



Searching for Cryptic Prey: A Dynamic Model

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SEARCHING FOR CRYPTIC PREY: A DYNAMIC MODEL¹

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Abstract. We present a dynamic model to examine sequential foraging decisions of predators searching for cryptic prey. We identify key elements of information processing and ecological factors determining the costs and benefits of two foraging alternatives. On the one hand, specializing on a single prey type while ignoring other types increases the distance a forager must move; this involves increased energy and time expenditures. On the other hand, switching between searching for several prey types has the obvious cost of an initial reduction in the probability of detecting prey immediately after switching. Switching also has the less apparent cost of a forager's reduced ability to assess the probability of prey presence. We show that if the cost of switching is sufficiently high, and a forager estimates that one prey type is more common than others, then the forager should search for this prey only, unless conditions change.

Key words: *dynamic programming; foraging; information processing; learning; prey detection; search patterns; switching.*

INTRODUCTION

The foraging patterns of predators searching for cryptic prey strongly affect populations and communities of animals and plants (Hassell 1978, Sih et al. 1985, Martin 1988, Crawley 1992). Such foraging patterns are shaped by constraints on the processing of information by these predators (Tinbergen 1960, Pietrewicz and Kamil 1981, Milinski 1990, Dukas and Ellner 1993, Getty and Pulliam 1993). Therefore, realistic theoretical and empirical understanding of predators' search patterns and their dynamics is essential.

Dukas and Ellner (1993) presented a model to examine how limitations on the simultaneous processing of information affect searching behavior. Their model indicates that a forager may be more successful if it searches simultaneously for items of only a single cryptic prey type while ignoring other cryptic types. However, Dukas and Ellner's model assumes that foragers constantly move through the environment and encounter new prey. The model does not explicitly address sequential searching decisions. Nonetheless, recent studies emphasize that the sequential searching behavior of many predators involves series of pauses and runs. Searching for, and detection of prey, occurs only during pauses (Anderson 1981, O'Brien et al. 1990, Getty and Pulliam 1991, 1993).

A forager that pauses to search for cryptic prey but does not detect any prey item after a short time can choose one of three alternatives. First, it may simply continue pausing and searching for the same prey type. Second, it may continue pausing, but switch to searching for another prey type. Third, it may move a certain distance, then pause again and resume search. We present here a model to examine the costs and benefits

associated with each alternative, and to predict the optimal searching strategy that foragers should employ. This extension of the model of Dukas and Ellner (1993) permits a more realistic examination of both the simultaneous and sequential problems of information processing underlying searching behavior.

THE MODEL

We assume that the foraging period is divided into T short time intervals ($t = 1, 2, \dots, T$); each interval is long enough to enable the forager to scan its effective visual field. We also assume that items of a few distinct and familiar cryptic prey types are randomly distributed, that the forager can find only a single item of prey of each type during the same pause, and the "prior" probability of encountering an item of any type i , per time period, while pausing, is p_e . Here "encountering" refers to physical proximity, e.g., a prey item is encountered when it comes within the visual range of the forager. The forager then may detect an encountered prey item with a probability p_d . The probability of detecting prey is a function of (1) the conspicuousness of this prey, defined as the degree of dissimilarity between the prey and its surrounding background (Gendron and Staddon 1983, Dukas and Ellner 1993), (2) the exact distance between the prey item and the forager during pausing (e.g., Getty and Pulliam 1993), and (3) the forager's search rate, defined as the area searched per unit of time (Gendron and Staddon 1983, Dukas and Ellner 1993, Reid and Shettleworth 1992). For brevity, we do not elaborate here on these issues. Rather, we concentrate on the effects of switching on the probability of detecting cryptic prey.

Behavioral and physiological studies indicate that humans and other animals show an initial reduction in performance after switching between sequential tasks

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(Wickens 1984, Baddeley 1986, Lewis 1986, Anderson 1990, Croy and Hughes 1991). For example, egg-laying *Colias* butterflies made 12% more mistaken landings on plants after a run of foraging on flowers (Stanton 1983). As another example, upon switching from one floral type to another familiar type, bumble bees (*Bombus bimaculatus* Cresson) increased initial handling times by 50–180% (Woodward and Lavery 1992). After switching to searching for prey of type i , the forager may regain its maximum probability of detecting items of this familiar type within several time intervals. We let y denote the number of time intervals since the most recent switching, and use a general learning model (e.g., Dukas and Real 1993a) to describe the association between the probability of detection (p_d) and y ,

$$p_d = a - be^{-\delta y}, \quad (1)$$

where a is the asymptote, $(a - b)$ is the intercept, and δ is the rate of re-learning. By presenting p_d as a function of number of time intervals, we assume that both finding and not finding prey are valuable experiences for the forager. Learning is typically presented as a function of overall experience, and this seems to be well justified in our specific case. While locating prey can clearly enhance subsequent performance, failing to detect prey may be equally helpful. Such failure can help the forager to re-learn (1) to ignore non-prey items that are similar to prey, (2) to search for prey in more suitable micro-sites, or (3) to attend to another prey attribute that makes it easier to detect this prey.

The forager's probability of finding a prey item i during the first time interval during a pause is therefore $p_d p_e$. The probability of finding an item i in any time interval during a pause can be calculated using Bayes' theorem (e.g., Berger 1980, McNamara and Houston 1980, Mangel and Clark 1988). First, the probability of not detecting prey i (even though it is present) during a pause is

$$\Pr(y, z) = (1 - p_d(y - 1))(1 - p_d(y - 2)) \dots (1 - p_d(y - z)), \quad 1 \leq z \leq y. \quad (2)$$

Also $\Pr(y, 0) = 1$, where, as before, y = time spent searching for prey type i , and z = time spent in unsuccessful search for prey i in the current pause ($0 \leq z \leq y$). Therefore, the probability that prey is present, given y and z , is

$$\lambda(y, z) = \frac{\Pr(y, z)p_e}{\Pr(y, z)p_e + 1 - p_e} \quad (3)$$

and the probability of finding a prey item is

$$R(y, z) = \lambda(y, z)p_d(y). \quad (4)$$

In words, the probability of finding prey in the first time interval during a pause is an increasing function of the time spent in the same search mode y (Fig. 1; upper curves). On the other had, if prey is not found

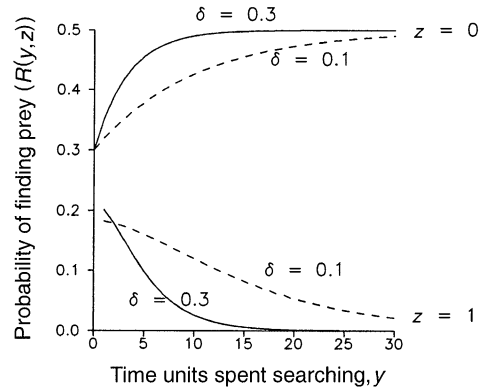


FIG. 1. The probability of finding a prey item of given type, $R(y, z)$, as a function of the time spent searching (y) for this prey type. The upper pair of curves describes $R(y, z)$ for the first time period during a pause ($z = 0$); the lower pair of curves describes $R(y, z)$ for the second time period ($z = 1$), following an unsuccessful search in the first period. The rate of re-learning (δ) is either 0.1 (broken line), or 0.3 (continuous line). Other parameter values are: $p_e = 0.5$, $a = 1$ and $b = 0.4$.

in the first time interval, the probabilities of finding prey in the second and subsequent time intervals during a pause may become decreasing functions (depending on parameter values) of the time spent in the same search mode y (Fig. 1; lower curves). Both the rates of increase and decrease in $R(y, z)$ are larger for larger values of δ , the rate of re-learning.

Evaluating the alternative searching strategies

Based on the above formulas, we developed a dynamic optimization model of searching behavior (see Appendix). Briefly, the model operates as follows. After pausing, the forager should always search for prey during the first time interval. If it does not find prey, it then may choose one of three alternatives: (1) continuing to search for the same prey, (2) switching to search for another prey, or (3) moving. With the parameter values of δ used here, the probability of finding the same prey in subsequent time intervals during a pause is low even for moderate values of y (Fig. 1; lower curves). Therefore, the forager should not continue pausing and searching for the same prey for long; rather, it should either move or switch. Moving has the advantage of keeping a high probability of detecting prey (Fig. 1; upper curves). However, moving involves an energetic cost and also expends some time not searching. On the other hand, switching incurs two other costs. First, the initial probability of finding prey is lower. Second, the forager has less reliable information about the probability of finding prey in the current pause position because its initial probability of detecting prey is lower. Therefore, after switching, the forager may spend a longer time pausing and searching even when prey is not present.

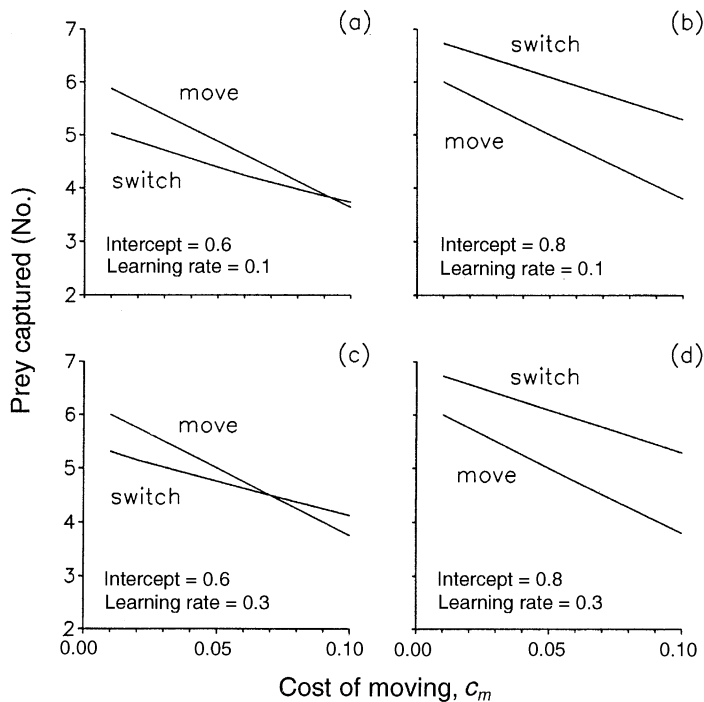


FIG. 2. The number of prey items captured while using either the "move" or "switch" strategy for a range of moving costs (measured as a proportion of the energy content per prey). The intercept ($a - b$) and rate of re-learning (δ) values are (a) 0.6 and 0.1, (b) 0.8 and 0.1, (c) 0.6 and 0.3, and (d) 0.8 and 0.3, respectively. Other parameter values are: $p_e = 0.25$, $a = 1$, $T = 50$.

RESULTS

The optimal search strategy

We define $F(x, y, z, t)$ as the forager's expected total energy gain from time t to T , where x indicates the prey type the forager is currently searching for, and y and z are described above. For simplicity, we now consider only two prey types which are distinct in all their attributes, $x = 1$ or 2 . Given x, y, z at time t , the forager then should choose the strategy that maximizes $F(x, y, z, t)$ (Appendix). After finding prey, or after some time intervals of pause and unsuccessful search, the forager may either move on and continue searching for the same prey, or it may continue pausing but switch to searching for the other prey type. Except for prey parameters, the optimal strategy is affected by three factors: the energetic cost of moving (Appendix), the intercept, and rate of re-learning (see Eq. 1). We express the cost of moving as a fraction of the energy gained from prey. Such cost may vary among species, and is also a function of the profitability and density of prey. We chose 10 values of moving cost (c_m) of 1–10% of the energy content per prey. These values cover a realistic range of observed parameters (Fedak and Seeherman 1979, Ellington et al. 1990).

The initial reduction in foragers' abilities to detect familiar cryptic prey and the rate of increase in probability of detection after switching have not been quantified experimentally. Based on indirect information (Pietrewicz and Kamil 1981, Baddeley 1986, Lewis 1986, Woodward and Lavery 1992) we chose two moderate values of 0.2 and 0.4 for the initial reduction in

probability of detection (b in Eq. 1) and rates of re-learning of 0.1 and 0.3 per time period (δ in Eq. 1).

Prey types with identical parameter values

First, we consider the simplest case, where the forager encounters two distinct prey types with identical parameters, i.e., items of each prey type are equally cryptic and have the same energetic content, handling time, and density. When the initial cost of switching is 0.4 (a 40% reduction in probability of detection), the forager captures more prey if it searches for only a single prey under most values of moving cost (Fig. 2a). Here, the gain from keeping the initial probability of detection high by not switching compensates for both the cost of moving and the lost opportunity of finding another prey. On the other hand, a 50% decrease in the initial cost of switching (from 0.4 to 0.2) makes switching the optimal searching strategy for the whole range of moving costs (Fig. 2b). An increase in the rate of re-learning from 0.1 to 0.3 reduces the overall cost of switching. Although the initial cost of switching is identical, re-learning is faster and, thus, the overall cost of switching is lower. This makes switching the optimal behavior for the higher range of moving costs when the initial cost of switching is 0.4 (Fig. 2c). However, increased rate of re-learning has little effect on the relative benefit of switching when the initial cost of switching is only 0.2 (Fig. 2d).

Prey types with different density

Next, suppose that prey types have different density, but share all other parameters, i.e., they are equally

cryptic and have the same energetic content and handling time. Note that prey density is represented in our model by the value of p_e , the "prior" probability of encountering prey. Fig. 3 presents the payoffs for using either the move or switch strategies for a range of densities of prey type 2, and for an intermediate moving cost of 0.05. When the initial cost of switching is 0.4, the forager captures more prey if it searches for only a single prey (Fig. 3a). Again, the gain from keeping the initial probability of detection high by not switching compensates for both the cost of moving and the lost opportunity of finding another prey. On the other hand, a 50% decrease in the initial cost of switching makes switching the optimal searching strategy, but only if the other prey is relatively abundant (Fig. 3b). Although an increase in the rate of re-learning from 0.1 to 0.3 reduces the overall cost of switching, it has relatively little effect on the optimal searching strategy (Fig. 3c, d).

DISCUSSION

The trade-off between the cost of switching and the cost of moving

The central concept we model here is that sequential search for cryptic prey involves a trade-off between the costs of switching and the costs of moving. Some aspects of this trade-off have been mentioned in previous theoretical and empirical investigations of foraging (Hughes 1979, McNair 1981, Lewis 1986, Waser 1986, Croy and Hughes 1991, Woodward and Laverty 1992, Dukas and Ellner 1993, Dukas and Real 1993a).

Nevertheless, as far as we know, no previous study has examined an overall analysis of the factors involved.

When items of several prey types are randomly distributed, searching for one type while ignoring others increases the distance foragers must move. This has the obvious costs of increased energetic expenditure and moving time. On the other hand, switching between searching for different prey types involves a widely recognized cost in terms of an initial reduction in the probability of detecting prey. This reduction also has a less apparent cost, resulting from the forager's reduced ability to assess the probability of prey presence. In other words, when the initial probability of detecting prey is low, the forager cannot know whether it has found prey because prey is not present, or because the forager's probability of detecting such prey is low. On the other hand, when the initial probability of detection is high, a forager who does not find prey can quickly conclude that prey is probably not present.

Another possible cost of switching is partial forgetting of information about spatial and temporal patterns of prey availability and profitability. Such a cost is irrelevant in our model, which assumes uniformly random distribution of prey items of identical quality. However, in many cases prey distribution is not uniformly random, and foragers of many species are able to adjust their behavior for exploiting patchily distributed food (e.g., Hassell 1978, Price and Reichman 1987, Dukas and Real 1993b). Therefore, a more realistic model should also account for the forager's knowledge about spatial and temporal prey parameters,

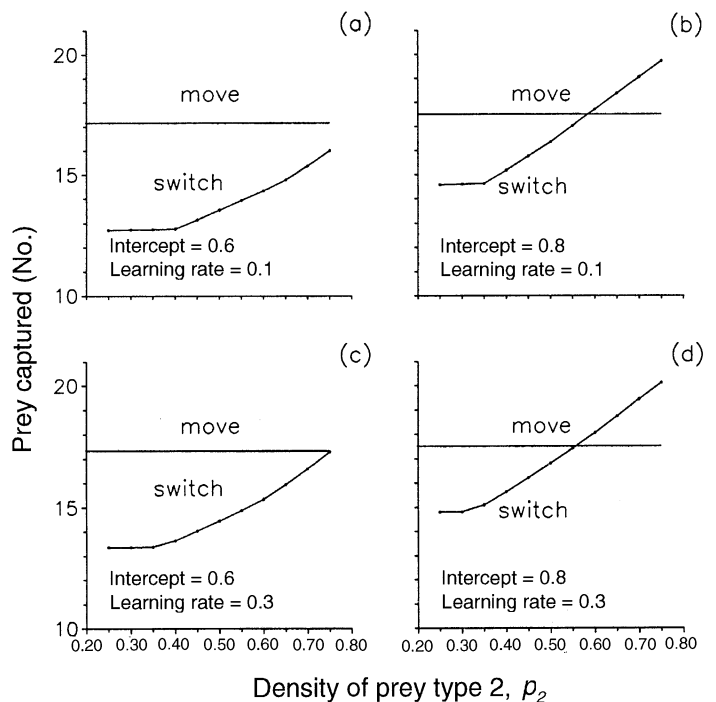


FIG. 3. The number of prey items captured while using either the "move" or "switch" strategy for a range of densities (probability of encountering prey) of prey type 2. The density of prey 1 is 0.75, the cost of moving is 0.05, and $a = 1$. See values for intercept and rate of re-learning in Fig. 2.

and the effect such knowledge has on the optimal searching behavior. The theoretical treatment of such problems might get rather complicated (McNamara and Houston 1985, 1987, Mangel 1990). Fortunately however, animals appear to use relatively simple decision rules which are based on limited amounts of information (e.g., Bouskila and Blumstein 1992). Such rules may be easier to incorporate into future models of searching behavior.

In our model, we allow the probability of prey detection to increase as a function of time periods whether prey items are detected or not. In other words, we regard each time period as a trial and take performance to be a function of the total number of trials. Changes in behavior due to experience are usually examined in regard to the entire experience, i.e., the total number of learning trials. Such trials most commonly include both successful and unsuccessful attempts. This is done for two major reasons. First, one loses the unbiased measure of experience if only positive trials are counted. Second, unsuccessful attempts may be as valuable or even more valuable than successful attempts. In other words, one may learn more from a failure than from success. For our specific model, a failure means not locating prey; this may result from (1) approaching and rejecting a non-prey item similar to the prey, (2) not searching for prey items at the best micro-sites, or (3) not attending to the best prey attribute which makes it easier to detect this prey. Experiencing any of these possibilities is likely to enhance subsequent prey detection. Thus the forager may re-learn to (1) ignore non-prey items, (2) search in alternate micro-sites within the same locality, or (3) attend to another prey attribute. Although we believe our above assumption is well justified, we do not know the relative value of success and failure for learning. Thus the assumption remains to be critically tested. At least one study on "search images" suggests that unsuccessful trials have negative effects on subsequent performance (Gendron 1986). Nevertheless, this proposition must be further evaluated under well-controlled experimental conditions.

We concentrated here on the problem of prey detection while assuming that manipulation of prey is trivial. For many foragers, however, both detection and manipulation of food items are difficult tasks. Two recent studies questioned whether increased handling costs after switching were sufficiently high to explain specialization (Croy and Hughes 1991, Woodward and Lavery 1992). Although handling costs alone may not be adequate, the combination of decreased detection and increased handling due to switching might be large enough to justify specialization.

The optimal search strategy

Our model suggests that the most important parameter affecting the trade-off between switching and moving is the initial reduction in probability of finding prey

after switching. A 40% reduction is sufficient to make specialization on a single prey the optimal strategy under a wide range of moving costs. Similarly, such reduction makes specialization on a single prey type optimal if other prey types are less common. In other words, if the cost of switching is sufficiently high and a forager estimates that one prey type is more common than others, then the forager should search for this prey only, as long as conditions do not change.

Ways of evaluating the model

In spite of the ecological importance of searching behavior, key parameters shaping such behavior have not yet been quantified. These include the relative costs of moving and the direct and indirect effects of switching on the probability of detecting prey. Quantifying such costs for prey types with a range of conspicuousness values must therefore precede a direct test of the model. The problem of searching for cryptic prey with negligible handling is most relevant for birds feeding on cryptic seeds or camouflaged insects. Several successful experimental paradigms using birds (Pietrewicz and Kamil 1981, Reid and Shettleworth 1992, Getty and Pulliam 1993) may therefore be adopted for evaluating our model's parameters and predictions.

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APPENDIX

THE DYNAMIC MODEL

We describe briefly the dynamic programming model used to obtain the results of this paper. In the model, time is treated as a discrete variable $t = 1, 2, \dots, T$; in a given time interval t the forager can either scan for prey during a pause, or move to a new location. We compare the effectiveness of two search strategies: (1) The "move" strategy, wherein the forager specializes on a single prey type; if a prey of this type is detected (and consumed) the forager then moves to a new location and resumes search; if no prey is encountered after n intervals of search in a given location, the forager also moves to a new location. Our model determines the optimal duration of unsuccessful search. The alternative strategy is (2) the "switch" strategy, in which the forager alternates between two prey types. Having found a prey of the first type, the forager then switches to search for the second type (rather than moving to a new location). Also, after n periods of unsuccessful search, the forager switches to the second type. Only after searching for both types does the forager relocate itself.

We refer to a sequence of consecutive time periods during which the forager continues to search for prey in a given location as a "pause." Moving between pauses is assumed to use up one time period t .

Three state variables are required in our dynamic programming model (see Mangel and Clark 1988):

$X(t)$ = number of prey types already detected and consumed (or, for the switch strategy, given up hope of finding) during the current pause,

$Y(t)$ = number of time periods spent in continuous search for current prey type,

$Z(t)$ = number of time periods spent in unsuccessful search for current prey type during current pause.

Thus, $Y(t)$ is incremented by one following a time period t of search for the same prey; $Y(t)$ is reset to 0 following a switch in prey type; and $Y(t)$ is unchanged when moving without switching. Similarly, $Z(t)$ is reset to 0 following either a switch in prey type or a move.

Move strategy.—For the move strategy, the forager searches only for the best prey type. Thus, $X(t)$ can take on the values 0 or 1 only. The forager's fitness function (assuming the move strategy) is defined as $F_m(x, y, z, t)$ = maximum expected number of prey recovered from period t to T inclusively, given $X(t) = x$, $Y(t) = y$, $Z(t) = z$. The maximization here refers to using the optimal length of time to spend in unsuccessful search before moving. The fitness function satisfies the following dynamic programming equations:

$$F_m(x, y, z, T) = \begin{cases} R(y, z) & \text{if } x = 0 \\ 0 & \text{if } x = 1, \end{cases} \quad (\text{A.1})$$

where $R(y, z)$ is the probability of finding a prey item, given y and z ; see Eq. 4. For $t < T$

$$F_m(0, y, z, t) = \text{maximum of:}$$

(1) continue search:

$$R(y, z)[1 + F_m(1, y + 1, 0, t + 1)] + (1 - R(y, z))F_m(0, y + 1, z + 1, t + 1) \quad (\text{A.2})$$

(2) move:

$$F_m(0, y, 0, t + 1) - c_m \quad (\text{A.3})$$

where c_m denotes the metabolic cost of moving (in units of prey item value). Also

$$F_m(1, y, z, t) = F_m(0, y, 0, t + 1) - c_m \quad (\text{A.4})$$

Let us describe briefly the logic behind these equations. Eq. A.1 asserts that the expected number of prey captured in the terminal period $t = T$ is just $R(y, z)$, unless prey has already been exhausted in the current location ($x = 1$). For $t < T$, if the forager chooses to continue searching (Eq. A.2), it will be successful with probability $R(y, z)$, in which case the number of food items found equals 1 plus the number expected from $t + 1$ on; this latter number is equal to $F_m(1, y + 1, 0, t + 1)$ because in this case $X(t + 1) = 1$, $Y(t + 1) = y + 1$, and $Z(t + 1) = 0$. Similarly, if no prey is detected in period t , future expected food recoveries are given by $F_m(0, y + 1, z + 1, t + 1)$. If the forager chooses to move, then $X(t + 1) = 0$, $Y(t + 1) = y$, $Z(t + 1) = 0$, leading to Eq. A.3. Finally, if $X(t) = x = 1$ (local prey already exhausted), the forager is forced to move (and not to switch prey type, for the present case), which leads to Eq. A.4.

Numerical computation of the fitness function $F_m(x, y, z, t)$ is carried out as usual by iteration of these dynamic programming equations. These iterations run backwards in time, starting at $t = T$; Mangel and Clark (1988) discuss the computational rationale and details of this standard procedure.

Switch strategy.—We consider the simplest case of two prey types with identical parameter values. After moving, it is always optimal to resume searching for the same prey type last searched for (whether successful or not). This is not nec-

essarily true when searching for prey types with different parameters. For brevity we omit discussion of the model equations for this case (Fig. 3). For the switch strategy, $X(t)$ can assume the values 0, 1, or 2. The fitness function $F_s(x, y, z, t)$ is defined as before, and the dynamic programming equations now become:

$$F_s(x, y, z, T) = \begin{cases} R(y, z) & \text{if } x = 0 \text{ or } 1 \\ 0 & \text{if } x = 2 \end{cases} \quad (\text{A.5})$$

and for $t < T$,

$$F_s(0, y, z, t) = \text{maximum of:}$$

(1) continue search:

$$R(y, z)[1 + F_s(1, 0, 0, t + 1)] + (1 - R(y, z))F_s(0, y + 1, z + 1, t + 1) \quad (\text{A.6})$$

(2) switch to second prey type:

$$R(0, 0)[1 + F_s(2, 0, 0, t + 1)] + (1 - R(0, 0))F_s(1, 1, 1, t + 1) \quad (\text{A.7})$$

and

$$F_s(1, y, z, t) = \text{maximum of:}$$

(1) continue search:

$$R(y, z)[1 + F_s(2, 0, 0, t + 1)] + (1 - R(y, z))F_s(1, y + 1, z + 1, t + 1) \quad (\text{A.8})$$

(2) move

$$F_s(0, y, 0, t + 1) - c_m \quad (\text{A.9})$$

Finally

$$F_s(2, y, z, t) = F_s(0, y, 0, t + 1) - c_m \quad (\text{A.10})$$

These equations are derived by arguments similar to those used before.