidating like terms, simplifies to:

$$s > r, \quad (8)$$

for all values  $s > 1$  (i.e., lower ranked prey are being added to the diet). It is also clear that the reverse of inequality (4) will be true when the reverse of inequality (8) is satisfied. Therefore when adding prey to the diet the direction of inequality (4) is determined entirely by the relation between  $s$  and  $r$ ; the actual values for  $\lambda$ ,  $E^*$ , and  $h^*$  do not affect the conclusions.

It is also possible to evaluate the consequences of rejecting (subtracting from the diet in eqq. [1] and [2]) higher ranked prey ( $s < 1$ ). Changing signs in equations (1) and (2), inequality (5) becomes:

$$\frac{A - (1/s)C}{B - D} > \frac{A - C}{B - sD} \tag{9}$$

which reduces to:

$$-s(s - 1) > -r(s - 1)$$

following the same logic outlined above. However,  $s$  is now less than one, thus dividing through by  $(s - 1)$  and multiplying by  $-1$  returns us to equation (8). As before, the reverse of inequality (9) will be true for values satisfying the reverse of inequality (8). In other words, regardless of whether prey types are being added to or rejected from the diet, inequalities (5) or (9) are both directly dependent on the relation between  $s$  and  $r$ .

To determine unconditionally whether the optimum will be passed on addition of the next lower ranked prey type, it is necessary to solve the following inequality:

$$Y_e > Y_o \tag{10}$$

where  $Y_e$  is the average yield after the next lower ranked prey type has been added to the diet, and  $Y_o$  is the average yield before it has been added. Using the substitutions described for inequality (5), inequality (10) becomes:

$$\frac{A + (1/s)C}{B + D} > \frac{A}{B}$$

which, upon cross multiplication, yields:

$$\frac{1}{s}BC > AD. \tag{11}$$

Multiplying through by  $s$ , substituting for  $BC$  from equation (6) and canceling terms reduces inequality (11) to:

$$r > s. \tag{12}$$

It is easily demonstrated that the inequality  $Y_h > Y_o$  also reduces to inequality (12). Further, reversing the direction of inequality (10), a consideration when higher ranked prey are being rejected from the diet, merely reverses the direction of inequality (12). Consequently, as lower value prey are added to the diet the unconditional characterization of the ascending portion of the harvesting curve is  $r > s$ ; for the descending portion of the curve it is  $r < s$ .

TABLE 1

EFFECT OF ADDING LOWER OR REJECTING HIGHER RANKED PREY TYPES ON AVERAGE YIELD ( $E_N/T$ ) IN DIFFERENT REGIONS OF A HARVESTING CURVE

POSITION OF PREDATOR'S PRESENT AVERAGE YIELD ON HARVESTING CURVE	PREDATOR DECISION	
	Add Next Lower Ranking Prey ( $s > 1$ )	Reject Next Higher Ranking Prey ( $0 < s < 1$ )
Ascending portion of harvesting curve ( $s < r$ ) . . . . .	(1) Correct decision, increase of average greater for varying $h^*$	(2) Incorrect decision, decrease of average greater for varying $h^*$
Descending portion of harvesting curve ( $s > r$ ) . . . . .	(3) Incorrect decision, decrease of average greater for varying $h^*$	(4) Correct decision, increase of average greater for varying $h^*$

NOTE.—Decisions 2 and 3 represent errors which result in reduced average energy intake.

INTERPRETATION AND PREDICTIONS

Table 1 summarizes the consequences of correctly or incorrectly adding or deleting prey types. From this table it is clear that correct decisions always result in a greater increase in the average yield where prey vary in handling time than where they vary in net energy, and that incorrect decisions result in a greater decrease in the average for prey that vary in handling time. The decrease in average yield associated with an incorrect decision may be considered a cost in terms of reduced potential growth when compared to an organism not making such an incorrect decision.

The implication of this analysis is intriguing. Other things being equal, predators whose prey vary primarily in handling time would be expected to make fewer errors (decisions 2 and 3, table 1) than predators whose prey vary primarily in net energy because the cost of making an error will be greater. In decision 3 for example, for the same number of decision errors a consumer of long handling-time prey will spend more time feeding on inappropriate prey than a predator consuming prey varying in net energy. This would be particularly important for predators that attempt to obtain a fixed amount of energy in the least amount of time (time minimizers, Schoener 1971).

Another prediction from this analysis is that predators in environments where prey availability fluctuates in space or time would be expected to reevaluate their average yield (Cowie 1977; Krebs 1977; Palmer 1980) over a shorter time interval or over fewer prey items if their prey vary in handling time as opposed to net energy (a consequence of decisions 1 and 4, table 1). In other words if prey availability suddenly increases (predator's present yield now to the right of the predicted optimum) or decreases (predator's present yield now to the left of the predicted optimum), decreasing the averaging time results in a greater increase in the average yield where prey value is handling-time dependent.

A final implication is that where predators are exposed to higher risks while in the process of feeding than while searching, these risks will be of greater importance to predators consuming prey whose value is handling-time as opposed to net-energy dependent. This is because a greater proportion of the total foraging time is being spent in the act of consuming prey, and risk while feeding is likely to be proportional to handling time. Thus, consumers of long handling-time prey would again be expected to make fewer prey-choice mistakes than consumers of prey varying in net energy. Such risks, however, would also be likely to alter the rankings of prey.

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