THE INFLUENCE OF PREDATION RISK ON WITHIN-PATCH FORAGING DECISIONS OF CRYPTIC ANIMALS

by

Robert Houtman

B.Sc., Simon Fraser University, 1986

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

April 1995

APPROVAL

NAME: **Robert Houtman**

DEGREE: DOCTOR OF PHILOSOPHY

TITLE OF THESIS:

THE INFLUENCE OF PREDATION RISK ON WITHIN-PATCH FORAGING DECISIONS OF CRYPTIC ANIMALS

Examining Committee:

Chair: Dr. A. S. Harestad

Dr. L. M. Dill, Professor, Senior Supervisor,
Department of Biological Sciences, SFU

Dr. R. C. Ydenberg, Associate Professor
Department of Biological Sciences, SFU

Dr. B. D. Roitberg, Professor
Department of Biological Sciences, SFU

Dr. C. W. Clark, Professor
Department of Applied Mathematics, UBC
Public Examiner

Dr. T. Getty, Associate Professor
W. K. Kellogg Biological Station, Michigan State Univ.
External Examiner

Date Approved April 19, 1995

PARTIAL COPYRIGHT LICENSE

Title of Thesis/Project/Extended Essay

The Influence of Predation Risk on Within-Patch
Foraging Decisions of Cryptic Animals.

Author:
(signature)

(name)

19 IV 1995
(date)

Abstract

Cryptic animals must trade-off foraging benefits with predation risk costs, because foraging movements reduce their crypsis, thus exposing them to predators. A forager's estimate of the predation risk associated with various foraging options will vary with its estimate of the probability that a predator is present ("ϕ"). In this thesis, ϕ is varied to examine the influence of predation risk on the foraging behavior of cryptic animals.

I show experimentally that the response of tidepool sculpins (*Oligocottus maculosus*) to conspecific skin extract (elevated ϕ) depends on their level of crypsis. Cryptic subjects (on sand substrate), for whom movement is risky relative to immobility, reduce their rate of movement more than non-cryptic ones (on white substrate), for whom movement is relatively safe (*i.e.*, relative to immobility).

I generate predictions about ϕ dynamics, prey capture distances, and diet selectivity mathematically. A Bayesian-updating model specifies how information influences ϕ, and predicts that following predator detection, ϕ generally decays to a non-zero asymptote, at rates dependent on an animal's vigilance and crypticity. A dynamic programming model (DPM), with state variables representing energy and ϕ state (the dynamics of which are specified by the updating model), determines the maximum prey capture distances which maximize the probability of surviving a foraging period. The model predicts that capture distances decrease with increasing energy state and ϕ state, and that the influence of ϕ on capture distances will increase with energy state. I show that sculpins capture brine shrimp (*Artemia* sp.) at shorter distances with skin extract present than without, supporting the prediction that prey capture distances decrease with ϕ. The DPM also predicts that the relationship between prey profitability and danger associated with prey capture influences how diet selectivity changes with ϕ. An experiment on juvenile coho salmon (*Oncorhynchus kisutch*) failed to demonstrate this effect. Finally, by coupling the DPM output with a forward simulation model, the effects of predator arrival probability, forager crypticity, and food availability on diet selectivity are examined.

To Dr. O., who I think would have liked the thesis, math notwithstanding,

and mom, who got me wondering.

Acknowledgements

I thank the many people who contributed intellectually, emotionally, and/or physically to this thesis. Here are some of them.

Larry Dill, my senior supervisor, was always a willing substrate for bouncing ideas off. To this end, he kept a permanently open door, and forgave me when his eyes glazed over. I will always value his guidance. However, I have yet to learn the finer points of softball from him.

Bernie Roitberg and Ron Ydenberg (my supervisors) contributed in many discussions and edits. Ron Ydenberg's efforts improving the writing went far above and beyond the duties of a supervisor. Discussions with Ron greatly bolstered my confidence as a researcher. I thank Ron for providing several opportunities to gain teaching experience, and especially for the two stints at Bamfield.

I thank Tom Getty (external) for being gentle (but not soft!), and wise enough to know that I should plan to rest the **day after** rather than entertain him. Colin Clark (public examiner) found a fairly cryptic contradiction in Chapter 4 not detected by the rest of us. During my studies, I have benefited from frequent discussions with Colin about my modeling approach.

I happily confirm the B.E.R.G reputation as an interactive group. My membership in the 'Association of Serious Scientists for Holistic Organismal Landmark Ecological Studies' enrolled me in all kinds of science discussions. Ralf Cartar and Bob Lalonde not only let me win the majority of rubbers of 'three-handed', but actually helped with science once or twice. Karen Price and Richard Pocklington made grad courses more fun. Darren Gillis and Tamara Grand explained stats, Guy Martel explained Mac's, and Nick Hughes and Dan Soluk explained anything. Mike Dehn treated me very colleagially, examining my models in depth.

A bunch of people helped run experiments, giving almost freely of their time, including Alex Fraser, Dorothy Hill, Ian Parnell, Maydianne Andrade, Kelly Reis, Greg Fong and Ann Rahme. Steve Halford did a great job stuffing a heron for me, and Vic Bourne was always willing to show me how to use the camera.

The Bamfield Marine Station, the Capilano Hatchery, and the Animal Care Facility at S.F.U. provided space and equipment for experiments, and Wildlife Rescue lent me some herons. I received financial support from S.F.U., Bamfield Marine Station, the F.A. Linville Institute in Sensory Research, and Larry's N.S.E.R.C. grant.

Sports have been my major work avoidance mechanism during my time at S.F.U., and I would like to thank all past Gougers, Big Boys and Hackers, Hi 5'ing White Guys and the Beckenbachs for great times on the diamond/pitch, rink, floor, and court, respectively.

Finally, I thank my family for continuous inspiration and support. Ann kept me going during the worst times, and helped me enjoy the good times. Tante Miep shared her home with Ann and I during our stint in Holland. Mom (John?) bought me a computer and provided other outstanding loans. And mom's Sunday dinners were a critical refuge where I could work out weekly stresses through a technique charitably described as 'discussion with raised voice'. Thanks.

Table of Contents

List of Tables

Table **Page**

List of Figures

Figure **Page**

Chapter 1

General introduction

In this thesis, I examine the influence of predation risk on the foraging decisions of cryptic animals. Cryptic animals will often face a predation risk-foraging tradeoff (Lima and Dill, 1990) because for them, prey capture activities are riskier than non-capture activities.

An important theme in this thesis is the approach of studying the influence of predation risk on foraging behavior by identifying the components of risk relevant to a particular foraging decision, and treating them as independent variables. The predation risk of an activity is the probability of death by predation during that activity. For death by predation to occur, a predator must be present, it must detect the animal, attack it, and capture it (*cf.*, Endler, 1991). Predation risk equals the product of the probabilities that each of these events occurs during a forager's activity. While foragers will rarely be certain whether a predator is present or not, they likely use information, such as vigilance information, to estimate the probability that a predator is present. I use ϕ to refer to this estimate. I denote the other probabilities as follows: Pr(predator detects forager | predator is present)= Pr(detection), Pr(predator attacks forager | predator detects forager)= Pr(attack), and Pr(predator captures forager | predator attacks forager)= Pr(capture).

Central to my approach is the notion that predation risk components can be classified as either 'activity-dependent' or 'activity-independent', according to whether their value depends on the activity performed. The classification of a particular component can change with the level of foraging behavior. For example, at the patch-choice level (with behavioral options forage in patch type 1, 2, etc.), ϕ will be activity-dependent when patch types differ in the probability that predators are present. However, ϕ will typically be activity-independent for within-patch foraging options. A predation risk-foraging trade-off exists only if the values of the activity-dependent predation risk components associated with the foraging options increase with the energetic return of those options.

A common approach to investigating whether predation risk influences a certain level of foraging behavior is to manipulate the value of a predation risk component which is activity-independent (at that level). Such a manipulation does not affect the relative predation risk costs of the behavioral options (set by the values of activity-dependent components), but alters the predation risk cost of all options relative to their energetic benefits. Throughout this thesis, ϕ is the activity-independent component of predation risk I vary in order to alter the predation risk costs of the behavioral options available to the forager.

In Chapter 2, I examine whether tidepool sculpins (*Oligocottus maculosus*) adjust their response to a sudden elevation in ϕ according to their degree of crypsis. ϕ is elevated by adding skin extract from a freshly killed conspecific (to which this species shows an alarm response; Hugie *et al.*, 1991) to a subject's tank. I manipulate the crypsis of sculpins by placing them in tanks with either sand or white substrates, and compare the change in movement rates in response to skin extract addition. The prediction tested is that sculpins on sand substrates (cryptic), for whom movement is risky relative to immobility, will reduce their movements more than those on white substrates (non-cryptic), for whom movement has no marginal cost.

An animal's estimate of the probability that a predator is present will change as new relevant information is obtained. In Chapter 3, I develop a Bayesian-updating model which calculates the magnitude of the change in ϕ appropriate for a particular initial ϕ level and 'piece' of information. Two sources of information are used to update the estimate. Vigilance information is obtained when the animal performs a scan for predators, and either detects one or not. Attack information is obtained when an animal performs a behavior for which Pr(detection) and Pr(attack) are greater than zero. Obviously, if the animal is attacked, ϕ=1.0 regardless of the initial ϕ. More interestingly, the absence of an attack during such a behavior provides information that justifies a decrease in ϕ. Predator arrivals and departures are modeled as a first order Markov process. I use this model to describe the change in ϕ, from a starting value of 1.0, over successive time periods if no predator detections or attacks occur.

In Chapter 4, I present a model which predicts the maximum distance to attack prey, as a function of the forager's ϕ and energy states. Previous models of the influence of predation risk on prey capture decisions (Gilliam, 1990; Godin, 1990) have treated ϕ as a static parameter. However, I feel it is important for the model to incorporate the dynamic nature of ϕ; therefore, I use a dynamic-programming approach with ϕ as a state variable. This model employs the Bayesian-updating model (Chapter 3) to calculate the change in ϕ state during an activity. The dynamic-programming model also treats the forager's energy reserve as a state variable. The model produces a decision matrix that specifies, for each combination of state variable values, the maximum prey attack/capture distance that maximizes the probability of survival to the end of a foraging bout. Chapter 4 also presents an experimental test of one prediction from the model, namely that prey capture distances decrease with increases in ϕ.

Four experiments have examined the influence of predation risk on diet selectivity, by comparing selectivities of animals foraging at different levels of activity-independent predation risk. Their results include increased selectivity, unchanged selectivity, and decreased selectivity. A possible explanation for this variation emerges from the realization that prey types available to a forager can differ not only in profitability, but also in the value of activity-dependent components of predation risk associated with capture (hereafter, 'danger'). I refer to the relationship between danger and profitability, for a given set of prey, as the 'DP slope'.

Although these four experiments differed in the DP slope of the prey used, they unfortunately differed in other ways as well; for example, they studied different species of forager, eating different types of prey, and used different methods to vary the activity-independent components of predation risk. Thus, it is impossible to conclude on the basis of these experiments that the variation in DP slope is responsible for the different results. I test, both theoretically (Chapter 5) and experimentally (Chapter 6), whether manipulating the DP slope from negative to positive can produce the entire range of diet selectivity responses. In Chapter 5, I use the dynamic-programming model (Chapter 4) to provide decision matrices for foragers eating two types of prey, differing in profitability. I manipulate the Pr(predator captures forager | predator is present) of the two prey types to adjust the DP slope. For each DP slope, the influence of ϕ on diet selectivity is determined.

Chapter 6 describes an experimental test of the influence of DP slope using juvenile coho salmon (*Oncorhynchus kisutch*). Diet selectivities of coho foraging on large (more profitable) and small (less profitable) brine shrimp (*Artemia* sp.), with and without predators visible, are determined in treatments representing negative, null, and positive DP slopes. The capture danger of prey is manipulated by presenting prey over either a white substrate (high danger) or a gravel substrate (low danger).

Chapter 7 departs from the central approach of examining the influence of ϕ directly, instead examining the influence of habitat characteristics on diet selectivity (and several other ecologically important variables). Three habitat characteristics are examined: predator arrival probability, forager crypticity, and food availability. A two stage process is used to determine the diet selectivity for each habitat type. In stage 1, I run the dynamic-programming model (Chapter 4) with a parameter set representing a particular environment, to produce a decision matrix optimal for that habitat. Stage 2 simulates foraging bouts in that environment, with foragers capturing prey according to the decision matrix rules.

Overall, the theoretical and empirical findings I present here demonstrate the usefullness of identifying the specific components of predation risk which potentially affect behaviors, and the importance of treating an animal's ϕ as a dynamic variable.

References

Endler, J.A. 1991. Interactions between predators and prey. In: *Behavioral Ecology* (J.R. Krebs and N.B. Davies, eds.), pp. 169-196. Blackwell, Oxford.

Gilliam, J.F. 1990. Hunting by the hunted: optimal prey selection by foragers under predation hazard. In: *Behavioural Mechanisms of Food Selection* (R.N. Hughes, ed.), pp. 797-818. Springer-Verlag, Berlin.

Godin, J.-G.J. 1990. Diet selection under the risk of predation. In: *Behavioural Mechanisms of Food Selection* (R.N. Hughes, ed.), pp. 739-769. Springer-Verlag, Berlin.

Hugie, D.M., Thuringer, P.L. and Smith, R.J.F. 1991. The response of the tidepool sculpin, *Oligocottus maculosus*, to chemical stimuli from injured conspecifics, alarm signalling in the Cottidae (Pisces). Ethology **89**: 322-334.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**: 619-640.

Chapter 2

The influence of substrate color on the alarm response of tidepool sculpins (*Oligocottus maculosus*; Pisces, Cottidae)

This Chapter has been published (Ethology **96**: 147-154), co-authored with Larry Dill

Abstract

For animals that use crypsis to avoid predators, immobility reduces the risk of detection. The magnitude of this immobility benefit depends upon the probability that a predator is present, since a predator must be present for crypsis to be valuable. Thus, cryptic animals typically reduce their movement rates upon detection of a nearby predator or signs of its activity. Such a response occurs in tidepool sculpins (*Oligocottus maculosus*) when presented with water-borne compounds released from the skin of injured conspecifics (Hugie *et al.*, 1991). The benefit of immobility should also depend upon the animal's background, or substrate, since animals on a matching substrate achieve a higher level of crypticity than those on a nonmatching substrate, and have more to gain by remaining still. Therefore, I predicted that the response of tidepool sculpins to conspecific skin extract would involve a greater reduction in movement rates for fish on sand (matching) than for those on white (nonmatching) substrate. The results of a laboratory experiment supported this prediction, with fish on sand showing a large decrease in movement rates in response to skin extract, while the movement rates of those on white substrate remained unchanged.

Introduction

Prey that rely on crypsis to avoid detection use a variety of behavior patterns to enhance the cryptic effect. For example, they commonly choose backgrounds upon which they will appear most cryptic (Donnelly and Dill, 1984; Feltmate and Williams, 1989; Mercurio *et al.*, 1985; Morey, 1990; Steen *et al.*, 1992; review in Edmunds, 1974). Feltmate and Williams (1989), Mercurio *et al.* (1985), and Morey (1990) provide experimental evidence that cryptic animals are less at risk on their chosen substrates than on rejected ones.

Typically, cryptic animals have low movement rates (Sih, 1987), because motion increases their probability of detection (Edmunds, 1974). For example, Morey (1990) compared the vulnerability of treefrogs (*Pseudacris regilla*) to visual predators (garter snakes, *Thamnophis elegans*) on matching (cryptic) and nonmatching (noncryptic) substrates. Treefrogs on matching substrates were safer when immobile, but at the same risk as frogs on nonmatching substrates when moving. Thus, low movement rates enable animals to maintain a high degree of crypsis.

When deciding whether to employ a specific crypsis-enhancing behavior, an animal must consider the relative costs and benefits of such behavior given its current situation. For animals that use crypsis to avoid detection by predators, these behavior patterns clearly have the greatest relative benefit when predators are near. Consider such an animal deciding whether or not to move (to forage, for example). The cost of not moving is lost foraging time, which is independent of whether or not a predator is present. However, the benefit of not moving depends on whether a predator is perceived to be nearby; if a predator has recently been detected, the benefit of remaining motionless, and thus cryptic, is high relative to when no predator has been detected. Thus, cryptic animals might be expected to reduce their movement rates upon detecting a predator. Such a response has been observed in a stonefly, *Baetis tricaudatus* (Kohler and McPeek, 1989), a goby, *Pomatoschistus minutus* (Magnhagen, 1988), and the juvenile salmon, *Oncorhynchus kisutch* (Dill and Fraser, 1984) and *Salmo salar* (Metcalfe *et al*., 1987). In addition, alarm responses to substances released from injured conspecifics are characterized by a reduction in movement rates in cryptic species (*e.g.*, Smith, 1979, 1982 a). Cryptic animals also adjust their response to predator detection in relation to their hunger level, reducing movement rates less when hungry, *i.e.*, when the relative costs of immobility are large (Dill and Fraser, 1984; Magnhagen, 1988; Smith, 1981).

The effect of a predator's presence on movement should depend on substrate characteristics. Animals on a matching substrate obtain a large increase in crypsis by becoming motionless. However, becoming motionless may not result in as great an increase in crypsis for animals on a nonmatching substrate, since they will still be very obvious. Thus, upon detecting a predator, animals on nonmatching substrates should reduce their movement rates less than those on matching substrates, since the benefit of remaining motionless on a nonmatching substrate is less and the opportunity cost is independent of substrate. In this chapter, I report an experiment to test this prediction, using tidepool sculpins (*Oligocottus maculosus*).

Tidepool sculpins appear to use crypsis to reduce their probability of detection by predators. They are adept at altering skin color to match their current substrate. For example, individuals who are green upon collection turn light grey within minutes of being placed in a container with a sand bottom (personal observation). Tidepool sculpins also move less when they perceive a predator to be near, and when immobile these fish are very difficult to detect, at least for humans. Like many species of fish and some invertebrates (see Smith, 1982 b for review), tidepool sculpins respond to water-borne chemicals released from the skin of injured conspecifics (Hugie *et al.*, 1991). This "alarm response" includes decreased movement and feeding rates and increased use of cover and burrowing into the substrate (Hugie *et al.*, 1991), and apparently indicates that the animals perceive a predator to be nearby. In this experiment, water flushed over the lacerated skin of sculpins ("skin extract") was added during trials to increase the subjects' perception of the likelihood that a predator was present.

Methods and Materials

Sculpins were collected on July 21, 1989, from tidepools at First Beach, on the east side of Trevor Channel, Barkley Sound, B.C., using dip nets and a 120 × 180-cm pole seine. Immediately after collection, the fish were inspected and any injured fish returned to the tidepools. The remaining fish were then transported to laboratory facilities at Simon Fraser University in white, 20-l buckets. In the lab, the sculpins were held in 20-, 40-, and 80-l aquaria with loose sand substrates and fed a diet of brine shrimp (*Artemia salina*) and broken mussels (*Mytilus edulis*). Water temperature was maintained between 11 and 14 °C.

The skin extract was prepared in a single batch on August 9, before the start of the experiment, and 5-ml aliquots frozen. This batch preparation method was used to reduce variation in skin extract aliquot potency caused by differences between donor fish or by differences in length and depth of lacerations (see below). Aliquots required cryo-preservation to prevent the potential deterioration of skin extract compounds. A preliminary experiment performed in July 1989 indicated that freezing did not affect skin extract potency: changes in movement rates in response to fresh and previously frozen preparations did not differ significantly (Mann-Whitney $U = 70.5$, $p > 0.6$, $n=12$ fish each).

For the present experiment, 10 donor fish (5 males and 5 females, 49-67.5 mm) were used to prepare 22 aliquots of skin extract. Each fish was killed by a blow to the skull, placed in a clean petri dish, and lacerated 50 times on each flank with a clean razor blade. Each flank was flushed with approximately 6 ml of sea water from a 5-ml syringe. The liquid from all 10 donors was poured into a 125-ml erlenmeyer flask, and stirred at low speed for one minute using a magnetic stirrer. Twenty-two 5-ml disposable syringes were filled, capped, and frozen at -14 °C. The entire procedure took 25 min, and was done in a cold room to minimize decay and evaporation rates.

Before each trial, the entire experimental apparatus was rinsed with hot tap water followed by two rinses with cold sea water. Four 20-l glass aquaria, each divided into two 23.9 h × 19.8 l × 19.8 w cm experimental chambers by a watertight, opaque white wall were used for the tests. Experimental substrates (see below) were placed in the chambers and the chambers filled to a depth of 10 cm with sea water passed through a hobby brewing filter (pore size < 50 μ), to remove all potential food items. Filling was done the day prior to use, to allow the water temperature to equilibrate with that of the cold room (11-14 °C). The tanks were placed in well-lit surroundings with white blinds on all sides. Aquarium airstones, adjusted to provide a moderate bubbling rate, were placed against the rear walls of each chamber, to ensure that the skin extract became well mixed upon addition to the tanks. Skin extract was introduced to the chambers through Tygon tubes leading from behind the blind to the water surface immediately above the airstones.

I built artificial substrates measuring 19.6 × 19.5 cm, designed to cover the entire chamber bottom and allow easy removal for cleaning. The matching substrate consisted of a 3-mm thick layer of Plexiglas, to which a solid layer of gray sand was glued using clear silicon sealant. These substrates were used with the Plexiglas side on top. The sand appeared grainy and wet through the Plexiglas, and provided a good simulation of the colors of loose sand and granite, tidepool substrates upon which *O. maculosus* are commonly found (Nakamura, 1976; personal observation). The sculpins were able to achieve a high degree of color match with this substrate. The nonmatching substrate was also topped with a 3-mm piece of clear Plexiglas, but had an opaque white sheet of the same thickness below it. White was used because it is a common substrate color in natural settings (accumulations of barnacle shells, etc.), but the sculpins could not become light enough to match it well.

The experiment consisted of 11 paired trials. Sculpins, starved between 19 and 24 h, were randomly assigned to a substrate treatment and placed singly in the appropriate chamber 2 h (± 5 min) prior to the beginning of trials, to allow acclimation. A minimum of 0.5 h prior to trial initiation, a VHS camera was set up inside the blind; no one entered the blinds between camera set-up and the end of a trial. The camera was positioned approximately 90 cm from the tanks, and at the same height, providing good resolution of the subject fish against the white blind behind the tanks. Each trial involved a pair of fish, in the two chambers of one tank, one with the sand substrate and the other with the white substrate (the tank side receiving the white substrate was determined randomly). Fifteen minutes after filming began, skin extract preparations, thawed completely (typically requiring 15-20 min in the cold room), were injected simultaneously into each chamber. Filming was continued for 15 min after skin extract addition. Subjects were 50-66 mm in total length. They were not reused.

The number of movements initiated per unit time is commonly used as an index of activity in alarm response experiments on benthic fish which do not swim continuously (*e.g.*, Smith, 1979, 1981, 1982 a; Hugie *et al.*, 1991). Preliminary tests indicated that for tidepool sculpins responding to skin extract, movement rates typically remained depressed for 15 to 30 min. I determined, from the videotapes, the numbers of movements initiated during the 2-min periods beginning 14, 9, and 4 min prior to skin extract addition, and during the complementary periods beginning 2, 7, and 12 min after skin extract addition. These periods were chosen arbitrarily, with the intention of minimizing the total amount of video-analysis required, while including a range of periods in order to minimize the influence of short bouts of atypical movement rates. Movements varied in intensity from change in position of the large pectoral fins to displacement of the fish's entire body. All were included in the analysis, since all decrease the crypsis of the sculpins (at least those on sand). The total number of moves each fish initiated in both the pre- and the post-skin extract addition observation periods (totalling 6 min each) was determined, and the alarm response subsequently calculated by subtracting the total number of moves pre-skin extract addition from the total moves post-skin extract addition. With this measure, 0 represents no response, while negative values indicate reduction in activity. The paired design was used to reduce several potential sources of variation, including (1) vibrations reaching the tank from investigator movements during skin extract addition, (2) the subjects' degree of acclimation to the lab environment and holding procedures, (3) hunger state, and (4) the subjects' activity patterns, naturally entrained to the tidal cycle (Green, 1971). The rhythmic activity patterns of *O. maculosus* continue in the lab, although entrainment is lost after 3 or 4 d (Green, 1971). Data were analyzed using Wilcoxon signed-ranks tests, appropriate for nonparametric, paired data (Darlington and Carlson, 1987).

Results and Discussion

Sculpins on the sand substrate decreased their movements from 31.6 ± 3.4 (mean ± SE) in the 6 min analyzed before skin extract addition to 20.3 ± 4.4 in the 6 min after skin extract addition. Movements of those on the white substrate increased slightly from 22.8 ± 3.6 before to 23.4 ± 5.3 after skin extract addition. The movement rate response to skin extract was significantly greater for fish on the sand substrate than for those on the white substrate (Wilcoxon signed-ranks test, $n = 11$, one-tailed $p = 0.007$; Fig. 2.1).

Thus, tidepool sculpins adjusted their movement rates in an adaptive manner in response to cues indicative of the presence of predators. Sculpins on the matching substrate became relatively inactive after detecting skin extract, presumably due to the large benefit of immobility in maintaining crypsis. In contrast, sculpins on nonmatching substrates did not change their movement rate. Against the white substrate, immobility would have provided relatively little improvement in crypticity. Therefore, movement rates did not decrease in response to skin extract, probably due to the lost opportunity costs of immobility. There may even be a benefit to movement for sculpins on nonmatching substrate upon detecting

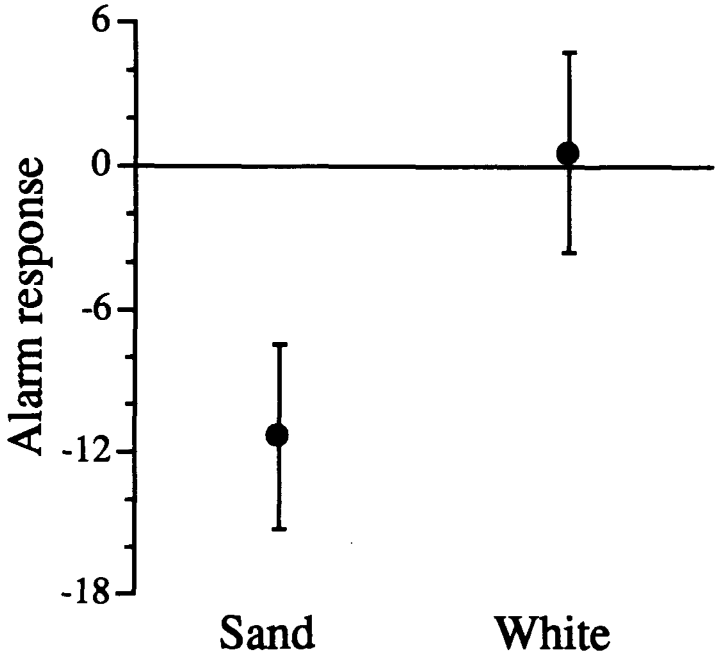

Figure 2.1. The alarm responses (mean ± SE) of tidepool sculpins on the two substrates, calculated by subtracting the number of moves initiated in the pre-skin extract addition observation periods from the number initiated in the post-addition observation periods (6 min each, in total). The horizontal line indicates the 'no response' level, and points below the line indicate reduced activity following skin extract addition.

predator cues -- it would allow them to search for physical cover, or matching substrate. This may have been a factor causing the sculpins on the white substrate to maintain high rates of movement after detection of skin extract, since there were no prey in the tanks, and thus no real opportunity cost of immobility.

Several other studies, all non-experimental, have examined the influence of degree of crypsis on the response to predators. Kettlewell (1973) searched for moths resting on trees in an area of burnt forest and an adjacent area of unburnt forest and found that moths were much easier to find in the burnt area, apparently due to different levels of crypsis on the two types of trees. The moths in the unburnt area "could be approached and captured without eliciting an escape response", while those in the burnt area "without exception ... took flight on approach and this when I was several yards distant" (*ibid.*, page 73). Heatwole (1968) determined the distance to which individuals of two species of anoles (*Anolis stratulus* and *A. cristatellus*) would allow a predator to approach before fleeing. This distance was significantly less for the more cryptic species, *A. stratulus*, than for *A. cristatellus*. Finally, Radabaugh (1989) examined the response to predator detection by males of three darter species, differing in the degree and nature of color change between the non-breeding and breeding seasons: *Etheostoma flabellare* change very little, *E. blennioides* develop bright green colors, while *E. spectabile* develop intense and contrasting orange, blue, yellow and red areas. Non-breeding and breeding *E. flabellare* and *E. blennioides*, and non-breeding *E. spectabile* all reduced their movement rates after predator detecton. However, breeding *E. spectabile* did not show a significant reduction in movement rates. Furthermore, they made more long distance moves after predator detection than any of the other darters. All of these results indicate that the extent to which an animal relies on crypsis during a predator encounter depends on the likelihood of remaining undetected during that encounter.

An unexpected result of this experiment was that prior to skin extract addition, sculpins on the white substrate had lower movement rates than those on the sand substrate. This difference was almost significant (p = 0.061, two-tailed Wilcoxon signed-ranks test). The opposite influence of substrate was expected, since when no predator cues have been detected, searching for matching substrates should be relatively cost-free for sculpins on the white substrate. In fact, Heinen (1985) found that juvenile ***Bufo americanus*** on nonmatching substrates had higher movement rates than those on matching substrates during periods in which the toads had not detected predators (equivalent to the pre-skin extract addition periods in my experiment). Further work is required to determine whether the present result was spurious and, if not, the adaptive explanation for the trend.

It may appear that this experiment lacked a proper control, consisting of water without skin extract. While such a control is neccessary and commonly used in experiments designed to test for an alarm response to skin extracts (*e.g.*, Hugie *et al.*, 1991;.Smith, 1982 a), the intention of my experiment was to determine the influence of substrate match on the response of a cryptic animal to detection of a predator cue, using skin extract as the cue. Thus, it is appropriate that in the experimental design and statistical analysis of the results, the two substrate colors were considered the "treatments", and that all subjects in both substrate treatments received skin extract.

Throughout this chapter, I have implied that the major benefit of immobility for tidepool sculpins is improved crypsis. Another potential benefit of immobility, or reduced activity rates in general, is that the animal can focus more of its visual attention on the detection of attacking predators (Godin and Smith, 1988; Milinski, 1984). These two mutually compatible benefits both generate the prediction that activity rates will decrease with increases in an animal's perception of the probability that a predator is present. Therefore, it is important to examine whether my results would be expected if the only benefit to sculpins of reduced activity were improved vigilance. The improvement in vigilance due to a given reduction in movement rates would presumably be independent of substrate, in which case one would expect no substrate effect. Further, if the fish on the white background perceived themselves to be less cryptic, and thus at a higher risk of predatory attack, they would be expected to show a greater reduction in movement rates than those on sand. My results clearly do not agree with these predictions. Thus, I conclude that for tidepool sculpins, the primary benefit of reduction in movement rates is the resulting improved crypsis which results.

Several studies have invoked one or the other of these benefits in the interpretation of responses of fish to predators (*e.g.*, Dill and Fraser, 1984; Godin, 1986; Ibrahim and Huntingford, 1989; Metcalfe *et al.*, 1987), often without explicit justification. In fact, in the interpretation of similar results using similar species, Dill and Fraser (1984) invoke the crypsis benefit while Metcalfe *et al.* (1987) invoke the vigilance benefit. In future studies, experiments similar to the present one could be used to determine the degree to which the two benefits of reduced activity rates apply to a particular species.

Throughout this chapter, I have avoided the use of the term "predation risk", although the experimental manipulations were obviously closely connected to predation risk. Instead, I have used terms such as "probability of detection" and "presence of predators". If predation risk is viewed as the probability of death in a certain time period, these two terms represent two component probabilities of risk. In this experiment, a sculpin's percieved predation risk depended both on substrate (influencing the probability of detection) and whether or not skin extract had been detected. Thus, referring to one or both of these components as predation risk would lead to confusion regarding the roles of the two manipulations. It is likely that experimental designs like this one, in which two or more components of predation risk are manipulated, have been overlooked because workers have not treated predation risk as a product of several components.

References

Darlington, R.B. and Carlson, P.M. 1987. *Behavioral Statistics: Logic and Methods*. The Free Press, New York.

Dill, L.M. and Fraser, A.H.G. 1984. Risk of predation and the feeding behaviour of juvenile coho salmon (*Oncorhynchus kisutch*). Behav. Ecol. Sociobiol. **16**: 65-71.

Donnelly, W.A. and Dill, L.M. 1984. Evidence for crypsis in coho salmon, *Oncorhynchus kisutch* (Walbaum), parr: substrate colour preference and achromatic reflectance. J. Fish Biol. **25**: 183-195.

Edmunds, M. 1974. *Defence in Animals*. Longman Inc., New York.

Feltmate, B.W. and Williams, D.D. 1989. A test of crypsis and predator avoidance in the stonefly *Paragnetina media* (Plecoptera: Perlidae). Anim. Behav. **37**: 992-999.

Godin, J.-G.J. 1986. Risk of predation and foraging behaviour in shoaling banded killifish (*Fundulus diaphanus*). Can. J. Zool. **64**: 1675-1678.

Godin, J.-G.J. and Smith, S.A. 1988. A fitness cost of foraging in the guppy. Nature **333**: 69-71.

Green, J.M. 1971. Field and laboratory activity patterns of the tidepool cottid *Oligocottus maculosus* Girard. Can. J. Zool. **49**: 255-264.

Heatwole, H. 1968. Relationship of escape behavior and camouflage in anoline lizards. Copeia **1968**: 109-113.

Heinen, J.T. 1985. Cryptic behavior in juvenile toads. J. Herpetol. **19**: 524-527.

Hugie, D.M., Thuringer, P. L. and Smith, R. J. F. 1991. The response of the tidepool sculpin, *Oligocottus maculosus*, to chemical stimuli from injured conspecifics, alarm signalling in the Cottidae (Pisces). Ethology **89**: 322-334.

Ibrahim, A.A. and Huntingford, F.A. 1989. Laboratory and field studies of the effect of predation risk on foraging in three-spined sticklebacks (*Gasterosteus aculeatus*). Behaviour **109**: 46-57.

Kettlewell, B. 1973. *The Evolution of Melanism: The Study of a Recurring Necessity.* Oxford University Press, London.

Kohler, S.L. and McPeek, M.A. 1989. Predation risk and the foraging behavior of competing stream insects. Ecology **70**: 1811-1825.

Magnhagen, C. 1988. Changes in foraging as a response to predation risk in two gobiid fish species, *Pomatoschistus minutus* and *Gobius niger*. Mar. Ecol. Prog. Ser. **49**: 21-26.

Mercurio, K.S., Palmer, A.R. and Lowell, R.B. 1985. Predator-mediated microhabitat partitioning by two species of visually cryptic, intertidal limpets. Ecology **66**: 1417-1425.

Metcalfe, N.B., Huntingford, F.A. and Thorpe, J.E. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. Anim. Behav. **35**: 901-911.

Milinski, M. 1984. A predator's costs of overcoming the confusion-effect of swarming prey. Anim. Behav. **32**: 1157-1162.

Morey, S.R. 1990. Microhabitat selection and predation in the Pacific treefrog, *Pseudacris regilla*. J. Herpetol. **24**: 292-296.

Nakamura, R. 1976. Experimental assessment of factors influencing microhabitat selection by the two tidepool fishes *Oligocottus maculosus* and *O. snyderi*. Mar. Biol. **37**: 97-104.

Radabaugh, D.C. 1989. Seasonal colour changes and shifting antipredator tactics in darters. J. Fish Biol. **34**: 679-685.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In: *Predation: Direct and Indirect Impacts on Aquatic Communities.* (W.C. Kerfoot and A. Sih, eds.), pp. 203-224. University Press of New England, Hanover, U.S.A.

Smith, R.J.F. 1979. Alarm reaction of Iowa and johnny darters (*Etheostoma*, Percidae, Pisces) to chemicals from injured conspecifics. Can. J. Zool. **57**: 1278-1282.

Smith, R.J.F. 1981. Effect of food deprivation on the reaction of Iowa darters (*Etheostoma exile*) to skin extract. Can. J. Zool. **59**: 558-560.

Smith, R.J.F. 1982 a. Reaction of *Percina nigrofasciata, Ammocrypta beani,* and *Etheostoma swaini* (Percidae, Pisces) to conspecific and intergeneric skin extracts. Can. J. Zool. **60**: 1067-1072.

Smith, R.J.F. 1982 b. The adaptive significance of the alarm substance - fright reaction system. In: *Chemoreception in Fishes.* (T.J. Hara, ed.), pp. 327-342. Elsevier Publishing Co., Amsterdam.

Steen, J.B., Erikstad, K.E. and Høidal, K. 1992. Cryptic behaviour in moulting hen willow ptarmigan *Lagopus l. lagopus* during snow melt. Ornis. Scand. **23**: 101-104.

Chapter 3

How risky is it? A Bayesian-updating model of how animals assess the probability that a predator is present.

Abstract

Animals frequently must assess the probability that predators are dangerously close. I examine this assessment procedure using a general, discrete, Bayesian-updating model of the probability that a predator is present (ϕ). The model proceeds in discrete steps, each composed of a behavioral action followed by a brief three-step updating process. The occurrence of an attack during the behavioral action in period t obviously contains information allowing the animal to update $\phi(t)$ (to 1.0). More interesting is the fact that the absence of an attack also carries information that may be used to arrive at an updated estimate of ϕ (to a lower level) using a Bayesian procedure. The impact that the event 'no attack' has on the revision depends on the probability that a predator, if present, attacks the animal. This information is used in the first step of the updating process to update $\phi(t)$ to $\phi(t')$. The second step updates $\phi(t')$ to $\phi(t'')$ based on the probability of arrival and departure of predators during the preceding behavioral action, modelled as a Markov process. In the third step the animal scans the surroundings and updates $\phi(t'')$ to $\phi(t''')$, based on whether a predator is detected during the scan ($\phi(t''')=1.0$), or not ($\phi(t''')\leq(\phi(t''))$). The impact of the event 'no detection' on the value of $\phi(t''')$ depends on the probability of detecting a predator, if present. The updated value of $\phi(t)$ applies during the next behavioral action, after which ϕ is revised again. I use the model to describe the dynamics of ϕ when no predators are detected for a prolonged period. In this case the value of ϕ decreases continuously to a non-zero asymptote. Increasing either the probability of being attacked by a predator (if present) or the probability of detecting a predator per scan (if one is present) increases the rate at which the asymptote is approached.

Introduction

Numerous studies have shown that animal decisions are strongly influenced by predation risk (see reviews by Dill, 1987; Lima and Dill, 1990). How animals determine what behavior is adaptive in particular situations is an important current area of study, in part because of the variable nature of predation risk. One variable component of predation risk that may be amenable to assessment is the probability that a predator is close enough to pose a threat. Animals have several potential sources of information regarding this, including their visual, chemical, and aural senses. In this Chapter, I present a model of the assessment of the probability that a predator is present (designated ϕ). For simplicity, I consider only one type of predator and I assume that a predator is either close enough to pose a risk (predator present) or is not (predator absent). The latter may be a reasonable approximation for certain situations, such as for animals in small patches (*e.g.*, tidepools, ponds), but not for cases in which risk varies continuously with predator-prey separation distance. I also present some numerical solutions of the model, and discuss the important predictions that emerge.

The Model

The model proceeds in discrete steps, each composed of a behavioral action followed by a brief three-step updating process. (Note that I do not specify the duration of the steps, only that they be of equal duration.) The ϕ value which applies for a particular time period t is denoted $\phi(t)$ and is determined at the end of the preceding period (t-1), by updating $\phi(t-1)$. Figure 3.1 presents a schematic overview of the updating process.

During the behavioral action in period t, the animal will either be attacked by a predator, or not. Both of these events provide the animal with information regarding the

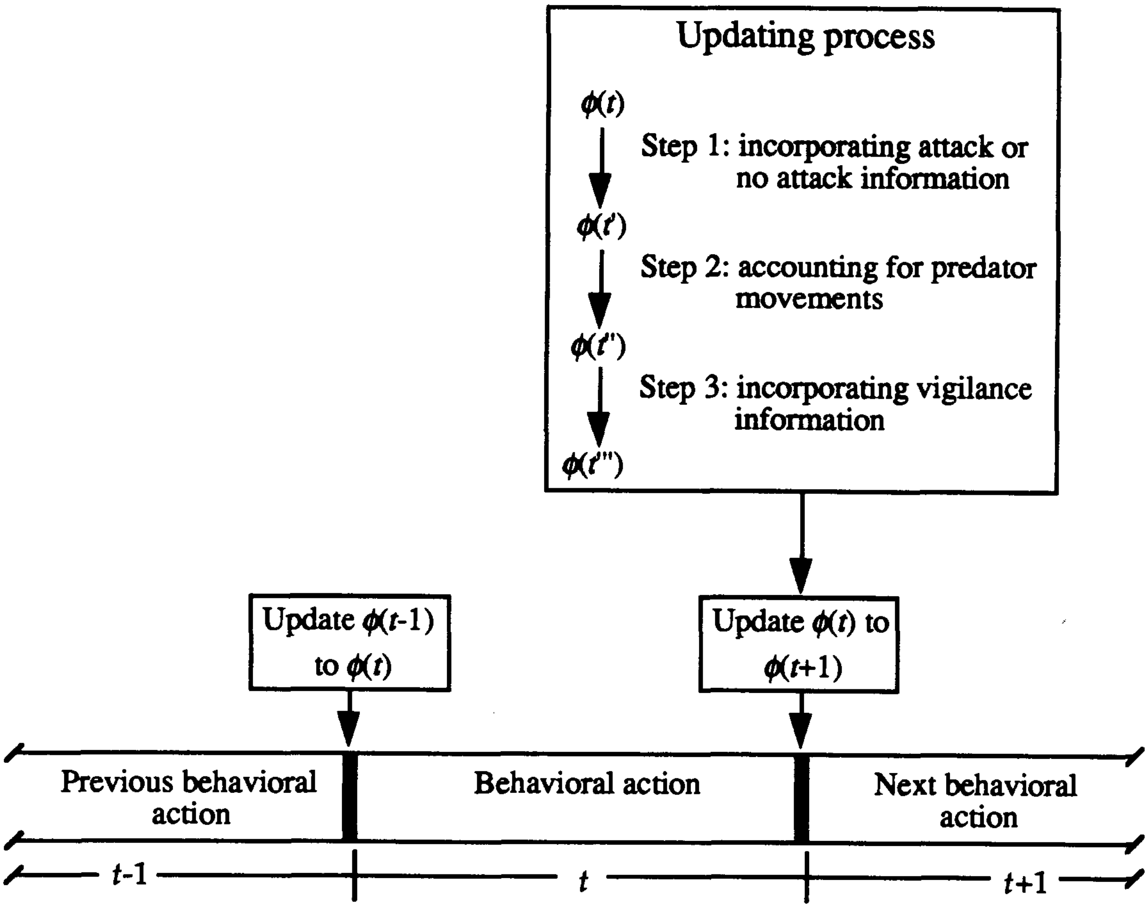

Figure 3.1. A schematic representation of the model, which updates ϕ after discrete time steps, each composed of a behavioral action followed by a three-step updating process.

probability that a predator was present during the behavioral action. Step 1 of the updating process incorporates this information, modifying $\phi(t)$ to $\phi(t')$. In Bayesian terminology, $\phi(t)$ and $\phi(t')$ are the 'prior' and 'posterior' values of step 1. An attack from which the animal escapes (the alternative does not allow subsequent assessment) indicates unambiguously that a predator was present; in such a case, $\phi(t')=1.0$.

I refer to the information provided by the event 'no attack' as 'no attack information'. This information is used to update $\phi(t)$ as follows. If an animal was not attacked, one of 3 events must have occurred: (1) a predator was present but did not detect the animal, (2) a predator was present, detected the animal, but did not attack, or (3) no predator was present. For simplicity, I assume that if a predator detects the animal in period t, it either attacks in period t or forgets where the animal is prior to period $t+1$. $\phi(t')$ is then calculated from the ratio of the animal's estimate of the probability that either event #1 or #2 occurs to that for any of the 3 events occurring. Let Pr(detection)=Pr(predator detects animal during behavioral action | predator is present), and Pr(attack)=Pr(predator attacks animal during behavioral action | predator detects animal). Then, the animal's estimate of the probability that event #1 occurs is $\phi(t)(1\text{-Pr(detection)})$, while that for event #2 is $\phi(t)\text{Pr(detection)}(1\text{-Pr(attack)})$, where 1-Pr(detection) and 1-Pr(attack) are the probabilities that the animal is not detected or not attacked (if detected), respectively, by a predator that is present. The probability of event #3 is simply $1-\phi(t)$. Therefore, when no attack occurs

$$\phi(t') = \frac{\phi(t)(1-\Pr(\text{detection})) + \phi(t)\Pr(\text{detection})(1-\Pr(\text{attack}))}{\phi(t)(1-\Pr(\text{detection})) + \phi(t)\Pr(\text{detection})(1-\Pr(\text{attack})) + (1-\phi(t))} \tag{1}$$

$$= \frac{\phi(t)(1-\Pr(\text{detection and attack}))}{1-\phi(t)\Pr(\text{detection and attack})},$$

where Pr(detection and attack)=Pr(detection)Pr(attack).

Step two of the updating process incorporates the probabilities of predator arrival and departure. Transitions between the states *predator present* or *absent* in period t and *predator present* or *absent* in period t+1 are assumed to occur during the interval between successive periods, and are described by a first order Markov process (see Table 3.1). During step 2, $\phi(t')$ is updated to $\phi(t'')$. It is convenient to view $\phi(t')$ and $\phi(t'')$ as the prior and posterior probabilities, respectively, although this step does not involve Bayes' formula.

I assume patches may contain at most one predator, and ignore higher level processes. There are two possible events which lead to a predator being present in period t+1. First, a predator present in period t may stay. The animal's estimate that this occurs is $\phi(t')$(1-Pr(leave)). Second, if no predator was previously present, a predator may arrive. The animal's estimate of the probability that this occurs is (1-$\phi(t')$)Pr(arrive). $\phi(t'')$ is the probability of either of these exclusive events occurring, which is simply the sum of their individual probabilities.

The third and final step of the updating process, updating $\phi(t'')$ to $\phi(t''')$, incorporates information from vigilance. (Implicit in making this the final step is the assumption that vigilance occurs only after predator movements have taken place). Four events may occur when an animal scans for predators, namely : 1) no predator is detected, and no predator is present; 2) no predator is detected, but one is actually present; 3) a predator is detected, and one is present; and 4) a predator is detected even though one is not present.

When no predator is detected, either event #1 or #2 must have occurred. In this case, $\phi(t''')$ (the posterior estimate of this step) will equal the estimated probability of event #2 divided by the sum of the estimated probabilities of either event #1 or #2 occurring. Let

Table 3.1. The probabilities of transitions from *predator present* or *absent* states in period *t* to *predator present* or *absent* state in period *t*+1. Pr(leave) is the probability that a predator leaves if one is present, while Pr(arrive) is the probability that a predator arrives if none is present.

		Period *t*+1	
		Predator present	*Predator absent*
Period *t*	*Predator present*	'Stays': 1-Pr(leave)	'Leaves': Pr(leave)
	Predator absent	'Arrives': Pr(arrive)	'No arrival': 1-Pr(arrive)

Pr(false alarm) represent the Pr(detect a predator | no predator present), and Pr(scan) the Pr(detect a predator | predator present). Then the animal's estimate of the probability that event #1 occurs is (1-$\phi(t'')$)(1-Pr(false alarm)). The estimate for event #2 is $\phi(t'')$(1-Pr(scan)). Then,

$$\phi(t''') = \frac{\phi(t'')(1 - \Pr(\text{scan}))}{\phi(t'')(1 - \Pr(\text{scan})) + (1 - \phi(t''))(1 - \Pr(\text{false alarm}))}. \tag{2}$$

If the animal detects a predator, either event #3 or #4 must have occurred, in which case $\phi(t''')$ equals the estimated probability of event #3 divided by the sum of the estimated probabilities of either event occuring. The animal's estimates of the probability of these events are $\phi(t'')$Pr(scan) and (1-$\phi(t'')$)Pr(false alarm), for events #3 and #4 respectively. Thus, if the animal detects a predator

$$\phi(t''') = \frac{\phi(t'')(\Pr(\text{scan}))}{\phi(t'')(\Pr(\text{scan})) + (1 - \phi(t''))(\Pr(\text{false alarm}))}. \tag{3}$$

The model assumes that the animal knows the exact values of the parameters involved in calculating ϕ. Extending the model to consider the influence of imperfect knowledge of these parameters would be worthwhile, but is outside the scope of this Chapter. Nevertheless, this simplyfying assumption may be reasonable in some situations.

One important consequence of the assumption of accurate knowledge of the parameters is that the value of ϕ will not be subject to error as it would if the parameters were estimates (with associated error). Further, although there are only two possible true states of a patch (predator present or absent), ϕ will equal zero or one only on the rare occasions when information is complete. More often, information will be incomplete and ϕ will have an intermediate value.

Numerical Solutions

I investigated the dynamics of the assessment by solving the equations iteratively, using the value of $\phi(t'')$ or $\phi(t''')$ as the value of $\phi(t+1)$ for the next period, and repeating the calculations. I used the following basic parameter values: Pr(detection and attack)=0.1, Pr(arrive)=0.05, Pr(leave)=0.4, and Pr(scan)=0.5. For simplicity, I set Pr(false alarm) at 0; therefore, when a predator is detected, $\phi(t''')=1.0$. Runs were started with $\phi(1) = 1.0$, thus modeling the change in $\phi(t)$, $t=1, 2, 3, \ldots T$, following a time period in which a predator was detected. Subsequent predator detections were not allowed, since these would simply reset ϕ to 1.0. As well, no predator attacks were allowed, since these would have a similar effect. In all runs performed, ϕ decreased asymptotically. I ended iterations when $\phi(t+1)-\phi(t)<1 \times 10^{-6}$.

I refer to the temporal patterns by which $\phi(t)$ changes following a predator attack or detection (as well as changes in the associated behavioral and physiological characteristics, discussed below) as 'recovery curves'. Two types of recovery curves were calculated. The recovery curve for a vigilant animal was calculated by setting $\phi(t+1)=\phi(t''')$, thereby modeling the dynamics of $\phi(t)$ for an animal using both vigilance and 'no attack' information. The recovery curve for a non-vigilant animal was calculated by setting $\phi(t+1)=\phi(t'')$, thereby modeling the dynamics of $\phi(t)$ for an animal who foregoes vigilance information. All parameter values were held constant during a run.

I also calculate the average probability that a predator is present in a patch, denoted Φ, which equals $\mathrm{Pr(arrive)}/\big(\mathrm{Pr(arrive)}+\mathrm{Pr(leave)}\big)$. Φ is presumably the best ϕ value for an animal without the ability to use information, or for an animal who has no relevant information, either due to lack of opportunity to gather it (*e.g.*, an animal just emerging from a safe refuge from which it could not detect predators) or to changes in the environment since data were last gathered (*e.g.*, at dawn, information regarding diurnal predators, gathered the previous day, could be completely irrelevant if predators move at night).

General Results

A general result of the model is that the ϕ recovery curves, both for vigilant and non-vigilant animals, decrease (from the initial value of 1.0) continuously towards an asymptote (Fig. 3.2). The asymptote is nonzero whenever Pr(arrive) > 0 and Pr(scan) < 1.0. When both criteria are met, $\phi(t)$ never reaches zero because there may always be undetected predators. The recovery curve shape depends upon the value of P(leave). When this probability has a high value (for example, 0.4), the curve approximates a negative exponential (Fig. 3.2A). However, when P(leave) is small (in this case, less than 0.1), the curve has an inflection point, thus approximating a negative logistic curve (Fig. 3.2B). Generally, however, $\phi(t)$ decreases monotonically toward an asymptote.

These results lead to predictions regarding behaviors whose rate (or intensity) of performance influences one or more components of predation risk (*e.g.*, Pr(detection) and Pr(attack)); otherwise, $\phi(t)$ values would not be expected to affect the performance of that behavior. Similarly, $\phi(t)$ may affect physiological characteristics whose level influences the animal's predation risk; heart rate and respiration rate in vertebrates are possible examples, since both influence an animal's preparedness for flight, and thus its probability of successfully escaping a predator, should one attack. The predictions will also apply to the physiological characteristics which represent an animal's 'informational state' (*cf.*, Blumstein and Bouskila, in prep.; Mangel and Roitberg, 1989) but do not directly influence it's predation risk; one possible example is the concentration of stress hormones in the blood.

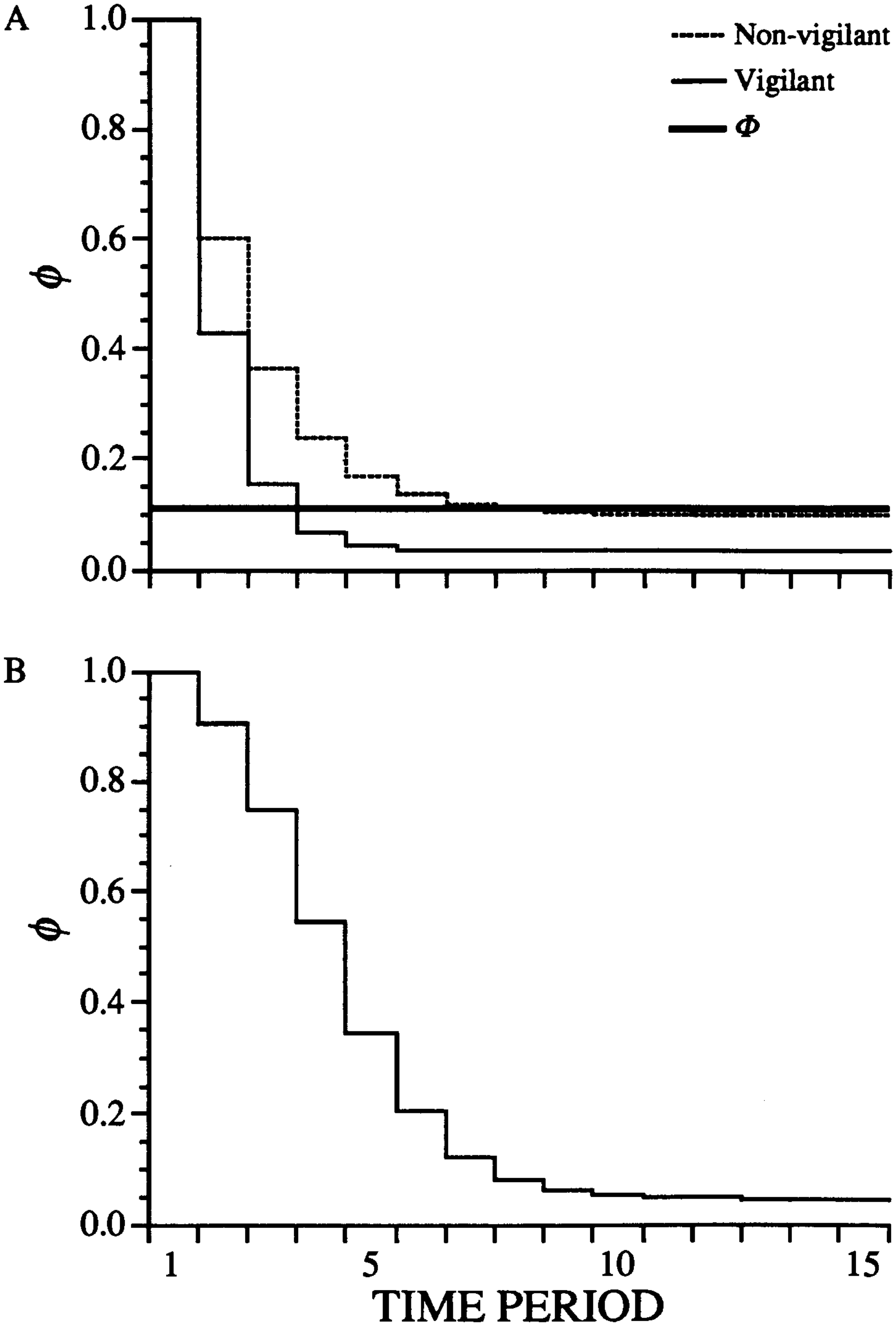

Figure 3.2. Typical ϕ recovery curves, generated using the basic parameter values (Pr(detection and attack)=0.1, Pr(arrive)=0.05, Pr(leave)=0.4, Pr(scan)=0.5, and Pr(false alarm)=0.0). The average Pr(predator present), or Φ, is shown for comparison. B presents a curve for a vigilant animal in which the negative logistic shape is clearly shown, generated using the same parameter values, except that Pr(leave) = 0.05.

One important prediction is that animals should rarely behave as if ϕ is 0.0. In other words, an animal's decisions, even after a long period without predator detection, should be based on the assumption of nonzero predation risks.

A second prediction is that the recovery curves of some behaviors and physiological states will be shaped like the $\phi(t)$ recovery curves illustrated in Fig. 3.2. The extent of this similarity will depend upon the nature of the tradeoff governing the rate or level examined. For example, a behavior may have such a small benefit that it is 'worth' performing only at the minimum ϕ value. In that case, I would expect that behavior to be performed only after a long period without predator detection; the recovery 'curve' of such a behavior would be a step function. Alternatively, the behavior may be worth performing only if ϕ is below some threshold level, in which case the rate of performance of that behavior will begin to change with time only after ϕ has decreased below that threshold. However, in many cases the recovery should be continuous.

This general result might explain findings like those of Metcalfe *et al.* (1987) concerning the post-predator-detection opercular beat rates of juvenile Atlantic salmon (*Salmo salar*), assuming that opercular beat rate reflects an animal's preparedness to flee and thus influences its predation risk. The recovery curves for the opercular beat rates of two fish were determined (Fig. 3.3); these curves are clearly continuous and asymptotic. Metcalfe *et al.* (1987) also studied the effect of time elapsed since predator detection upon the proportion of passing prey that were eaten, and concluded that "the response of the salmon to predators is ... of a continuous (rather than discrete) nature, with fish constantly updating the trade-off between foraging and predator avoidance with changes in perceived predation risk".

In Fig. 3.2A, the curves for both vigilant and non-vigilant animals are shown for one set of parameter values. The difference between the asymptote for the recovery curve for a non-vigilant animal and Φ is small (10%) which might suggest a limited effect of 'no

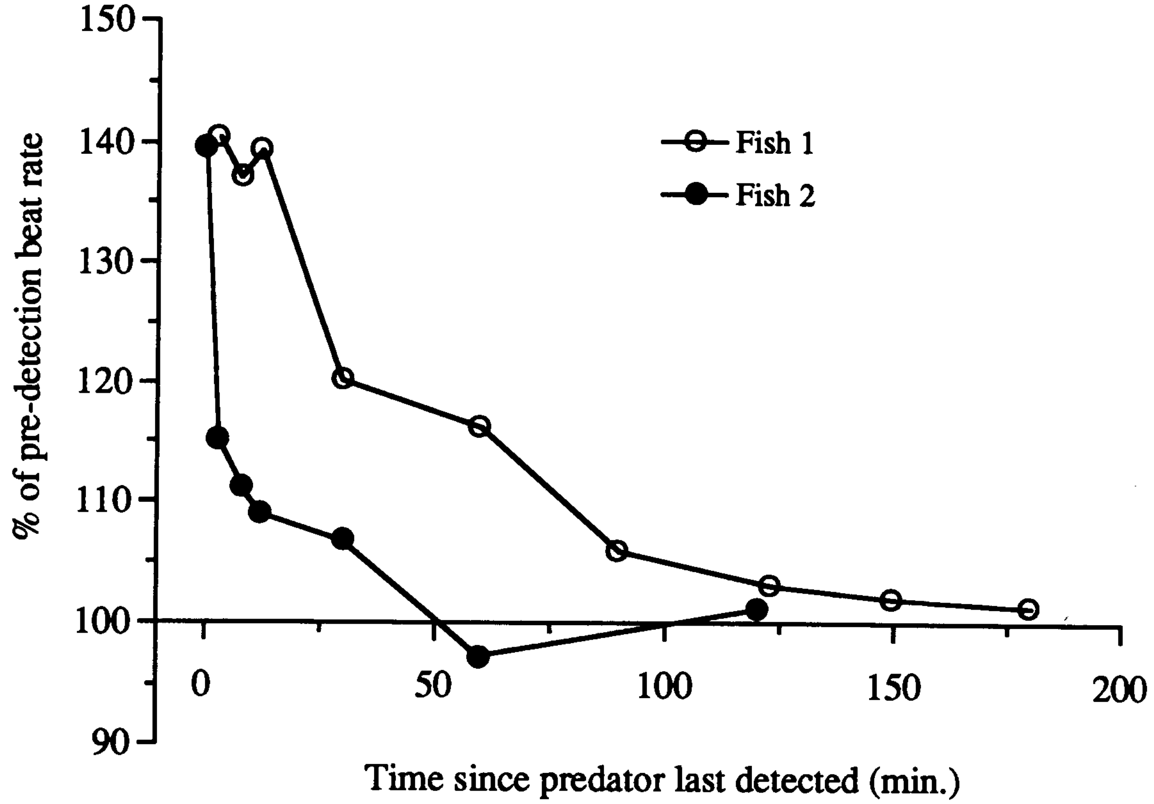

Figure 3.3. The opercular beat rate recovery curves for two juvenile Atlantic salmon (*Salmo salar*) following predator detection (modified from Metcalfe *et al.*, 1987).

attack' information. However, 'no attack' information should also influence the rate of recovery. In order to investigate the influence of 'no attack' information on the recovery curve, I varied the parameter influencing the information gain from this source, Pr(detection and attack) (Fig. 3.4). Although Pr(detection and attack) has only a small influence on the asymptotic value of the curve for a vigilant animal, it strongly influences the rate at which the curves approach their asymptotes; this rate increases with increasing Pr(detection and attack) (Fig. 3.4). Thus, 'no attack' information is expected to influence behavior most in the period soon after a predator has been detected.

Although ϕ recovery rates increase with Pr(detection and attack), this does not neccessarily mean that recovery rates of behavioral and physiological levels should also increase with this parameter. For behavioral and physiological levels which depend on predation risk, current levels will depend on both ϕ and Pr(detection and attack) (both are components of predation risk). To determine the influence of Pr(detection and attack) on perceived predation risk, I multiplied each ϕ recovery curve by the Pr(detection and attack) value used to produce it. This provides an index of actual predation risk (assuming that Pr(capture | attack)=1.0). The value of this index at any time t actually increases with the value of Pr(detection and attack). Therefore, recovery rates of behavioral and physiological levels should decrease with increasing Pr(detection and attack). Effectively, the direct influence of Pr(detection and attack) on predation risk is greater than its indirect influence through ϕ.

Different behaviors will often have different associated Pr(detection and attack). For example, for a cryptic animal, Pr(detection) will generally be greater when the animal is in motion than when it remains still. Pr(attack) values may also depend on the animal's behavior. For example, Fitzgibbon (1989) found that cheetahs tended to attack Thomson's gazelles that were less vigilant than their nearest neighbours. In such cases, the value of Pr(detection and attack) may influence an animal's choice of behavior in two ways. First,

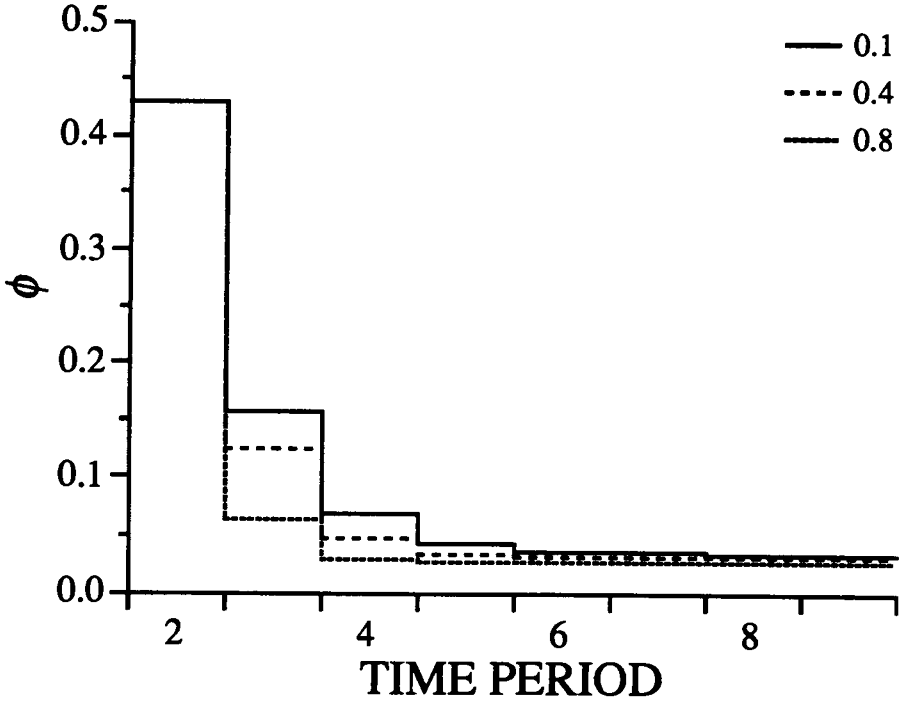

Figure 3.4. The influence of Pr(detection and attack) on the ϕ recovery curves for vigilant animals. Curves are shown for three values of Pr(detection and attack). The basic values were used for the other parameters. To improve resolution, $\phi(1)$ (1.0 in all cases) is not shown.

since this parameter is a component of predation risk, decisions which are influenced by the predation risks of the choices will be affected by the Pr(detection and attack) values of those choices. Second, the potential 'no attack' information gain available from each of the options will differ, and animals may choose behaviors with higher Pr(detection and attack) than would otherwise be adaptive, if the resulting depressed ϕ (assuming no attack occurred) confers sufficient advantages in the future. For example, the energy intake rate a foraging animal can achieve may depend on its certainty that the patch is predator free. In such a case, the energetic benefits derived while foraging with a relatively low ϕ value may outweigh the predation risk costs incurred during the performance of the initial high Pr(detection and attack) activity. This suggestion is equivalent to the patch (or prey) sampling problem in the foraging literature, in that costs incurred in gathering information can be repaid through optimized behavior in the future (*e.g.*, Shettleworth *et al.*, 1988; see Stephens and Krebs, 1986, for a full discussion). The results of my simulations suggest that the potential long-term effect of 'no attack' information is small, and it is therefore likely that the potential information benefits of incurring a high Pr(detection and attack) (and thus a high predation risk) are small, and will not influence behavior significantly. However, I recommend a more complete analysis before this possibility is ruled out.

The influence of an animal's scanning ability (Pr(scan)) on the recovery curves for a vigilant animal was also examined (Fig. 3.5). As expected, the curves become more depressed as Pr(scan) increases. The curve when Pr(scan) = 0.0 is identical to the curve for a non-vigilant animal for the same parameter set, since in this case no information is gained from vigilance. This curve also represents a non-vigilant animal's recovery curve for the other three parameter sets used in Fig. 3.5, since the values of all three parameters involved in the $\phi(t'')$ calculation are constant. Therefore, by comparing any of the curves in Fig. 3.5 to the curve for Pr(scan) = 0.0, the influence of vigilance can be estimated for

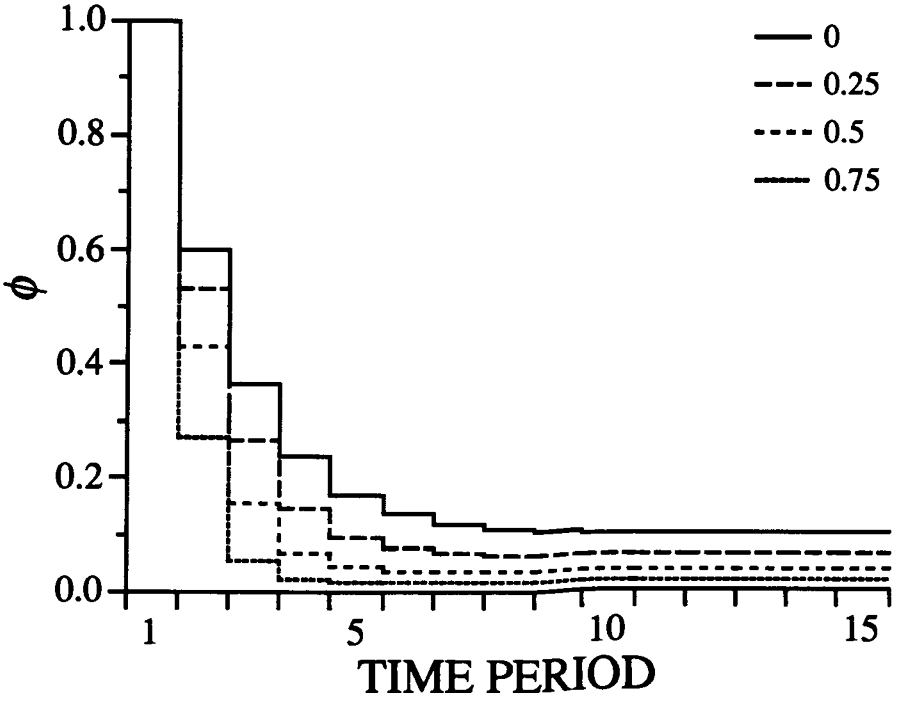

Figure 3.5. The influence of scanning ability on the ϕ recovery curves. Curves are shown for four values of Pr(scan). The basic values were used for the other parameters.

animals with different scanning abilities; not surprisingly, the effect of vigilance increases with increased scanning ability.

Discussion

Mangel (1990) suggests that "an information processing theory should include: (i) a decay of memory, so that events which happened a long time ago have less impact on the estimate than more recent events, (ii) succinctness of the estimate, so that the organism can summarize its encounter history in an efficient way, and (iii) flexibility of the estimate, through a consistent treatment of uncertainty." A memory decay mechanism is important because in changing environments (*i.e.*, where learning is important), as an observation becomes older, it becomes increasingly likely to have been sampled from a habitat which has subsequently changed (or from which the animal has departed). Several previous models have achieved this goal by incorporating *ad hoc* rules governing the weighting of information gained in previous time periods. Two common types of weighting rules are a continuous weighting function (*e.g.*, negative exponential, McNamara and Houston, 1985, 1987), or a 'sliding memory window', in which all data inside the memory window are weighted equally, but any older data are 'forgotten' (*e.g.*, Cowie and Krebs, 1979; Roitberg *et al.*, 1992). In the model presented in this Chapter, no specific memory rules are involved. Nevertheless, observations have a decreasing influence upon the ϕ estimate as the time since they were current increases. The model also is sensitive to the rate of change in the environment, due to the influence of the two parameters relating to predator movements. As shown in Fig. 3.2, the recovery curve's shape depends upon Pr(leave), which will influence the rate of change of ϕ since with smaller Pr(leave) values, once a predator is present it is likely to remain longer. Thus, in Fig. 3.2B, with lingering predators, the ϕ value drops slowly initially, which is equivalent to weighting the predator detection several time periods in the past more heavily than in a habitat in which predators are less likely to linger (Fig. 3.2A).

The same approach could be applied to other sorts of assessment models, by inclusion of parameters which specify the rate of change of the habitat feature of interest. As an example, consider the assessment of the maximum long-term reward rate for animals foraging in patches, when that reward rate varies unpredictably (in the short term) through time. McNamara and Houston (1985) modelled this problem using a negative exponential function to weight older data less strongly. The alternative suggested by my approach is to incorporate parameters that specify the probability that a change in the habitat maximum reward rate occurs. In such a model, the weighting given to older data would be exactly proportional to the probability that the habitat had not changed since those data were collected.

The second desirable characteristic of an assessment model, that of succinctness of the estimate (Mangel, 1990), is also achieved by the present model, since the only value an animal is required to remember is the ϕ value from the last time period. Mangel's third desirable characteristic ("flexibility of the estimate, through a consistent treatment of uncertainty") is achieved as well. The estimate is flexible in that it changes as each piece of information is added to it. Furthermore, because the model uses Bayes' theorem, the change in ϕ resulting from incorporation of a given piece of information is "consistent" in that it is justified probabilistically.

It was this feature of Bayes' theorem that led me to use it to model this problem. However, there is also some empirical evidence that animals behave as if they are using a Bayesian assessment strategy. Valone and Brown (1989) and Valone (1991) examined patch leaving decisions in seven species of birds and mammals and found that four of them foraged in qualitative agreement with the predictions of a Bayesian strategy. This type of evidence would be strengthened by tests of quantitative predictions.

An animal's estimate of the probability that a predator is present (ϕ) is only one component of perceived predation risk; the three other components are Pr(detection), Pr(attack), and Pr(capture | attack by predator), some of which may have sub-components. A common experimental treatment in behavioral ecology is to elevate the perceived predation risk of subjects by manipulating one of these components (or sub-components). Most often, subjects are allowed to detect a predator (*e.g.*, Fraser and Huntingford, 1986; Godin, 1986) or predator model (*e.g.*, Dill and Fraser, 1984; Godin and Sproul, 1988), thus elevating their ϕ. Less commonly, one of the other components is manipulated. For example, Heinen (1985) manipulated Pr(detection) by altering the substrate upon which juvenile toads (*Bufo americanus*) were placed, thus making them more or less cryptic. Lima *et al.* (1985) and Dill and Houtman (1989) manipulated the Pr(capture | attack by predator) of gray squirrels (*Sciurus carolinensis*) by altering the distance from the nearest tree (refuge) at which food was presented.

Such manipulations are typically referred to as alterations of the perceived predation risk, without specifying which of its components is actually being altered. This is not invalid, since manipulating a single component will influence perceived predation risk in a direct manner. However, this approach obscures the possibility of experiments in which more than one of the components are varied; such experiments allow determination of the influence of one component conditional on the values of other components. For example, in Chapter 2 I found that the movement rate responses of tidepool sculpins (*Oligocottus maculosus*) to detection of a predator cue depended on substrate color (matching vs. non-matching). This experiment indicated that the influence of ϕ (elevated using the predator cue) depended on Pr(detection) (manipulated through substrate match). Such an experiment would not have been considered if the manipulations were considered simply alternative methods of altering perceived predation risk, since then either would have sufficed.

Sih (1992) also modelled learning of ϕ (which he denoted z). In his model, prey learned from vigilance information, equivalent to the third step of the present model ($\phi(t'') \rightarrow \phi(t''')$). However, his model differed from mine in two important aspects. First, there was no chance of new predator arrivals after the initial predator departed. This approach assumes "either that these events are rare or that prey detect returning predators immediately" (Sih, 1992). This difference explains his result of a decay in ϕ to an asymptote of zero; in my model, the possibility of undetected, recently arriving predators prevents the recovery curves from reaching zero. Second, Sih did not incorporate learning from 'no attack' information. This is reasonable for the situation he modelled, in which prey are learning while in a refuge, but only if the refuge is completely safe (since then Pr(detection and attack) = 0 and the 'no attack' event provides no information).

Surprisingly, Bouskila and Blumstein (1992) demonstrated that the fitness costs of relatively large errors in assessment of habitat-specific long-term predation risks (mediated through the forager's behavior) can be very small, suggesting that selection for more accurate assessment will be relatively weak. It is not known whether this result applies to the problem of estimating the current ϕ (a component of an animal's short-term predation risk), addressed in this Chapter; a similar analysis to that of Bouskila and Blumstein (1992) would be required.

The model presented here leads to several testable predictions, including the expected shape of recovery curves and the expected influence of an animal's Pr(detection and attack) and Pr(scan) values on these recovery curves. Furthermore, the general continuous and asymptotic shape of the ϕ recovery curves is intuitively appealing and matches patterns reported in the literature (eg. Kotler, 1992). However, several simplifying assumptions were incorporated into the model which could be relaxed. For example, the assumption that predators are discretely present or not could be relaxed by making ϕ and its components a function of predator-prey separation distance. Such efforts will result in further novel predictions.

References

Blumstein, D.T. and Bouskila, A. In prep. Information assessment and decision making: a conceptual model to clarify mechanistic processes.

Bouskila, A. and Blumstein, D.T. 1992. Rules of thumb for predation hazard assessment: predictions from a dynamic model. Am. Nat. **139**: 161-176.

Cowie, R. and Krebs, J.R. 1979. Optimal foraging in patchy environments. In: *Population Dynamics* (R.M. Anderson, B.D. Turner and L.R. Turner, eds.), pp. 183-205. Blackwell, Oxford.

Dill, L.M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. Can. J. Zool. **65**: 803-811.

Dill, L.M. and Fraser, A.H.G. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behav. Ecol. Sociobiol. **16**: 65-71.

Dill, L.M. and Houtman, R. 1989. The influence of distance to refuge on flight-initiation distance in the gray squirrel (*Sciurus carolinensis*). Can. J. Zool. **67**: 232-235.

Fitzgibbon, C.D. 1989. A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. Anim. Behav. **37**: 508-510.

Fraser, D.F. and Huntingford, F.A. 1986. Feeding and avoiding predation hazard: the behavioural response of the prey. Ethology **73**: 56-68.

Godin, J.-G.J. 1986. Risk of predation and foraging behaviour in shoaling banded killifish (*Fundulus diaphanus*). Can. J. Zool. **64**: 1675-1678.

Godin, J.-G.J. and Sproul, C.D. 1988. Risk taking in parasitized sticklebacks under threat of predation: effects of energetic need and food availability. Can. J. Zool. **66**: 2360-2367.

Heinen, J.T. 1985. Cryptic behavior in juvenile toads. J. Herpetol. **19**: 524-527.

Kotler, B.P. 1992. Behavioral resource depression and decaying perceived risk of predation in two species of coexisting gerbils. Behav. Ecol. Sociobiol. **30**: 239-244.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**: 619-640.

Lima, S.L., Valone, T.J. and Caraco, T. 1985. Foraging-efficiency-predation-risk trade-off in the grey squirrel. Anim. Behav. **33**: 155-165.

Mangel, M. 1990. Dynamic information in uncertain and changing worlds. J. theor. Biol. **146**: 317-332.

Mangel, M. and Roitberg, B.D. 1989. Dynamic information and host acceptance by a tephritid fruit fly. Ecological Ent. **14**: 181-189.

McNamara, J.M. and Houston, A.I. 1985. Optimal foraging and learning. J. theor. Biol. **117**: 231-249.

McNamara, J.M. and Houston, A.I. 1987. Memory and efficient use of information. J. theor. Biol. **125**: 385-395.

Metcalfe, N.B., Huntingford, F.A. and Thorpe, J.E. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. Anim. Behav. **35**: 901-911.

Roitberg, B.D., Reid, M.L. and Li, C. 1992. Choosing hosts and mates: the value of learning. In: *Insect Learning* (D.R. Papaj and A. Lewis, eds.), pp. 174-194. Chapman and Hall, New York.

Shettleworth, S.J., Krebs, J.R., Stephens, D.W. and Gibbon, J. 1988. Tracking a fluctuating environment: a study of sampling. Anim. Behav. **36**: 87-105.

Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. Am. Nat. **139**: 1052-1069.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, U.S.A.

Valone, T.J. 1991. Bayesian and prescient assessment: foraging with pre-harvest information. Anim. Behav. **41**: 569-578.

Valone, T.J. and Brown, J.S. 1989. Measuring patch assessment abilities of desert granivores. Ecology **70**: 1800-1810.

Chapter 4

Prey capture distances of cryptic foragers: a dynamic-programming model and an experimental test.

Abstract

I investigate the foraging behavior of cryptic animals using a dynamic-programming model, in which prey capture elevates risk of predation. Two state variables, energy and information state, are incorporated into the model. The information state variable represents the forager's assessment of the probability that a predator is present. The value of this variable depends upon information which the forager has obtained in the recent past. Predator detection elevates the information state value to 1.0, while not detecting predators and the survival of risky activities provide information used to update the information state variable in a Bayesian manner. The model determines the survival-maximizing response (accept and capture, or reject) to each of four possible types of prey encounter (one prey type at four capture distances). Trends within the resulting decision matrices are used to predict the effects of the two state variables on maximum prey capture distance. I address three predictions: 1) as the energy state increases, and 2) as the information state increases, maximum capture distance will decrease, and 3) as the energy state increases, the influence of the information state on maximum capture distance will increase (*i.e.*, hungry animals will be less sensitive to predation risk). Comparisons between decision matrices are used to predict the influence of three parameters (corresponding to predator arrival probability, relative danger of prey capture, and food availability) on prey acceptance. Increasing habitat riskiness causes an increase in prey capture distances and an increase in the area of the state-space within which prey are captured. Increasing both the relative danger of prey capture and food availability has the opposite effect. An experimental test of the predicted influence of the perceived probability that a predator is present on maximum capture distances, using tidepool sculpins (*Oligocottus maculosus*), is described. Capture distances decreased with the perceived probability that a predator is present, as predicted.

Introduction

Recently, investigations of foraging behavior have begun to address the influence of conflicting behavioral demands (Dill, 1987). The conflict most commonly considered is that between predation risk and energy intake rate. Several mechanisms can lead to such a conflict. For example, predators may be more abundant in more profitable habitats or patches. The influence of such a scenario on 'where to forage' decisions (*cf.*, Lima and Dill, 1990) has received much attention, both theoretical (*e.g.*, Gilliam, 1982; Gilliam and Fraser, 1987; Mangel and Clark, 1988) and experimental (reviewed by Dill, 1987 and Lima and Dill, 1990). Predation risk-foraging trade-offs influencing within-patch 'what to eat' decisions have received much less attention.

Before considering why such trade-offs exist, it is useful to examine predation risk more closely than is commonly done, in the process defining some terms I will use repeatedly. The predation risk of an action is the probability of death by predation during that action. For death by predation to occur, a predator must be present, it must detect the animal (termed 'the forager'), attack it, and capture it (*cf.*, Endler, 1991). Predation risk equals the product of the probabilities that each of these events occurs during the action. In the model presented here, I assume that the forager knows the probabilities of the latter three events, but estimates the probability that a predator is present. I will refer to these probabilities as follows: the forager's perceived Pr(predator is present)= ϕ, Pr(predator detects forager | predator is present)= Pr(detection), Pr(predator attacks forager | predator detects forager)= Pr(attack), and Pr(predator captures forager | predator attacks forager)= Pr(capture). For simplicity, this formulation assumes that upon detection of a forager, predators either attack immediately or forget the location of the forager- otherwise, an action could influence the risk experienced by the forager even after the action is completed.

Within-patch (*e.g.*, 'what to eat') foraging decisions may represent a trade-off between predation risk and foraging because prey capture activities often have high associated values of Pr(detection) and/or Pr(capture), relative to non-capture activities. Pr(capture) will be elevated during prey capture actions whenever they reduce a forager's ability to detect an attacking predator, and thus to escape. Milinski (1984) has shown for sticklebacks (*Gasterosteus aculeatus*) foraging on *Daphnia*, that the frequency with which individuals detect model predators decreases with prey capture frequency and prey swarm density (see also Godin and Smith, 1988). Further, several studies have shown that animals alter their foraging behavior in response to predators, apparently due to the influence of feeding on Pr(capture) (*e.g.*, Milinski and Heller, 1978; Godin, 1986; Lima, 1988). Pr(detection) will be elevated during prey capture if foragers use physical cover to avoid detection by predators, and need to leave refuge to capture prey. More generally, the movements involved in prey capture and handling may expose foragers to predators (increase Pr(detection)), and this will be especially true of cryptic animals (Edmunds, 1974). Several studies have shown that movement increases predation risk, apparently because of increased Pr(detection) (*e.g.*, Herzog and Burghardt, 1974; Wright and O'Brien, 1982; Poulin *et al.*, 1987; Morey, 1990; Martel and Dill, in press).

Two models (Gilliam, 1990; Godin, 1990) have examined the influence of predation risk on diet selectivity. In this Chapter, I generate predictions regarding prey capture distances of cryptic foragers, using a dynamic programming model. I chose this method for two reasons. First, this technique allows the influence of several conflicting behavioral demands to be considered because it expresses the various costs and benefits of all behavioral options in a common currency (Mangel and Clark, 1986; Houston *et al.*, 1988). Second, the technique allows the influence of forager states to be investigated. This was necessary because I felt that the forager's ϕ state should be incorporated as a state variable (see Discussion for justification of this approach). This allows the influence of ϕ

on foraging behavior to be determined. The forager's energy level is also treated as a state variable, in order to incorporate the energetic benefits of prey capture, and because several studies have indicated that the effect of predation risk on foraging behavior is influenced by the energetic state of the forager (*e.g.*, Dill and Fraser, 1984; Godin, 1990; Heller and Milinski, 1979; Magnhagen, 1988). The predictions from this model are intended to be relatively general, applying to a wide range of animals.

After developing the predictions, I describe an experiment performed to test the influence of ϕ on prey capture distances of a cryptic forager, the tidepool sculpin (*Oligocottus maculosus*; Pisces, Cottidae).

The Model

The problem facing the forager is to survive to the end of a foraging interval. The foraging interval is divided into discrete time periods, indexed as t=1, 2, 3, ...T. In each time period, for all state variable value combinations, the model determines the optimal behavior (capture or reject) to perform upon encounter of each of the possible prey types (see below). The optimal choice is defined as the behavior that results in the maximum probability of survival from the present time t to T. The forager can die in two ways: by starving, or by being captured by a predator. Capture and ingestion of prey provides the forager with energy, which reduces the risk of starvation. However, foragers capturing prey have a higher per time period probability of detection by predators (given that predators are present), or $\mathrm{Pr(detection)}_c$, than do foragers who are not capturing prey ($\mathrm{Pr(detection)}_0$), because they are more cryptic in the latter case. Thus, foragers capturing prey experience a higher predation risk (the fundamental trade-off being modeled).

The model is presented in four steps. First, the state variables and their dynamics are described. Second, the calculations of predation risks associated with different activities are detailed. Third, the dynamic programming equation is developed. Finally, the details of running the model and generating predictions are explained.

The State Variables

The value of the energy state variable in time period t is designated $E(t)$. The energy state ranges from 0 (*i.e.*, forager completely empty) to *CAP* (*i.e.*, the forager's energy reserves are full to capacity). Further, for $E(t) \leq E_{\text{crit}}$, the forager is considered to have died from starvation. The forager's metabolic rate, m, is equal to one energy unit per time period, regardless of the activity performed.

The 'non-capture' activity is performed if no prey item is encountered, or if an encountered prey item is rejected. This activity has a duration, τ_0, of 1. Following a non-capture, $E(t+1) = E(t) - m$.

The forager gains energy by capturing prey. Prey have a gross energy content of G energy units and can be encountered at any of four distances, d_i, i=1, 2, 3, or 4. The capture time required for prey encountered at distance d_i is τ_i (for all runs presented here, I use $\tau_i = i$). The net energy gain from capturing a prey at distance d_i is $Y_i = G - \tau_i m$. The probability of encountering a prey at distance d_i is λ_i per period. Following a capture of a prey item at distance d_i, $E(t + \tau_i) = E(t) + Y_i$. The energy state and time consequences of capturing a prey item at each of the four capture distances (*i.e.*, times) and of non-capture, are shown in Fig. 4.1. Several assumptions regarding prey encounter and capture are inherent in this formulation. First, prey are always captured if attacked. Second, either prey items are never encountered simultaneously, or if they are, foragers instantly determine which is the most profitable item and disregard all others. Last, encounter probabilities are constant, thus assuming that prey are not depleted.

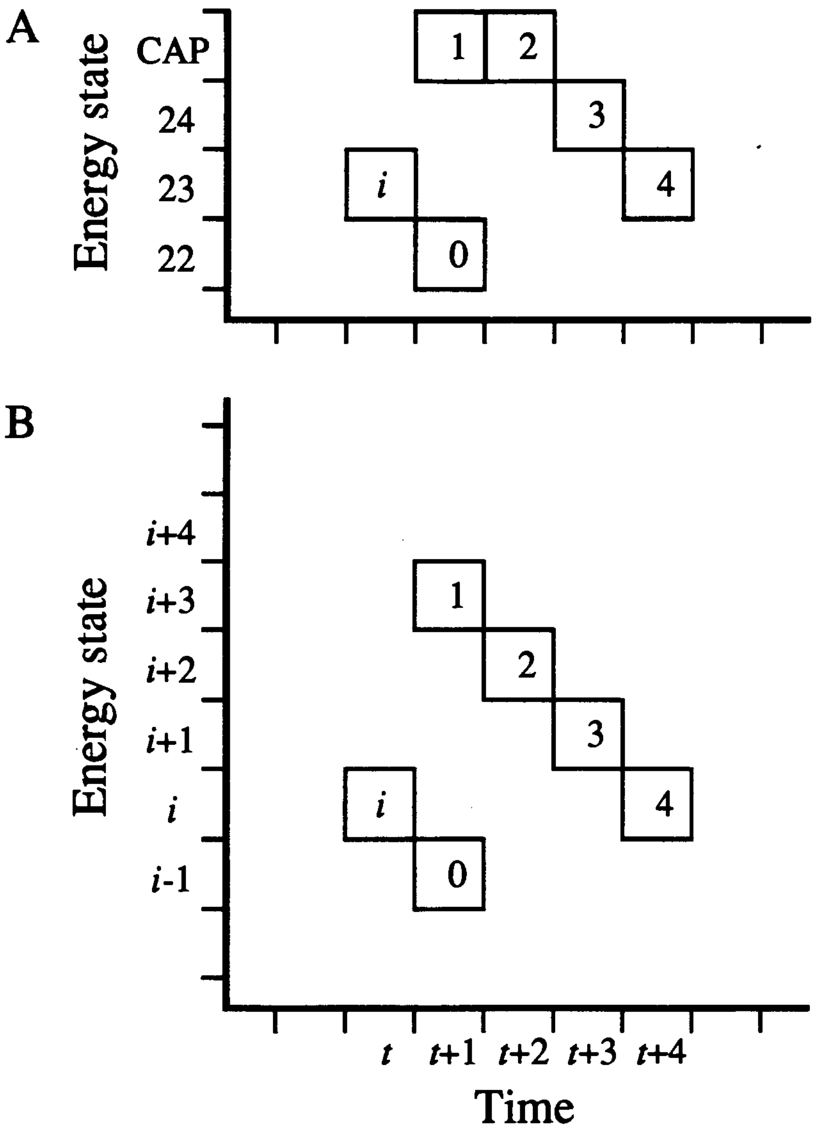

Figure 4.1. The energy state and time consequences of capturing prey at each of the four capture times (indexed 1-4), and of non-capture (indexed 0), for a forager with $E(t)=i$ (in the cell labeled '*i*'). B represents the consequences when the *CAP* boundary is not involved (*i.e.*, for $E(t)\leq 22$). In A, the influence of the *CAP* boundary is shown for a forager with $E(t)=23$.

Special conventions are necessary near the boundaries *CAP* and *T*. First, if $E(t) + Y_i \geq CAP$, then $E(t + \tau_i)$ is set equal to *CAP* (Fig. 4.1A). Second, when $t + \tau_i > T$, prey are rejected.

The model also treats ϕ as a state variable. The value of this variable represents the result of an assessment by the forager of the probability that a predator is present; thus, it represents an 'information state' (*cf.*, Blumstein and Bouskila, in prep.; Mangel and Roitberg, 1989). The value of the information state during period t is denoted $\phi(t)$. The information state ranges from 0 (when the forager is certain no predator is present) to 1.0 (when the forager is certain a predator is present). In model runs presented here, nine discrete information state levels were used, with values of 0, 0.125, 0.25, 0.375, 0.5, 0.675, 0.75, 0.975, and 1.

The assessment model developed in Chapter 3 is used to determine the information state dynamics. That model uses a three-step procedure to update $\phi(t)$ to $\phi(t+1)$. The first step updates $\phi(t)$ to $\phi(t')$, incorporating the information gained from either being attacked or not being attacked during a time period. If an attack occurs, a predator is certainly present ($\phi(t)$=1.0). If no attack occurs, ϕ is reduced, the size of the reduction increasing with the value of $\Pr(\text{detection}) \times \Pr(\text{attack})$ of the forager during period t. The second step updates $\phi(t')$ to $\phi(t'')$ by accounting for predator movements. The two parameters which specify predator movements are Pr(arrive)=Pr(predator arrives | no predator is present), and Pr(leave)=Pr(predator leaves | one is present). $\phi(t'')$ equals the sum of the probabilities 1) that a predator which is present stays or 2) if no predator is present, that one arrives. The third step updates $\phi(t'')$ to $\phi(t''')$ by incorporating information gained from scanning for predators. On a scan for predators, the forager can either detect a predator or not. If a predator is detected, $\phi(t''')$=1.0 (assumes no false alarms). If no predator is detected, ϕ is reduced, the size of the reduction increasing with the value of Pr(detect a predator | predator present), or Pr(scan).

I make three assumptions in applying the assessment model to describing the information state dynamics. First, I set Pr(capture)=1.0; therefore, I need not evaluate the post-attack ϕ dynamics. Second, I assume Pr(attack | detection)=1.0 for both prey capture and non-capture activities. Notice that the change in ϕ in step 1, when no attack occurs, then depends only on Pr(detection). Further, since $\Pr(\text{detection})_c > \Pr(\text{detection})_0$, the reduction in ϕ will be greater after a time period spent capturing prey than one spent in non-capture activity. Finally, I assume that the forager only scans for predators upon completion of activities.

The latter assumption specifies the ϕ values which apply in each time period of an action (periods t to $t+\tau-1$) and in the period immediately following an action ($t+\tau$). During the first period of any action, t, $\phi(t)$ applies. During all other periods of actions (for which $\tau>1$), indexed $t+j$ for $1 \leq j < \tau$, $\phi(t+j)=\phi(t+j-1'')$ because no scanning information is obtained in these time periods. However, since the forager scans for predators at the end of an action, $\phi(t+\tau)=\phi(t+\tau-1''')$. Examples of ϕ dynamics during capture of a prey with $\tau=4$ are shown in Fig. 4.2.

Predation Risk Calculations

Once the ϕ values applying for each time period of an action are known, the probability of death by predation (predation risk) during that action can be obtained. The total predation risk, β, of any action equals the sum of the probability of dying by predation in each of the time periods of the action, t to $t+\tau-1$, or

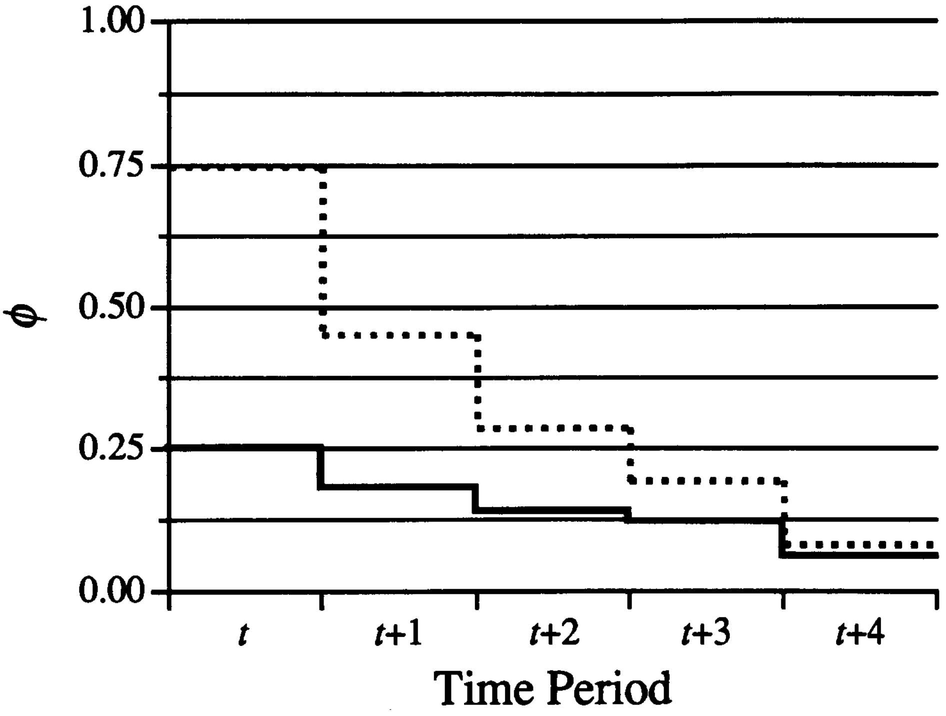

Figure 4.2. Information state dynamics during and after a capture at τ=4, for two initial $\phi(t)$ states, 0.75 and 0.25, represented by the dotted and solid lines respectively. The horizontal lines indicate the discrete ϕ levels. During periods t+1 to t+3, $\phi(t')$ values apply (and are shown) because no vigilance information is gained during prey capture. During t+4, $\phi(t'')$ values apply (and are shown) because the forager scans immediately after prey capture (between t+3 and t+4).

$$\beta = \sum_{j=0}^{\tau-1} \beta(t+j) \tag{1}$$

where

$$\beta(t+j) = \Pr(\text{alive at start of period } t+j) \times \ \phi(t+j) \times \Pr(\text{detection}) \tag{2}$$

since Pr(attack)=1.0 and Pr(capture)=1.0.

$$\Pr(\text{alive at start of period } t+j) = \begin{cases} 1.0 \text{ when } j = 0 \\ 1.0 - \sum_{k=0}^{j-1} \beta(t+k) \text{ when } j \geq 1 \end{cases}. \tag{3}$$

Thus, the predation risk for the non-capture activity, denoted β_0, is

$$\beta_0 = \phi(t) \times \Pr(\text{detection})_0, \tag{4}$$

since τ_0=1. The predation risk of capturing a prey item at distance d_i, denoted β_i, is

$$\beta_i = \sum_{j=0}^{\tau-1} \beta_c(t+j), \tag{5}$$

where $\beta_c(t+j)$ is obtained from equations (2) and (3), the subscript c indicating that $\Pr(\text{detection})_c$ is used in equation (2).

Table 4.1 lists all of the model parameters, with their values in the baseline parameter set. The Appendix presents the entire set of D_0, $\phi(t'')_0$, and predation risks, for all combinations of initial$\phi(t)$, activity type and τ, for the baseline parameter values.

Table 4.1. The model parameters (defined in the text) and their values in the baseline parameter set.

Parameter	**Basic value**
Prey parameters*	
G	4
Y_{0-4}	-1, 3, 2, 1, 0
τ_{0-4}	1, 1, 2, 3, 4
λ_{0-4}	.2, .08, .16, .24, .32
Forager parameters	
Pr(scan)	0. 5
m	1
E_{crit}	1
CAP	25
Number of ϕ levels	9
Predator parameters	
Pr(arrive)	0.05
Pr(leave)	0.4
Pr(detection)$_0$	0.01
Pr(detection)$_c$	0.1

* Prey parameter subscripts refer to the following: subscripts 1-4 refer to encountering and/or capturing a prey item at the four τ, λ_0 is the probability of not encountering a prey item per time period, and τ_0 and Y_0 are the duration and net energy change, respectively, of non-capture.

The Dynamic Programming Equation

Fitness at time t, energy state $E(t)$, and information state $\phi(t)$ is designated $F(E, \phi, t, T)$. Recall that this is equal to the maximum probability of survival from t to T. Recall also that only one prey item (or none) can be encountered in a time period. Thus, the fitness at time t is

$$F(E,\phi,t,T) = \sum_{i=0}^{4} \lambda_i \,\mathrm{MAX} \begin{Bmatrix} \Pr(\text{survive } t \text{ to } T, \text{ if reject}) \\ \text{OR} \\ \Pr(\text{survive } t \text{ to } T, \text{ if accept}) \end{Bmatrix}, \tag{6}$$

or the sum of the fitnesses realized for no encounter (i=0), or encounter of a prey item at one of the four d_i, weighted by their probabilities of occurrence. Note that if no prey item is encountered the two terms of the maximization are equal.

The Pr(survive t to T), given that an activity of duration τ is initiated at time t, equals the product of the probability of surviving the activity, from t to t+τ, and the probability of surviving from t+τ to T. The forager survives the activity if it avoids being eaten. The probability of not being preyed upon, during some activity with predation risk β, is simply $(1 - \beta)$. Thus, expanding equation 6,

$$F(E,\phi,t,T) = \sum_{i=0}^{4} \lambda_i \,\mathrm{MAX} \begin{Bmatrix} (1-\beta_0)\Pr(\text{survive } t+1 \text{ to } T, \text{ if reject}) \\ \text{OR} \\ (1-\beta_i)\Pr(\text{survive } t+\tau_i \text{ to } T, \text{ if accept}) \end{Bmatrix} \tag{7}$$

where the β values are dependent upon $\phi(t)$. The forager survives from $t + \tau_i$ to T if it neither starves nor succumbs to predation during that time. This probability is

$$\Pr(\text{survive } t+\tau_i \text{ to } T) = \sum_{j=0}^{1} D_j \times F\left(E(t)+\Upsilon_i, \phi_j, t+\tau_i, T\right), \tag{8}$$

where D_j represents the probability that scan outcome j occurs and ϕ_j represents $\phi(t+\tau_i)$ (*i.e.*, after the action) if outcome j occurs, where $j=0$ (no detection) or 1 (detection). The probability that the forager detects a predator on the scan following an action of duration τ, is

$$D_1 = \phi(t+\tau-1'') \times \Pr(\text{scan}), \tag{9}$$

while the probability that no predator is detected is $D_0=1-D_1$.

Note that ϕ_0 will rarely equal one of the discrete values of ϕ. In order to obtain the value of $F(E(t)+Y_i,\ \phi_0,\ t+\tau_i,\ T)$, I use linear interpolation. Thus, if $\phi(x)<\phi_0<\phi(x+1)$ (where $\phi(x)$ represents the value of ϕ at the x^{th} discrete ϕ level), and

$$p = \frac{\phi(x+1)-\phi_0}{\phi(x+1)-\phi(x)}, \tag{10}$$

then

$$F\left(E(t)+Y_i, \phi_0, t+\tau_i, T\right) = \left\{ \begin{matrix} p\left(F\left(E(t)+Y_i, \phi(x), t+\tau_i, T\right)\right) \\ + \\ (1-p)\left(F\left(E(t)+Y_i, \phi(x+1), t+\tau_i, T\right)\right) \end{matrix} \right\}. \tag{11}$$

The complete dynamic programming equation is obtained by substitution of equation (8) into equation (7). Thus,

$$F(E,\phi,t,T)=\sum_{i=0}^{4}\lambda_i\ \mathrm{MAX}\begin{Bmatrix}(1-\beta_0)\sum_{j=0}^{1}D_j\times F\big(E(t)-1,\phi_j,t+1,\ T\big)\\ \text{OR}\\ (1-\beta_i)\sum_{j=0}^{1}D_j\times F\big(E(t)+Y_i,\phi_j,t+\tau_i,\ T\big)\end{Bmatrix} \qquad (12)$$

where the D_j and ϕ_j values are dependent upon $\phi(t)$ and the activity type and duration.

The dynamic programming method of 'backwards iteration' (Mangel and Clark, 1988) allows this equation to be evaluated at any time t. This method involves calculating the fitnesses, for all state combinations, backwards in time from T - 1, at which time the fitness consequences of all activities are pre-defined with a 'terminal fitness function'. Thus, at any time t, all future fitness outcomes $F(E(t)-1, \phi_j, t+1, T)$ and $F(E(t)+Y_i, \phi_j, t+\tau_i, T)$ have already been calculated, and the equation can be solved.

Generating Predictions

As the program solves the dynamic programming equation, the optimal (survival-maximizing) behavior (accept or reject) for each encounter type (capture time) is recorded in a decision matrix. In this Chapter, I discuss only the 'stationary' sections of such decision matrices. A decision matrix is stationary when the decision set depends only upon the state variable values, and not upon time (Mangel and Clark, 1988). As the model runs (iterating backwards through time from T), the decision matrices converge upon a stationary decision set. I defined stationarity operationally as the first (iterating backwards) decision matrix which was unchanged for 20 time periods. The three dimensions of the decision matrices are energy state, ϕ state, and capture time/distance.

I examined the influence of Pr(arrive), Pr(detection)$_0$, and food availability (FA) on capture distances, by comparing the decision matrices produced by running the model with different parameter sets. *FA* is defined as the expected energy state increment resulting from an encounter, including encounter of no prey, *i.e.*, $FA = \sum_{i=0}^{4} \lambda_i \times Y_i$ (this assumes capture of encountered prey). To manipulate *FA*, different sets of λ_i were used, maintaining the probabilities in the proportion 1:2:3:4 for capture distances of 1, 2, 3, and 4, respectively. The feature of the decision matrices which was compared to determine the influence of these variables was the extent of the region in the matrices in which the optimal behavior was to capture encountered prey (at $\tau_i \geq 1$): I refer to this region as the 'capture region'.

The Predictions

Several predictions emerge from the decision matrices regarding the influence of the two state variables on maximum distance at which prey will be captured (*e.g.*, Fig. 4.3); I discuss three which I consider to be the most significant and general. Note that, due to the discrete nature of the model, the decision matrices are discrete, but I discuss the predictions as if the trends in the matrices were continuous.

The first prediction is that as $E(t)$ increases, the maximum capture distance decreases, for all $\phi(t)$. This trend can be seen in Fig. 4.3 by comparing maximum capture distances from left to right across a single $\phi(t)$ level. This prediction results from the decrease in the relative value of the energy gain from prey capture with increasing $E(t)$. The forager must capture prey to avoid starvation when its energy reserves are low; thus, at low $E(t)$, the forager captures prey at all τ. As the forager's energy state increases, the forager can afford to ignore prey encountered at longer τ and wait to encounter prey at shorter distances (safer and more profitable captures), and for ϕ to decrease.

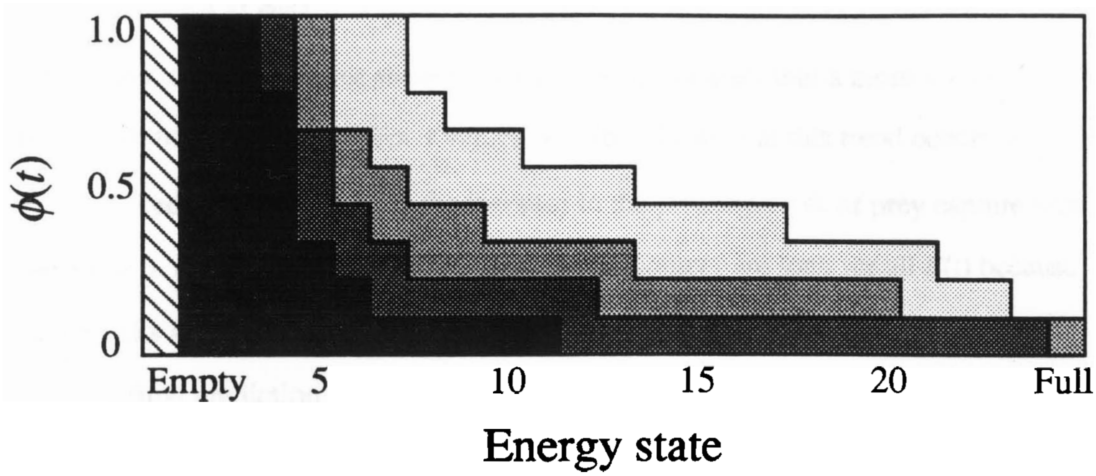

Figure 4.3. The stationary decision matrix for the baseline parameter set. Shaded regions represent state combinations at which encountered prey will be captured. The darkness of the shading indicates the maximum capture time (assumed equal to capture distance) at which the prey types will be captured, from lightest for τ=1 to darkest for τ=4. In the unshaded region, prey are rejected at all capture distances. If the forager enters the hatched region, it dies from starvation.

The second prediction which emerges from the decision matrices is that as $\phi(t)$ increases, maximum capture distance decreases. For example, at $E(t)=10$, maximum capture distance=4 at $\phi=0$, 3 at $\phi=0.125$, 2 at $\phi=0.25$, and 1 for $\phi=0.375$ to 0.625 (Fig. 4.3). Although this trend is not shown at $E(t)=2$ or 3, I suspect that a more sensitive analysis, with more ϕ levels and/or τ values, would indicate that this trend occurs at all $E(t)$ levels. This prediction results from the increase in the predation risk of prey capture with increasing $\phi(t)$. At low $\phi(t)$, the maximum capture distances are long for all $E(t)$ because predation risks are small.

The final prediction concerns the effect of the forager's energy state on the strength of the influence of $\phi(t)$ on maximum capture distances. As energy state increases, the influence of $\phi(t)$ on maximum capture distance increases (Fig. 4.3), because the forager can increasingly afford to wait to encounter prey at closer distances, and for the $\phi(t)$ state to decrease due to information gain and predator departure.

The effects on the capture region of manipulating Pr(arrive), Pr(detection)$_0$, and FA are presented in Table 4.2. First, as Pr(arrive) increases, the capture region expands. As Pr(arrive) increases, the forager reaches the lower $\phi(t)$ levels less frequently, and the total time spent at these levels decreases, due to more frequent predator sightings elevating the $\phi(t)$ to 1.0. Therefore, in order to avoid starvation, the forager must capture prey at higher $\phi(t)$ levels, explaining the expansion of the capture region. Second, an increase in the value of Pr(detection)$_0$ also causes the capture region to expand. As Pr(detection)$_0$ increases, the safety benefit of rejecting prey (and remaining cryptic) decreases. At the extreme, a forager whose Pr(detection)$_0$=Pr(detection)$_c$ experiences no increase in predation risk due to prey capture movement; thus, in the run with Pr(detection)$_0$=Pr(detection)$_c$=0.1, maximum capture distance=4 for all cells of the decision matrix. Thus, the capture region expands because of the decreasing marginal predation risk cost of prey capture with increasing Pr(detection)$_0$. Third, the capture region decreases with increases in habitat richness. With

Table 4.2. The parameters which were varied, the values used, and their influence upon the capture region of the decision matrix.

Parameter varied	Parameter values used	Influence on the capture region of increasing the parameter value
Pr(arrive)	0.01, 0.05*, 0.1, 0.2	Capture region expands
Pr(detection)$_0$	0.001, 0.005, 0.01*, 0.025, 0.05, 0.1	Capture region expands
Food availability[1]	0.2, 0.4, 0.6*, 0.8, 1.0	Capture region contracts

[1] See text for an explanation of this parameter.

* The value of this parameter in the baseline parameter set.

increased food availability, there is less risk of starvation in rejecting encountered prey when the $\phi(t)$ level is high, and it is more often better to wait to capture prey until the risk has decreased.

Experimental Test

I tested the prediction that prey capture distances decrease with ϕ (the second prediction of the model), for two sizes of prey, using tidepool sculpins (*Oligocottus maculosus*). Several aspects of the biology of this species indicate that crypsis is an important defense against detection by predators. Sculpins change their skin color to match their current substrate. As well, they reduce their activity rates upon detection of a predator (an approaching human; pers. obs.) or predator stimulus (conspecific 'skin extract'; Hugie *et al.*, 1991), an appropriate response for a cryptic animal. I have shown (Chapter 2) that their 'alarm response' to skin extract depends on substratum color; sculpins on sand respond by reducing their movement rate, while sculpins on a white background (for whom immobility will provide little improvement in crypsis) show no such reduction. This indicates that the reduction in movement rates in response to predator detection is motivated by the increase in crypsis, and not by any improved ability to detect an attacking predator (Chapter 2).

The prediction from the model is stated in terms of the maximum distance at which prey will be captured. In this experiment, however, I measure average capture distances. This approach is reasonable since average and maximum capture distances will generally be positively correlated, and are in the case of the model's assumptions.

Methods

In the model used to make the prediction being tested by this experiment, I allowed for predator detection through 'vigilance scans'. While this implies visual detection, detection of predator cues by any sense would produce the same prediction. In the present experiment, I use skin extract as a predator stimulus, *i.e.*, as the manipulation to elevate ϕ. Five ml skin extract aliquots were prepared by squirting seawater from a 5 ml syringe over the skin of a freshly killed sculpin, which had been lacerated 25 times on each flank, and subsequently redrawing the seawater into the syringe. 'Control' fluid consisted of plain seawater.

Two sizes of live brine shrimp were used as the prey in this experiment. Brine shrimp, ranging from nauplii to adults, were size sorted by passing them through a series of Nytex filters. Brine shrimp that were caught by a 1000 µ mesh represented the large size class, while those that passed through an 850 µ mesh, but were caught by a 710 µ mesh made up the small size class.

The experiment was performed between 5 Oct. and 25 Nov., 1991, in a refrigerated laboratory (11-14°C) at Simon Fraser University. Sculpins were collected 20 Sept., 1991 at Wizard Island, Barkeley Sound, B.C., using dip nets. Subjects (59-72 mm long) were housed individually in 1 liter containers, and fed brine shrimp (*Artemia* spp.) and broken mussels (*Mytilus edulis*) *ad libidum*. Skin extract donors (55-81 mm long) were housed in two 40-l aquaria on the same diet. Four experimental chambers, measuring 38 cm H x 60 cm W x 4.5 cm front-to-back, with 3 glass walls and one long wall of green plexiglas (the back wall), were used. This shape was chosen to restrict motion in one dimension, allowing attack distances to be measured by viewing through the long, glass side. Substrata were 3-mm clear plexiglas sheets, 4.5 cm x 60 cm, on the underside of which a solid layer of sand was attached using silicon sealant. Chambers were filled with seawater to a depth of 15 cm, surrounded by a white blind, and equipped with an airstone (set at a low rate) positioned at the middle of the green wall. A Tygon tube leading from behind the blind to the water surface allowed treatment and control fluids, and prey, to be added to the chambers with minimal disturbance; the tube was positioned above the airstone, to ensure that fluids and prey would disperse throughout the tank rapidly in the bubble-induced current.

Sculpins, starved approximately 48 h, were put in chambers individually, 2 h prior to beginning the trials. A VHS camera was set up inside the blind at least 0.75 h prior to the beginning of a trial, and thereafter the blind remained closed until trial completion. The appropriate fluid was added to a chamber 3- 4 min prior to prey addition, to allow time for the sculpins to detect any skin extract. 25 brine shrimp, of the appropriate size class, were added to start a trial. A trial was repeated at a later time if a subject made less than 10 captures.

The experiment was a repeated measures design, with each of 8 subjects experiencing each of the 4 treatment combinations (2 fluid types x 2 prey size classes). Prey capture distances were measured from a video monitor. The brine shrimp could not be seen on video, so behavior sequences typical of sculpins capturing brine shrimp were assumed to represent prey captures. Such a sequence includes a moderately rapid straight swim, ending in an acceleration or 'lunge', followed by a reduction or cessation in forward velocity and a change in direction. Capture distances were taken as the straight-line distance from the point at which the sculpin initiated the capture sequence, to the point at which the lunge ended. Captures were not measured if they appeared to be directed ≥ 45° from the plane of the screen (< 5% of captures). The capture distances for all acceptable captures, up to the fifteenth (subsequent captures were ignored), were used to calculate the average capture distance for a particular fish in a particular treatment combination.

Results

The results of this experiment are shown in Fig. 4.4. Both prey size and fluid type have a significant effect on capture distances (2-way, repeated measures ANOVA, $p<0.05$). The effect of ϕ is in the direction predicted by the dynamic-programming model, with capture distance greater in the low ϕ (control fluid) treatments than in the high ϕ (skin extract) treatments. As well, capture distances were greater for large than small prey.

The latter result, while sensible ecologically, is contrary to the prediction of the current model. Running the model with a larger prey type (larger G), holding prey encounter probabilities constant, would increase food availability. This model predicts that prey capture distances reduce with increasing food availability (Table 4.2). This contradiction would likely be resolved by modifying the model to incorporate the temporary nature of the change in food availability which occurs in the experiment. As well, incorporating benefits of energy gain other than starvation avoidance, such as growth and/or reproduction effects, may change the prediction.

Discussion

I consider the predictions of this model to be relatively general, for three reasons. First, since time does not influence the decisions at stationarity, these predictions will apply to species with different ecologically appropriate time period and foraging bout durations. Second, at stationarity the decision set is independent of the shape of the terminal fitness function (Mangel and Clark, 1988), which specifies the fitness the forager realizes at the end of the foraging bout, for each energy state; therefore, the predictions derived here will apply to animals with different terminal fitness functions. Finally, the predictions regarding the influence of the state variables are robust over a large range of parameter values. Thus,

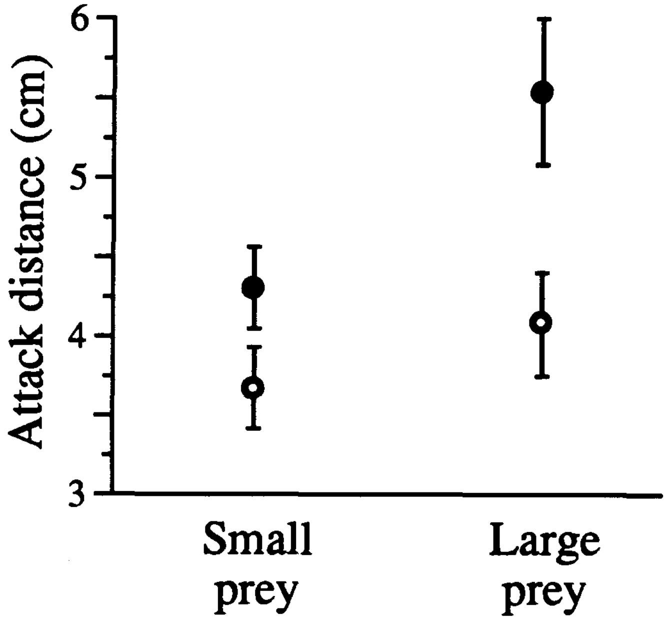

Figure 4.4. The influence of skin extract and prey size on attack distances (mean± S.E.) of tidepool sculpins. Filled and empty circles represent mean attack distances in control fluid and skin extract trials, respectively.

the predictions should apply to cryptic foragers generally (whose biology meets the other assumptions of this model) during the early portion of their foraging bouts.

Experimental evidence supports the three predictions regarding the influence of the information and energy state variables. Four experiments have determined the effect of predator (or model, or cue) detection on prey capture distances. The experiment described here demonstrated that tidepool sculpins have lower average prey capture distances when their $\phi(t)$ level is elevated using conspecific skin extract. Dill and Fraser (1984), Metcalfe *et al.* (1987), and Gotceitas and Godin (1991, 1993) have demonstrated that juvenile salmonids, who are also relatively cryptic (see Donnelly and Dill, 1984), reduce their prey capture distances when $\phi(t)$ is elevated using predator models. As well, Magnhagen (1988) has shown that the relatively cryptic goby *Pomatoschistus minutus* has a lower feeding rate in the presence of predators. She also reported lower movement rates when predators were present; it is probable, therefore, that the reduction in feeding rates was caused in part by reduced attack distances. Overall, I consider the existing evidence as strong support for this prediction.

Two experiments provide data appropriate for testing the prediction that capture distance (or τ) will decrease with increasing $E(t)$. Dill and Fraser (1984) demonstrate this effect for juvenile coho salmon (*Oncorhynchus kisutch*) foraging at high ϕ; however, no effect of energy state was found at low perceived risk. Magnhagen (1988) found that *P. minutus* foraged at a lower rate when well fed than when previously starved for one week. Again, her feeding rate data are only relevant to my prediction if the influence of risk on feeding rate is mediated primarily through reduced attack distances. Clearly, this prediction requires further experimental evidence before its validity can be determined.

These two experiments also provide support for the prediction regarding the mediating effect of energy state on the influence of $\phi(t)$ on capture distances. For juvenile coho salmon, the difference in mean capture distances, between foragers at low and high risk, increases with the number of prey captures (and thus energy state; Dill and Fraser, 1984). Similarly, for *P. minutus*, the effect of predator presence on foraging rates is lower for starved than for well fed subjects (Magnhagen 1988; *cf.* Fig. 4.3). I recommend that further tests of this prediction be performed, on animals other than fish, so that the generality of this effect of energy state can be established.

The above predictions regarding the influence of the energy and information state variables should also be tested on animals in habitats with different values of Pr(arrive), Pr(detection)_0, and food availability. As shown above, the size of the capture region of the decision matrix depends on the value of these variables. An expansion of the capture region causes a reduced effect of $\phi(t)$ and of $E(t)$, the latter both on capture distance directly, and through its mediation of the $\phi(t)$ effect on capture distance. My predictions regarding the influence of Pr(arrive), Pr(detection)_0, and *FA* are apparently novel and no data have been found with which they can be tested. However, experimental tests of these predictions should be relatively straightforward. Subjects' perceived Pr(arrive) could be manipulated by acclimation to different rates of predator (or cue) detection. A forager's Pr(detection)_0 could be manipulated by varying the background on which it is allowed to forage, and subjects could be held at different feeding levels prior to testing to determine the influence of *FA* (ensuring that gut fullness at the time of testing was held constant).

An important feature of the model presented here is the incorporation of $\phi(t)$ as a state variable, with a Bayesian-updating model used to determine its dynamics. This method serves three important functions. First, it partially removes the assumption of complete knowledge, often regarded as a flaw of optimality models (Stephens and Krebs, 1986). Second, it allows for behaviors of animals with intermediate values of ϕ to be studied. Most importantly, it realistically allows $\phi(t)$ to vary with time due to information gain.

In fact, I suggest that the dynamic nature of ϕ must be incorporated into any theoretical study of behavior at different ϕ levels. An alternative approach to modeling changes in behavior with predator detection, is to run a model (static with respect to ϕ) with two parameter sets, one with low predation risks appropriate for a low ϕ (probably no predator present) situation, the other with high predation risks representing a high ϕ situation. Such an approach may seem reasonable for experimental conditions in which treatments either have predators present and in full view of subjects or no predators present. However, it does not simulate natural conditions in which predators can continually arrive and depart, and the forager must assess the probability that a predator is present at any given time.

The static ϕ approach will result in incorrect predictions for the following reason. Consider a forager who has just detected a predator and thus has a high $\phi(t)$. In a natural environment, altering its behavior in the short term, by foregoing risky activities, is adaptive for the forager because $\phi(t)$ will decrease (due to the increasing probability of the predator's departure). This response to predator detection can be viewed as waiting for conditions to improve enough for risky activities to be resumed. However, conditions cannot improve in a (model) environment in which predators are always present; in this case, risky activities can be performed as safely now as later. Therefore, the difference in forager behavior between 'predator always present' and 'predator never present' environments is expected to be smaller than the difference between high $\phi(t)$ level and low $\phi(t)$ level behavior. To test this, I modified my model by making the ϕ state static, and ran it with the basic parameter set, once with the predation risks which apply when $\phi(t)=0$ and once with those applying when $\phi(t)=1$. Comparing the difference in capture distances between $\phi(t)=0$ and 1, predicted by the dynamic and static versions (Fig. 4.5), supports my expectation: the behavioral difference is much reduced in the static runs.

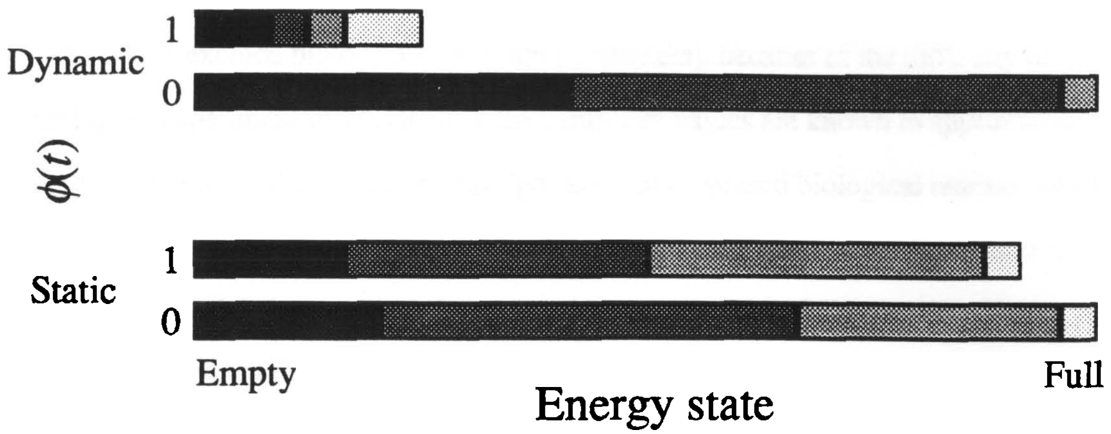

Figure 4.5. A comparison of two approaches to modelling the influence of the probability that a predator is present. The two approaches are referred to as 'dynamic' (the model as developed here, with $\phi(t)$ as a dynamic state variable) and 'static' (in which the forager's ϕ state is fixed at one level). See Fig. 4.3 for an explanation of the shading. Note that the bars for the dynamic runs are the same as the top and bottom ϕ slices from Fig. 4.3.

A valuable aspect of the dynamic-programming approach is that during formulation of a model, all parameters relevant to a question are acknowledged. Initially, this may appear to make accurate testing of such models more difficult than is the case for simpler models (which exclude biologically relevant parameters), because of the difficulty of designing an experiment in which all of the parameter values are known to approximate the values used in the model. However, this 'problem' of increased biological realism should not burden experimental tests. Tests of simpler models more easily meet the requirements because these models ignore many important parameters. Essentially, the simplifying assumptions of which features are critical to a problem are made during the modeling stage for simpler models, but during the testing stage for dynamic-programming models.

References

Blumstein, D.T. & Bouskila, A. In prep. Information assessment and decision making: a conceptual model to clarify mechanistic processes.

Dill, L.M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. Can. J. Zool. **65**: 803-811.

Dill, L.M. and Fraser, A.H.G. 1984. Risk of predation and the feeding behaviour of juvenile coho salmon (*Oncorhynchus kisutch*). Behav. Ecol. Sociobiol. **16**: 65-71.

Donnelly, W.A. and Dill, L.M. 1984. Evidence for crypsis in coho salmon, *Oncorhynchus kisutch* (Walbaum), parr: substrate colour preference and achromatic reflectance. J. Fish Biol. **25**: 183-195.

Edmunds, M. 1974. *Defence in Animals*. Longman Inc., New York.

Endler, J.A. 1991. Interactions between predators and prey. In: *Behavioral Ecology* (J.R. Krebs and N.B. Davies, eds.), pp. 169-196. Blackwell, Oxford.

Gilliam, J.F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Ph.D. thesis, Michigan State University, East Lansing, USA.

Gilliam, J.F. 1990. Hunting by the hunted: optimal prey selection by foragers under predation hazard. In: *Behavioural Mechanisms of Food Selection* (R.N. Hughes, ed.), pp. 797-818. Springer-Verlag, Berlin.

Gilliam, J.F. and Fraser, D.F. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology **68**: 1856-1862.

Godin, J.-G.J. 1986. Risk of predation and foraging behaviour in shoaling banded killifish (*Fundulus diaphanus*). Can. J. Zool. **64**: 1675-1678.

Godin, J.-G.J. 1990. Diet selection under the risk of predation. In: *Behavioural Mechanisms of Food Selection* (R.N. Hughes, ed.), pp. 739-769. Springer-Verlag, Berlin.

Godin, J.-G.J. and Smith, S.A. 1988. A fitness cost of foraging in the guppy. Nature **333**: 69-71.

Gotceitas, V. and Godin, J.-G.J. 1991. Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.): effects of social status and hunger. Behav. Ecol. Sociobiol. **29**: 255-261.

Gotceitas, V. and Godin, J.-G.J. 1993. Effects of aerial and in-stream threat of predation on foraging by juvenile Atlantic salmon (*Salmo salar*). In: *Production of juvenile Atlantic salmon,* Salmo salar, *in natural waters* (R.J. Gibson and R.E. Cutting, ed.). Can. Spec. Publ. Fish. Aquat. Sci. **118**: 35-41.

Heller, R. and Milinski, M. 1979. Optimal foraging of sticklebacks on swarming prey. Anim. Behav. **27**: 1127-1141.

Herzog, H.A. and Burghardt, G.M. 1974. Prey movement and predatory behavior of juvenile western yellow-bellied racers, *Coluber constricter mormon.* Herpetologica **30**: 285-289.

Houston, A., Clark, C., McNamara, J. and Mangel, M. 1988. Dynamic models in behavioural and evolutionary ecology. Nature **332**: 29-34.

Hugie, D.M., Thuringer, P.L. and Smith, R.J.F. 1991. The response of the tidepool sculpin, *Oligocottus maculosus*, to chemical stimuli from injured conspecifics, alarm signalling in the Cottidae (Pisces). Ethology **89**: 322-334.

Lima, S.L. 1988. Vigilance and diet selection: a simple example in the dark-eyed junco. Can. J. Zool. **66**: 593-596.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**: 619-640.

Magnhagen, C. 1988. Changes in foraging as a response to predation in two gobiid fish species, *Pomatoschistus minutus* and *Gobius niger*. Mar. Ecol. Prog. Ser. **49**: 21-26.

Mangel, M. and Clark, C.W. 1986. Towards a unified foraging theory. Ecology **67**: 1127-1138.

Mangel, M. and Clark, C.W. 1988. *Dynamic Modelling in Behavioral Ecology*. Princeton University Press, Princeton, U.S.A.

Mangel, M. and Roitberg, B.D. 1989. Dynamic information and host acceptance by a tephritid fruit fly. Ecological Ent. **14**: 181-189.

Martel, G. and Dill, L.M. In press. Influence of movement by coho salmon (*Oncorhynchus kisutch*) parr on their detection by common mergansers (*Mergus merganser*). Ethology.

Metcalfe, N.B., Huntingford, F.A. and Thorpe, J.E. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. Anim. Behav. **35**: 901-911.

Milinski, M. 1984. A predator's costs of overcoming the confusion-effect of swarming prey. Anim. Behav. **32**: 1157-1162.

Milinski, M. and Heller, R. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). Nature **275**: 642-644.

Morey, S.R. 1990. Microhabitat selection and predation in the Pacific treefrog, *Pseudacris regilla*. J. Herpetol. **24**: 292-296.

Poulin, R., Wolf, N.G. and Kramer, D.L. 1987. The effect of hypoxia on the vulnerability of guppies (*Poecilia reticulata*, Poeciliidae) to an aquatic predator (*Astronotus ocellatus*, Cichlidae). Envir. Biol. Fish. **20**: 285-292.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, U.S.A.

Wright, D.I. and O'Brien, W.J. 1982. Differential location of *Chaoborus* larvae and *Daphnia*: the importance of motion and visible size. Am. Midl. Nat. **108**: 68-73.

Appendix. The information state dynamics and the predation risks for all combinations of initial $\phi(t)$, activity type and τ, for the baseline parameter set (see Table 4.1). β_0 and β_i refer to the predation risks of non-capture and capture activities, respectively. $\phi(t'')_0$ denotes the value of ϕ after an action if no predator is detected on the scan following the action, while D_0 denotes the probability of this outcome. See text for details.

	τ	Initial $\phi(t)$								
		0	0.125	0.25	0.375	0.5	0.625	0.75	0.875	1.0
Non-capture										
β_0	1	.0000	.0013	.0025	.0037	.0050	.0063	.0075	.0088	.0100
D_0	1	.9750	.9397	.9043	.8688	.8332	.7975	.7618	.7259	.6900
$\phi(t'')_0$	1	.0256	.0642	.1058	.1510	.2002	.2538	.3127	.3775	.4493
Capture										
β_i	1	.0000	.0125	.0250	.0375	.0500	.0625	.0750	.0875	.1000
	2	.0050	.0238	.0427	.0615	.0804	.0992	.1181	.1369	.1558
	3	.0125	.0346	.0566	.0786	.1006	.1226	.1446	.1666	.1886
	4	.0213	.0449	.0684	.0919	.1154	.1390	.1625	.1860	.2096
D_0	1	.9750	.9425	.9092	.8751	.8400	.8040	.7670	.7290	.6900
	2	.9621	.9452	.9276	.9093	.8902	.8703	.8496	.828	.8055
	3	.9554	.9466	.9373	.9276	.9174	.9067	.8955	.8836	.8712
	4	.9519	.9473	.9424	.9373	.9319	.9262	.9202	.9139	.9072
$\phi(t'')_0$	1	.0256	.0610	.0998	.1428	.1905	.2438	.3037	.3717	.4493
	2	.0394	.0580	.0781	.0998	.1233	.1490	.1770	.2077	.2415
	3	.0467	.0565	.0669	.0781	.0900	.1029	.1167	.1317	.1479
	4	.0505	.0556	.0611	.0669	.0731	.0796	.0867	.0942	.1023

Chapter 5

The influence of predation risk on diet selectivity: a theoretical analysis.

Abstract

Several studies have examined whether experimental increases in predation risk influence diet selectivity; results range from decreased to increased diet selectivities. A possible explanation for these disparate results emerges from an examination of the prey sets used in these studies, which differed in the relationship between the values of risk components associated with the capture ('danger') of different prey types, and their profitabilities. When less profitable prey were more dangerous, selectivity increased with risk. When prey were equally dangerous, selectivity did not change. Finally, when the more profitable prey were more dangerous, selectivity decreased with risk. Here, I examine theoretically the influence of a forager's estimate of the probability that a predator is present (ϕ) on the selection of diets from prey sets with varying danger-profitability relationships. A dynamic programming model (presented in Chapter 4) is used to determine the maximum capture time (distance) for each of two types of prey, differing in their energetic content, for a range of forager energy state and ϕ levels. Then the diets which would result if foragers attacked prey according to the rules provided by the dynamic model are determined. The model results indicate that the prey danger-profitability relationship determines the diet selectivity response to ϕ, confirming that variation in this relationship could be responsible for the range of experimental results. The results also indicate that the diet selectivity response to ϕ depends on the forager's energy state: at low energy levels, the diets do not differ between low and high ϕ values, for any danger-profitability relationship, because at these states the forager must place energetic gain before safety.

Introduction

Prediction and explanation of animal diet selectivity in different situations is an important research area in behavioral ecology. First generation studies of this problem considered only the energetic benefit-time cost tradeoff (Stephens and Krebs, 1986). Recently, studies have begun to investigate the importance of other, higher-level tradeoffs. One such tradeoff is that between foraging benefits (net energy intake) and predation risk costs. Prey capture actions will have an associated predation risk cost in many situations. For example, an animal's vigilance is often compromised when attacking and/or handling prey, decreasing the probability that the animal will detect an attacking predator (Milinski, 1984), and presumably resulting in reduced chances of escape (see Godin and Smith, 1988). A second example concerns cryptic animals; for them, prey capture movements may reduce or completely eliminate their crypsis, increasing the probability of detection by predators and thus predation risk (Edmunds, 1974; Morey, 1990).

The term "predation risk" has several different meanings. Here, the predation risk of a given action is the probability of death by predation during the execution of the action, which is the product of the probabilities of the components of predation risk. These components correspond to the steps leading to an animal's death by predation: a predator is present (close enough to detect and attack the animal), it detects the animal, attacks the animal, and captures the animal. (For simplicity, I assume that predators attack immediately upon detection of prey; thus, the predation risk after completion of an action is not influenced by that action.) An animal will often not be certain whether or not a predator is present, but will have an estimate of the probability that one is, based on the information it has. I refer to the animal's estimate of this probability as ϕ (Chapter 3). Many authors use "predation risk" synonymously with ϕ; however, this can lead to confusion and hinder new insights regarding the effects of predation risk. I refer to the probabilities of each of the final three steps as Pr(detection), Pr(attack), and Pr(capture), respectively. (Note that these three probabilities are all conditional on the steps earlier in the sequence.)

Typical tests of whether predation risk influences diet selectivity involve determining subjects' diet selectivities in two treatments: i) high ϕ - a subject's ϕ is elevated to close to 1.0 by presenting a predator or predator cue during a trial, and ii) low ϕ, achieved by having no predator cue present. I use the term 'diet selectivity response' to refer to the difference in diet selectivity at high minus low overall risk.

To date, four studies have measured diet selectivity responses. Godin (1990) studied guppies (*Poecilia reticulata*) foraging on *Daphnia* of three different size classes. Godin found that the guppies' handling times and attack success on the three sizes differed between predator present and absent situations. However, profitabilities (including the time and energy cost of failed capture attempts) were likely greatest for small *Daphnia*, least for large, and intermediate for the medium size class, in both situations. During trials with a predatory fish visible to the subjects (high ϕ), guppies captured relatively more small, profitable prey than in trials with no predator present (low ϕ); thus, in this study, the diet selectivity response was positive.

In a similar study, Ibrahim and Huntingford (1989) determined diet selectivities of sticklebacks (*Gasterosteus aculeatus*) foraging on chironomids and *Bosmina*, with and without a predatory fish visible. For sticklebacks, *Bosmina* are less profitable than chironomids (Ibrahim and Huntingford, 1989). Subjects in the predator-present treatment ate a larger proportion of *Bosmina*, and thus were less selective than control subjects (*i.e.*, a negative diet selectivity response).

I determined the diet selectivities of tidepool sculpins (*Oligocottus maculosus*: Pisces, Cottidae), foraging on two size classes of brine shrimp, with and without conspecific skin extract (to which these fish are known to show an alarm response) present in the water. (Details of this experiment are presented in the Appendix, as it is important to the argument presented here, but will not be published separately.) For sculpins, the larger size class of brine shrimp is more profitable. I found no effect of skin extract on the proportion of the two prey size classes captured, and thus on diet selectivity (*i.e.*, a null diet selectivity response).

Lima (1988) examined diets of juncos (*Junco hyemalis*) foraging on whole millet seeds and millet "bits". In his study, Lima compared the diets of individuals foraging in different flock sizes. He reasoned that "an increase in group size effectively reduces an individual's risk of predation because other flock members are also vigilant, and the chance of death in the event of a successful attack decreases with group size" (Lima, 1988, p 594). Thus, his comparisons of diet selectivities of birds in different group sizes can be viewed as comparisons at different predation risks (with risk increasing with decreasing flock size). He found that the proportion of whole seeds in the diets increased with decreasing flock size. Since seeds were less profitable than bits, diet selectivity decreased with decreasing flock size, a negative response. Lima's study was unique in two regards. First, he determined diets at 10 different flock size classes, and found that selectivity decreased continuously with increasing flock size. Second, for each flock size, he determined diets for birds foraging on three different bit-whole seed pairings, distinguished by the size of bits (bit profitability increases with bit size). He found that at all flock sizes, diet selectivity (proportion of bits in diet) increased with bit size. Further, he found that there was "a significant interaction between the effects of flock size and bit size; the effect of flock size was progressively smaller as bit size increased" (Lima, 1988, p 595). Thus, the diet selectivity response (to a given decrease in flock size) decreased with increasing bit size, although it was always negative.

In summary, the results of these studies include positive, null, and negative diet selectivity responses to manipulations of overall predation risk. All of these studies used different species of foragers and prey, and manipulated different predation risk components. Thus, there are several potential causes for the range of results. However, the variable most likely responsible is the relationship between the 'dangers' associated with capturing prey and their profitabilities.

In Godin's (1990) study, handling time increased with size of *Daphnia*. Therefore, he argued that larger prey were more dangerous to capture, because the prey handling probably reduced the guppies' ability to detect attacking predators. Since larger prey were also less profitable, the slope of the prey danger versus profitability relationship ('DP slope') was negative in his study (Fig. 5.1A).

In my experiment on sculpins, the two prey size classes had similar handling times (Appendix) and thus were likely equally dangerous to capture. Note that for sculpins, the major predation risk component elevated by prey capture is likely Pr(detection), as these animals are relatively cryptic when immobile (see Chapter 2). Thus, the sculpins were presented with a null DP slope (or close to null; Fig. 5.1A).

In the study by Ibrahim and Huntingford (1989), capture of the more profitable chironomids likely had higher associated values of Pr(capture) than did *Bosmina* (and thus a positive DP slope; Fig. 5.1A), for two reasons. First, prey handling likely reduces the sticklebacks' probability of detecting attacking predators, and chironomids required much longer handling times. As well, "feeding on benthic chironomids requires the sticklebacks to assume a head-down posture which reduces their chances of detecting predatory attacks" even further (Ibrahim and Huntingford, 1989, p 52).

In Lima's study (1988), the less profitable whole millet seeds were safer, because during handling to remove the shell, the juncos assumed a head-up posture and thus could scan for predators. In contrast, the entire handling time of bits (of all three sizes) was spent with the head down. Thus, the juncos also were presented with positive DP slopes. Because profitabilities of the bits increased with size, but their dangers were relatively

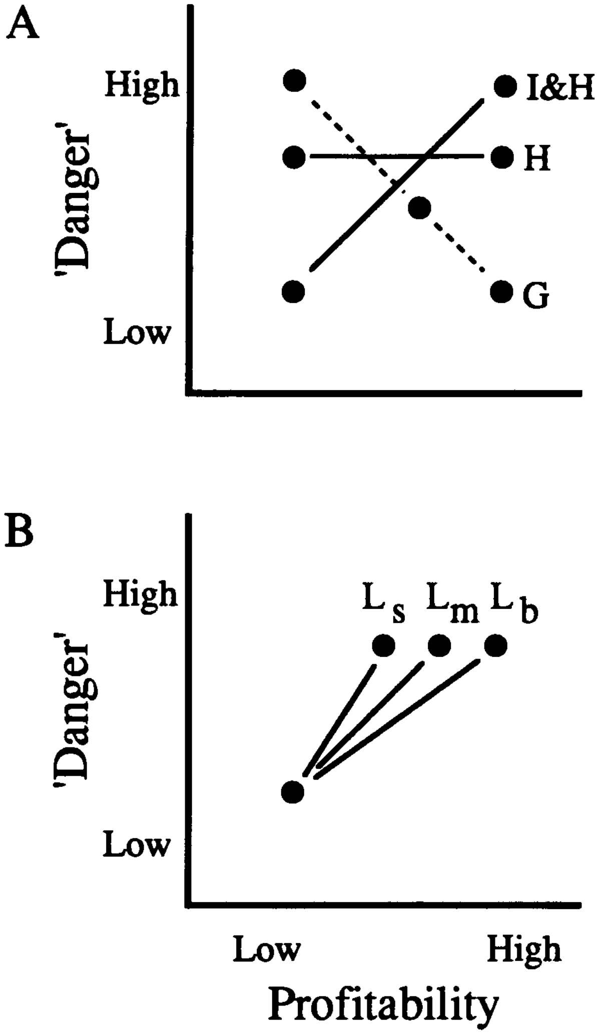

Figure 5.1. The relative positions of prey on the prey capture "danger" versus profitability axes in the four experiments which have examined the influence of predation risk on diet selectivity. (G= Godin, 1990, H= my study, reported in the Appendix, I&H= Ibrahim and Huntingford, 1989, and L= Lima, 1988). The dotted line connecting Godin's three prey types is used to indicate that the actual relationship between the three prey may well have been non-linear. In B, the three millet seed-bit pairings which Lima (1988) presented to juncos are represented (s, m, and b indicate pairings consisting of seeds and small, medium, and big bits, respectively). By changing a bit's size and therefore its profitability, Lima produced three different positive DP slopes.

constant (*i.e.*, they had similar handling times), the three different seed-bit pairings represented different (positive) DP slopes, as shown in Fig. 5.1B.

Summarizing, positive, null, and negative diet selectivity responses occurred in experiments that presented foragers with prey falling on a negative, null, and positive DP slope, respectively (Fig. 5.2). Such a relationship is intuitively reasonable, considering that in the experiments with positive and negative responses, the foragers always biased their diets more toward safer prey in situations with elevated values of overall predation risk (Godin, 1990: Ibrahim and Huntingford, 1989; Lima, 1988); thus, foragers reduced their rate of energy gain in exchange for increased safety. Further, in my experiment on sculpins, in which prey did not differ in danger, a change in diet selectivity would not have increased the sculpins' safety (although a decreased total prey capture rate, which was shown, would have).

The ideal test of the hypothesis that the DP slope is the cause of the different diet selectivity responses reported would determine responses in negative, null, and positive DP slope situations in a single study system. I use a dynamic programming model (see Mangel and Clark, 1988) to determine prey attack policies for a forager maximizing its probability of survival to the end of a foraging period, for a range of DP slopes. These policies specify the maximum capture times (or distances) at which two types of prey should be attacked, over a range of hunger and ϕ levels. By comparing the selectivities at high and low ϕ levels, the diet selectivity responses to an increase in ϕ is determined. In general, I use ϕ levels of 0 and 1.0, because they should approximate the levels perceived by subjects in experiments in which diet selectivities are measured in high (predator stimulus present) and low (no stimulus present) 'predation risk' treatments.

I use the dynamic-programming approach because it allows for various aspects of an animal's state to be incorporated as state variables, and generates behavioral predictions

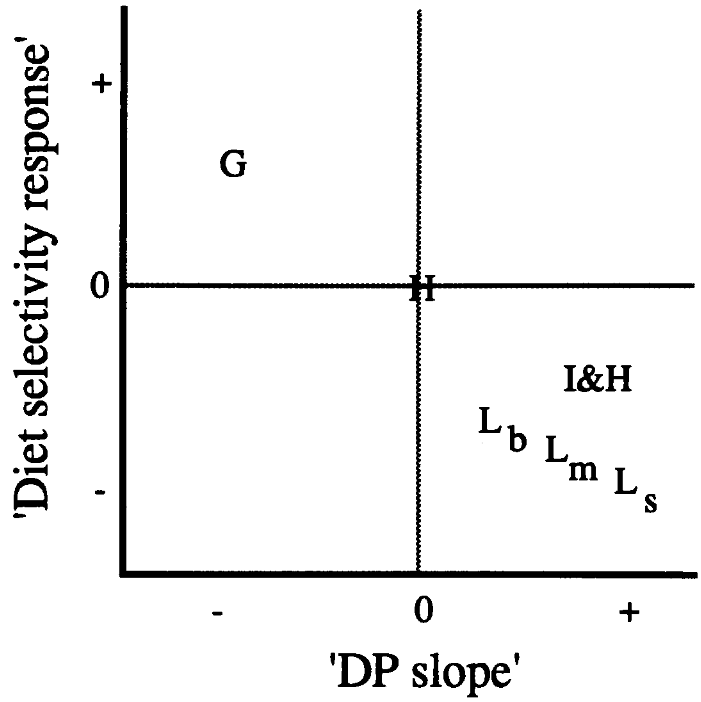

Figure 5.2. The diet selectivity responses to an increase in the value of overall predation risk versus the DP slope, in the four experiments reviewed (labels are the same as for Fig. 5.1). The plot is intended only to indicate the positions of the points relative to the origin. Although the nature of the relationship is not known, the three points from Lima's (1988) study suggest that the diet selectivity response should change continuously with DP slope. Note that in Lima's study, selectivities were obtained at a whole range of flock sizes (*i.e.*, overall predation risk levels); the responses shown represent the relative change in diet selectivity for any change in flock size in the 3 millet seed-bit pairings.

which are functions of these variables. Earlier work (Chapter 4) demonstrated the importance of treating ϕ as such a state variable.

The Dynamic-Programming Model

The dynamic programming model used here differs in only two details from the one fully described in Chapter 4. Therefore, I provide only a brief description of the model here, while fully detailing the changes.

The dynamic programming model considers a forager feeding on two types of prey, differing in their energy content, during a foraging bout made up of discrete time periods (in Chapter 4, a one prey-type version of the model was presented). Prey type I has a higher energy content than type II. Both prey types can be encountered at any of four capture times, corresponding to 1, 2, 3, and 4 time periods. When a prey item is encountered, the forager has the option to 'accept' it (*i.e.*, attack it and, it is assumed, capture it with probability=1.0) or 'reject' it. The dynamic model determines which of these two options maximizes the probability of survival from the current time period to the end of the foraging bout, for each prey type-capture time combination. This is done for each possible combination of values for two state variables, which describe the forager's energy and ϕ states.

The forager's energy state ($E(t)$) can vary over 25 levels. Unless prey are captured, the forager's energy state decreases one level each time period, due to metabolic costs; if $E(t)$ reaches the lowest level, the forager dies of starvation. It is this feature which provides the 'impetus' for the forager to attack prey. When prey are captured, the energy state is incremented by the gross energy content of the prey item minus the metabolic cost of capture (equal to one energy state level per time period). Note that this last feature makes the profitability of a prey capture dependent not only on the prey type attacked, but also on its capture time.

The information state at time t, denoted $\phi(t)$, represents the forager's assessment of ϕ in period t. The value of this variable changes as the forager gains information from scanning for predators and from not being captured by a predator (Chapter 3). This ϕ state has 9 discrete levels, the lowest representing $\phi = 0$ (certainty that no predator is present), the highest $\phi = 1.0$ (certainty that a predator is present). The value $\phi = 1.0$ applies during a period immediately after a predator detection; the lowest level is only reached after several consecutive periods without predator detection.

All of the activities which the forager can perform have associated predation risks. These are calculated as the sum of the probabilities of dying in each time period of an action. The probability of death in a particular time period, in turn, equals the product of Pr(alive at start of period), ϕ (which applies during that time period), Pr(detection), Pr(attack), and Pr(capture). Chapter 4 describes the predation risk calculations completely, and also lists the predation risk values corresponding to the run here with baseline parameter values (Table 5.1) and equal prey dangers.

I use Pr(capture | pp) (where 'pp' abbreviates 'predator present') to refer to the product of Pr(detection), Pr(attack), and Pr(capture). Here, I vary the value of Pr(capture | pp), to vary the 'danger' of different actions. As in Chapter 4, Pr(capture | pp) is always relatively low when the forager is not attacking a prey item, modeling (for example) a cryptic forager for whom Pr(detection) when not moving < Pr(detection) when attacking prey. In the present version, however, the value of Pr(capture | pp) associated with attacking the two prey types can be varied, in order to manipulate the DP slope. The energetic content of the two prey types, and thus their profitabilities at any given capture time, are held constant in all runs, making the DP slopes dependent only on the relative dangers of capture associated with attacking prey type I and II. Since the profitabilities of

Table 5.1. The dynamic programming model parameters (other than prey dangers) and their baseline values.

Parameter	Baseline value
Prey parameters	
Energy content of prey (in energy state units)	
Prey type I	5
Prey type II	3
Encounter times of prey type I and II (in time periods)	1-4
Encounter probabilities for encounter times of 1-4 (same for both prey types)	.04, .08, .12, .16
Probability of encountering no prey	0.2
Forager parameters	
Metabolic rate (energy state units per time period)	1
$E(t)$ at which forager starves (E_{crit})	1
Maximum E(t)	25
Number of information state levels	9
Pr(forager detects predator on a single scan | predator present)*	0. 5
Pr(capture | pp) when not attacking prey	0.01
Predator parameters	
Pr(predator arrives | no predator present)*	0.05
Pr(predator leaves | predator present)*	0.4

* For an explanation of these parameters, see Chapter 4.

the two prey types vary with capture time, actual danger-profitability slopes could not be defined. I use the difference in Pr(capture | pp) for the two prey types (prey type I minus prey type II) as an index of the DP slope. This index has the desired properties: i) the difference is negative when the energetically richer prey (type I) is safer, and positive in the opposite situation, and ii) larger values represent steeper slopes, either negative or positive, while a value of zero represents a situation in which prey have equal dangers.

The dynamic programming model was run with a variety of different DP slopes (Table 5.2), holding all other parameters constant. In each run, the model was run (backwards through time; see Mangel and Clark, 1988) until the decision matrix became stationary (defined as 20 time periods over which the decision matrix did not change). I determined diet selectivities for foragers at particular ϕ levels from these decision matrices.

Obtaining Diet Selectivities

The dynamic programming model provides decision matrices which specify maximum capture times at which both prey types should be attacked, for all combinations of $E(t)$ and $\phi(t)$. I use two methods to determine the diet selectivities which will result when an animal forages according to these rules.

The first method determines the diets of foragers whose ϕ level is fixed, but whose energy state fluctuates according to the energetic consequences of captures and non-capture activities. This is done by simulation, modeling foraging bouts which are terminated when 10 prey have been captured or the forager's energy state reaches E_{crit} (and it starves). In the simulation, 'foragers' begin a foraging 'bout' with $E(t)$=10. An encounter type i (no prey or one of the eight prey type-capture time combinations) is chosen randomly. If no prey is encountered, the energy state is decreased by one. If a prey item is encountered, the

Table 5.2. The combinations of prey-specific Pr(capture | pp) values ('dangers') and resulting danger-profitability slopes* used in model runs reported here.

Prey type I danger	**Prey type II danger**	**DP slope**
0.1	0.1	0
0.075	0.125	-0.05
0.125	0.075	+0.05
0.05	0.15	-0.1
0.15	0.05	+0.1
0.025	0.175	-0.15
0.175	0.025	+0.15
0.0	0.2	-0.2
0.2	0.0	+0.2

* See text for explanation of DP slope calculation.

appropriate cell of the decision matrix is consulted to determine whether that prey class is to be accepted or rejected. If the prey is rejected, the energy state is decreased by one. If that prey class is to be accepted, the energy state is increased by the prey item's gross energy content minus 1 unit per handling time period.

To provide a relatively stable estimate of diet selectivities, the program continues simulating foraging bouts until a total of 5000 prey have been captured. Using the total number of each prey type (I and II) encountered and captured during all of the simulated foraging bouts, a 'simulated selectivity' value is calculated using the formula for Chesson's α (Chesson, 1978), *i.e.*,

$$\text{Simulated selectivity} = \frac{\frac{r_{\mathrm{I}}}{p_{\mathrm{I}}}}{\frac{r_{\mathrm{I}}}{p_{\mathrm{I}}} + \frac{r_{\mathrm{II}}}{p_{\mathrm{II}}}}, \tag{1}$$

where I and II indicate the two prey types, and r_i and p_i represent the proportion of prey type *i* eaten and encountered, respectively. To test the variation in simulated selectivities, I ran the simulation twice for both the $\phi = 0$ and $\phi = 1.0$ levels of the decision matrices, for 7 different DP slope situations. The differences of these 14 pairs of selectivities had a mean of 0.0023 (S.E = 0.0013), indicating very low variance.

In order to examine the influence of energy state on the diet selectivity response, I use a second method of calculating diet selectivity, which represents the selectivity which would result if a forager's $E(t)$ and $\phi(t)$ remained constant for an extended period; I refer to such values as 'cellular selectivity' values, since they represent the selectivity produced by the prey capture rules in a single 'cell' of the decision matrix.

While it is possible for an animal to remain at one of the two $\phi(t)$ levels examined for an extended period, if predators were either never detected during that period (ϕ would remain at 0) or always detected during every scan (ϕ would remain at 1.0), energy state will fluctuate with prey captures (except when the net energy gain=1). Therefore the situation modeled, in which energy state is fixed, is an impossibility. I feel this analysis is worthwhile, however, because experimental measures of selectivity of animals at different average hunger levels may approximately meet this assumption (if prey captures cause little change in energy state relative to the difference in hunger levels between treatments).

Cellular selectivity is calculated as the ratio of prey type I to total prey occurring in the diet, which can be obtained using the formula

$$\text{Cellular selectivity} = \frac{\sum_{i=1}^{\tau_{max}(\mathrm{I})} \lambda_i}{\sum_{j=\mathrm{I}}^{\mathrm{II}} \left(\sum_{i=1}^{\tau_{max}(j)} \lambda_i \right)}, \qquad (2)$$

where $\tau_{max}(j)$ is the maximum capture time at which prey type j should be accepted, and λ_i is the probability of encountering either prey type at capture time i. The selectivity value calculated using this formula is equivalent to Chesson's α, since encounter rates of the two prey are equal. I then calculate the diet selectivity response to elevated ϕ for any energy state i by subtracting the cellular selectivity at $\phi = 1$, $E(t)=i$ from that for $\phi = 0$, $E(t)=i$. I examine the influence of energy state on the diet selectivity response by comparing selectivity responses across energy state levels.

Notice that cellular selectivities, and thus selectivity responses, can only be calculated for cells in which the $\tau_{max} \geq 1$ for at least one prey type. This requirement is often not met for cells at $\phi > 0$, and moderate and high $E(t)$ levels, because at these state combinations the forager can afford to wait for ϕ to decrease before capturing prey (*cf.*, Chapter 4). Selectivity responses can only be calculated at energy states for which both the

ϕ =0 and 1.0 cells have some prey acceptance. Thus, the analysis of the effect of energy state on the diet selectivity response can only examine the effect over the lower range of energy states.

Cellular selectivities cannot vary continuously, since only a limited number of prey encounter times were modeled and many combinations of $\tau_{max}(I)$ and $\tau_{max}(II)$ give equal selectivities. In fact, typical decision matrices contain only 7 different cellular selectivities. Therefore, I use cellular selectivities only to examine the influence of energy state on the diet selectivity responses. I use the simulated selectivities described above, which can vary continuously (as can the resulting diet selectivity responses), to examine the relationships of diet selectivity versus ϕ and diet selectivity response versus DP slope.

Although both methods of obtaining diet selectivities do so at a fixed ϕ level, the prey capture rules provided by the dynamic-programming model represent the optimal decisions for the given ϕ level, when ϕ is a dynamic variable. Thus, the diet selectivities obtained in this way will represent those for foragers who 'expect' ϕ to change in the future.

Results

The relationship between diet selectivity and ϕ, for danger-profitability (DP) slopes ranging from -0.15 to 0.15, is shown in Fig. 5.3. With a slope of 0, diet selectivity remains relatively constant with increasing ϕ. When slopes are negative, diet selectivities generally increase with ϕ, although a slight decrease is shown at higher ϕ values for DP slope= -0.05. Similarly, for positive DP slopes, selectivities decrease (at a decelerating rate) with increasing ϕ values. Further, for any given ϕ level, selectivities decrease with the DP slope. Note that these two features, for the three positive DP slope curves, are found in

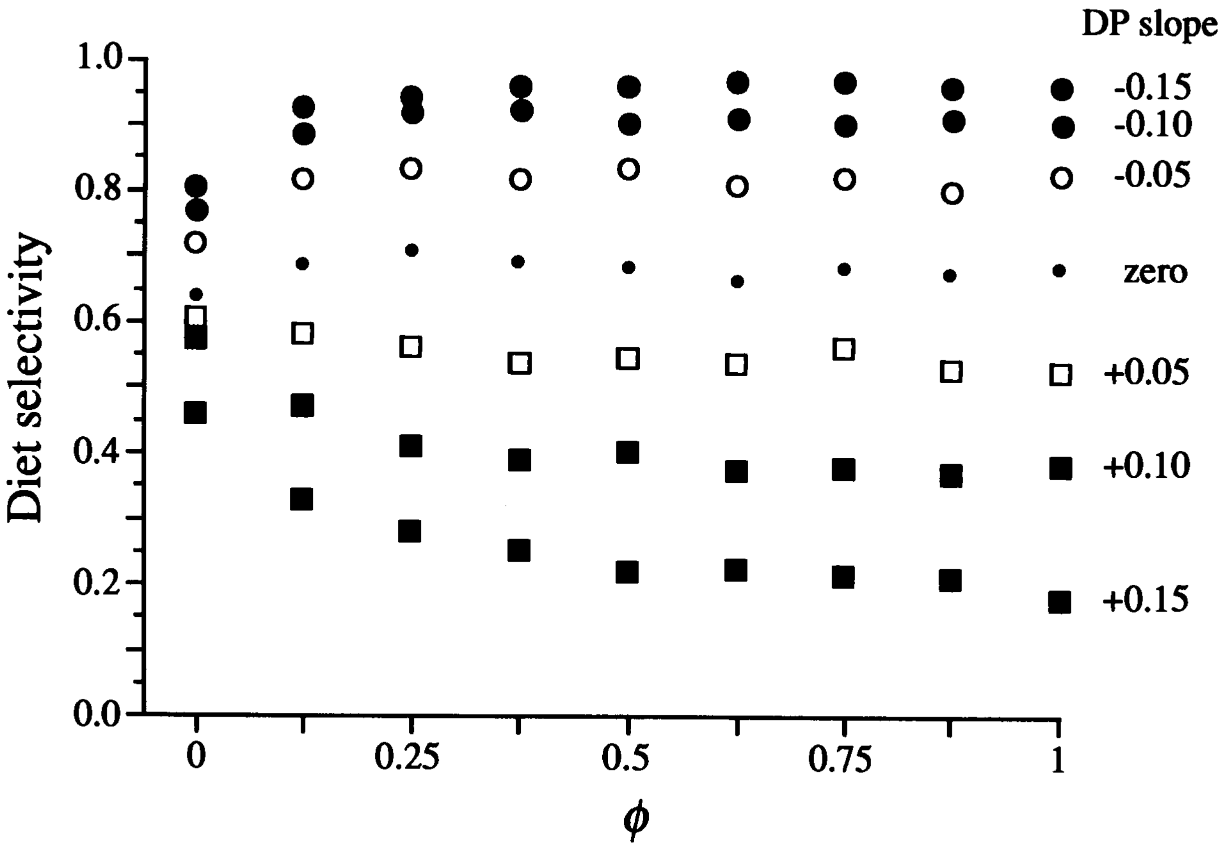

Figure 5.3. The relationship between 'simulated' diet selectivity values (see text) and ϕ, the forager's perceived probability that a predator is present, for DP slopes ranging from -0.15 to +0.15.

Lima's (1988) analogous results (discussed above), although in his study ϕ was not used to manipulate overall predation risk.

Figure 5.4 shows the relationship between the diet selectivity response and the DP slope. These responses equal the simulated selectivity at $\phi = 1.0$ minus that at $\phi = 0$. The overall negative relationship, with a near-zero y-intercept, is as expected from the empirical evidence reviewed in the introduction. This graph also indicates that the relationship is relatively continuous, although for $|\text{DP slope}| \geq 0.1$, the response appears to be relatively independent of the DP slope. Finally, the two extra series plotted on the graph, for runs with Pr(arrive)=0.1 and Pr(scan)=0.25 (double and half the baseline values, respectively) indicate that the result is relatively robust to changes in these variables.

While the model predicts a slightly positive diet selectivity response at a DP slope of zero, for all parameter sets tested, I believe this result to be a consequence of the limited number of discrete prey capture time options. Examination of the decision matrix for the zero DP slope situation indicates that prey type I is generally captured at longer capture times (resulting in selectivities above 0.5 at all ϕ values; Fig. 5.3). This is reasonable, since prey type I is the more profitable one. At $\phi = 1$, neither prey is captured at $E(t)>9$ (for the baseline parameter set), because at these energy states, the forager does better waiting until ϕ decreases before capturing prey. At energy states of 8 and 9, prey type I has a $\tau_{\max}$ (maximum capture time at which it should be accepted) of 1, while that for prey type II is zero. Again, this is as expected given the equal prey dangers, and the constraint that prey can only be encountered at discrete capture times. However, this disparity (between $\tau_{\max}(\text{I})=1$ and $\tau_{\max}(\text{II})=0$) is likely greater than the optimal one at those energy states for a situation with continuous $\tau_{\max}$ options, and causes diet selectivities to be greater than those that would be predicted by a continuous model.

Note that this problem is not limited to cases where $\tau_{\max}(\text{I})$: $\tau_{\max}(\text{II})=1{:}0$; however, at this ratio, the effect will be more severe than at less extreme ratios. This problem is also

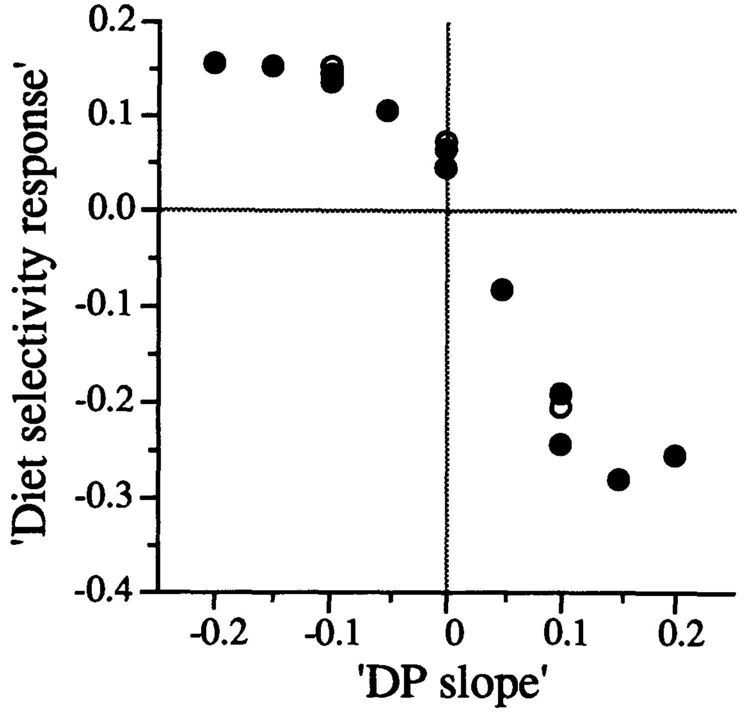

Figure 5.4. The relationship between diet selectivity responses and DP slope values, for responses calculated using 'simulated selectivities' for $\phi = 0$ and 1.0 (see text). Black circles represent values based on decision matrices produced by model runs using the baseline parameter set (Table 5.1). Gray and white circles represent values produced using parameter sets identical to the baseline set except that Pr(predator arrives | no predator present)=0.1, or Pr(forager detects predator on a single scan | predator present)=0.25, respectively.

not limited to the run with DP slope=0. Similar extreme ratios occur in all decision matrices when $\phi \geq 0.125$, although they are reversed (prey type II remains in the diet after type I has been dropped) when the DP slope is positive. Thus, the actual effect of ϕ on diet selectivity will be less severe than indicated in Fig. 5.3, and the relationship between the selectivity response and the DP slope (Fig. 5.4) is expected to be less steep, with an intercept closer to zero.

The influence of energy state on the diet selectivity response (calculated using 'cellular' selectivities) is shown in Fig. 5.5, for DP slopes of -0.1, 0, and 0.1. At an energy state of 2, responses for all three DP slopes are zero. This reflects the need for foragers at this energy state to obtain energy, since failure to do so will result in certain death through starvation. As the starvation threshold becomes more distant, the forager is more able to respond to the need to avoid predation, by avoiding the more dangerous prey. This results in the curves for the negative and positive DP slopes tending away from the zero response with increasing energy state. The curve for the positive DP slope decreases, due to diets at high ϕ values that are more biased toward the safer, less profitable prey than those at low ϕ values. The opposite occurs in the case of the negative DP slope, although the trend shows a slight reversal at $E(t)=8$. Although the relationship for the 0 DP slope situation is generally the closest to zero, it is very unstable, rising, falling, and rising above a zero response with increasing energy state. The cause of this instability is not known, but I again implicate the small number of possible capture times for each prey type (4), which causes cellular selectivities to change relatively abruptly.

Discussion

The results of this theoretical analysis strongly support the role of the prey danger-profitability relationship (DP slope) on the diet selectivity response to an increase in overall

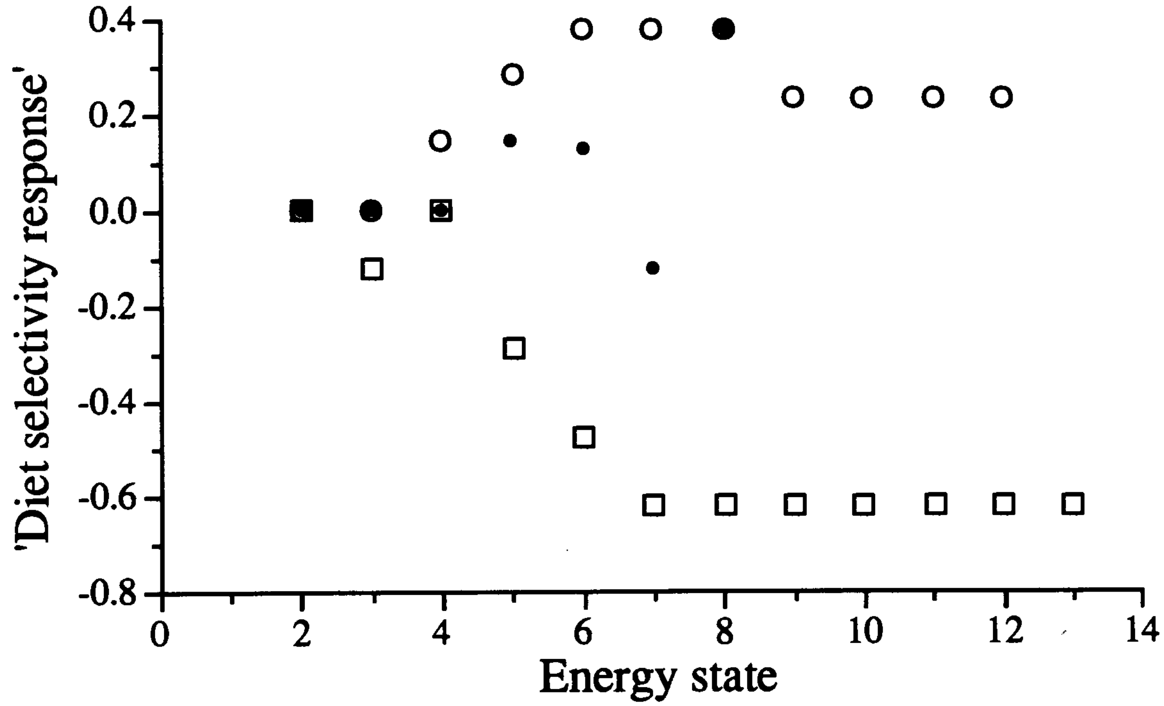

Figure 5.5. The relationship between diet selectivity responses and energy state, calculated using 'cellular selectivities' (see text). Circles, dots, and squares represent responses for -0.1, 0, and 0.1 DP slope situations, respectively. Responses could not be calculated at $E(t)>12$, 8 and 13 for the -0.1, 0, and 0.1 DP slope situations respectively, because at these higher energy states, for $\phi = 1.0$, the survival maximizing behavior is to reject both prey at all encounter times, and no 'diet selectivity' can be determined.

predation risk. Viewed more generally, this result is equivalent to the results of most studies which have investigated foraging-predation risk trade-offs (reviewed in Lima and Dill, 1990); when overall predation risks are elevated (*e.g.*, due to increased ϕ, during exposure to a predator for example) foragers tend to accept reduced energetic intake rates for reduced predation risk. For many foraging decisions, such as when or where to feed (*cf.*, Lima and Dill, 1990), the behavioral option with the highest energetic return often has the highest associated predation risks. The case of prey choice, considered here, is interesting in that there is no *a priori* reason why alternative prey must represent an energy-risk trade-off (only the positive slope represents a trade-off).

In his review of the literature on the influence of predation risk on diet selection, Godin (1990) comes to a similar conclusion regarding the importance of the relationship between prey danger and profitability on diet selectivity. However, his conclusion is stated more specifically, regarding only cases where vigilance and prey handling are incompatible, and handling time increases with prey size. Indeed, this influence of prey size on the probability of detecting a predator attack, and thus on Pr(capture), may be a common cause of prey-specific dangers. However, the realization that the value of other predation risk components may vary with prey-type reveals the more general nature of the hypothesis.

Two other studies have examined the influence of predation risk on diet selectivity theoretically. Gilliam (1990) determined diet selectivity for foragers minimizing 'μ / f' (the ratio of mortality rate to energy intake rate), when the predation risks of handling different prey types and of searching can differ. His analysis involved incorporating predation risks of search and handling into the basic prey model (for review see Stephens and Krebs, 1986). Gilliam (1990) applied this model to comparing diet breadths predicted by the basic prey model (with the optimization criterion maximize 'f') to those of the modified version.

Applying that model to the problem addressed here, that of predicting shifts in diets with changes in the probability that a predator is present, would require running it with two sets of predation risk values (for search and handling of all prey types), one with low values representing a low ϕ situation and one with higher values representing a high ϕ situation. The most reasonable assumption for assigning the values in the high ϕ set would be to multiply all of the risk values in the low ϕ set by the same factor, representing the elevation in ϕ. However, in this case, Gilliam's (1990) model would predict no change in diet selectivity with ϕ, regardless of difference in prey capture dangers. This is because the μ values for all possible diet breadths would increase by the same factor, and the diet minimizing μ / f would not change.

Gilliam cautioned "that just comparing diets in the presence and absence of visible predators may not form a suitable test" of the model, since foragers may adjust parameters associated with prey (*i.e.*, encounter probabilities, net energy gain, and/or handling time). Thus, the model would need to be run with different parameter sets to make appropriate predictions. It is interesting to note that in the current model, such an adjustment (in capture distances of the two prey types) is the mechanism which allows diet selectivity to vary with ϕ.

Godin (1990) also examined the influence of predation risk on diet selectivity, using a dynamic programming model. His approach was similar to mine in that predation risk per time period was greater during prey capture (his "β_H") than during non-capture actions ("β_S"). Because of the apparent similarity between my approach and Godin's, I will carefully contrast the two models. Godin (1990) presents his model as comparing predator-present and absent situations. This comparison is made by running his model with two sets of β_S and β_H, one with low values representing a predator-absent situation, and one with high values representing a predator-present situation. I will refer to Godin's two scenarios as predator-present and absent (or $\phi = 1$ and 0, respectively).

Godin's model was intended to predict diets of guppies foraging on *Daphnia*, with and without predators present. He found that guppies "required significantly more time, on average, to successfully attack, pursue and ingest a large *Daphnia* than a small one" (p. 751). Thus, the capture time values used in the model (obtained from observations of foraging guppies) increased with prey size, and an attack of a larger prey type required that the forager incurred the higher predation risk, β_H, for a longer time. Although β_H values were equal for all three prey sizes, this difference in capture time resulted in the three prey having different associated dangers: total capture danger increased with prey size. Since profitability decreased with prey size, the three prey fell along a negative DP slope. Godin's model predicted an increase in selectivity (increased proportion of small *Daphnia* in the diet) from predator-absent to predator-present situations, which agrees with the result of my model for this slope situation.

However, besides greater values of β_S and β_H in the predator-present runs than the predator-absent runs, Godin also varied two other features of the foraging environment, making it difficult to conclude that the effect was due to "predator presence" alone. First, profitabilities of the three prey classes differed in the two situations, based on measured handling times of guppies. These different profitabilities would have had an influence on diet selectivity independent of that of predator presence. Second, the ratio between β_S and β_H, differed between predator-absent and present situations. Godin (1990) used β_S and β_H values of 1×10^{-6} and 2×10^{-6}, respectively, for the predator-absent run, and 1×10^{-3} and 2×10^{-2}, respectively, for the predator-present run. Thus, prey capture was twice as risky as non-capture when no predator was present, but 20 times as risky when a predator was present; no rationale for this difference was provided. Since predation risk equals the product of ϕ and the probability of being captured given a predator is present (danger), this ratio should have remained constant if only the value of ϕ changed. This inconsistency may have exaggerated the influence of "predator presence" on diet selectivity predicted by Godin's model.

An important difference between Godin's (1990) approach and mine is the state variable approach used in my dynamic programming model to simulate the dynamics of $\phi(t)$. In Godin's simpler model, the predation risks (of capture and non-capture) have low values when simulating the absence of predators, and high values when simulating predator presence. It may appear that this formulation is reasonable for the experimental conditions that Godin was simulating (in which treatments either had predators present and in full view of subjects, or no predators present). However, since the predation risk parameters are fixed, Godin's model essentially represents a forager who knows that predators either will never arrive in the future ('predator absent') or will never leave ('predator present'). Such certainty is unlikely in nature, and no foragers are likely to have been designed with such knowledge. Instead, uncertainty of the type modeled here is more likely to be the rule, and a state-variable approach is likely to be more generally applicable.

References

Chesson, J. 1978. Measuring preference in selective predation. Ecology **59**: 211-215.

Edmunds, M. 1974. *Defence in Animals*. Longman Inc., New York.

Gilliam, J.F. 1990. Hunting by the hunted: optimal prey selection by foragers under predation hazard. In: *Behavioural Mechanisms of Food Selection* (R.N. Hughes, ed.), pp. 797-818. Springer-Verlag, Berlin.

Godin, J.-G.J. 1990. Diet selection under the risk of predation. In: *Behavioural Mechanisms of Food Selection* (R.N. Hughes, ed.), pp. 739-769. Springer-Verlag, Berlin.

Godin, J.-G.J. and Smith, S.A. 1988. A fitness cost of foraging in the guppy. Nature **333:** 69-71.

Hugie, D.M., Thuringer, P.L. and Smith, R.J.F. 1991. The response of the tidepool sculpin, *Oligocottus maculosus*, to chemical stimuli from injured conspecifics, alarm signalling in the Cottidae (Pisces). Ethology **89**: 322-334.

Ibrahim, A.A. and Huntingford, F.A. 1989. Laboratory and field studies of the effect of predation risk on foraging in three-spined sticklebacks (*Gasterosteus aculeatus*). Behaviour **109**: 46-57.

Lima, S.L. 1988. Vigilance and diet selection: a simple example in the dark-eyed junco. Can. J. Zool. **66**: 593-596.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**: 619-640.

Mangel, M. and Clark, C.W. 1988. *Dynamic Modelling in Behavioral Ecology*. Princeton University Press, Princeton, U.S.A.

Milinski, M. 1984. A predator's costs of overcoming the confusion-effect of swarming prey. Anim. Behav. **32**: 1157-1162.

Morey, S.R. 1990. Microhabitat selection and predation in the Pacific treefrog, *Pseudacris regilla*. J. Herpetol. **24**: 292-296.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, U.S.A.

Zar, J.H. 1984. *Biostatistical Analysis*. 2nd Ed. Prentice-Hall, Englewood Cliffs, U.S.A.

Appendix. An experiment on the influence of conspecific skin extract on the diet selectivity of tidepool sculpins.

Here, I describe a study of the diet selectivity response of tidepool sculpins (*Oligocottus maculosus*: Pisces, Cottidae) to elevated ϕ levels, performed from June to July, 1991 at the Bamfield Marine Station (Bamfield, B.C., Canada). I manipulated ϕ using skin extracts of injured conspecifics, to which these fish show an alarm response (Hugie *et al.*, 1991). Skin extract (prepared as in Chapter 2) was added to experimental aquaria 2-5 min prior to prey addition for high ϕ trials; untreated water was added in low ϕ trials.

Sculpins, measuring 44 to 60 mm, were collected from tidepools and beaches at Ross Islets, Barkley Sound, B.C., using dip nets and a 120 × 180-cm pole seine. Fish were held in a 150 × 150 × 50 D cm tank with flow-through seawater and sand substrate, and fed a diet of mussels (*Mytilus edulis*) and brine shrimp (*Artemia*). Sculpins were collected at least 4 days and not longer than 14 days prior to use in trials.

To control for hunger level, subjects were fed *ad libidum* on mussels and brine shrimp until 45-48 hours prior to trials, after which they were starved until the trial. Approximately 2 h prior to trials, sculpins were placed individually into experimental aquaria measuring 24 cm high X 19.8 X 19.8 cm, filled to a depth of 10 cm with seawater. In an earlier experiment (Chapter 2) I showed that one aspect of the alarm response of tidepool sculpins - the decrease in movement rate - depended on the substrate on which a fish was held: the movement rate decreased significantly more for sculpins on a sand substrate than for ones on a white background. Therefore, I also used sand substrates in the present experiment. To minimize disturbance during trials, the experimental aquaria were surrounded on all sides by a blind, and treatment fluids and prey were introduced to each aquarium through a tygon tube leading from outside the blind to the water surface.

Two sizes of live brine shrimp, sorted using Nytex filters, served as prey. The large size class consisted of shrimp which passed through a 710 μ mesh, but not a 600 μ mesh, while the small size class were shrimp which passed through a 500 μ mesh, but not a 400 μ mesh. Both size classes were swallowed almost instantaneously by the sculpins; thus, the large brine shrimp, with much more mass, were the more profitable prey type.

To determine diet selectivity, subjects were presented with 50 brine shrimp, 25 of each size class. Trials were terminated by removing the subject before feeding was completed (while ensuring that no remaining prey were removed). The remaining prey were then collected, sorted into size classes, and counted to determine by subtraction the number eaten. Seperate, blind trials, demonstrated the accuracy of the counts of the number of each prey type remaining. In order to minimize prey depletion effects and changes in subjects' hunger state, only those trials in which 6-15 prey captures occurred were considered in the analysis: 41 trials (20 skin extract and 21 seawater trials) met this criterion. The proportion of large prey of all prey captured in a trial was taken as that trial's diet selectivity. This measure equals Chesson's α (Chesson, 1978) when prey are equally available.

The diet selectivities did not differ significantly between the skin extract and control fluid treatments ($p=0.1001$, 2-tailed *t*-test, 39 df). However, power analysis (Zar, 1984) indicated that the experiment had a reasonably high probability of detecting treatment effects (δ) of a magnitude typical of the diet selectivity responses produced by the model presented here. For δ values of 0.1, 0.125, and 0.15, the power values were 0.67, 0.84, and 0.94, respectively. Despite this, sculpins in the skin extract treatment took significantly longer to capture a given number of prey than those in the seawater treatment, suggesting that the treatment did influence the sculpins' perception of predation risk.

Chapter 6

The influence of predation risk on diet selectivity: an experimental test.

Abstract

Experiments which have examined the influence of predation risk on diet selectivity have produced variable results. This variation can be explained by considering the relative danger associated with capture of alternative prey types. In those studies in which prey differed in danger, diets became more biased toward the prey type(s) with lower danger as overall predation risk increased. In the one study in which prey did not differ in danger associated with capture, diet selectivity did not change. Here, I present an experiment intended to test the influence of relative prey capture dangers of alternative prey on the diet selectivity response to the presence of a predator. The diet selectivity of juvenile coho salmon (*Oncorhynchus kisutch*), foraging on big (B) and small (s) brine shrimp, was determined with and without predators present, in three different relative prey capture danger treatments. Prey capture dangers were manipulated by varying the substrate over which a prey size was presented. Prey were presented either over white plexiglas (W: relatively dangerous) or gravel (G: relatively safe). The three treatments used were (i) B over G, s over W, (ii) B/G, s/G, and (iii) B/W, s/G. Data were obtained in all 3 treatments for 13 subjects, while 3 subjects were only tested in one treatment. Overall, the treatment had no significant effect on the diet selectivity response to predator presence. However, data collected in 1993 tended to support the prediction, while those collected in 1994 showed the opposite trend. Possible explanations for this difference are considered.

Introduction

Several experimental studies (Godin, 1990; Chapter 5, Appendix; Ibrahim and Huntingford, 1989; Lima, 1988) have examined the influence of predation risk on diet selectivity. In these studies, diet selectivities are determined at different predation risk levels, created in most cases by altering the subjects' perceived probability that a predator is present, or 'ϕ' (see Chapter 4, for details; see Lima, 1988, for an alternative approach). The results of these studies include increased, unchanged, and decreased diet selectivity as predation risk increases.

A review of these studies (Chapter 5) reveals a possible explanation for this variation. Alternative prey presented to foragers in three of the studies differed not only in profitability, but also in their associated danger of capture (hereafter, 'danger'). In the single study in which selectivity increased, danger decreased with profitability (a negative danger-profitability relationship; hereafter, 'DP slope'). In the two studies which found decreased selectivity, foragers were presented with a choice in which the more profitable prey was also more dangerous than the alternative (a positive DP slope). In a fourth study, in which selectivity did not change, the alternative prey types likely had similar capture dangers (a null DP slope). Thus, a negative relationship appears to exist between the 'diet selectivity response' (selectivity at high predation risk minus that at low predation risk) and the DP slope.

However, the four experiments studied different forager species, using different prey and different methods of manipulating overall predation risk. In theory (Chapter 5) the variation in DP slope is sufficient to produce the observed variation in diet selectivity response, but the hypothesized influence of the DP slope on diet selectivity should be tested in an experiment with at least three DP slope treatments (positive, null, and negative), holding all other components constant. Here, I report such a test.

One method of manipulating the DP slope would involve altering the handling times of the alternative prey (for example, by placing food items in different types of covers). If a species of forager was used for which handling and vigilance (for predators) were wholly or partially incompatible, capture danger would be proportional to handling time. However, while this approach could potentially provide the desired range of DP slope treatments, altering handling time also alters the profitability of prey. Thus, this approach confounds profitability and danger.

One design which allows the profitabilities of alternative prey to remain constant while their dangers are altered involves manipulating the level of crypsis the forager experiences while capturing each prey type. A negative DP slope, for example, can be achieved by presenting prey in such a way that the forager is more cryptic while capturing and/or handling the more profitable prey than while capturing and/or handling the less profitable prey type. This is the approach used in the experiment reported here, in which juvenile coho salmon (*Oncorhynchus kisutch*) serve as foragers. These fish have been shown to rely on crypsis to avoid detection by predators, and to be sensitive to the substrate color over which they swim (Donnelly and Dill, 1984).

Materials and Methods

The experiment was performed at the Capilano Hatchery, in North Vancouver, B.C., in August and September of 1993 and 1994. Two large rooms, each with 4 stream channels measuring 120 cm wide and 8 m long, were used for holding subjects and for running trials. Fluorescent lights, controlled by an outdoor sensor, maintained natural light/dark periods. Clear river water, at 9-10°C, supplied the channels.

Juvenile coho salmon, measuring 62-73 mm FL were collected by pole seine in Brothers Creek, near its confluence with the Capilano River. The coho were held communally in one of the stream channels (depth- 20 cm; flow- approx. 2 cm/sec.), and fed thawed krill and occasional brine shrimp, at least 4 days and no longer than 14 days prior to use in the experiment.

Steelhead (1993) and rainbow trout (1994) (both *Oncorhynchus mykiss*) served as predators: they ranged from 20-28 cm FL in size. The steelhead were obtained from the

Capilano Hatchery, while the rainbow trout were obtained from the Dept. of Fisheries and Oceans laboratory in West Vancouver. While not in use, predators were held in a separate stream channel, and fed thawed krill. Juvenile coho have been shown elsewhere (Dill and Fraser, 1984) to respond to rainbow trout as predators.

From the beginning of the pre-trial training period, until the end of trials (see below), coho subjects were held individually in stream enclosures (Fig. 6.1). Four such enclosures were constructed, and placed centrally in stream channels (1 per channel). The enclosures measured 94 cm w x 22 cm h x 70 cm, and had white opaque sidewalls. The upstream and downstream walls consisted of Nytex mesh (5 mm). A clear plexiglass sheet served as the enclosure bottom. The walls extended 5 cm below the enclosure bottom, providing a space below for placement of experimental substrates.

The enclosures were divided into three cells by clear plexiglass walls placed 24 cm from each sidewall. The larger center cell held the subject coho; predators were placed in the two side cells during 'predator present' trials. On the midline of each enclosure, 6 cm from the downstream mesh panel, a black PVC tube (6 cm o.d.) with bevelled ends (13.5 cm long on top, 2.5 cm on the bottom) was attached to the bottom to provide a covered holding station for the subjects. Two prey outlets were placed at the water surface, 10 cm left and right of the midline, and 2 cm downstream of the upstream mesh panel. In early feeding tests, some subjects would wait directly downstream of one prey outlet, ignoring the other outlet. To prevent this, an aluminum mesh panel (pore size approx. 5 mm) was positioned across the center cell, 16 cm downstream of the upstream mesh panel. The enclosures were positioned to achieve a water depth (to the plexiglass bottom) of 10-12 cm, and water velocity was set at ca. 6 cm/s (3.5 cm/s for the first set of 4 fish). Water flow was relatively laminar through the enclosures, and prey tended to drift straight downstream from the prey outlets.

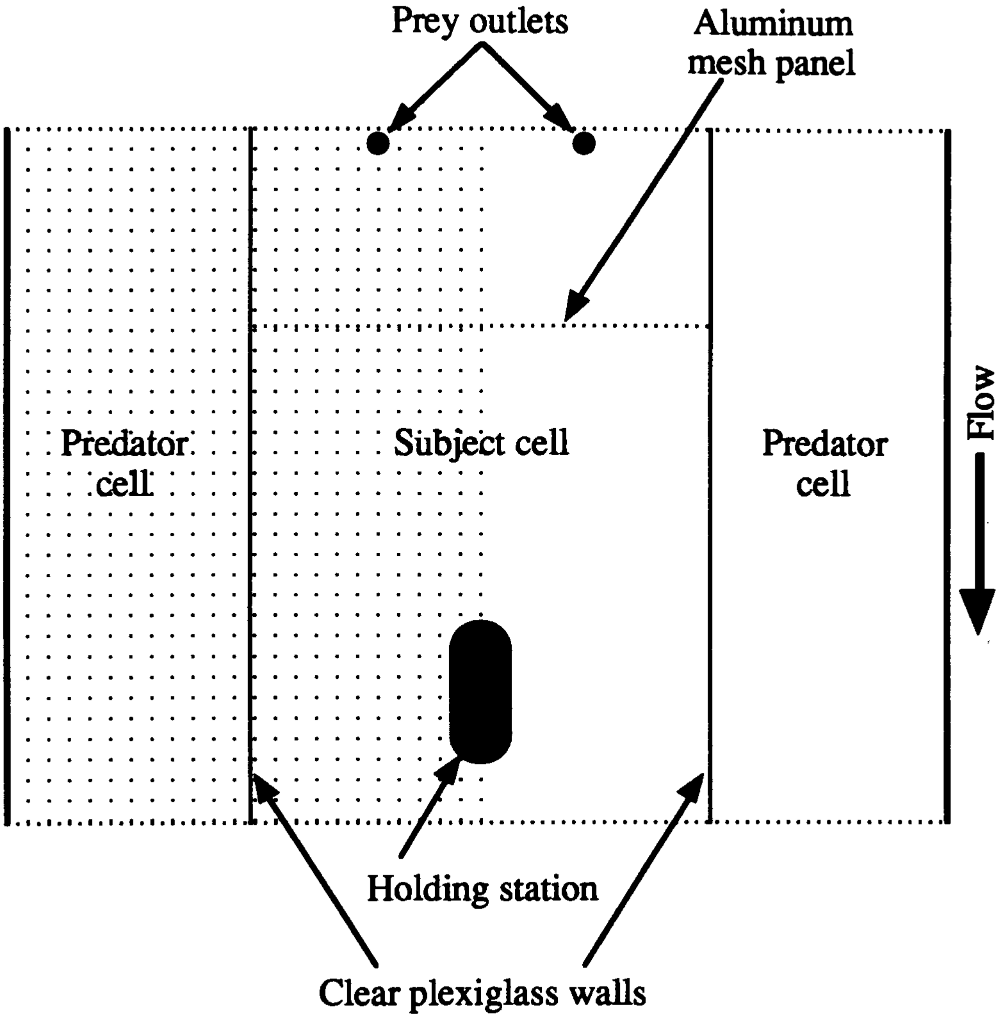

Figure 6.1. A top view of an enclosure. The outer sidewalls were opaque white, while the upstream and downstream walls consisted of 5 mm nytex mesh. The stippled area indicates the position of one substrate (see text for details). Notice that the substrates lie below a clear plexiglass raised bottom.

Two size classes of brine shrimp (*Artemia* sp.), sorted using Nytex screens, served as prey. The smaller size class consisted of brine shrimp which passed through a 1310 μ filter but not a 1000 μ filter, while the larger size class consisted of shrimp which did not pass through a 1600 μ filter. The shrimp were killed before use by placing them in hot tap water for 60-90 s. The coho used in the experiment ingested both size classes without handling and thus handling times were equal (*i.e.*, zero); therefore, the larger shrimp, with greater energy content, were the more profitable prey.

Two substrates were used to manipulate the danger of prey capture. Loose 4-8 mm round gravel, grey-brown in color, held in a aluminum tray, provided a substrate over which the subjects appeared relatively cryptic. This substrate closely matches the color of the substrates coho encounter naturally, and is similar to the gravel color most preferred by juvenile coho in the study by Donnelly and Dill (1984). An opaque white plexiglass sheet served as the other (dangerous) substrate. Substrates were shaped such that two fit side by side under each enclosure, with the junction directly below the midline of the enclosure.

The three DP slope treatments were produced by presenting the prey over different substrate combinations. For the positive and negative DP slope treatments, the gravel substrate was placed on one side of the enclosure and the white substrate was placed on the other. The positive DP slope situation was achieved by releasing large prey from the prey outlet on the side with the white substrate, and small prey from the other. The opposite arrangement produced the negative DP slope. For the null DP slope treatment, gravel was placed on both sides of the enclosure (Fig. 6.2). (Note that the null treatment could also have been achieved by presenting both prey over white substrates).

Feeders were based on the design used by Abrahams and Dill (1989). They consisted of 4 l Erlenmeyer flasks with a 6 mm (i.d.) spout attached near the bottom. Eight mm (i.d.) tygon delivery tubes led from the feeders to the prey outlets in the enclosures. Before trials, feeders were filled with 2 l of water and 25 brine shrimp. The feeders were

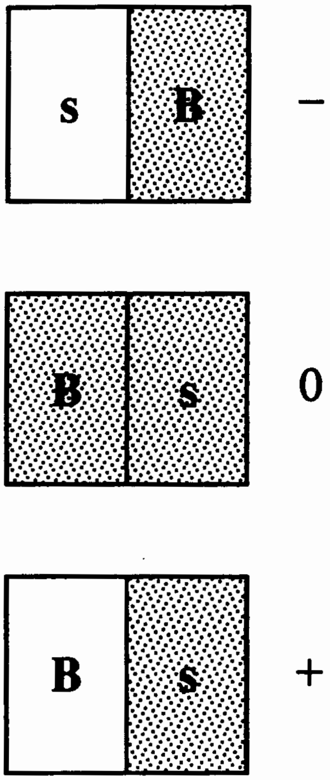

Figure 6.2. A schematic representation of the three treatments. Stippled and white rectangles represent the gravel and white substrates, and B and s refer to big and small prey, respectively. The DP slope acheived by each arrangement is indicated to the right of each scheme.

sealed with rubber stoppers, each penetrated by a 24 gauge needle (with syringe attached). Feeders were placed 160 cm above the water surface, on magnetic stir plates. The stirrers were turned on at a low rate, causing the suspension of the brine shrimp. With this arrangement, feeding is initiated by removing the plunger from the syringe. Air is then sucked into the flask and prey-bearing water flows down the delivery tube. These feeders delivered prey at haphazard intervals, until the water level in the flask dropped sufficiently far that air entered the delivery tube. Preliminary tests indicated that this occurred after approximately 5 min.; therefore, trials were stopped at 4.5 min.

Prior to the initiation of trials, subjects were trained to treat the PVC tube as a holding station, and were given experience feeding on both types of prey and over both bottom types. A typical training period progressed as follows. Day 1: subjects placed in the enclosures (with one gravel and one white substrate in place) and chased (once) into the PVC tubes. Days 2-4: subjects fed by dropping single adult brine shrimp over the midline of the enclosure, near its upstream end. Subsequent brine shrimp were withheld until the subject returned to the tube after a capture. Day 5: subjects presented with 4- 5 freshly killed brine shrimp of each size class, large on one randomly chosen side and small on the other. This was done by setting up the feeders as described above, but with no prey in the flask and with a portal set in the delivery tube to allow individual prey to be injected. These feedings were done between 1100 and 1300 h, the same time period that trial feedings would be performed. Beginning on day 5, and continuing daily until completion of trials with a subject, subjects were fed adult live brine shrimp to satiation between 1400 and 1530 h to control their hunger level. Satiation was defined operationally to have occurred when the fish had rejected three brine shrimp which passed within 3 cm of its nose. On day 5, after the satiation feeding, substrates were rearranged appropriately for the first treatments (if they happened to be in the correct arrangement, they were removed and replaced to control for the disturbance). This allowed the subject to experience the actual feeding situation it would be presented with, on its first trial, on day 6. Day 6: subjects presented with 4- 5 freshly killed brine shrimp of each size class, with the two size classes presented over the same substrates as they would be in the first treatment. Day 7: a mock trial was performed, in order to provide the subjects with experience foraging on the prey at arrival rates typical in trial feedings (the trial procedure is described below). Many subjects required extra training days at certain stages. Training periods were extended by up to 3 days for such fish; if this was insufficient, the subjects were discarded.

After training, the diet selectivity response of the fish to the presence of a predator was determined in each of the treatments. Due to the relatively long pre-trial training period the subjects required, I used a repeated measures design, in which each subject was tested in all three of the DP slope treatments. The order of treatments each subject experienced was assigned randomly. In two cases, subjects would not eat any prey after testing in the first treatment; data for these subjects are not presented here. After the initial trials with the final set of fish (n=3), it was clear that the hypothesis would be rejected. Therefore, these fish were not tested in other treatments, but their diet selectivity responses in the first trials are included.

To determine the diet selectivity response in a particular treatment, a fish's diet selectivity was measured twice, once with no predators present, and once with predators present (1 trout in each of the side cells); these tests were done on consecutive days. In order to ensure that a subject had similar hunger levels at the start of all selectivity measurements, measurements were performed at the same time each day (±15 min.), between 1100 and 1300 h. This procedure deprived subjects of food for 20-22 h.

After the predator present test (second day) of the first treatment, the substrates were changed (if neccessary) in preparation for the next treatment. Then, before sating the subjects that day, they were fed 4-5 of each type of prey, with the prey types fed on the side that they would be over during the next treatment. These feedings were performed between 1300 and 1400 h. This procedure was carried out again between the second and third treatments.

Diet selectivity tests were conducted as follows. Predators (if present) were placed in the outside cells of the enclosure 2 min. prior to the beginning of the test. The test began when syringes were removed from the two feeders, delivering prey to the subject's enclosure. During the test, counts were made of the numbers of each prey type entering the center cell and the numbers eaten. These observations were made by two people, from a blind at the side of the stream channel, one counting only large prey, the other counting only small prey. A test was terminated after 20 prey had been captured or after 4.5 min. had elapsed. Predators (if present) were removed within one minute after the test ended. Trials were repeated the following day if a subject ate less than 2 prey items (this occurred 5 times).

Diet selectivities (DS) were calculated for each test, according to the equation

$$DS = \frac{\frac{r_B}{p_B}}{\frac{r_B}{p_B} + \frac{r_s}{p_s}},$$

where r_i and p_i refer to the proportions of prey type i eaten and available, respectively (available prey are those entering the center cell), and B and s refer to big and small prey, respectively. The index of diet selectivity provided by this calculation (equivalent to Chesson's α; Chesson, 1978) ranges from 0, if no big prey are eaten, to 1 when no small prey are eaten. A value of 0.5 represents a diet in which the two prey types are eaten in proportion to their availability. A diet selectivity response, for a particular subject in a given treatment, equals the DS with predators present minus the DS without predators present. A positive value means that the fish are more selective of big prey when predators are present; a negative value implies the opposite.

Results and Discussion

This experiment tests the prediction that the negative, null, and positive DP slope treatments will produce positive, null, and negative diet selectivity responses, respectively. The combined 1993 and 1994 data clearly do not support this prediction (Fig. 6.3). However, the results differed notably between the two years, so I will report the results for each of the two years separately.

The data for 1993 provided relatively strong support for the prediction (Fig. 6.3A). I used single degree-of-freedom polynomial contrasts (Wilkinson, 1990), for polynomial order=1, to test for a linear effect of DP slope on diet selectivity response; this gave a 1-tailed p=0.068. While not quite significant, two features of the results are compelling. First, the (non-significantly) outlying data point in the positive DP slope treatment (0.452) has an extremely large influence on the significance level (1-tailed p=0.007 with all data for that fish removed). Second, the positions of the mean responses in all three treatments are as predicted. In the negative slope treatment the average response is positive (0.107±0.047: mean±S.E.), while in the negative slope treatment it is negative (-0.028±0.063 for all data, -0.076±0.046 with the extreme value removed). Further, the mean of the responses in the null slope treatment (-0.05±0.037) is not significantly different from 0 (2-tailed p=0.2145; t-test).

In 1994, the treatment had no effect, and even showed a trend opposite to that predicted (Fig. 6.3B). Diet selectivity responses in the positive DP slope treatment are all rather large and positive, although negative responses were predicted.

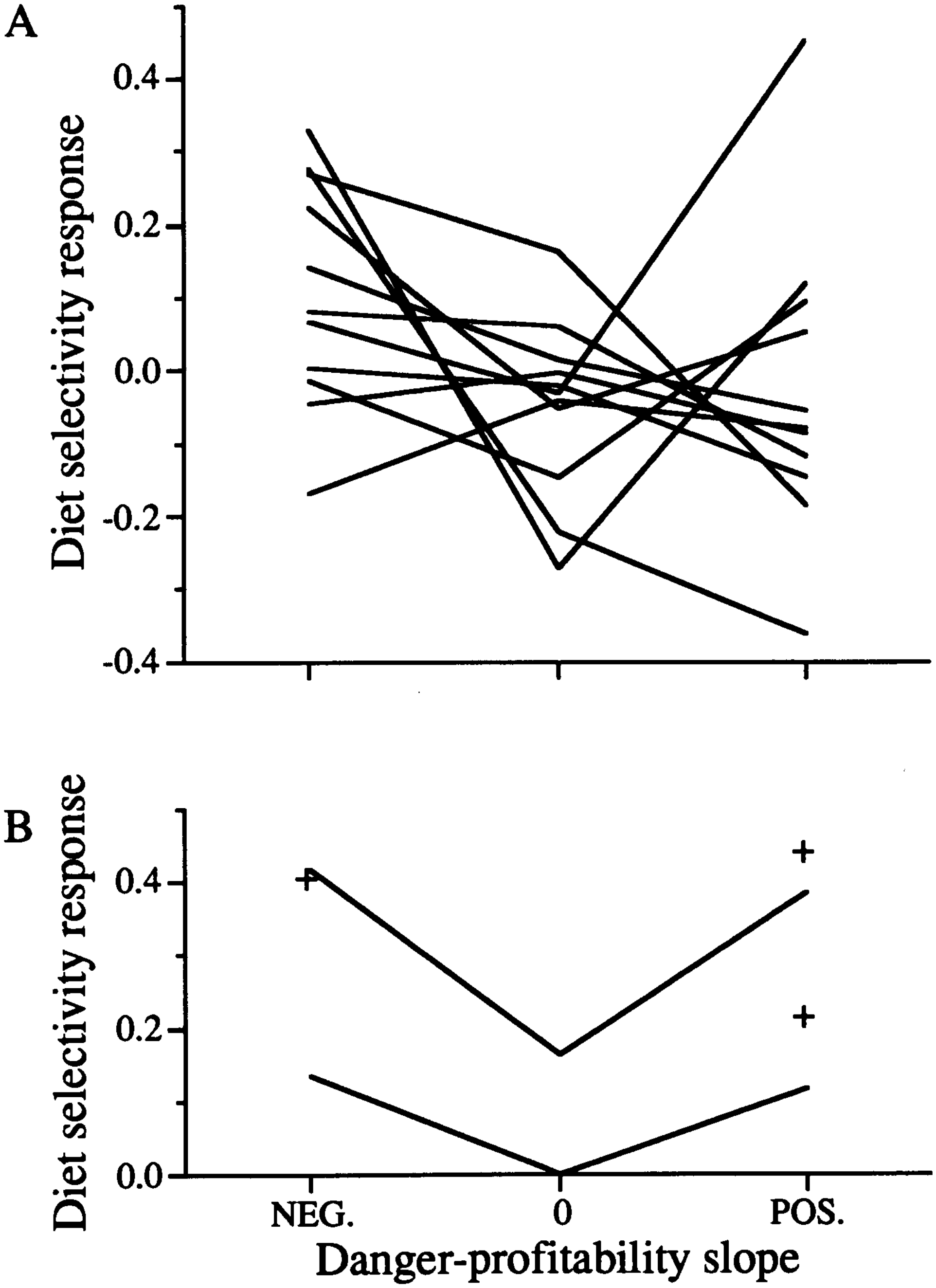

Figure 6.3. The relationship between the diet selectivity response and the danger-profitability slope (see text for an explanation of both terms), for 1993 (A) and 1994 (B) data. Lines connect repeated measures of the same subject. Crosses represent responses for subjects tested in only one danger-profitability slope treatment.

1994 fish also had more extreme diet selectivities than did 1993 fish when predators were present, tending to drop small prey from the diet completely. In 1993, in 33 trials (11 subjects in each of three treatments), only once did a subject eat some large prey, but no small prey. (That trial gave the high response value in the positive DP slope treatment.) In 1994, when only 9 trials were run, this occurred 7 times. This difference is significant (χ^2 test, p=0.0002). (It never happened that a subject ate some small prey but no large prey.)

The prediction in the current experiment was that the proportion captured of the more dangerous prey (those presented over the white substrate) would be lower with predators present than without. Studies of other behavioral changes in response to predator detection make equivalent predictions, in that animals are generally expected to reduce the time spent in relatively dangerous activities. Such studies tend to provide strong support for their predictions (reviewed by Lima and Dill, 1990). Thus, the prediction tested here had a reasonably strong foundation, and possible explanations for the lack of support should be considered. Since the 1993 data tended to support the prediction, it is neccessary to consider possible causes for the changes in behavior between years.

I made a strong effort to use the same procedures in both years of the study. Only one change was made consciously: in 1993, steelhead were used as predators, while in 1994, rainbow trout were used because steelhead of the appropriate size were not available. As steelhead and rainbow trout are the anadromous and non-anadromous morphs, respectively, of the same species, and do not differ morphologically, it is unlikely that this change would be responsible for the different results. It is possible that subtle changes were made which influenced behavior; however, the length of subjects and predators, water temperature, duration of pre-trial holding periods, photoperiod and light levels were all very similar in the two years.

The fact that the behavioral responses differed so much between years, but were relatively consistent within years, suggests that two different types of fish may have been used. It is known that juvenile coho salmon may forage in one of two ways: (i) as territory holders (Chapman, 1962), or (ii) as 'floaters' (Puckett and Dill, 1985). Nielson (1992) has shown that floaters hold positions and forage in areas of lower water velocity (<0.06 m/s) than territory holders. If floaters' habitats are also deeper (likely, given the lower velocities), it is possible that floaters would be less concerned about substrate color than territory holders would be.

I made an effort on all collection trips to collect only territory holders. However, when the subjects for the first set of trials of 1994 were collected, low capture success forced inclusion of fish collected from a deep pool in which they were apparently behaving as floaters; ca. 80% of the fish captured on that trip were from this one pool. After the first set of trials, the results of which appeared very different from 1993, a second collection trip was made, and only fish appearing to be territory holders were taken for the second set of trials. Since results from the first and second sets of trials in 1994 were similar (Fig. 6.3B), the likelihood that the difference in results between years was due to the use of different behavioral types is diminished, but since so few cases were collected in the second set, the possibility cannot be completely ruled out.

However, it seems unlikely that 1994 subjects were using a different foraging strategy, during trials, than 1993 subjects. Subjects spent at least 7 days solitarily in enclosures before trials began. During this time, subjects that perceived their social status as too low to hold a territory while living in a group likely learned that the enclosures were devoid of competitors. Thus, any subjects that entered the enclosure as floaters probably switched to foraging as territory holders; at least, they had the opportunity to do so.

At this point, I do not believe that the hypothesis should be considered disproven. The 1994 fish differed not only in their diet selectivity responses, but also in their tendency to drop small prey completely from their diets when predators were present. Since the 1994 results countered the trend shown by the 1993 data, and are mainly responsible for the failure of the prediction, it will be important to determine the cause of the difference between years before final judgement is passed on the hypothesis.

References

Abrahams, M.V. and Dill, L.M. 1989. A determination of the energetic equivalence of the risk of predation. Ecology **70**: 999-1007.

Chapman, D.W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. **19**: 1047-1080.

Chesson, J. 1978. Measuring preference in selective predation. Ecology **59**: 211-215.

Dill, L.M. and Fraser, A.H.G. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behav. Ecol. Sociobiol. **16**: 65-71.

Donnelly, W.A. and Dill, L.M. 1984. Evidence for crypsis in coho salmon, *Oncorhynchus kisutch* (Walbaum), parr: substrate colour preference and achromatic reflectance. J. Fish Biol. **25**: 183-195.

Godin, J.-G.J. 1990. Diet selection under the risk of predation. In: *Behavioural Mechanisms of Food Selection* (R.N. Hughes, ed.), pp. 739-769. Springer-Verlag, Berlin.

Ibrahim, A.A. and Huntingford, F.A. 1989. Laboratory and field studies of the effect of predation risk on foraging in three-spined sticklebacks (*Gasterosteus aculeatus*). Behaviour **109**: 46-57.

Lima, S.L. 1988. Vigilance and diet selection: a simple example in the dark-eyed junco. Can. J. Zool. **66**: 593-596.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**: 619-640.

Nielson, J.L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Trans. Amer. Fish. Soc. **121**: 617-634.

Puckett, K.J. and Dill, L.M. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behaviour **42**: 97-111.

Wilkinson, L. 1990. *SYSTAT: The System for Statistics*. SYSTAT, Evanston, U.S.A.

Chapter 7

Simulated diets of cryptic foragers: the influence of predator arrival probability, forager crypticity, and food availability.

Abstract

I present a forward simulation model that predicts the diets of cryptic foragers capturing prey according to a prey capture strategy set provided by a dynamic-programming model. The strategy set specifies the maximum capture distance at which each of two prey types (differing in energy value) should be captured, for all combinations of the forager's energy state and its information state (perceived probability that a predator is present). During a simulation, the forager's state levels fluctuate according to events such as prey capture or detection of a predator. For each iteration of a simulated foraging bout, the encounter type (no prey, or prey type I or II at a specified capture distance) is determined randomly. If a prey item is encountered, the rule contained in the strategy set for the forager's present state levels is used to determine if that prey will be attacked (all attacked prey are captured). The total numbers of each prey type captured during a foraging bout are then used to calculate diet selectivity. The influence of three habitat parameters on diet selectivity was investigated by repeating the simulation using strategy sets produced by the dynamic-programming model run with different parameter sets. The three habitat parameters varied were predator arrival probability, forager crypticity, and food availability. Diet selectivity increased with both predator arrival probability and forager crypticity. With increasing food availability, however, selectivity increased to a maximum and then decreased rapidly, a result different from that of "classical" optimal foraging models.

Introduction

Early prey choice models considered only the energy gain (benefit) versus time (cost) trade-off (reviewed in Stephens and Krebs, 1986). Recently, foraging theorists have begun to consider other trade-offs. Three models of diet selection have incorporated the predation risk-energy gain trade-off. Gilliam (1990) extended the classical prey choice model by incorporating handling and search specific mortality rates. Dynamic-programming models by Godin (1990) and myself (Chapter 5), examined diet selection of foragers for whom predation risk is elevated during the act of prey capture. Both these analyses concluded that the probability of predator presence could influence diet selectivity. However, no state-dependent models incorporating predation risk have examined the influence of habitat parameters on diet selectivity, to make predictions equivalent to the predictions of the early prey choice model concerning the effect of increasing encounter rates with the more profitable prey.

In this chapter, I examine the influence of three habitat parameters on the diet selectivity of cryptic animals foraging in homogeneous patches in which predators are occasionally present. The model simulates foraging bouts using prey capture/rejection rules provided by a dynamic-programming model (DPM). The habitat parameters examined are predator arrival probability, forager crypticity, and 'food availability' (defined below).

Dynamic Model and Strategy Sets

A DPM similar to the one described in Chapter 4 is used to determine the survival-maximizing prey capture decisions for a cryptic forager feeding on two types of prey. The only choices available to the forager are to capture or reject encountered prey; if no prey are encountered, the fitness consequences are identical to rejection of a prey item. If a rejection occurs, the forager remains motionless and cryptic, and thus has a lower Pr(detection by predator| predator present, not attacking prey) (Pr(detection)$_0$) than when capturing prey (Pr(detection)$_c$). The predation risk the forager faces during a particular time period equals the product of the perceived probability that a predator is present in that time period (ϕ) and the Pr(detection) of the activity performed. Thus, a trade-off exists between prey capture and predation risk. At any time, the forager can encounter no prey or either of two types of prey, distinguished by their gross energy value; these values are 5 and 3 energy state units for prey types I and II, respectively. Each prey type can be encountered at any of four capture times (τ=1, 2, 3, or 4 time units) resulting in eight prey type-τ combinations, or prey 'classes'. I assume that prey capture distances are proportional to capture times, and refer to them interchangeably. The probability of encountering prey class i is represented by λ_i, while λ_0 represents the probability of not encountering any prey. The DPM determines the survival-maximizing option for each potential encounter-type, for the entire forager state-space.

Two variables describe the forager's state. The energy state variable (denoted $E(t)$) represents the forager's energy reserves and ranges from 1, at which the forager dies from starvation, to 25, at which its reserves are full. The energy state increases due to prey capture and decreases when metabolic costs are not recovered. The second state variable (denoted $\phi(t)$) represents the forager's perceived probability that a predator is present. The $\phi(t)$ state is updated in a Bayesian fashion (according to the model presented in Chapter 3), modifying the previous estimate in light of new information. Because the value of this state variable results from information gain, it is also referred to as the information state variable (*cf.*, Blumstein and Bouskila, in prep.; Mangel and Roitberg, 1989). Two sources of information are used to update ϕ. First, survival of activities with non-zero Pr(detection) provides information since it is possible that there was no predator present to detect (and attack) the forager. This is referred to as 'no attack' information (Chapter 3). Second, vigilance 'scans', performed at the end of all activities, provide information whether or not a predator is detected. The ϕ state variable reaches its highest level (1.0) immediately after predator detection, but decreases asymptotically to a low level after several consecutive time periods with no predator detections. In Chapter 4, I provide a complete description of a model identical to the DPM used here except for two details (described in the Appendix) which have a very minor influence on the output.

In order to investigate the influence of the three ecological parameters on long-term diet selectivity, I use the stationary portion of the decision matrix generated (hereafter, the 'strategy set'; see Mangel and Clark, 1988). Strategy sets are obtained by repeated runs of the DPM with parameter sets differing only in the value of the variable under investigation; all other parameters take the values of the baseline parameter set, shown in Chapter 4. In order to examine the influence of predator encounter rate, the value of Pr(predator arrives| no predator present) (Pr(arrive)) is varied between 0.01 and 0.2. The forager's crypticity is varied by altering the value of Pr(detection)$_0$. I perform two series of runs, with Pr(detection)$_c$=0.1 in one, and 0.2 in the other. Pr(detection)$_0$ is varied from 0.0001 to 0.1 in the first series, and from 0.01 to 0.2 in the second series. Note that when Pr(detection)$_0$=Pr(detection)$_c$, the tradeoff between foraging and predation risk disappears, since not capturing prey is as dangerous as prey capture. The third parameter, food availability, is defined as the expected energy state increment resulting from an encounter (assuming capture), which equals the average net energetic value of all encounter types (including encountering no prey) weighted by their encounter probabilities. I manipulate food availability from 0.2 to 1.0 by altering prey encounter probabilities, subject to two rules. First, the encounter probabilities of prey type I and II at any given capture distance are kept equal (thus maintaining equal overall encounter rates with the two prey types). Second, the probabilities of encountering prey at τ=1, 2, 3, and 4 are always in the proportion 1:2:3:4, respectively.

Simulation Procedure

I use a forward simulation model (FSM) to simulate foraging bouts of 50 time periods in duration, in which the animals forage according to the strategy set provided by a particular run of the DPM, in a 'habitat' defined by the parameters used for that DPM run. The simulation is performed using a Waterloo Basic program running on a mainframe computer. The FSM is shown schematically in Fig. 7.1.

Step 1 (numbers correspond to those in Fig. 7.1) sets the forager's state variable levels at the beginning of each foraging bout. The initial energy state is set to 10 units, an intermediate level. The ϕ state is set to the discrete level closest to the long-term expectation that a predator is present (see Chapter 3), the best-guess level for animals who have no information pertaining to current ϕ.

The remaining steps are repeated until either the foraging bout is completed, or the forager dies (by predation or starvation). Step 2 randomly determines the type of encounter that occurs in the present time period. If a prey item is encountered, a check is made to ensure that it can be captured in the time remaining in the foraging bout. If not, the prey item is rejected.

If a prey item is encountered when sufficient time remains to capture it, the strategy set is consulted to determine whether the prey item ought to be captured (step 3).

Step 4 determines if the forager dies by predation during the resulting behavior (capture or rejection), using a random number generator. If the forager is eaten, the simulation returns to step one, and begins simulating the next foraging bout. (Deaths by predation were modeled in order to assess mortality rates in different habitats.)

If the forager survives the selected activity, the next step (step 5) updates the time state and the forager's energy state. I assume that all prey capture attempts are successful. If the forager starves (energy state dropped to a value of 1) or if the foraging bout is

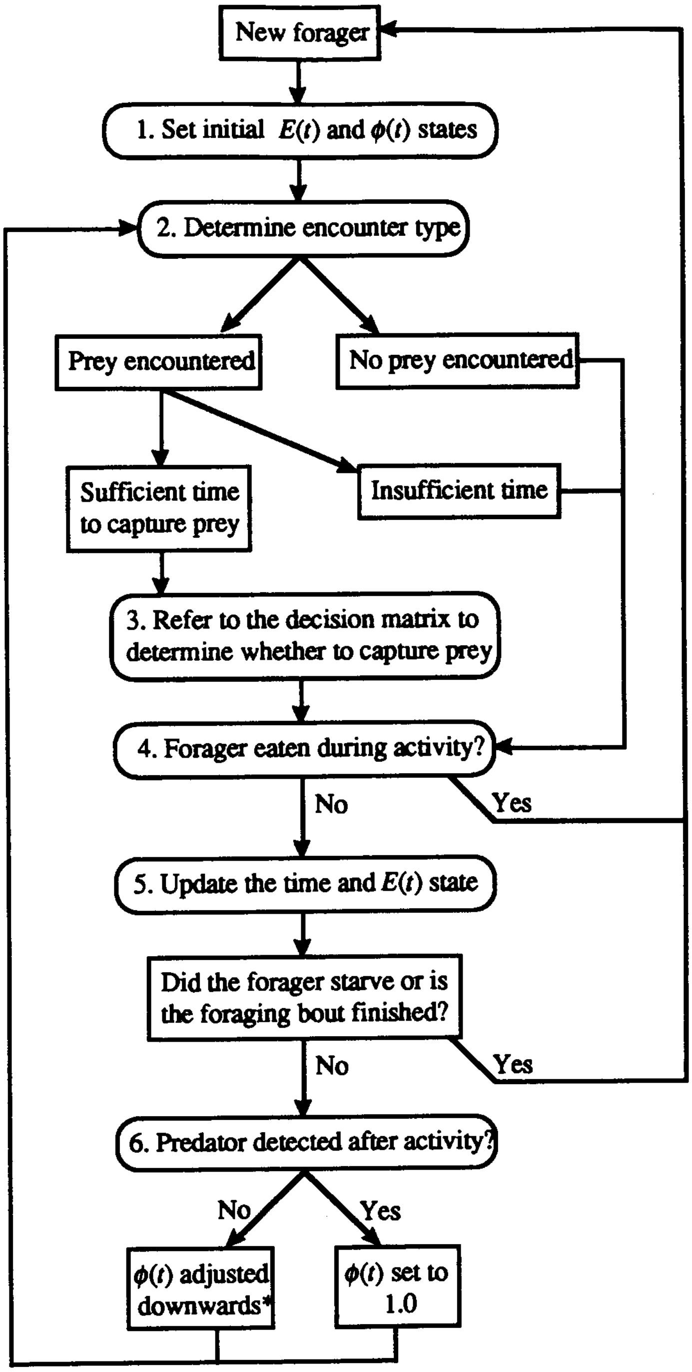

Figure 7.1. A schematic representation of the simulation procedure. The step numbers correspond to those in the text. *The value of ϕ which applies if no predator is detected is determined using a model which describes the ϕ dynamics (see text for details).

completed, the simulation returns to step one, to begin the next foraging bout.

Otherwise, the ϕ state is updated (step 6). When the forager scans for predators upon completion of an activity, there are two possible outcomes: either a predator is detected or not. If a predator is detected, ϕ=1.0, since I assume that false alarms do not occur. If no predator is detected, ϕ is revised downward to a level depending on i) the pre-activity level (because ϕ decays asymptotically), ii) the activity type (since the decrease in ϕ depends on the value of Pr(detection)), and iii) activity duration (see Chapter 4 for more details). The FSM determines the ϕ state transition type (predator detection or not) randomly. The simulation continues with the updated state variable and time state values, repeating steps 2 through 6 until the forager dies or completes the foraging bout.

The simulation is repeated for 1000 complete foraging bouts (*i.e.*, bouts which the forager survives for the full 50 time period duration), in order to obtain relatively stable diet selectivity estimates. During this procedure, the total numbers of each prey type captured in those 1000 bouts (50,000 time periods) are tallied. Diet selectivity is then calculated as the ratio of prey type I captured to total prey captured. This measure of selectivity corresponds to the selectivity index 'α' recommended by Chesson (1978), since encounter rates with the two prey types are equal. The program also calculates the average number of times a predator is detected per completed foraging bout, and the average energy state ($\overline{E(t)}$) during completed foraging bouts. $\overline{E(t)}$ equals the sum of the all $E(t)$ values experienced by foragers during completed foraging bouts, divided by the total number of time periods spent foraging (50,000). While $E(t+\tau_i)$ values are defined, the model does not calculate values of $E(t+j)$ for j=1 to τ_i. For the purpose of calculating an average energy state, I estimate $E(t)$ values for these intermediate time periods by linear interpolation. Thus, for any activity with duration τ, beginning in time period t, the energy state in period $t+j$ equals

$$E(t+j) = E(t) + j\left[\frac{E(t+\tau) - E(t)}{\tau}\right].$$

Finally, the program records the number of bouts ending in death by predation and starvation during a run.

I repeat the above simulation procedure 10 times for every strategy set. The influence of the three habitat characteristics on diet selectivity is large relative to the variation in selectivities at any single strategy set; therefore no statistical tests are performed.

Results

Predator Arrival Probability

Diet selectivity increases with the Pr(predator arrives| no predator present), from 0.634 at Pr(arrive)=0.01 to values between 0.697 and 0.707 for Pr(arrive)≥0.0625 (Fig. 7.2). However, this increase is discontinuous, occurring almost completely in the interval Pr(arrive)=0.05 to 0.0625. The cause of this discontinuity is unknown. The strategy sets, predation risks associated with all activities, and ϕ dynamics all change continuously with Pr(arrive).

Figure 7.3 presents the influence of Pr(arrive) on the other 4 variables measured during simulation bouts. As Pr(arrive) increases, the number of predators detected (7.3A) and the number of foraging bouts ending in predation (7.3C) and starvation (7.3D) increase, while the mean energy state decreases (7.3B). Note that although average ϕ state was not calculated, it will clearly increase with increasing Pr(arrive) due to increasing frequency of predator detections (7.3A) and decreasing rates of ϕ decline (due to increasing

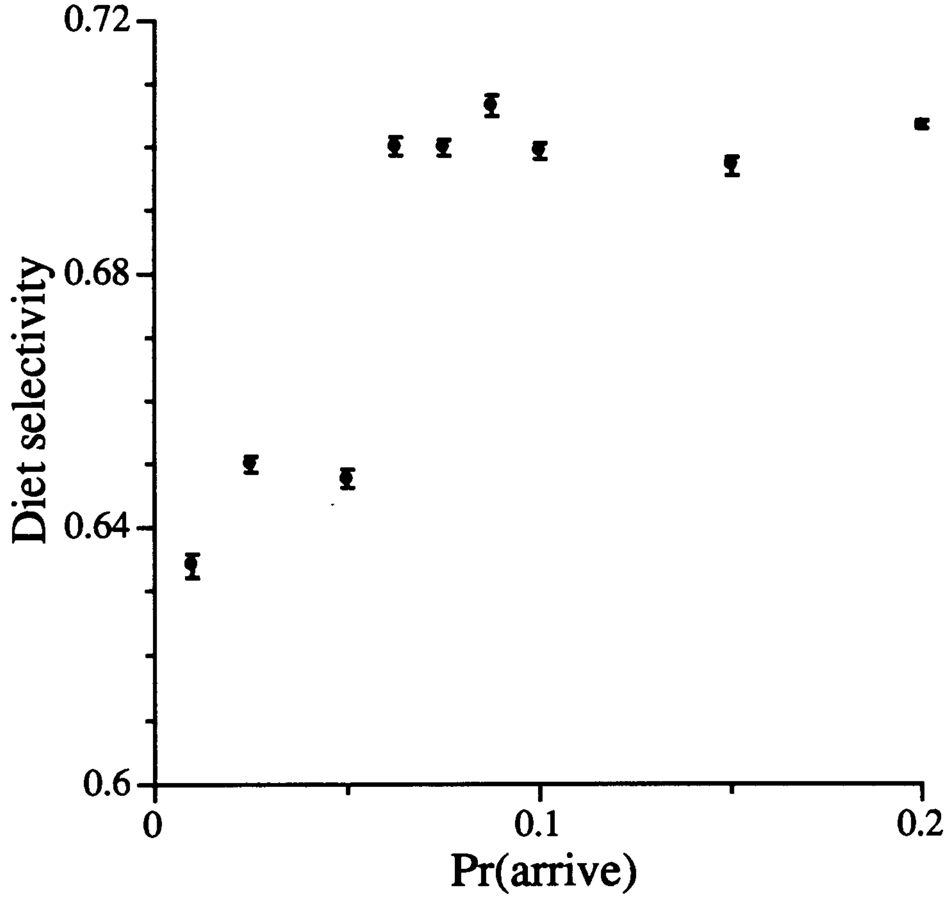

Figure 7.2. The relationship between diet selectivity and Pr(arrive) (the Pr(predator arrives| no predator present)). Points are means (±S.E.) of 10 runs, each simulating 1000 foraging bouts.

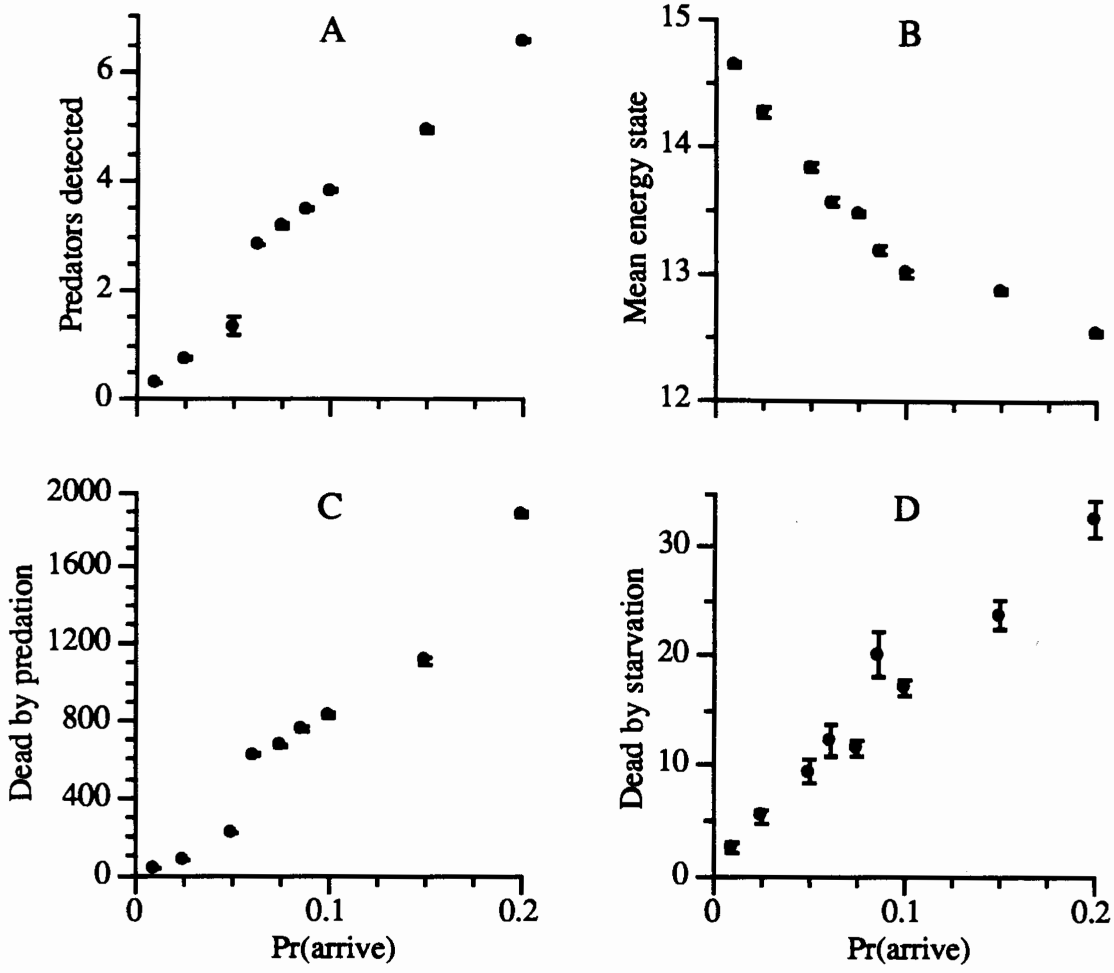

Figure 7.3. The influence of Pr(arrive) on the number of predators detected per foraging bout (A), the mean energy state of foragers (B), and the number of foraging bouts ending in death by predation (C) or starvation (D), per simulation (1000 complete foraging bouts). Points are means (±S.E.) of 10 (or fewer; see below) simulation runs. In A, the point at Pr(arrive)=0.05 represents the mean of only 2 runs, while the points at Pr(arrive)=0.01, 0.025, 0.1, 0.15, and 0.2 represent the means of 9 simulation runs. In the other panels, the points at Pr(arrive)=0.05 represent the means of 8 runs. Mean energy state is defined in the text.

probabilities of new arrivals). Thus, increasing Pr(arrive) effectively increases the predation risk experienced by a forager, and the results in Fig. 7.3 are all sensible.

Forager Crypticity

Diet selectivity decreases with increasing Pr(detection)_0, or decreasing forager crypticity, for $\text{Pr(detection)}_c = 0.1$ and 0.2 (Fig. 7.4). This effect is undoubtedly due to the relationship between the predation risk cost of prey capture and crypticity. When $\text{Pr(detection)}_0 = \text{Pr(detection)}_c$, there is no predation risk cost of prey capture (since the risks of capture and rejection are equal) and such foragers can be relatively unselective. With increasing Pr(detection)_c, the predation risk cost of prey capture increases, causing foragers to increase their selectivity (Fig. 7.4). However, since selectivities at $\text{Pr(detection)}_c = 0.2$ are greater than at $\text{Pr(detection)}_c = 0.1$, for equal relative predation risk cost of prey capture (equal $\text{Pr(detection)}_c/\text{Pr(detection)}_0$), the change in relative capture costs does not fully account for the relationship.

Diet selectivity appears to asymptote as crypticity increases (*i.e.*, at Pr(detection)_0 values below 0.05, for $\text{Pr(detection)}_c = 0.1$, for which a sufficiently large range of Pr(detection)_0 values were tested). However, this pattern may represent insensitivity of the model past threshold Pr(detection)_0 values.

The number of predator detections per completed foraging bout increases with crypticity (Fig. 7.5A). The most likely cause is that as crypticity increases, foraging bouts in which predator detections occur are decreasingly likely to end in predation (Fig. 7.5C); thus, the number of detections in survived bouts tends to increase.

Mean energy state is independent of crypticity (Fig. 7.5B). This result is surprising, since as crypticity decreases, the predation risk cost of prey capture decreases. The decrease in mean energy state from $\text{Pr(detection)}_c = 0.1$ to 0.2 is reasonable for this

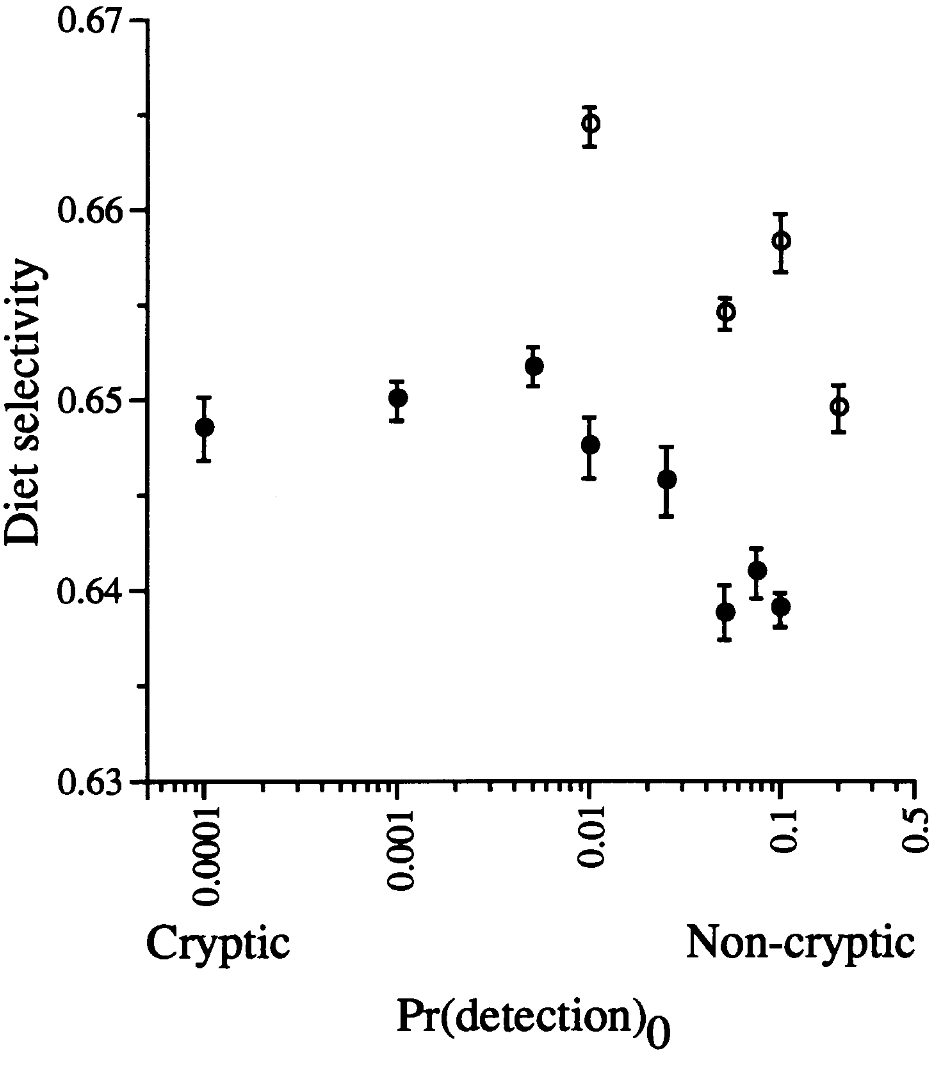

Figure 7.4. The relationship between diet selectivity and the Pr(detection by predator| predator present, not attacking prey) (Pr(detection)$_0$). The filled and open points represent selectivities for Pr(detection by predator| predator present, attacking prey) (Pr(detection)$_c$) of 0.1 and 0.2, respectively. Note: for Pr(detection)$_0$=Pr(detection)$_c$, prey capture has no predation risk cost. Points are means (±S.E.) of 10 runs, each simulating 1000 foraging bouts.

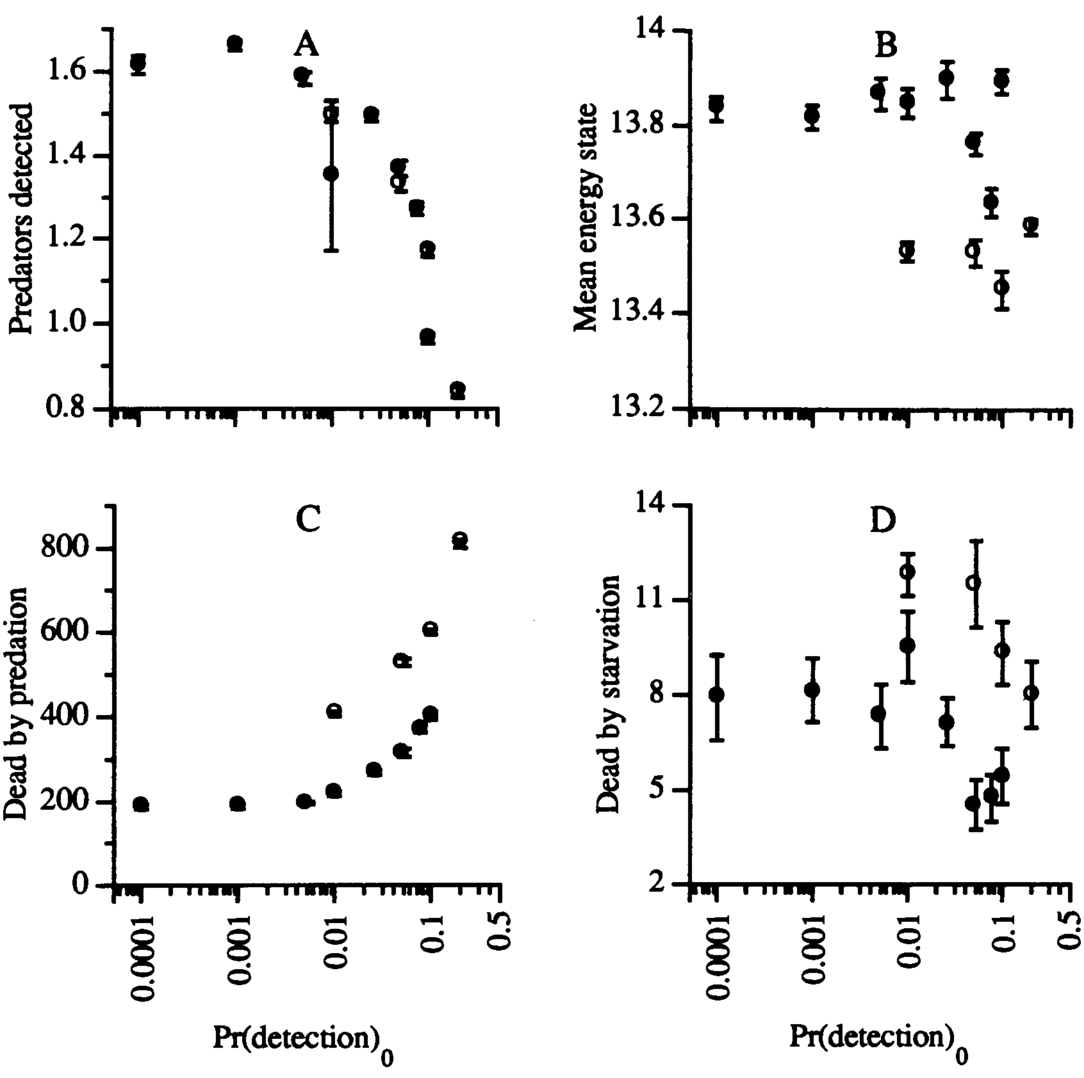

Figure 7.5. The influence of Pr(detection)$_0$ on the number of predators detected per foraging bout (A), the mean energy state (B), and the number of foraging bouts ending in death by predation (C) or starvation (D), per simulation (1000 complete foraging bouts), for Pr(detection)$_C$=0.1 (filled) and 0.2 (open). Points are means (±S.E.) of 10 (or fewer; see below) simulation runs. In A, for Pr(detection)$_C$=0.1, the point at Pr(detection)$_0$=0.01 represents the mean of only 2 runs, while the points at Pr(detection)$_0$=0.0001, 0.001, 0.005, 0.05, and 0.1 represent the means of 9 simulation runs. In the other panels, for Pr(detection)$_C$=0.1, the points at Pr(detection)$_0$=0.01 represent the means of 8 runs. Mean energy state is defined in the text.

reason. Furthermore, the number of foragers starving decreases with Pr(detection)$_0$ and increases with Pr(detection)$_c$ (Fig. 7.5D), also as expected based on relative cost of capture (capture becomes relatively less dangerous with increasing Pr(detection)$_0$ and more dangerous with increasing Pr(detection)$_c$).

Food Availability

Increasing food availability causes selectivity to increase to a maximum and then decline rapidly (Fig. 7.6). The increasing portion of this curve clearly results from the increasing freedom of the forager to forego capture of the lower value prey due to the increasing rate of encounter with prey type I. The cause of the sudden decline, however, is not known.

As food availability increases, average prey capture distances decrease (data not presented), allowing foragers to perform vigilance scans at increasing rates (Fig. 7.7A). Mean energy state also increases (Fig. 7.7B), because fewer time periods pass with no prey encounter, and since prey captured at shorter distances provide higher net energy gain. The number of foraging bouts ending in predation decreases (Fig. 7.7C), both because the forager, at higher $E(t)$ values, will more often be able to respond to predator detections by foregoing feeding opportunities, and because more vigilance scans are performed, making it more likely that predators will be detected. Finally, with increasing food availability, the number of foragers starving decreases (Fig. 7.7D), as expected.

Discussion

In Chapter 5, I predicted that when alternative prey types have equal capture dangers (the situation modeled here), diet selectivity should remain constant as ϕ increases.

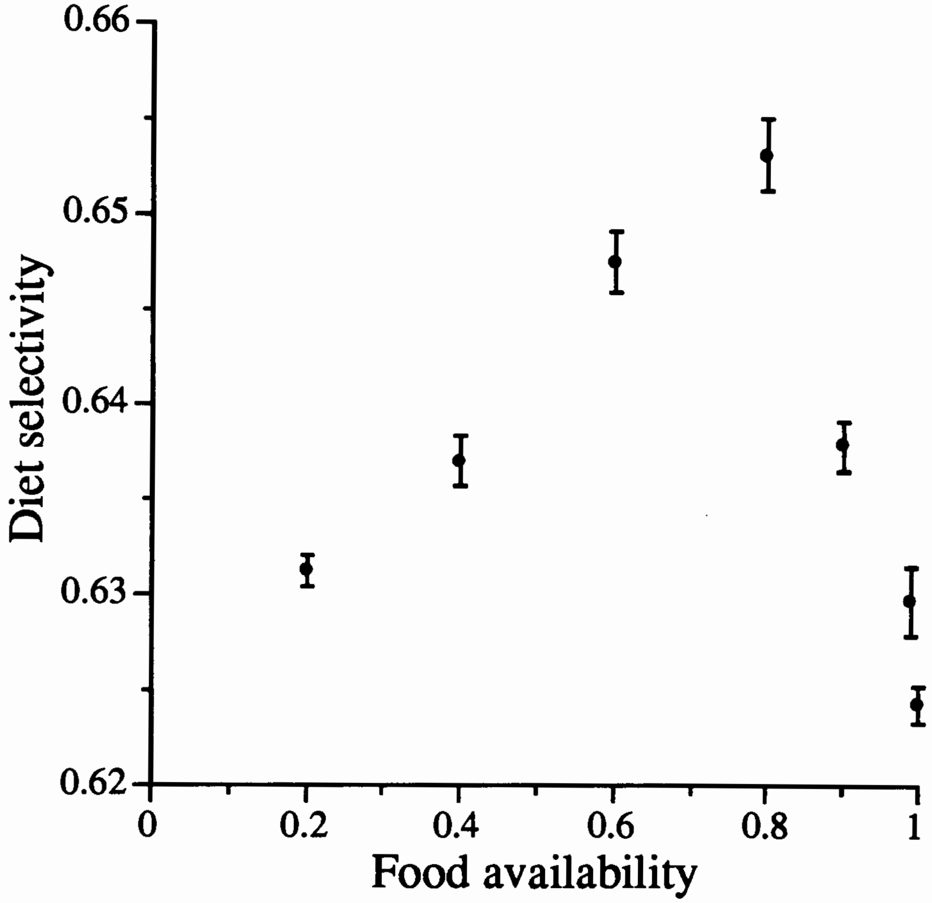

Figure 7.6. The relationship between diet selectivity and food availability. Food availability equals the expected net energy gain (if encountered prey are captured) per time period. Points are means (±S.E.) of 10 runs, each simulating 1000 foraging bouts.

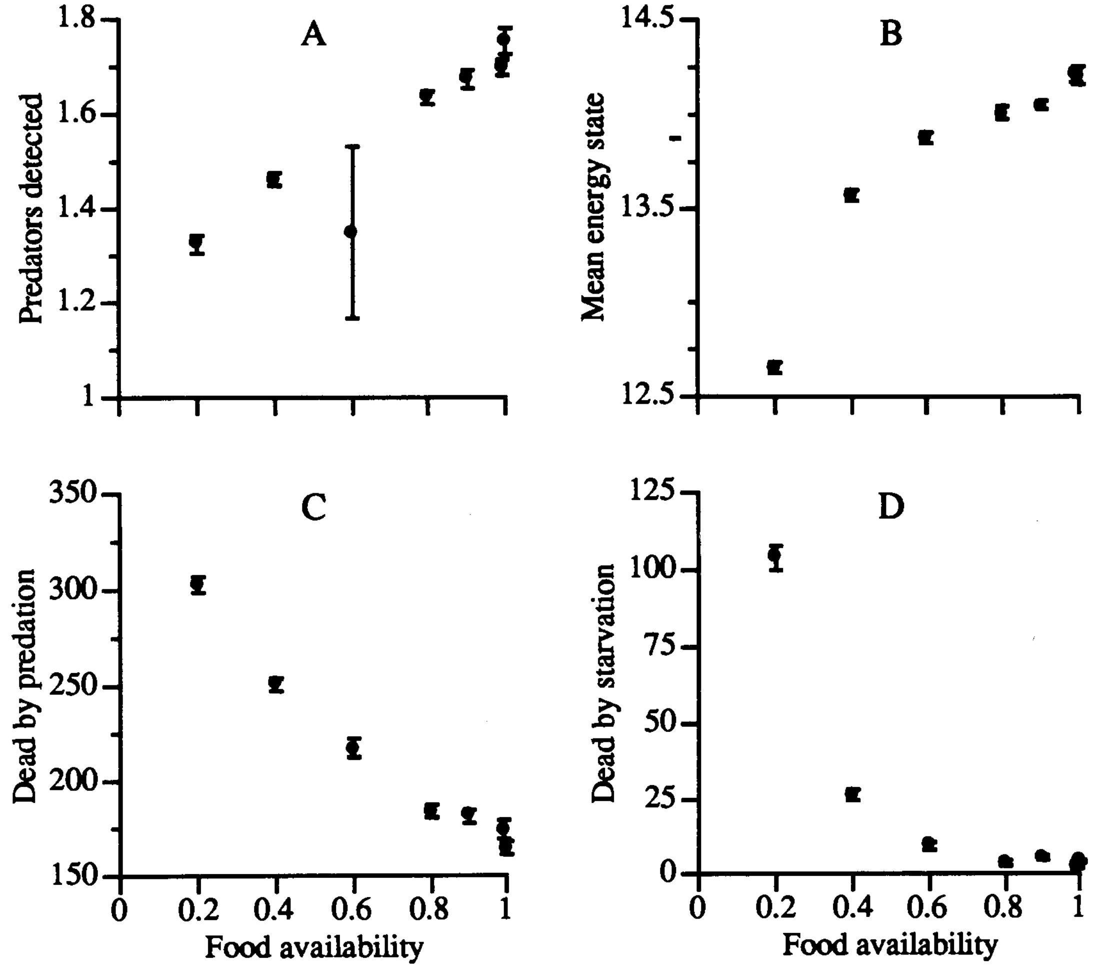

Figure 7.7. The influence of food availability on the number of predators detected per foraging bout (A), the mean energy state of foragers (B), and the number of foraging bouts ending in death by predation (C) or starvation (D), per simulation (1000 complete foraging bouts). Points are means (±S.E.) of 10 (or fewer; see below) simulation runs. In A, the point at food availability=0.6 represents the mean of only 2 runs, while the points at availabilities of 0.2, 0.4, 0.8, and 1.0 represent the means of 9 simulation runs. In the other panels, the points at Pr(arrive)=0.6 represent the means of 8 runs. Mean energy state is defined in the text.

That analysis determined diets of foragers at different fixed ϕ states (whose attack decisions were optimal for foragers with dynamic ϕ states) foraging in a single habitat type. Here, the forager's ϕ state is dynamic, but diet selectivities are obtained for foragers in habitats differing in Pr(arrive) values. Thus, although the average ϕ state will increase with Pr(arrive) (discussed above) the results from these two analyses are not necessarily contradictory.

The three diet selectivity predictions from this study are novel. No evaluation of the influence of forager crypticity on diet has been performed previously, and while Godin (1990) and I (Chapter 5) considered the influence of ϕ within a habitat, no study has evaluated the influence of predator arrival rate on diets. The classical prey choice model does make a prediction regarding food availability, namely that selectivity should increase with increasing encounter rate with more profitable prey (*e.g.*, Stephens and Krebs, 1986). However, the prediction from this model, that with increasing prey availability selectivity will increase to a maximum and then decrease, is novel.

The ability of this model to make novel predictions is appealing. However, several features of the results concerning diet selectivity are difficult to reconcile ecologically, and indicate the need for further work with the model. In particular, the causes of the discontinuity and the stability above Pr(arrive)=0.0625 in Fig. 7.2, the apparent asymptote below $\text{Pr(detection)}_0=0.005$ in Fig. 7.4, the decline at high food availabilities in Fig. 7.6, and the relatively small 'effect sizes' in all three cases, need to be ascertained. A feature of the model which may be responsible for several of these characteristics is the limited number of prey attack distances (4 for each prey type), dictated to a large extent by the need to limit computing time.

For all runs of the simulation, predation rates were much greater than starvation rates (compare panels C and D of Fig 7.3, 7.5, and 7.7). This difference probably results from the choice of parameter values in the model and is not presented as a robust prediction.

No data relating diet selectivity to Pr(arrive) or Pr(detection)$_0$ have been found; however, both experimental and comparative tests of the influence of these variables are possible. Acclimation with different rates of predator (or predator model) presentation would allow manipulation of the foragers' perception of Pr(arrive), assuming that foragers update their estimate of this parameter. Experimental tests of the effect of Pr(detection)$_0$ require that foragers estimate their current degree of crypsis. This requirement will likely be met in animals which rely heavily on crypsis to avoid predation, since such animals exhibit substrate choice (Donnelly and Dill, 1984; Feltmate and Williams, 1989) and colour change to improve background match (Edmunds, 1974), and differential responses to predator cues depending on substrate match (Chapter 2). Comparative tests could compare selectivities of foragers in spatially or temporally separated habitats that differ in one of the parameters. For example, determining changes in diet with seasonal emigration or immigration of predators into the foragers' habitat would provide a test of the influence of Pr(arrive). Seasonal changes in background, due for example to changes in foliage or snow cover, could provide a 'manipulation' of forager crypticity.

Many empirical studies have determined the influence of food availability on diet selectivity (reviewed by Stephens and Krebs, 1986). The results of these studies have generally been "partially or qualitatively consistent" with the classical prey choice model (Stephens and Krebs, 1986). However, these tests are not applicable to the prediction of the current model because, in most or all cases, the foragers were not exposed to predator stimuli during trials. Thus, the subjects' ϕ would have remained relatively constant, at some unknown but low level. Further runs with this model, with Pr(arrive)=0 are required to determine if the predicted influence of food availability is dependent on the occasional presence of predators and resulting fluctuating ϕ. If so, experiments which allow ϕ to fluctuate during trials due to predator arrivals (and subsequent detection by foragers) and departures, are required to test this prediction. However, if the model's prediction is qualitatively similar (*i.e.*, the selectivity versus food availability curve decreases after an initial increase) when Pr(arrive)=0, the lack of correspondence between the prediction and the results of the experiments considered above would bring the model's validity into question.

McNamara and Houston (1987) have pointed out, for animals under a foraging-predation risk trade-off, that predation and starvation rates are not independent (see also Lima, 1986). This dependence is shown in the simulation results presented here. As food availability increases, the number of foraging bouts ending in both predation and starvation decreases (Fig. 7.7C and D). Similarly, as Pr(arrive) (one component of predation risk) increases, the number of foraging bouts ending in both predation and starvation increases (Fig. 7.3C and D).

Predation and starvation rates are affected differently by Pr(detection)$_c$ and Pr(detection)$_0$ (the other component of predation risk in the model). With increases in the former, both predation and starvation rates increase (Fig. 7.5C and D). However, increasing Pr(detection)$_0$ causes predation rates to increase and starvation rates to decrease. Predation and starvation rates increase with predation risk when reduced feeding 'buys' the forager a degree of safety at the cost of reduced energy state. As Pr(detection)$_0$ increases, the gain in safety from foregoing prey capture decreases. Essentially, at high Pr(detection)$_0$, foragers can do nothing about predation but can increase survival chances by capturing prey, warding off starvation.

Selectivity increases with Pr(arrive) (Fig. 7.2), but decreases with Pr(detection)$_0$ (Fig. 7.4), even though both are factors of predation risk. These results, and the results discussed above (regarding the influence of the two factors on predation and starvation rates) illustrate the importance of considering the influence of predation risk components, not simply predation risk itself. For example, had the analysis (in an attempt to determine the influence of predation risk on diet selectivity) manipulated only one of the components, opposite predictions would have been made depending on the component chosen. Thus, care must be taken in attributing behavioral responses to predation risk rather than to the particular components of risk manipulated.

References

Blumstein, D.T. and Bouskila, A. In prep. Information assessment and decision making: a conceptual model to clarify mechanistic processes.

Chesson, J. 1978. Measuring preference in selective predation. Ecology **59**: 211-215.

Donnelly, W.A. and Dill, L.M. 1984. Evidence for crypsis in coho salmon, *Oncorhynchus kisutch* (Walbaum), parr: substrate colour preference and achromatic reflectance. J. Fish Biol. **25**: 183-195.

Edmunds, M. 1974. *Defence in Animals*. Longman Inc., New York.

Feltmate, B.W. and Williams, D.D. 1989. A test of crypsis and predator avoidance in the stonefly *Paragnetina media* (Plecoptera: Perlidae). Anim. Behav. **37**: 992-999.

Gilliam, J.F. 1990. Hunting by the hunted: optimal prey selection by foragers under predation hazard. In: *Behavioural Mechanisms of Food Selection* (R.N. Hughes, ed.), pp. 797-818. Springer-Verlag, Berlin.

Godin, J.-G.J. 1990. Diet selection under the risk of predation. In: *Behavioural Mechanisms of Food Selection* (R.N. Hughes, ed.), pp. 739-769. Springer-Verlag, Berlin.

Lima, S.L. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. Ecology **67**: 377-385.

Mangel, M. and Clark, C.W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton, U.S.A.

Mangel, M. and Roitberg, B.D. 1989. Dynamic information and host acceptance by a tephritid fruit fly. Ecological Ent. **14**: 181-189.

McNamara, J.M. and Houston, A.I. 1987. Starvation and predation as factors limiting population size. Ecology **68**: 1515-1519.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, U.S.A.

Appendix. Differences between the DPM version used here and the model described in Chapter 4.

The ϕ state variable is updated in a three-step procedure (see Chapter 3). Step two calculates $\phi(t'')$, the probability that a predator is present after predator movements have occurred, from $\phi(t')$, the ϕ value which applies before predator movements occur. In Chapters 3 and 4

$$\phi(t'')=\phi(t')(1\text{-Pr(leave)})+(1-\phi(t'))\text{Pr(arrive)},$$

where Pr(leave) is the probability that a predator (which is present) leaves, per time period. This formulation models predator movements as a first order Markov chain with no higher order terms (the two terms of the summation equal the probabilities that a predator was present and stayed and that no predator was present and one arrived, respectively). In the DPM version used here, a single higher order term is added, accounting for the probability that a predator was present, leaves, and is immediately replaced. The probability of the third event equals $(1-\phi(t'))$Pr(leave)Pr(arrive), and is always small relative to the other two events, since it equals the product of three probabilities. Therefore, this difference has a small influence on the dynamics of ϕ.

In the model described in Chapter 4, Pr(survive $t+\tau_i$ to T) (the probability of surviving from the end of an activity of duration τ_i to the time horizon) is determined by linear interpolation between the values of that probability for the discrete ϕ values immediately above and below the actual $\phi(t+\tau_i)$ (see Mangel and Clark, 1988, for details of this approach). In the current DPM, $\phi(t+\tau_i)$ is rounded up or down to the nearest discrete ϕ value, and the Pr(survive $t+\tau_i$ to T) for that ϕ value is used. Several comparisons between the output of the two models indicate that this difference has only a very small influence on the strategy sets.

In both respects, the current DPM is ancestral: the model described in Chapter 4 represents an improved version of the DPM used here. While it would be preferable to redo all of the runs reported here with a DPM identical to the model in Chapter 4, it would be time consuming and I expect the differences in results to be very minor, due to the small effects of both, and to the qualitative nature of my conclusions.

Chapter 8

General conclusions

For cryptic animals, foraging movements increase the probability of detection by predators. Every possible prey item must therefore be evaluated against the danger that capturing it brings. This thesis has examined the influence of this trade-off on several aspects of foraging behavior.

Foragers will rarely know for certain whether a predator is dangerously close. However, they usually have information with which to make an estimate of the probability that one is present (ϕ). Animals maintain such estimates, and should adjust their foraging behavior, because ϕ alters the predation risk costs of the foraging options relative to their benefits. Most of this thesis is concerned with the nature of the adjustments made by cryptic foragers in response to changing ϕ.

In Chapter 2, I showed experimentally that the response of tidepool sculpins (*Oligocottus maculosus*) to conspecific skin extract (elevated ϕ) depended on their level of crypsis. Cryptic subjects (on sand substrate), for whom movement was risky relative to immobility, reduced their rate of movement more than did non-cryptic ones (on white substrate), for whom movement was relatively safe. The results of this experiment are consistent with those from three non-experimental studies of species relying on crypsis to avoid predation (moths, lizards, and darters), suggesting that this influence of crypsis on the response to predator detection is fairly general.

Chapter 3 presented a Bayesian updating model that determined the dynamics of ϕ for foragers using vigilance and attack information. While this model was motivated by the need to specify the dynamics of ϕ as a state variable in a dynamic-programming model (see below), it led directly to two important insights. First, if an animal performs an action without being attacked, a reduction in ϕ is justified. Second, as time since the last predator detection increases, ϕ decays asymptotically, to a value greater than zero.

The dynamic-programming model presented in Chapter 4 calculated maximum prey attack distances as a function of a forager's ϕ and energy states. Three predictions emerged directly from the resulting decision matrices: maximum attack distances should decrease with increasing (i) energy state, and (ii) ϕ state, and (iii) the influence of ϕ state should increase with increasing energy state. The model indicated that foragers will attack prey at longer distances and in an increasing proportion of the energy-ϕ state space, with increasing predator arrival probability, decreasing forager crypticity (when not capturing prey), and decreasing food availability. Finally, the influence of ϕ on maximum prey attack distances was extremely reduced in runs with a static ϕ relative to runs with a dynamic ϕ, demonstrating the importance of treating ϕ as a dynamic variable.

In Chapter 5, I used this dynamic-programming model to show that the influence of ϕ on diet selectivity depends on the relationship between prey capture danger and prey profitability (DP slope). Specifically, selectivity increases with ϕ when the more profitable prey are relatively safer (DP slope is negative), remains unchanged when alternative prey are equally dangerous to capture (DP slope of zero), and decreases when the more profitable prey are more dangerous to capture (DP slope is positive). This result provided support for a hypothesis developed to explain the varying results of four experiments, all of which determined the influence of ϕ on diet selectivity.

In order to obtain experimental support for this hypothesis, I performed an experiment (Chapter 6) comparing the difference in diet selectivity of coho salmon (*Oncorhynchus kisutch*) in trials with predator present and absent, in three DP slope treatments (negative, zero, and positive). The results of this experiment, collected over two years, were not significant. However, the general trend in the data from the first year agreed with the hypothesis. Subjects in the second year of study appeared to forage differently than those in the first year, suggesting either that the subjects or the experimental design differed in some important respect. Therefore, I feel that further work is required before rejecting the hypothesis.

In Chapter 7, I developed predictions regarding the influence of three habitat characteristics on diet selectivity, using a two stage modeling process. In stage 1, the dynamic-programming model generated habitat-specific maximum prey capture distance policies. Stage 2 simulated foraging bouts of animals feeding in a particular habitat type, capturing prey according to the optimal policy appropriate for that habitat. Increasing the predator arrival probability and decreasing the forager's Pr(detection | not moving) caused diet selectivity to increase, while increasing food availability caused selectivity to increase to a maximum, and then decline. Currently, several features of these trends cannot be satisfactorily explained, and further work is required. The simulation measured several parameters other than selectivity, including the number of predators detected per foraging bout, the mean energy state of foragers during bouts, and the number of foragers dying by predation and starvation (until a certain number of bouts were completed). The effects of the habitat parameters on these variables were intuitively reasonable in most cases, suggesting that the simulation was operating as intended.

Throughout the thesis, I have stressed the importance of treating predation risk as a product of several component probabilities. One benefit of this approach is that the components of risk responsible for a particular trade-off can be identified. Knowledge of which components are activity-independent provides direction for manipulations appropriate for studying a particular trade-off. Another benefit of this approach was demonstrated in Chapter 7: increasing the predator arrival probability and decreasing the forager's Pr(detection | not moving) had opposite effects on diet selectivity, although predation risk increases with both parameters. Thus, the approach advocated here increases the likelihood of discovering interesting alternative effects on behavior of different predation risk components, that have so far not been comprehensively treated.