FORAGING BEHAVIOUR

OF

THE INTERTIDAL BEETLE THINOPINUS PICTUS (STAPHYLINIDAE)

by

LAURA JEAN RICHARDS

B.Sc(Hons.), Dalhousie University, 1976 M.Sc., The University of British Columbia, 1979

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY in THE FACULTY OF GRADUATE STUDIES (Department of Zoology)

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA May 1982

🕝 Laura Jean Richards, 1982 -

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of ______

The University of British Columbia 1956 Main Mall Vancouver, Canada V6T 1Y3

Date ______ 3/82_

ABSTRACT

Optimal foraging models generally assume that predators are capable of making appropriate foraging decisions and that these decisions affect fitness. Ι tested these assumptions in a study of the intertidal beetle Thinopinus pictus Leconte (Staphlyinidae). Adult beetles live on sand beaches in temporary burrows from which they emerge at night to prey on amphipods Orchestoidea californiana (Brandt). I also present isopods Alloniscus perconvexus Dana, some data for а less important prey species. I measured amphipod activity patterns by pitfall trapping, and beetle activity patterns by direct counts of the number of beetles active on the beach in 1-h searches. In general, there was a good correspondence between beetle and amphipod temporal and spatial activity patterns. However, by manipulating the spatial distribution of prey, Ι showed that beetles arrived at foraging sites independently of prey availability. Prey capture rate was low, with a mean of 75 min between captures, so that beetles were not always successful in obtaining food during a night. Food deprivation intervals did not affect beetle survival or for up 4-d to oviposition rates in laboratory experiments.

I constructed models of amphipod size selection by beetles, using the size distributions of amphipods measured on the beach, and the results of laboratory experiments on capture success, reaction distance and feeding rates. Capture success decreased and the probability that an amphipod was detected increased with increasing amphipod size. Beetles observed during beach searches selected larger sizes of amphipods than predicted from availability and vulnerability of different sizes. To apply an optimal foraging model, I estimated the profitability of different sizes of amphipods from the number of amphipods of a given size required to satiate a beetle in the laboratory. Profitability was highest for large amphipods and lowest for small amphipods and isopods. However, amphipod abundance on the beach was always below the threshold at which specialization on larger sizes was predicted to occur.

Male beetles were active longer than female beetles during the night, and fewer male beetles were observed feeding. Male beetles tended to be found higher on the beach and to include more isopods in their diet than female beetles. In laboratory experiments I showed that amphipods were highly preferred over isopods by both sexes of beetles. Male and female beetles were approximately the same size and consumed equal numbers of prey items. I conclude that male foraging behaviour was altered by search for mates.

Ι present an optimal diet model for two prey types, based on the expected foraging time required for a predator to reach satiation. Predictions differ in some cases from a model based maximization of the rate of energy intake. Foraging time on may be minimized by a predator which begins as a specialist and then expands its diet to include lower value prey when it is near satiation. Laboratory experiments on Thinopinus give weak support for these predictions, but I present alternative interpretations of the results. I suggest that most

iii

invertebrate predators which forage on active prey are limited in their ability to assess variations in prey abundance. Future studies should emphasize how patchiness in prey availability affects foraging behaviour.

TABLE OF CONTENTS

ABSTRACT ii
LIST OF TABLESviii
LIST OF FIGURES ix
LIST OF SYMBOLS x
ACKNOWLEDGEMENTSxii
Chapter 1: General introduction 1
Background to the problem 1
The study animals 4
The study site 6
Chapter 2: Prey patchiness and foraging
Introduction
Materials and Methods 8
Predator and Prey Activity Patterns
Behaviour at a patch 10
Laboratory feeding experiments 12
Survival and oviposition rates
Results
Temporal changes in amphipod activity
Beetle activity patterns
Behaviour at a patch 27
Laboratory feeding experiments
Survival and oviposition rates
Discussion
When where and how to forage

Sex differences	48
Relation to theory	49
Chapter 3: Prey selection	51
Introduction	51
Models	53
Materials and Methods	56
Field data	56
Vulnerability	57
Feeding experiments	59
Results	60 -
Vulnerability	60
Feeding rates	62
Field results	68
A test for prey selection	82
Mechanistic model	82
Frequency-dependent model	84
Optimal diet model	84
Discussion	89
Why did the optimal diet model not work?	92
Isopods versus amphipods	93
Chapter 4: Hunger and Optimal diet	95
Introduction	95
The model	96
A test with Thinopinus1	05
Discussion1	11
Chapter 5: Concluding remarks1	15
Literature cited	17

vi

 • • • • • • • • • • • • • • • •	Appendix A
 ••••••	Appendix B

LIST OF TABLES

.

Table	I. Time budgets for male and female beetles	25
Table	II. Results of patch experiments	37
Table	III. Results of the oviposition experiment	43
Table	IV. Capture success	61
Table	V. Feeding data	65
Table	VI. Feeding data for beetles fed to satiation	68
Table	VII. Parameter values for exact fit	85
Table	VIII. Parameters for the optimal diet model	86
Table	IX. Foraging times generated by the model	88
Table	X. Values of c	09

• •

.

LIST OF FIGURES

Figure	1. Temporal activity of amphipods and beetles 15
Figure	2. Nightly changes in amphipod size distributions 19
Figure	3. beetle and amphipod abundance 23
Figure	4. Frequency distribution of move durations 29
Figure	5. Proportion of time in active mode
Figure	6. Frequency distribution of attacks/min 35
Figure	7. Mean number of amphipods eaten
Figure	8. Survivorship curves 41
Figure	9. Reaction distances 63
Figure	10. Mean number of isopods eaten
Figure	11. Monthly changes in amphipod size distributions . 70
Figure	12. Morphological comparisons of male and female
beet	les
Figure	13. Mandible spread 76
Figure	14. Scavengers and amphipod size
Figure	15. Predicted and available amphipod distributions . 80
Figure	16. Expected total foraging times
Figure	17. Expected total foraging times for the general
case	e
Figure	18. Mean numbers of amphipods eaten

LIST OF SYMBOLS

A	probability that an encountered prey item is attacked
с	coefficient of preference (Murdoch 1969)
c(i)	probability that prey of size i are captured when
	detected
С	in the optimal diet model, the probability that a prey
	item is captured, given that it is attacked
d(i)	maximum reaction distance for a prey of size i
D	total food value required by a predator
e(i)	food value of a prey of size i
f(i)	relative encounter frequency with prey of size i
h(i)	handling time for a prey of size i
Н	total time spent in handling prey items
K	proportionality constant which depends on the shape of
	the reactive field of the predator
N	total number of prey items eaten
p(i)	proportion of prey of size i in the diet of a
-	non-selective forager
p(i)'	proportion of prey of size i observed in the diet of a
	non-selective forager
r(i)	proportion of prey of size i observed in the diet
R	prey encounter rate
S	total time spent in prey search
v(i)	vulnerability of prey of size i to the predator
w(i)	number of prey of size i eaten in preference
	experiments

х

- x(i) number of prey of size i presented in preference experiments
- a(i) preference for prey of size i (Chesson 1978)

ACKNOWLEDGEMENTS

I would like to thank my supervisor, First and foremost Judy Myers, for making this study possible. Jamie Smith deserves special mention for helpful comments and advice at most stages. thank the staff of Bamfield Marine Ι also wish to Station and the members of my supervisory committee, Drs. т.н. Carefoot, C.J. Krebs, C. Levings, W.E. Neill and J.D. McPhail for help in various ways. I also benefited from discussions with Lee Gass, Sarah Groves, Peter Morrison, Pamela Mace, Richard Palmer, and Jens Roland, and from the mathematical expertise of John Parslow. Elizabeth Boulding and Bruce Till assisted in the field in 1979 and 1980 respectively. The Coastal Missions provided the coffee and moral support to keep me awake at night in 1979, and all the people with whom I shared accommodation let me sleep in the morning. I was supported by a NSERC Science Scholarship and a H.R. MacMillan Family Fellowship. Research costs were met by NSERC and NAHS grants to J.H. Myers. Finally I wish to express my appreciation to Roy Getman for the song "The Moonlight Beach Bug Ball".

xii

CHAPTER 1: GENERAL INTRODUCTION

1

Background to the problem

Predation is one of the major processes which structure communities (Brooks and Dodson 1965, Connell 1975). The success of a predator in finding suitable prey items will not only affect its own fitness, but will also have consequences on the dynamics of the community in which it resides. One good example of how this process can operate is a study by Inouye <u>et al</u>. (1980). In a series of predator removal experiments, they showed that seed predation affected the diversity of annual plants in the Sonoran Desert. The outcome differed however, depending on whether the predators were rodents or ants or both.

The overall importance of predation has lead to a search for general rules which govern predator behaviour. One such attempt is known as optimal foraging theory (for reviews see Schoener (1971), Pyke et al. (1977), and Krebs (1978)). Optimal foraging theory is based on the premise that foraging behaviour evolved through natural selection. Observed behaviours has reflect the outcome of this selection, and should approximate the behaviours which maximize individual fitness. To apply this approach, the investigator must first identify the constraints the animal, such as time or energy on limitation. The optimization procedure is then applied subject to these constraints.

Optimal foraging theory has been severely criticized for several reasons. One major criticism is that the hypothesis that animals optimize in some way is not falsifiable (Maynard Smith 1978). The hope, rather, is that informed modelling of the behaviours can lead to some insight into their evolution. Given this restriction it is surprising, as stressed by Ollason (1980) and Hanski (1980), that in most studies the optimization approach is followed without consideration of alternate hypotheses.

A second major criticism of the theory is the general lack of fit between quantitative predictions of the theory and the actual behaviours observed, although the gualitative predictions Most of these tests have been conducted met. may be on vertebrates, especially birds, under highly controlled conditions. Schluter (1981) has recently reviewed the (lack of) evidence for optimal diets, and concluded that foraging studies of (mainly) vertebrates conducted in the field do not support predictions of the theory. One reason is that the necessary decisions are often too complex for the animal to make. Another reason is that the energy content of a prey item, used by most investigators to assign prey value, is not always a sufficient index of its value to a predator.

I chose to conduct a field study of foraging in an insect predator, the beetle Thinopinus pictus LeConte (Staphylinidae). My general aims were (1) to assess the ability of this beetle to make complex foraging decisions (2) to assess the importance of ability to individual fitness (3) to test predictions of this optimal diet models against an alternative model based on differential vulnerability. Thinopinus prey lives in а

2

structurally simple environment, the sand beach. Adults are ambush predators of beach invertebrates (Craig 1970), mainly the amphipod <u>Orchestoidea</u> <u>californiana</u> (Brandt) and the isopod <u>Alloniscus perconvexus</u> Dana. I chose this system because of its structural simplicity. I could directly observe foraging of the beetles, and I could measure the sizes of prey items of beetles. I could also manipulate amphipod availability by moving patches of drift seaweed.

This thesis is divided into 3 main sections. In Chapter 2, I describe the behaviour and activity patterns of the beetle and its major prey. I test two assumptions of optimal foraging models: (1) that predators can assess and respond to variations in prey availability, and (2) that short-term foraging success is closely linked to fitness. In Chapter 3, I consider the problem of diet selection. This aspect of foraging theory has received the most attention, probably because its predictions are the simplest to test experimentally. I construct an optimal and a simple mechanistic model of prey selection, and test diet these models against behaviours observed in the field. In Chapter 4, I present a new version of an optimal diet model. This model illustrates how the addition of one assumption can alter predictions of the model. I test these predictions in simple laboratory experiments. The last chapter contains a few general remarks on the future of optimal foraging theory.

3

The study animals

<u>Thinopinus pictus</u> inhabits exposed sand beaches on the west coast of North America. Adult beetles are active on the sand surface only at night. They spend the day in temporary burrows on the upper part of the beach. After dark they emerge from these burrows and move down the beach to the high tide level where they forage. Beetles generally wait within a few cm of drift seaweed and attack prey items moving on or off the weed by lunging and grasping the prey in their mandibles. They feed by injecting digestive enzymes and sucking the digested material from their prey. This leaves a carcass which can be identified and measured.

I frequently observed mating beetles throughout the summer. When a male and female meet, the male lunges forward and attempts to grasp the female in its mandibles, as it would a prey item. The male then mounts the back of the female and links genitalia. The total time required for copulation is approximately 2 min. Females usually resist the mating attempt and may continue other activities such as burrowing, feeding, or attacking prey items while mating. More than one male may attempt to mate with a female, and males often attempted to mount other males. Sexes of Thinopinus can be distinguished by a cleft in the last abdominal segment of the male.

Female <u>Thinopinus</u> lay their eggs singly in damp sand (Craig 1970). Eggs weighed on average 4.4 ± 0.1 mg ($\pm1SE$) (n=25, live weight) and hatched in approximately 3 wks at laboratory temperatures (16-20°C). I was unable to rear larvae in the

laboratory to determine the number or duration of instars. Larvae were not active on the sand surface at night and so were not included in this study. I occasionally observed larvae running across the sand surface in late afternoon, or found them in burrows on the upper part of the beach.

natural history of sand beach amphipods on The the California coast has been studied extensively by Bowers (1964) and Craiq (1971,1973a,b). The predominant species at my field site was Orchestoidea californiana. This amphipod digs burrows in the soft sand on the upper part of the beach in which it spends the day, similar to the pattern shown by Thinopinus. At dusk, Orchestoidea californiana emerges and moves down the beach the drift line left by the previous high tide. It is to omnivorous, although it feeds mainly on drift seaweed. It sometimes forms large feeding aggregations. Juvenile amphipods do not burrow, but remain under drift seaweed during the day. Juveniles are active mainly at dawn and dusk.

Isopods, <u>Alloniscus</u> <u>perconvexus</u>, show an activity pattern similar to amphipods. Isopods tend to burrow in drier sand higher on the beach than amphipods, and to feed on dried seaweed.

Apart from <u>Thinopinus</u>, there are several other beetles of the families Staphylinidae, Carabidae, and Curculionidae which comprise the beetle community on the beach. These other beetles often join <u>Thinopinus</u> in feeding on a prey item. The most frequent scavengers are an unidentified staphylinid and Dyschirius obesus LeC., a carabid, both about 2 mm in length. Amphipods and isopods occasionally join in the scavenging as well. <u>Thinopinus</u> reacts to the presence of scavengers by shaking its prey or carrying it away from the site of capture, sometimes as much as several meters.

The study site

field data were collected between April and September Most of 1979 to 1981. The main study site was located at Pachena (48°53'N lat., 125°7'W long.) near Bamfield, on the west Beach coast of Vancouver Island, Canada. This is a wide fine-grained beach about 1 km long. Tides in this region are mixed sand semi-diurnal. The two daily high tides usually differ in height, and each leave a line of drift seaweed. I divided the beach into upper and lower sections based on the position of the drift line left by the previous higher high tide. The upper beach extended above this line to the backshore and included all burrows from of amphipods. The lower beach included the drift line and extended down to the water. For a given night the width of the upper beach remained constant, but that of the lower beach varied as the tide moved in and out.

CHAPTER 2: PREY PATCHINESS AND FORAGING

Introduction

environment of a foraging animal is characterized by The patchiness in prey distribution (e.q. Wiens 1976, Hassell and Southwood 1978). This patchiness extends over a range of spatial temporal scales. The ability of a predator to respond to and patchiness will determine in part, its foraging success. The major attempt to incorporate patchiness into an optimal foraging model was made by Charnov (1976b). His Marginal Value Theorem predicts that a predator will leave a patch when its capture the patch decreases to the habitat average. This model rate in has been moderately successful in controlled laboratory (Cowie 1977, Cook and Cockrell 1978), but has been experiments found inappropriate in more complex field situations (Zach and Falls 1976, Hanski 1980, Morse and Fritz 1982). Apart from the argument of whether or not an optimization approach is correct, there are two simple explanations for the failure of this model. First, there is always variability among patches. Second, the forager is limited in its ability to assess this variability.

The need for predators to sample their environment has been suggested repeatedly to account for deviations between observed and predicted values in tests of optimal foraging theory (Heinrich 1976, Davidson 1978, Krebs <u>et al</u>. 1978). Yet only a few authors (e.g. Pyke 1978) have considered how foragers might learn about their environment. In this chapter I use <u>Thinopinus</u> <u>pictus</u> to test the assumption inherent in the model that predators can assess and respond to habitat variation. I then relate short-term predator success to fitness. The specific aims of this chapter, then, are to (1) correlate temporal patterns of beetle and amphipod activity, (2) measure the effect of temporal and spatial distributions of prey on foraging success, and (3) relate foraging success to predator fitness in terms of survival and oviposition rates.

Materials and Methods

Predator and Prey Activity Patterns

Once each month in 1980 I monitored beetle and amphipod activity over the amphipod activity period. Dry nights were chosen as rain reduced activity of beetles and amphipods. I formed two rows of pitfall traps spaced 3 m apart. One row was set along the drift line left by higher high tide of the day, here written as HW, and the second row along the drift line left by the highest high tide of the month, here written as HHW, about 10 m towards the backshore from HW on the nights chosen. May sample there were two rows of 12 traps 5 m apart For the with the rows spaced 1 m apart. Pitfall traps consisted of plastic cups (8.5 cm diameter, 7.5 cm deep) filled to one-third with seawater (Craig 1970, 1973a, b, Hayes 1970). The water prevented animals from escaping once they fell in the traps. This method sampled the relative abundance of active amphipods beetle sitting motionless on the sand. which would pass a Alternating traps were placed in position or removed each hour, so that 10 traps in each row were set at any given time. I counted and released the numbers of amphipods (estimated as ≥ 10 mm), and the numbers of beetles which were caught each hour. I then counted the number of beetles found between the backshore and the water in a 10 m wide beach section at each end of the row of traps. Each 2 h I collected and preserved amphipods from additional traps at the end of each row. Amphipod size was measured from the anterior of the head through the third abdominal segment, allowing for body curvature (Bowers 1963).

On 6 July 1980, I compared the sizes of amphipods feeding on weed patches and caught in pitfall traps. Before amphipod activity began, I selected five weed patches and positioned a pitfall trap 15 cm from each patch. These traps were placed after peak amphipod activity had occurred. One hour later I collected and preserved amphipods from both the traps and weed patches.

Ι collected additional activity data on beetles in 57 1-h searches on 22 nights between May and July 1981. For each search I wore a headlight and walked systematically in a series of transects. As only a small portion of the beach could be covered one at in hour, searches were begun the same location to minimize local variation in beetle density. I scored sex. behavior (sitting, feeding, mating) and beach position (upper, lower beach) for each beetle found. The sitting behavior category also included a few beetles which were moving when first observed.

For each search I recorded day of year, temperature, time

in hours after sunset, and amphipod abundance. These variables were used in backwards multiple regression analysis (Draper and Smith 1966). Amphipod abundance was estimated from the mean of the number of amphipods caught in 6 to 10 pitfall traps set at the high water level.

Mark-recapture experiments tested if male and female beetles active on one night were equally likely to emerge from the following night and if feeding on one night burrows influenced emergence on succeeding nights. On 7 and 19 July, all searches early in beetles were collected in two the night, separated according to sex, and divided into two groups. One group was left undisturbed, and the second group was provided abundance of amphipods. At the end of the night, 2-3 h with an later, beetles were marked with enamel paint on the thorax according to treatment group (food, no food) and released. The following night, three surveys were conducted to search for marked beetles.

Behaviour at a patch

During 1979 and 1980 I made observations of individual beetles, generally for 10 min periods, for a total of 62 h. To observe beetles I covered the lamp of the headlight with red cellophane to reduce light intensity. I was careful to not move or shine the light directly on the beetles during observations. Using a stopwatch and coding sheet, I obtained a chronology of all beetle activities. I eliminated records of beetles which were observed for periods of less than 5 min, and of beetles

10

which responded by movement towards my headlight. Beetles selected for observation were located near weed patches at HW.

In 1980 I conducted a series of experiments to test which composition of weed patches attract sizes or beetles. Ι constructed patches with the test characteristics from drift seaweed and Phyllospadix collected from the beach. Patches were spaced along HW, alternating patch types. A pitfall trap was set beside each patch to catch beetles. These traps were not filled with water. Amphipods could escape from the traps, but beetles could not. I counted and released beetles caught in these traps each half hour for a total of five or six times in the first part of the night. On 6 August, I tested patches of 20 cm, 40 cm and 60 cm diameter using the most common patch type on the beach, a mixture of mainly Fucus distichus and Phyllospadix scouleri. I compared Fucus-Phyllospadix with Egregia menziesii patches on 15 August and with Nereocystis luetkeana patches on 19 August. These patches were 40 cm in diameter. As a control, on 19 August I constructed 40 cm diameter patches from plastic garbage bags.

I measured the attractiveness of <u>Phyllospadix</u> and these species of seaweed to amphipods in a separate series of experiments. Two species of drift plants were compared at a time. Similar sizes of patches of each species were paired and placed along HW. One to two hours later I counted the numbers of feeding amphipods.

Laboratory feeding experiments

Feeding experiments tested if male and female beetles consumed the same numbers of prey items under similar conditions the laboratory. Twelve beetles of each sex were placed in individually in glass jars (8 cm diameter, 10 cm deep) and covered with a 3 cm layer of damp sand. Each jar also contained 2, 4, 6, 8 or 10 large (16-19 mm) amphipods. Jars were covered to prevent amphipod escape and left overnight for 20-22 h under natural photoperiod at laboratory temperatures. The number of amphipods in each jar were then counted, and the number live eaten determined by inference. There were two treatments. One group was preconditioned by holding for three days without food. The other group had been fed the previous night. Each beetle was only used once in each treatment. The rate of search, a, and the time spent handling prey, h, were estimated by non-linear regression techniques using Rogers' (1972) random predator equation

ahE-aTE = N[1-e]

where E is the number of amphipods eaten, N is the number of amphipods presented, and T is total time and is set to one. Use of this equation enabled comparisons to be made between male and female beetles for search rates and handling times. The equation is similar to the disc equation (Holling 1959) but compensates for removal of consumed prey from those available.

Survival and oviposition rates

I collected beetles for these experiments on 4 July 1980 and 10 May 1981 respectively, from Tapaltos Beach, about 4 km from the main field site. Prior to beginning the experiment, beetles were left with amphipods for one day to standardize satiation levels. I then placed beetles in individual jars (8 cm diameter, 10 cm deep) filled to one-half with damp sand. Beetles were kept under natural photoperiod at laboratory temperatures (16-20°C).

I measured the effect of temperature and a regular feeding regime on survival rates with five treatments of eight beetles of each sex per treatment. These were (1) food at 2-d intervals (2) food at 4-d intervals (3) food at 8-d intervals (4) no food (5) no food at low temperature (10-12°C). To feed beetles I placed three 12-15 mm amphipods in each jar. The following day amphipods were removed and beetle survival was scored. This procedure was followed for 28 days.

Beetles deposit their eggs singly in damp sand (Craig 1970). I measured the effect of regular feeding on oviposition rates with three treatments of 20 female beetles each: (1)continuous food (2) food at 3-d intervals (3) food at 6-d intervals. Amphipods were replaced in treatment 1, and the jars were checked for eggs on the day following feeding in treatment 2. After 30 days, the remaining beetles were dissected to determine the state of egg development in the ovaries.

Means for all experimental results are shown with one standard error, except where indicated. Proportions used in statistical tests were first transformed by arcsine square root. All tests were two-tailed with a significance level of 0.05, except where indicated. Non-parametric tests were used when assumptions of parametric tests were not met and included X^2 , median test, sign test and Spearman rank correlation coefficient which are described in Siegel (1956). All times are given as Pacific Daylight Time.

Results

Temporal changes in amphipod activity

numbers of amphipods caught in pitfall traps at HW The peaked just after dark on most nights (Fig. 1, solid line). Abundance then declined gradually with a second peak near dawn nights, such as shown in Fig. 1D. The peak on some was associated with emergence of amphipods from burrows on the upper part of the beach and migration to HW, or with the return to the upper beach from HW. While at HW, amphipods fed on drift seaweed. They sometimes formed large aggregations, especially on kelp patches. These feeding amphipods could not be sampled by the pitfall trap method. Amphipods caught in traps in the middle of the night were moving between patches or returning to the upper beach. The numbers of amphipods trapped at HHW (Fig. 1, dotted line) were lower and less variable than at HW. A few amphipods did feed on patches of dried weed at HHW. However, most amphipods caught in these traps were probably moving between the upper beach and HW.

14

Figure 1. The mean ±1SE numbers of amphipods caught in pitfall traps at HW (solid line) and HHW (dotted line) at each hour over the night, and the number of beetles observed (open circles). Beetle data were summed from pitfall trap and transect counts. Arrows indicate the approximate time of high tide. The heavy line gives the period of maximum darkness. (A) 6-7 May 1980 (B) 19-20 June 1980 (C) 13-14 July 1980 (D) 18-19 August 1980. Note the scale changes for amphipods in (B) and for beetles in (D).





. 17

Amphipod activity was affected by weather and tide patterns. The small peaks 0300 at in Fig. 1B and D were associated with incoming fog and a 1-2°C rise in temperature. Repeated observations indicated that a few amphipods only were active on rainy nights (Craig 1973b). When a high tide occurred early in the night (before about 0100), amphipod activity was delayed until after high tide. When the high tide occurred later in the night, there were activity peaks both before and after high tide (Bowers 1964, Craig 1973b). Fig. 1C shows an the intermediate stage in this transition.

The size distribution of active beetles varied over the night and with beach position (Fig. 2). Juvenile amphipods were 2 mm in length when released from the female brood pouch, and sexes could be distinguished at 12 mm. Juveniles were active primarily at dusk and dawn. They were trapped in low numbers only over the period of the night when beetles were active. Juveniles did not burrow but remained under weed patches during the day (Craig 1971), so that few juveniles were trapped at HHW. The peak at juvenile HHW at midnight (Fig. 2) probably represented the brood of a female which was released when the female fell into the trap.

Beetle activity patterns

I did not find active beetles each night until after amphipod activity had begun (Fig. 1, open circles). Otherwise the overall activity patterns of beetles and amphipods were

18

Figure 2. The frequency distribution of the sizes of amphipods caught in pitfall traps on 19-20 June 1980 at different times of night at HW and HHW. Mean ±1SE size (n) is given for each time.





similar. Maximum numbers were counted just after dark, and the number of active beetles decreased gradually over the night. For the data collected in 1981, I found a correlation of 0.273 (Fig. 3, n=57, p<0.05) between the number of beetles counted on the lower part of the beach and the number of amphipods trapped. Part of the variation in this relation can probably be accounted for by differences in recruitment patterns of beetles and amphipods over the summer. I was unable to scale beetle counts size of the beetle population. I also found important to total fine scale differences between beetle and amphipod activity. For example, beetles did not delay activity when a high tide occurred in the middle of the night (Fig. 1C). Craig (1970) similarly reported peaks in beetle activity both before and after a high tide.

A more detailed analysis of the beetle activity pattern was obtained from the 1981 search data, which indicated differences between male and female beetles in the amount and location of surface activity. A mean of 58.8±2.2 males and 50.4±2.0 females were counted during these searches (Table I). There were no differences in the mean number of males counted on either the upper or lower beach, but significantly more of the females were counted on the lower beach. Hence, the sex ratio was skewed towards males on the upper beach and towards females on the lower beach. This suggested that female beetles fed and then returned to the upper beach to burrow, while males were active longer during the night. A multiple regression on the proportion of males in the upper beach counts included date (r = -0.425)

Figure 3. The number of beetles counted on the lower beach in 1981 as a function of the number of amphipods caught in pitfall traps at the time the beetle count was made (r=0.275, n=57, p<0.05).


Table I: Time budgets for male and female beetles at different beach positions. Values given are for the mean proportion of time spent sitting, mating, and feeding, for the mean number of beetles counted, and for the mean proportion of males in 57 searches. All male-female comparisons for a given beach position are significant (paired t-test, p<0.01) as are all upper-lower beach comparisons on proportions for males (p<0.05), but not for females (p>0.10). For upper-lower beach comparisons on total counts, differences are significant for females (p<0.001), but not for males (p>0.10).

	uppe: <u>males</u>	r beach females	lowen <u>males</u>	r beach <u>females</u>	beac <u>males</u>	h total <u>females</u>
sitting	0.973	0.856	0.934	0.885	0.941	0.865
feeding	0.023	0.133	0.050	0.103	0.044	0.116
mating	0.004	0.011	0.016	0.012	0.015	0.019
total	28.6	11.6	30.4	38.7	58.9	50.4
prop. male	0.	735	0.4	425	0.	542

n=57, p=0.001), temperature (r=0.329, n=57, p=0.014) and time after sunset (r=0.280, p=0.039) with $r^2=0.230$ (n=57, p=0.003). On the lower beach, the regression included temperature only (r=0.344, n=57, p=0.009). The total number of beetles counted on the lower beach also increased with temperature (r=0.387, n=57, p<0.01). Proportionately more males were active on warmer nights and later in the night, and fewer males were active relative to females later in the summer.

Males and females also differed in the proportion of times they were observed performing each behaviour. A mean of 11.6% of females were observed feeding in surveys compared to 4.4% of males. Females were observed sitting, feeding and mating in similar proportions at either beach position. Males, however,

spent significantly less time sitting, and more time feeding and mating when on the lower beach. Males on the lower beach fed in significantly lower proportions than did females at the same beach position.

In an attempt to determine if active beetles were foraging, beetles were placed in open buckets on the beach containing amphipods. Rejection of amphipods would suggest that active beetles were not searching for food. There were no differences response of male beetles from the upper or lower beach, when in beetles were collected early in the evening, before feeding had begun. Forty-five percent (n=20) of males from the upper beach and 40% from the lower beach (n=20) accepted prey items. When this experiment was repeated with males collected in the middle of the night, after males did have the opportunity to move to the lower beach and feed, 33% (n=12) of males on the upper beach (n=20) on the lower beach accepted amphipods $(X^2=11.3,$ and 95% df=1, p<0.01). Foraging males were more likely to be on the lower beach, although some males on the upper beach did feed as well. Insufficient numbers of females were found on the upper beach on these nights to perform comparative tests.

Mark-recapture experiments tested if male and female beetles marked on one night were equally likely to emerge the following night, and if feeding affected emergence. In the 7 July experiment, the recapture rate was 14.4% (n=208) with no difference between sexes ($X^2=0.18$, df=1, p>0.10). Twice as many recaptures were beetles which had not fed the previous night, but this difference was not significant ($X^2=2.88$, df=1, p>0.10).

For the 19 July experiment, the recapture rate was 50.3% (n=195) with 58% of males and 43% of females recaptured (X^2 =3.84, df=1, p=0.05). Recapture success did not depend on whether beetles had fed the previous night (X^2 =0.18, df=1, p>0.10). Differences between the experiments can probably be attributed to weather. On 8 July conditions were less favorable for beetle activity with impending rain and a temperature of 9°C, compared to overcast and 13°C on 20 July.

Behaviour at a patch

Continuous observations of beetles at HW suggested that beetles alternated between active and ambush foraging modes. I classed beetles in ambush mode when they made moves of no longer than 2 s in duration. These moves were probably a response to prey items detected at a distance and were of three types:

(1) forward move - the beetle moved forward 1-3 cm

(2) turn - the beetle changed its facing direction, usually by 180°

(3) lunge - the beetle appeared to attack, although I did not observe any prey items within striking distance.

Because I could not detect whether or not beetles which remained motionless on the sand were in fact foraging, the ambush category also included beetles which may have been engaged in other activities, such as mate search or digestive pause.

I classed beetles in active mode when at least one move in a sequence was greater than 2 s in duration and pauses were less than 2 s between successive moves. Most moves made by beetles were less than 1 s in duration but moves ranged up to 78 s in duration for beetles which I observed in active mode (Fig. 4). For these longer moves beetles generally maintained a constant forward direction, either in weed patches, or on the sand along or between weed patches. Beetles in active mode could also be considered moving between patches, but they attacked as amphipods they encountered while moving. Hence, patches could not always be considered as discrete units.

Individual beetles spent on average 3.2-4.7% (95% confidence interval, n=362) of the observation time in active mode. The attack rate increased with the proportion of time active (Spearman rank correlation coefficient = 0.168, n=362, p<0.01, Fig. 5). To test whether beetles moved until they located a good foraging site, or in response to unsuccessful attacks on amphipods, I compared the proportion of time spent in mode by beetles before and attacks on amphipods. There active was a weak tendency for beetles to be more active following an attack (Mann-Whitney U-test, n=248, p=0.08). This unsuccessful suggested that active foraging mode was frequently a response to the detection of amphipods. The duration of individual moves did not differ before and after an attack (t=1.16, df=3350, p>0.10).

Male and female beetles spent similar proportions of time active (Mann-Whitney U-test, n=141,168, p>0.10). However, only 27% (n=141) of male beetles attacked amphipods compared to 52% (n=168) of females (X^2 =18.6, df=1, p<0.001). There was no difference between sexes in the proportion of attacks which resulted in capture (X^2 =0.06, df=1, p>0.10). I presented

Figure 4. The frequency distribution of the duration of individual moves made by beetles observed to attack amphipods. The mean is 2.5±0.1 s (n=3389).



Figure 5. Frequency distributions of the proportion of time spent in active mode by beetles which did (white bars, n=149) and did not (black bars, n=213) attack amphipods.



amphipods directly to beetles in an experiment to test whether differences in attack rates between males and females resulted from behaviour differences or differences in encounter rates with prey. Male and female beetles were collected early in the evening before feeding had begun. They were separated according sex and grouped in open buckets on the to beach with an abundance of amphipods. Male and female beetles had an equal opportunity to attack prey items. However, 63% (n=78) of the females captured amphipods compared to 30% (n=76) of the males $(X^2=15.1, df=1, p<0.01).$

the differences in activity patterns Because of of different sizes of amphipods (Fig. 2), the activity and position of a beetle will determine the sizes of amphipods it encounters. On 6 July 1980 the mean size of amphipods collected from weed patches was 6.1±0.1 mm (n=388), in contrast to a mean of 12.6±0.2 mm (n=275) from pitfall traps. There were also significant local differences in the size distributions of amphipods within the five samples taken from weed patches $(X^2=31.6, df=12, p<0.001)$ and pitfall traps $(X^2=26.8, df=8, df=8)$ p<0.001). Beetles observed on sand, captured amphipods with a 10.3±0.8 mm (n=32), compared to 6.5±0.8 mm (n=8) mean size of for beetles moving over weed patches (t=3.23, df=21, p<0.001 one-tailed).

On average beetles attacked 0.147 ± 0.019 (n=362) amphipods/min and captured 9.1% (n=440) of the amphipods attacked. Hence, beetles could expect to wait 6.8 min between attacks and 75 min between captures. The frequency distribution

attack rates (Fig. 6) however, was significantly different of $(X^2=430, df=5, p<0.001)$ from random for fit to Poisson). Fifty-nine percent of beetles did not attack during the observation period, and more beetles had high attack rates than expected. This suggested that most foraging sites were of low quality. Either beetles were relatively unsuccessful in finding high quality sites, or they did not detect, or did not respond to amphipods at a site. Further, overall amphipod abundance did not influence foraging success. I found no relationship between either the number or proportion of beetles observed feeding during surveys in 1981 and mean amphipod abundance (Spearman rank correlation coefficient = -0.009 and -0.087 respectively, n=57, p>0.10).

Beetles were not attracted to foraging sites on the basis of patch size. There were no differences in the total number of beetles caught in pitfall traps by patches of 20, 40 or 60 cm diameter (Table II). However, species composition of the patch influenced the number of beetles trapped. Significantly more beetles were caught in traps near Egregia or Nereocystis than Fucus-Phyllospadix patches. I used plastic garbage bags as near a control for a patch type which did not attract amphipods. Beetles were caught in traps near these patches, but significantly fewer were caught than near Fucus-Phyllospadix patches. This result suggests that beetles were initially attracted to all patch types, but that they remained longer and so were more likely to be trapped near Egregia and near, Nereocystis patches than near Fucus-Phyllospadix patches, and

Figure 6. The frequency distribution of the number of amphipods attacked/min by beetles during observations in 1979 and 1980 (n=362). Dotted lines give predicted values for a Poison distribution with the same mean (0.147 amphipods/min).



Table II: The numbers of beetles caught in pitfall traps located near patches of different size or species composition, and sample sizes for each type (F-P, Fucus-Phyllospadix; E, Egregia; GB, garbage bag; N, Nereocystis). Probability levels are for ANOVA. Date No. of beetles counted n patch size comparisons 20 cm 40 cm 60 cm 6 Aug. 6.1±1.6 5.6±0.8 10 4.7±1.1 p>0.10 patch composition comparisons F-P E 15 Aug. 12 12.2±1.1 8.8±0.9 p<0.05 GB F-P Ν p<0.0001 19 Aug. 12 4.1±0.5 6.6±0.8 10.3±1.0 near Fucus-Phyllospadix patches than near garbage bags. Patches near which I trapped more beetles were also more attractive to amphipods. In the amphipod experiments, more amphipods were counted on Nereocystis than on Egregia (n=24,

p<0.001), on Nereocystis than on Phyllospadix (n=22, p<0.001),

Egregia

Phyllospadix than on

than

on

matched-pairs signed-ranks test, one-tailed).

on

Phyllospadix (n=14, p<0.05), and

Fucus (n=16, p<0.005, all Wilcoxon

37

on

Laboratory feeding experiments

Laboratory feeding experiments tested if there were differences in the number of amphipods eaten at different amphipod densities for male and female beetles which had been starved or fed. The number of amphipods eaten by starved beetles number of amphipods presented increased with the (Fig. 7). Beetles which had fed the night prior to the experiment consumed fewer amphipods than those which had been starved. There was a weak tendency for fed females to consume more amphipods than fed males, but this trend was not consistent at all densities. There were no differences between male and female beetles either in attack rate or handling time for either the estimates of treatment (t-test, df=117, p>0.10).

Survival and oviposition rates

In laboratory experiments beetles survived at least 8 days without food at laboratory temperatures, and at least 24 days at the lower temperature which more closely approximated conditions on the beach (Fig. 8). Only one of the beetles which was fed at 2- or 4-d intervals died during the experiment, and there were no differences in percent weight loss of beetles between these two treatments (Mann-Whitney U-test, n=16,15, p>0.10). Fifty-six percent of the beetles fed at 8-d intervals died between days 10 and 28.

A total of nine beetles died or were lost in the oviposition experiment. Oviposition rates were low for the

Figure 7. The mean ±1SE number of amphipods eaten at each amphipod density for starved (A) and fed (B) beetles during a 20-22 h period. As differences between male and female beetles were not significant, male and female data were combined for curve fitting. The equations are E = N(1 - exp(0.447E - 1.860)) E = N(1 - exp(0.253E - 1.072))(A)

(B)



Figure 8. Survivorship curves for beetles according to food treatment: (a) food at 2-d intervals (b) food at 4-d intervals (c) food at 8-d intervals (d) no food (e) no food at low temperature (10-12°C).



remaining beetles (Table III). When I dissected beetles I found

Table III. Results of the oviposition experiment. The table gives the number of beetles, the proportion which laid eggs, the proportion with at least one mature egg in their ovaries, the total number of eggs laid, and the mean egg dry weight for each treatment: (1) continuous food (2) food at 3-d intervals (3) food at 6-d intervals.

	<u>1</u>	Freatment	3
n	15	20	16
prop. laid eggs	0.33	0.35	0.19
prop. eggs in ovar.	0.60	0.60	0.06
no. eggs	12	18	3
mean egg dry weight (mg)	6.2±0.2	5.3±0.2	5.0±0.3

60% of the beetles which were fed continuously or at 3-d that intervals, and one of the beetles fed at 6-d intervals had a mature egg in the common oviduct. This suggested that conditions the jars were not favourable for oviposition. However, there in were no differences in the proportion of beetles which either laid eggs, or had at least one egg in their ovaries, for beetles fed continuously or at 3-d intervals. I combined these data to test for the effects of feeding at 6-d intervals. There was no difference in the proportion of beetles which laid eggs $(X^2=0.64, df=1, p>0.10)$, but fewer beetles which were fed at 6-d intervals had at least one mature egg in their ovaries $(X^2=20.4,$ df=1, p<0.001).

Beetles which were fed continuously laid eqqs of significantly greater dry weight than beetles fed at 3-d intervals (t=3.03, df=28, p<0.01). There was no correlation between beetle size (measured as head capsule width) and mean egg dry weight (r=-0.023, n=15, p>0.10), between beetle size and the number of eggs laid (r=-0.295, n=15, p>0.10), or between mean egg dry weight and the number of eggs laid (r=0.054, n=15,p>0.10).

Discussion

When where and how to forage

Although the sand beach habitat is structurally simple, amphipod abundance varied over a range of temporal and spatial scales. Patterns of abundance could largely be accounted for by weather and tide factors, and the distribution of different types of weed patches. In general, a qood correspondence occurred between the timing of beetle and amphipod activity, but there were important discrepancies. Beetle abundance did not perfectly track amphipod abundance. In order to apply an optimal foraging model, it is necessary to assume that the predator can assess or "know" prey abundance both at a patch, and for the habitat average. Foraging beetles could encounter very different numbers of amphipods at the same time and at similar sites on consecutive nights. This must complicate any assessment process. One additional feature of this system was that the location and quality of patches changed each night. There was no benefit to a beetle gained by remembering the time or location of a success on the previous night.

If beetles and amphipods use different cues to initiate or maintain surface activity, beetles may be unable to respond to night-to-night differences in the times of amphipod activity. Alternatively, it is possible that beetles need to forage during periods of both high and low amphipod availability, to increase the probability of eventual prey capture. Foraging in ambush mode may be sufficiently inexpensive that the probability of prey capture outweighs any energetic cost. However, beetles foraging before high tide were occasionally hit and washed away by waves. This may be an important mortality factor.

Insects have well-developed chemical responses. I was unable to elicit any response from Thinopinus to seaweed odors in preliminary experiments. Beetles may be using visual cues such as silhouettes to find patches, as they were attracted to patches moved to least 20 m below HW. In addition, Craig at (1973a) showed that Thinopinus, Orchestoidea californiana and Alloniscus perconvexus all moved up-slope when exposed to wet slopes of 5° in the laboratory. These animals may simply move up or down beach according to the slope of the beach and degree of wetness of the sand until they encounter some object such as a weed patch. None of these mechanisms for finding patches provide information on amphipod abundance. Beetles arrived at all types of patches in my experiments, including garbage bags, whether or not these patches were attractive to amphipods. In general, cues

used by insects to find food patches provide little information on relative prey availability at the patch (Hassell and Southwood 1978). Selection of ambush sites by movement from patch-to-patch until a site with high prey availability is located, has been suggested for web-building spiders (Turnbull 1964) and damselfly nymphs (Crowley 1979).

Although I counted more beetles at patches which were also more attractive to amphipods, beetles were probably limited in their ability to assess amphipod abundance once at a patch. The attack frequency tended to be too low to act as a useful index of amphipod abundance. For example, one attack soon after arrival at area of low amphipod abundance could lead to a an spurious impression of high amphipod abundance. Scorpions detect prey through substrate vibrations (Brownell and Farley 1979). use a similar mechanism. Short moves and turns-Thinopinus may made by beetles suggested responses to amphipods detected at а distance. However, the number of amphipods on a patch, if they the are not moving, may not be a indicator of dood number available to a beetle in ambush mode. Amphipod abundance also changed over the night independently of beetle activity.

I counted more beetles on the lower beach on warmer nights. Mark-recapture experiments suggested that this was because more beetles emerged from burrows on successive nights at higher temperatures. Polis (1980) found a similar relation between temperature and surface activity of desert scorpions. <u>Thinopinus</u> probably required more food at higher temperatures as survival during starvation was enhanced at low temperatures in laboratory

experiments. For example, dasmselfly larvae (Thompson 1978a) and mites (Everson 1980) increase their attack rates on prey items at higher temperatures. Temperature probably affects activity indirectly through its affect on hunger.

Hunger has been shown to lead to increased activity for a number of different types of predators (Beukema 1968, Grüm 1971, Calow 1974). Akre and Johnson (1979) and Crowley (1979) suggested that hungry damselfly nymphs shifted from ambush to active foraging modes at low prey densities. This could also be true for <u>Thinopinus</u>, as the proportion of time spent in active mode tended to increase following an unsuccesful attack.

Active foraging mode did have associated disadvantages. As well as the energetic cost, active beetles on seaweed disturbed amphipods, depleting abundance at the patch. This is what Charnov <u>et al</u>. (1976) have termed resource depression. Other beetles in ambush mode near the patch could potentially benefit from the resulting increase in prey activity.

Toft (1980) studied foraging behaviours of several species of tropical anurans and found that species which were active foragers took smaller prey items and captured more prey per unit time than species which were ambush foragers. This was also true for <u>Thinopinus</u>. Beetles which were active on seaweed encountered a higher proportion of juvenile amphipods, and captured smaller amphipods on average, than beetles in ambush mode. One beetle I observed by a kelp patch rapidly captured and consumed two 5 mm amphipods in a 15 min observation period. In chapter 3, I show that one large amphipod (>15 mm) is sufficient to satiate most beetles, while up to six juvenile amphipods are required. Feeding on small amphipods could lead to a significant increase in the total time required for foraging at low amphipod abundance or in areas of mostly juveniles.

Sex differences

Sex differences in activity, attack rates, beach feeding experiments and mark-recapture experiments, indicated that either (1) male beetles fed less on the beach or (2) that they spent a greater proportion of their non-foraging time active on the sand surface, or (3) both. I did not find differences in of male and female beetles feeding rates in short-term laboratory experiments to suggest that females had a greater food requirement. However, there may be long-term differences. Females which were fed continuously laid heavier eggs than those females fed at 3-d intervals (Table III). For the cinnabar moth, egg weight is related to hatching success under adverse conditions (Richards and Myers 1980). A similar relationship in Thinopinus may have selected for more frequent feeding in females.

As well, male beetles must spend more of their non-foraging time active, and they probably devote this extra time to mate search. I observed mating throughout the summer. The problem of mate search for male beetles is similar to the problem of searching for amphipods (Parker and Stuart 1976), and they may attempt to perform both behaviours simultaneously.

If males are searching for food and/or mates, the reasons

for the spatial differences between male and female activity are not obvious, as both prey items and female beetles were more abundant on the lower beach. Mating may sometimes occur in burrows, so I may have underestimated mating success of males on the upper beach. Even if the probability of obtaining a mate on the upper beach is lower, sitting on the upper beach had several advantages. It was energetically cheap, compared to a return trip of about 50 m to the lower beach. Females emerged from and return to burrows in the same area. The last male to mate with a female in a night probably fertilizes eggs laid that night (Schlager 1960, Parker 1970, Smith 1979).

Relation to theory

То а casual observer, amphipods might appear as an unlimited food resource. Certainly, some beetles were successful in finding patches of high amphipod abundance. I have shown this not to be true in general. Beetles foraged at times and in locations of low amphipod abundance. Mean attack rates and were also low, and beetles were probably capture success frequently unsuccessful in prey capture during a night. Beetles were obviously limited in their ability to assess quality of a foraging site, and any assessment process may have been confounded by the variability which could exist on successive nights. As one critical assumption of the optimality approach is that foragers can assess quality of a patch, it is not possible to design a test of optimal patch choice model in this an system. Any deviation between the observed and predicted values

could be accounted for by either sampling of the beetle or by lack of fit of the model. Morse and Fritz (1982) reached similar conclusions in their study of crab spiders on milkweed. They found spiders at good sites more frequently than random, but spiders did not immediately leave poor sites when better sites were provided. They claimed that spiders which moved to new flowers or stems had little information available to them other than the number of insect arrivals at their previous site.

A second critical assumption of the optimality approach is not met with <u>Thinopinus</u>. In most foraging studies the claim is made that foraging success does affect short-term fitness. I found no differences in survival, weight changes, or oviposition rates for beetles fed in the laboratory at up to 4-d intervals over a 28-30 d period. In general, low foraging success on a few nights appears unlikely to affect oviposition or survival rates in this beetle.

Hanski (1980) found that movements of dung beetles between pats could be accounted COW for more closely by a simple stochastic model than by a model based on maximization of net energy intake. Mechanistic or stochastic models. based on specific systems and which incorporate sensory information, are likely to be useful in future as tools to predicting foraging behaviours. They should at least be considered as alternate hypotheses. In the next chapter I compare predictions of optimal diet and mechanistic models in prey choice of Thinopinus.

CHAPTER 3: PREY SELECTION

Introduction

There is abundant evidence that animals discriminate among the range of potential prey types, or sizes of a given prey type available to them (e.g. see Pyke et al. 1977). Any difference distribution of prey types in the between the diet and availability in the environment is a measure of prey selection (Eggers 1977). Selection may result directly through active choice by the predator (e.q. Zach 1978) or indirectly through differential vulnerability of prey types (e.g. Pastorok 1981). In this chapter I describe a field study of predation by the beetle Thinopinus pictus Leconte (Staphylinidae) on different size classes of amphipods Orchestoidea californiana (Brandt). I some data for beetle predation on also present isopods, Alloniscus perconvexus Dana. I test first whether beetles select certain sizes or types of prey, and second whether this selection results from differential vulnerability of different prey types or from active choice.

Theoretical attempts to predict diet selection fall into two general classes: (1) frequency-dependent models (2) optimal diet models. Frequency-dependent models (Murdoch and Oaten 1975, Greenwood and Elton 1979) are based on the hypothesis that the predators feed disproportionately on the most abundant prey items. Abundant items will be over-represented in the diet, and rare items will be under-represented relative to availability.

Optimal diet models (Pyke et al. 1977, Krebs 1978) first

assume that prey items can be ranked according to some measure their profitability, such as the ratio of energy value to of handling time. Prey types are added to the diet in their rank The optimal diet consists of the subset of prey types order. which results in optimization of some criterion chosen by the investigator, such as the net rate of energy intake. Predictions low value prey will be eaten only when more are that (1) profitable prey are rare (2) as the abundance of profitable prey increases, predators become more specialized (3) profitable prey will always be eaten and unprofitable prey never eaten when encountered (Pulliam 1974, Charnov 1976a).

Field tests of these models are often difficult due to changing conditions and problems in measurement of prey availability and diet. I chose to measure prey selection in Thinopinus because I could observe this beetle feeding directly in its natural habitat, a sand beach. The aims of this chapter are (1) to develop a simple mechanistic model of prey selection based on differential prey vulnerability (2) to develop an optimal diet model based on active choice (3) to compare Thinopinus behaviour in the field with predictions of the mechanistic, frequency-dependent and optimal diet models. The mechanistic model provides a null hypothesis against which selection in general, and the frequency-dependent and optimal diet models in particular can be tested.

Models

The mechanistic model predicts the frequency distribution of n sizes of a prey type in the diet of a predator, as determined by an observer. For a predator which does not use active choice, the proportion of prey items of size i expected in the diet is given by

$$p(i) = \frac{v(i)f(i)}{n}$$

$$\sum_{i=1}^{n} v(i)f(i)$$

where v(i) is the vulnerability of size i prey and f(i) is the relative frequency with which size i prey are encountered by the predator. The term in the denominator ensures that

$$\sum_{i=1}^{n} \Sigma_{p}(i) = 1$$

The vulnerability of size i prey can be determined from the product of c(i), the probability that a size i prey is captured given that it is detected, and the probability that a size i prey is detected.

The probability that a size i prey is detected is proportional to the area of reaction of a predator. It is given by

$Kd(i)^2$

where K is a constant of proportionality which depends on the shape of the reactive field of the predator, and d(i) is the maximum reaction distance for a size i prey, measured directly in front of the predator (Holling 1966). Hence

$$v(i) = Kd(i)^{2}c(i)$$

Because of the manner in which I collected data, I must add another term to the model. This is the probability that an observer will score a feeding event on a size i prey and is proportional to h(i), the handling time, or the time between prey capture and completion of feeding. Then

$$p(i)' = \frac{c(i)d(i)^{2}f(i)h(i)}{\sum c(i)d(i)^{2}f(i)h(i)}$$

$$i=1$$

is the proportion of prey items of size i I expect to observe in the diet of a predator which does not use active choice.

A suitable index for measuring deviations from the expected proportions is the standardized forage ratio (σ) (Chesson 1978). Let r(i) be the actual proportion of prey items of size i observed in the diet. Then preference for size i prey can be expressed as

$$\sigma = \frac{r(i)/p(i)'}{n}$$

$$\Sigma[r(i)/p(i)']$$

$$i=1$$

This index has the advantage that it varies between 0 and 1 and is independent of prey availability (Paloheimo 1979).

The optimal diet model I develop here is based on the total foraging time T(r) required for a predator to reach satiation, when the diet may include prey with sizes of rank 1 through r only. I define j as the rank of a size i prey item, based on some measure of the value of the prey item to the predator. The optimal diet is the set of sizes which minimize T(r). A rationale for this approach will be presented later. T(r)includes both searching and handling times. If prey are randomly

distributed, the expected search time for each prey item can be derived from the mean of the exponential distribution with rate parameter λ given by

$$\lambda = R \cdot A \cdot C$$

Here R is the encounter rate, measured in prey items/time. A is the probability that the encountered prey is attacked, that is, that it has a size of rank j to be included in the optimal diet, so

$$A = \sum_{j=1}^{r} f(j)^{2} f(j)$$
$$\underbrace{j=1}_{p} f(j)^{2} f(j)$$
$$\underbrace{j=1}_{j=1}$$

C is the probability that the encountered prey item is captured, given that it has a size of rank j to be included in the diet, so

$$C = \sum_{\substack{zc(j)d(j)^{2}f(j)\\j=1}}^{r}$$

$$\sum_{j=1}^{r}$$

$$\sum_{j=1}^{r}$$

The term in the denominator ensures that the maximum value of C is 1 if c(i)=1 for all i.

If a mean of N items is eaten and the total handling time is H, then

 $T(r) = N/[R \cdot A \cdot C] + H$

Materials and Methods

Field data

I collected field data between May and August 1980 and May July 1981. During these months regular searches for beetles and were conducted (see also page 9). For each search I wore a headlight and walked systematically in a series of transects. I scored time of night, beach position, prey type, prey length (for amphipods), beetle sex, and beetle length for each beetle found feeding. Amphipod length was measured from the anterior of the head through the third abdominal segment, allowing for body (Bowers 1963). As a check on measurement error of the curvature lengths of partially consumed amphipods estimated on the beach, T fed 20-22 mm amphipods to beetles in the laboratory and compared lengths measured before and after beetle feeding. There was a weak tendency to underestimate amphipod length, with а mean difference of -0.8 ± 0.6 mm (n=15).

estimated amphipod abundance from the mean of the number T of amphipods caught in 1 h in 6 to 10 pitfall traps placed at level. Pitfall traps consisted of plastic cups the high water (8.5 cm diameter, 11 cm deep) set into the sand and filled one third full of seawater (Craig 1973a,b). The water prevented animals from escaping once they fell into the traps. This method sampled the relative abundance of active amphipods which would beetle sitting motionless on the sand. In 1980, traps pass a were set one night each month. In 1981, traps were during set the period when searches were conducted.

To measure the sizes of amphipods available to beetles, I collected amphipods from two pitfall traps on one night each month. These traps were left throughout the period of beetle surface activity. Samples from the two traps were combined and preserved in 5% formalin. I grouped the amphipods into 4 mm size classes: (1) 4-7 mm (2) 8-11 mm (3) 12-15 mm (4) 16-19 mm (5) 20-22 mm. Juveniles were 2 mm in length when first released from the female brood chamber. However, 4 mm amphipods were the smallest I could observe when caught by beetles.

Vulnerability

I measured the reaction distance of beetles to amphipods of different sizes, and the capture success for detected amphipods in laboratory experiments. To standardize for hunger levels, I held beetles at laboratory temperatures without food for two to three days prior to these experiments. Experiments were conducted at night in buckets or trays containing a layer of damp sand. The overhead fluorescent lights were covered with filters to reduce light intensity.

To measure reaction distance I formed a grid of 0.6 cm² blocks in the sand. A live amphipod of known size was tied on a thread and dragged in a line perpendicular to the head of the beetle at approximately the walking speed of the amphipod. Three presentations at a given distance were made, moving towards the beetle at one block intervals until a response was obtained. I defined reaction distance as the maximum number of blocks at

which the beetle responded by movement towards the amphipod. Each beetle was tested once only for each amphipod size.

For capture success experiments, one beetle and a few amphipods of a given size were placed in buckets. I observed the beetle and counted the number of attacks required to capture an amphipod up to a maximum of 10 attacks. I defined an attack as a forward lunge by the beetle which resulted in contact with the amphipod. This was a conservative definition as it did not include misdirected lunges. I determined the probability of successful capture from the product of (a) the frequency of captures/attack for successful beetles, and (b) the frequency of success within 10 attacks.

I tested for the importance of beetle size for 16-19 mm amphipods only, by recording the number of captures made in 20 successive attacks by each beetle. Amphipods were removed manually between captures. Beetle size was estimated from the width of the head capsule, measured with vernier calipers. Beetle size in these experiments ranged from 3.9 to 5.6 mm. Head capsule width (W) was a more consistent measure of size than body length (L) used in beach measurements. They are related by the following equations

W = -0.04 + 0.23L for males (p<0.001, n=40)

W = 1.57 + 0.13L for females (p<0.001, n=40)

As a control for the use of overhead lighting, I repeated the experiments with blinded beetles, whose eyes had been covered with enamel paint. Beetles were permitted to recover for a few hours before these trials began. To determine capture success, I used 12-15 mm amphipods only and recorded the number of successful captures made by each beetle in 20 attacks. To determine reaction distance, I used 16-19 mm amphipods only, and followed the procedure described above.

Feeding experiments

I measured feeding rates for beetles covered with a thin layer of damp sand and placed in individual jars. I weighed beetles to the nearest 0.1 mg and allowed them to recover for about one hour prior to experimentation. They were then presented with amphipods or isopods of known size. Ι used amphipods 4-22 mm in length and isopods 8-11 mm in length. Isopods larger than this could not be held by beetles and were always rejected as food items. I recorded handling times to the nearest minute for the time between prey capture and completion of feeding. Beetles were immediately reweighed and gross consumption was estimated from the difference of the two weights. There were no appreciable weight changes in beetles which did not feed.

To determine the number of amphipods of a given size required to satiate a beetle, I presented amphipods continuously to beetles until they refused further food, at a maximum of 6 amphipods. Beetles were reweighed at the end of the experimental period.

I could not measure the number of isopods required to satiate a beetle, as beetles tended to reject isopods presented to them. A beetle would grasp the isopod between its mandibles
and release it, although it would readily accept an amphipod. Isopod experiments tested for differences in preference between male and female beetles for isopods and amphipods. The design was similar to the feeding experiments described in chapter 2 (page 12). Each jar contained one beetle, 10 isopods (under 12 mm in length), and 0, 2, 4, or 6 amphipods. Only starved beetles were used and two sizes of amphipods (8-11 mm and 16-19 mm) were offered.

Results

Vulnerability

The mean and the variance of the number of attacks required to capture an amphipod increased with increasing amphipod size (Table IV). For the three smallest size classes, all beetles tested captured an amphipod in less than 10 attacks (see Table IV, "prop. of beetles" column). For larger amphipods, some beetles were unsuccessful. The probability of prey capture/attack decreased with increasing amphipod size (see Table IV, "prob. of capture" column).

Beetle size also affected the frequency with which large amphipods were captured. The correlation between the number of 16-19 mm amphipods captured in 20 attacks and beetle size was 0.447 (n=41, p<0.01). Such relationships between capture success and predator and prey size are typical for insects (Evans 1976, Griffiths 1980).

Small amphipods were captured easily as the entire body of

Table IV. Capture success as a function of amphipod size. The table gives the mean and variance of the number of attacks required for capture by beetles which were successful within 10 attacks, the number of beetles tested, the proportion of beetles which were successful, and the combined probability of prey capture/attack.

size (mm)	size class	mean	var.	n	prop. of beetles	prob. of capture
4-7	1	1.53	0.81	30	1.000	0.652
8-11	2	1.88	1.75	40	1.000	0.533
12-15	3	3.25	6.58	32	1.000	0.308
16-19	4	3.84	8.81	48	0.646	0.168
20+	5	4.14	8.98	23	0.304	0.073

the amphipod fit between the mandibles of the beetle. For larger amphipods, beetles grasped the amphipod with their mandibles and maintained a position on its dorsal surface until the amphipod was subdued. Amphipods responded to capture by repeated flexing uropods. Maximum lengths of of the such escape responses observed in timed bouts were 40 s for an 11 mm amphipod, 80 S for а 14 mm amphipod, and 96 s for an 18 mm amphipod. In the last example the amphipod escaped. Large male amphipods also defended themselves with their second (enlarged) gnathopods and their antennae. These could prevent the beetle from grasping the body of the amphipod.

The overhead lighting used to conduct these experiments had no effect on capture success. Beetles which had been blinded captured 6.33±0.32 amphipods (n=15) in 20 attacks, or had a frequency of 0.317 captures/attack for amphipods in size class 3. This value was not significantly different from the observed

value of 0.308 for beetles which had not been blinded (t=0.56, df=14, p>0.10).

Beetles responded to large amphipods at much greater distances than small amphipods (Fig. 9). The responses of blinded beetles were not significantly different from those of beetles which had not been blinded (t=1.48, df=73, df=73, p>0.10).

Feeding rates

There were no differences in gross consumption, handling time or feeding rate between male and female beetles feeding on amphipods or isopods (t-test, p>0.05). I combined results from males and females for the following analyses. Gross consumption, handling time and feeding rates increased over the first 3 amphipod size classes and then remained constant for the two largest size classes (Table V). Beetles required more than twice the amount of time to feed on a large amphipod as they did on a small one. Feeding rates on isopods were only marginally greater than for the smallest amphipods.

One large amphipod was sufficient to satiate most beetles. All but one beetle tested on each of amphipod size classes 4 and 5 rejected additional amphipods (Table VI). Beetles which were fed on a sequence of the smallest amphipods consumed 3.6 amphipods on average. Handling times were also significantly greater for the smallest size classes, with an overall correlation of -0.429 (n=96, p<0.01) between amphipod length and handling time. Handling times for feeding to satiation did not Figure 9. The maximum presentation distance at which beetles responded to amphipods by movement towards the amphipod. Means are given with 95% confidence intervals (n=50). The value for blinded beetles (n=25) is given for 16-19 mm amphipods (closed circle).



Table V. Feeding data for beetles fed one amphipod or isopod. The table gives means, standard errors and sample sizes. The superscripts define levels which are not significantly different by Duncan's multiple range test.

size	size	gross	handling	feeding
(mm)	class	consumption	time	rate
		(mg)	(min)	(mg/min)

	•	٠		-	
$\sim m$	m m	•	50	~	~
~ ~ 111	1 1 1 1		1 16 1	(1	~
		-		~	~
	+		÷-		

_			(-)	.		
4-7	1	8.6±1.2'	(15)	12.0±1.4'	(14)	0.70±0.08'
8-11	2	26.8±2.3 ²	(18)	20.7±1.5 ²	(17)	1.38±0.15 ²
12-15	3	43.0±2.5 ³	(28)	22.8±2.0 ²	(28)	2.17±0.16 ³
16-19	4	49.6±3.4 ³	(25)	28.8±2.4 ³	(25)	2.01±0.20 ³
20+	5	48.8±3.8 ³	(21)	27.1±2.5 ²³	(21)	1.93±0.15 ³
		i	isopods			
		13.7±1.2	(25)	19.3±1.4	(25)	0.74±0.06

include the search time between successive prey items. The inclusion of search time would inflate the difference in total foraging time between small and large amphipods.

There were no differences in total gross consumption for beetles fed to satiation on different size classes. Gross consumption was related to initial beetle weight (r=0.505, n=96, p<0.01). The correlation between feeding rate and beetle weight was not significant (r=0.178, n=96, p>0.05).

In the experiments testing for preference of beetles between amphipods and isopods, male beetles consumed more isopods than female beetles when no amphipods were available (Fig. 10, open and closed squares, t=2.19, df=18, p<0.05), suggesting that males were either more successful in capturing Figure 10. The mean ±SE number of isopods eaten at densities of 10 isopods and 0, 2, 4 or 6 large amphipods (16-19mm, closed circles, n=20) and small amphipods (8-11mm, open circles, n=13). Male and female beetles differed in the number of isopods eaten in the absence of amphipods only (closed or open squares). For other amphipod densities, male and female data were combined.



Table VI. Feeding data for beetles fed to satiation on one amphipod size class. The superscripts define levels which are not significantly different by Duncan's multiple range test.

size (mm)	size clas	no. Seaten		gross consumption (mg)	handling time: (min)	f (eeding rate mg/min)
4-7	1	3.61±0.341	(18)	39.6±4.21	46.3±4.41	(14)	0.98±0.13 ¹
8-11	2	2.42±0.23 ²	(21)	48.6±3.6 ¹	38.7±3.4 ¹²	(16)	1.38±0.161
12-15	3	1.30±0.11 ³	(20)	51.2±3.8 ¹	26.5±2.5 ³	(20)	2.19±0.19²
16-19	4	1.04±0.04 ³	(25)	50.6±3.4 ¹	30.4±2.8 ²³	(25)	1.99±0.21 ²
20+	5	1.05±0.05 ³	(21)	49.5±3.8 ¹	27.4±2.6 ³	(21)	1.93±0.15 ²

isopods, or were less likely to reject isopods as prey. In the presence of large or small amphipods, only a few beetles ate any isopods (Fig. 10, open and closed circles). There were no differences in the number of isopods eaten by each sex. The rapid decrease in isopod consumption and corresponding increase in amphipod consumption with increasing amphipod abundance suggested strong preference for amphipods. Beetles observed in feeding experiments would attack an isopod dropped in front of them, and then reject the isopod, even small isopods that they could capture easily.

Field results

In 1980, beetles fed almost exclusively on <u>Orchestoidea</u> <u>californiana</u>. Of 423 observations, only four were on related amphipod species (<u>Orchestoidea</u> <u>pugettensis</u> and <u>Orchestia</u> traskiana) present on the beach in low numbers. One beetle only

was found feeding on an isopod, Alloniscus perconvexus. The pattern was different in 1981 and there were also differences between male and female beetles. Amphipods comprised 73.1% (n=175) of the diet of males, compared to 91.4% (n=336) for females ($X^2=28.8$, df=1, p<0.01). Mainly isopods comprised the remainder of the diet. In addition in 1981, there were four observations of males feeding on Dyschirius obesus LeC. (Carabidae), and two observations on Emphyastes fucicola Mann. (Curculionidae), both species about 2 mm in length. For females, there were three observations of feeding on larval Thinopinus pictus. These were the only three larvae observed on the surface at night in 1981, and they had probably been forced out of their burrows in the sand near HW by an incoming tide.

In 1981, 67% (n=114) of the feeding observations on amphipods and isopods for male beetles, and 71% (n=236) for female beetles, were on the lower beach ($X^2=0.76$, df=1, p>0.10). However, males on the upper beach were found feeding on isopods 42% (n=55) of the time, compared to 16% (n=114) on the lower beach ($X^2=12.3$, df=1, p<0.01). This was probably because isopods were relatively more abundant on the upper beach. Female beetles showed the same trend but the difference, 12% (n=97) compared to 6% (n=236), was weak ($X^2=3.12$, df=1, p<0.10).

The relative abundance of different sizes of amphipods changed as the summer progressed (Fig. 11). The largest amphipods disappeared after May, and juveniles were recruited to the population throughout June and July. There were also year to year differences. The modal size was larger in 1981 than in

Figure 11. Size-frequency distributions of amphipods caught in pitfall traps for each month in 1980 (A) and 1981 (B).





В

1980. The mean length of captured amphipods was also greater in 1981 (14.0 \pm 0.12 mm) than in 1980 (12.3 \pm 0.2 mm, t=11.5, df=802, p<0.001). Beetle length was also greater in 1981 (21.9 \pm 0.1 mm) than in 1980 (21.6 \pm 0.1 mm, t=3.20, df=802, p<0.01). Beetle length and the length of the captured amphipod were significantly correlated in both years (r=0.356, n=419, p<0.01 for 1980; r=0.190, n=385, p<0.01 for 1981).

Male and female beetles did not differ in mean body weight $(0.237\pm0.009 \text{ g}, n=25 \text{ for males}, 0.242\pm0.008 \text{ g}, n=27 \text{ for females})$, but males had greater head widths than females of the same weight (Fig. 12). As head width was related to how far apart mandibles could be spread (Fig. 13), this could affect the maximum size of prey captured. In beach observations, the mean and variance of the size of amphipods on which males and females were observed feeding did not differ (t=0.8, df=417, p>0.10 for 1980; t=0.0, df=383, p>0.10 for 1981). However, beetles found feeding on amphipods were significantly larger than beetles feeding on isopods for both males (t=2.29, df=142, p<0.05) and females (t=2.50, df=304, p<0.05).

The frequency with which scavengers joined beetles in feeding was related to the size of amphipod captured (Fig. 14, $X^2=13.4$, df=4, p<0.01). Beetles feeding on larger amphipods were more likely to attract various scavengers, mainly an unidentified staphylinid and <u>Dyschirius obesus</u>, a carabid (see page 6), and there was more space for attachment of scavengers on larger carcasses. In 1980, <u>Thinopinus</u> was joined in feeding in 7% of the observations. This figure was greater in 1981 with

Figure 12. Morphological comparisons of a sample of male and female beetles collected 4 June 1981. Weights were measured 9 h after collection. The slopes, but not the intercepts of the regression lines are significantly different (p<0.05). Regressions are y = 3.06 + 8.23x for males, r²=0.853 y = 3.26 + 5.87x for females, r²=0.751



Figure 13. Maximum mandible spread for male and female beetles (r=0.937, n=56). Measurements were made on relaxed beetles using vernier calipers.



Figure 14. The frequency distribution of the sizes of captured amphipods in 1981 when scavengers were present or absent.

.



Figure 15. The observed frequency distribution of amphipod size classes in the population obtained by weighted averages of pitfall trap catches from each month (white bars), the predicted distribution of amphipods captured according to the mechanistic model (striped bars), the observed distribution of captures (black bars), and the standardized forage ratios (inset, see page 54) for both years of data. The dotted line gives the expected forage ratios in the absence of preference.



scavengers present in 27% of the observations ($X^2=57$, df=1, p<0.001). Only 5% of the beetles feeding on isopods in 1981 were joined by scavengers.

A test for prey selection

obtained an average distribution for the sizes Ι of amphipods available to beetles in each year by weighting the frequency of each amphipod size in each month by the number of feeding observations made on beetles in that month (Fig. 15, white bars). The observed distributions of the sizes of captured amphipods (Fig. 15, black bars) differed from the sizes available for both years ($X^2=376$, df=4 for 1980, $X^2=128$ for 1981 p<0.001). Beetles did not capture sizes of amphipods in proportion to the relative abundance of those sizes. I used the model described above to test whether this resulted from differences in the relative availability of different sizes to beetles, or by active selection by the beetles.

Mechanistic model

The mechanistic model was based on p(i)', the proportion of amphipods of size i, I expected to observe in the diet of a beetle if the beetle did not use active selection. To predict p(i)', I combined data on the sizes of amphipods available (Fig. 15, white bars) with laboratory values for vulnerability and handling times (Fig. 9, Table IV, Table V). Predicted values of p(i)' differed between the two years (Fig. 15, striped bars). The observed distributions of the sizes of captured amphipods (Fig. 15, black bars) also differed between years $(X^2=34.8 \text{ df}=4)$, p<0.001), but showed similar trends in both years and differed from p(i)' (X²=540, for 1980; X²=85 for 1981, df=4, p<0.001). The pattern of food selection is seen most clearly by examining the standardized forage ratios (Fig. 15, inset). With five prey size classes, а size class which is neither selected preferentially nor avoided has a ratio of 0.20. In both years beetles appeared indifferent to the smallest size class, avoided at least one of the middle size classes, and showed strong preference for the largest size class.

The apparent preference for large amphipods could result if I underestimated capture success for these sizes. To test this possibility, I recalculated p(i)' using data on the probability of capture/attack from beetles which were successful only. This would overestimate the true probability. As the numbers of amphipods captured in the largest two size classes were underestimated by this calculation, measurement error was still insufficient to account for the preference observed. The new distributions of p(i)' did however conform more closely to the observed distributions ($X^2=239 p<0.001$, for 1980; $X^2=14$, p<0.01for 1981).

It is possible to choose parameter values which force agreement between p(i)' and the observed distributions. Values which result in an exact fit for a change in one parameter are given in Table VII. For example, very high values for d(i) or h(i) for size class 5, relative to the other size classes, could

improve the fit of the model. None of the values for parameters listed in Table VII were within the range of values obtained from experiments. However, it is still possible that errors in different parameters could combine to produce a spurious but significant difference between p(i)' and the observed distributions.

Frequency-dependent model

The frequency-dependent model could also be tested by a comparison of p(i)' and the observed distribution of the sizes of captured amphipods. According to the predictions of this model, the most abundant size classes should be over-represented in the diet relative to their availability, and conversely for the least abundant size classes. The data showed the opposite trends. Preference appeared to be strongest for the largest and least abundant size class.

Optimal diet model

For most optimal diet models, the profitability of each prey type is defined as the ratio of net energy intake to handling time. I approximated this ratio by the feeding rate for each size class and could not distinguish between the largest 3 size classes. This simple form of the model was clearly inappropriate, as I measured differences in selection between size classes 3 and 4. An alternative method I chose was to rank prey items based on the number of amphipods of a given size

Table VII. Parameter values for f(i), h(i), d(i) and c(i) which result in an exact fit of the observed distribution of the sizes of captured amphipods to p(i)'. These values were calculated for a change in the listed parameter only. Other parameters used in calculation of p(i)' were those obtained from the experiments. Values for h(i), d(i) and c(i) were standardized to a maximum value of 1. Values are shown for both 1980 and 1981 data.

i	f(i)	h(i)	d(i)	c(i)
1980	data			
1	0.3995	0.1646	0.0333	1.0000
2	0.1038	0.1147	0.0387	0.3304
3	0.1764	0.0429	0.0245	0.0648
4	0.1921	0.2323	0.1741	0.1510
5	0.1281	1.0000	1.0000	0.3009
1981	data			
1	0.1663	0.1715	0.0347	1.0000
2	0.0870	0.1259	0.0425	0.3478
3	0.1960	0.2786	0.1581	0.4009
4	0.3597	0.4965	0.3722	0.3095
5	0.1910	1.0000	1.0000	0.2888

class required to satiate a beetle. This was because an increase in the number of items eaten would increase the total search time required. I could still not distinguish between size classes 4 and 5 however, and these size classes shared a rank of one.

I calculated the expected foraging times, T(r), for beetles feeding to satiation on different sets of size classes as described on page 54. When beetles fed on mixtures of size classes I used the data in Table VI to estimate the mean numbers of items eaten and the handling times (Table VIII). I combined

è

Table VIII. Parameter values for the optimal diet model. The table gives all possible combinations of size classes of prey items in the diet, and the mean handling time h(i), and the mean number of items eaten (N) for each combination. Combinations are listed as the number of the size class in the order of capture for a maximum of four items eaten.

order <u>1</u>	of <u>2</u>	capture <u>3</u>	4	handling <u>time(min</u>)	no. <u>eaten</u>
1	1	1	1-2	42.2	3.6
1	1	1	3-5	39.4	3.6
1	1	2		42.4	3.0
1	1	3-5		36.6	3.0
1	2	1-2		42.2	3.0
1	2	3-5		38.0	3.0
1	3-	-5		32.5	2.0
2	1	1-2		42.2	3.0
2	1	3-5		38.0	3.0
2	2	1-2		42.2	2.4
2	2	2-5		39.4	2.4
2	3-	-5		33.8	2.0
3	1-	·2		32.5	1.3
3	3-	-5		28.3	1.3
4-5				28.3	1.0

data on handling times for size classes 1 and 2 and for size classes 3, 4 and 5 where differences were not significant. When feeding occurred on mixtures of size classes with distinct handling times, I used an average feeding time, weighted by the proportion of the total food intake from the different size classes.

prediction of optimal diet models, is that only the One subset of sizes which minimize foraging time are included in the optimal diet. Using 1980 data, T(r) was minimized (Table IX) when all size classes were included in the diet for encounter rates less than 60 amphipods/h, and for encounter rates less than 68 amphipods/h for 1981 data. At higher encounter rates, foraging time was minimized by excluding the smallest two size classes from the diet. The long foraging times for a beetle which fed on the two largest size classes only, resulted because these size classes were less abundant and required a longer search time.

test predictions from this model with the field data, I То used the numbers of amphipods caught in pitfall traps on the beach as an estimate of the amphipod encounter rate. The size of the trap opening approximated the area of reaction of a beetle. For 1981 data, the maximum encounter rate measured was 30 amphipods/h. According to Table IX, this rate was well below the threshold at which selection should occur. This result had two important implications. First, I could not distinguish the optimal diet prediction from the null hypothesis. A good fit to the model could result if beetles were foraging either optimally or simply according to prey availability. Second, for the range encounter rates observed, foraging time differences between of most strategies were within one standard error of experimental

Table IX. Foraging times (min) generated by the optimal diet model for beetles feeding to satiation on all combinations of size classes. (A) the generalist (B) size classes 2-5 only (C) size classes 3-5 only (D) size classes 4-5 only. Encounter rates are in amphipods/h. Calculations are shown based on amphipod size distributions for 1980 and 1981. * indicates the lowest value.

encounte <u>rate</u>	er <u>A</u>	B	<u>C</u>	<u>D</u>
198 1	30 data 258.4*	308.7	358.2	2187.7
10	52.8*	57.4	61.2	244.2
20	41.4*	43.4	44.8	136.2
30	37.6*	38.8	39.3	100.2
40	35.7*	36.4	36.5	82.2
60	33.8	34.1	33.8*	64.3
100	32.3	32.2	31.6*	49.9
198 1	81 data 291.1*	311.7	431.4	754.6
10	56.4*	58.3	68.6	100.9
20	43.4*	44.2	48.4	64.6
30	39.0*	39.5	41.7	52.5
40	36.9*	37.2	38.3	46.4
.60	34.7*	34.9	35.0	40.4
100	32.9	33.0	32.3*	35.5

values for mean handling time. The only testable prediction from Table IX was that beetles would not specialize on size classes 4 and 5. In fact, the proportion of captured amphipods in size classes 4 and 5 increased with amphipod encounter rate for May and June 1981 (Spearman rank correlation coefficient = 0.410, n=23, p<0.05). This was not true for July 1981 (Spearman rank correlation coefficient = 0.038, n=25, p>0.10), probably because small amphipods were relatively more abundant in July. It is possible that I underestimated encounter rates. This would be especially true if prey were clumped. However, beetles I observed continuously in 1979 and 1980 had a mean encounter rate of 8.8 amphipods/h (page 33).

The feeding rate on isopods was similar to the feeding rate Bv on the smallest size class of amphipods (Table V). the criteria defined above, isopods and size class 1 amphipods share isopods should be eaten as encountered and the same rank whenever the smallest size class of amphipod is included in the optimal diet. For amphipod abundances less than 10 amphipods trapped/h in 1981, 18% (n=135) of the feeding observations were on isopods. Above this level only 6% of the feeding observations were on isopods $(X^2=10.7, df=1, p<0.01)$.

Discussion

I have shown that the distribution of sizes of amphipods in Thinopinus differed significantly from a null the diet of hypothesis model based on differential vulnerability. However, the pattern of prey size selection could not be accounted for by frequency-dependent or optimal diet models. In order to either model reject the null hypothesis model, I must assume that the both complete and that the parameters were correctly is the parameters that assume evaluated. In particular Ι must in the laboratory accurately reflect behaviour in the measured field. A combination of estimation errors in any of the parameters could result in an apparent preference or indifference for some size classes.

One potential source of error is in the assessment of the amphipods available. This is because the predictions sizes of were based on means. I can only state that on average, beetles not perform as predicted. In chapter 2, I argued that local did spatial and temporal variations in the sizes of amphipods did occur and were important to the success of foraging beetles. I did not monitor these beetles continuously and I did not know the actual densities or sizes of amphipods encounted by each beetle. In particular, the sizes of amphipods caught in pitfall traps did not sample the sizes of amphipods encountered by a beetle in active mode (see page 33).

I describe a more precise test of preference between size and 4 in laboratory experiments in Chapter 4. I was classes 2 able to measure weak preference only for size class 4 by starved beetles, and I could not measure any preference of beetles which suggested that beetles had not been starved. This were predominantly opportunistic, and that measured deviations from mechanistic model were statistically, but only weakly the biologically, significant. Beetles which I observed on the beach always attack amphipods near them. This was true for did not large as well as small amphipods. I did not observe beetles to capture and then reject amphipods of any size.

In order for a beetle to actively select certain sizes of prey, it must have the ability to distinguish prey size. The ability to distinguish prey size has been well documented in

vertebrates (salamanders, Jaeger and Bernard 1981; fish, Gardner 1981; birds, Zach 1978, Goss-Custard 1977; shrews, Barnard and also some evidence for invertebrates There is 1981). Brown 1978). (crabs, Elner and Hughes 1978; ants, Davidson Brownell (1979) demonstrated that the desert scorpion and Farley detects prey through substrate-borne Paruroctonus mesaensis vibrations. Thinopinus may use a similar mechanism. There were blind and no differences in the reaction distance of sighted vibrations could also provide Such sand-borne beetles. information on prey size. This mechanism would work most amphipod walked toward a beetle. Frequently effectively if an amphipods jumped. Beetles rapidly attacked amphipods which landed near them. Hence, the potential for error in judging prey judging prey profitability are Mistakes in size was high. an explanation for the discrepancies frequently cited as observed in tests of optimal diet predictions (e.g. Elner and Hughes 1979, Jaeger and Barnard 1981).

There were advantages to feeding on small amphipods which I did not account for in measuring profitability of different amphipods for the optimal diet model. Small amphipods sizes of tended to be clumped and several could be captured in one area time interval. Large amphipods were more costly to in short а capture, as a struggle frequently ensued between the amphipod beetle feeding on a large item also attracted a and beetle. Α variety of scavengers. This led to struggles and a loss of а portion of the prey item, with associated time and energetic costs.

Why did the optimal diet model not work?

This is a case in which I measured all the necessary values and did everything "correctly". Yet, the optimal diet predictions were identical to the null hypothesis. Pastorok (1981) reported results similar to those I have presented here. He constructed an optimal diet model for <u>Chaoborus</u> feeding on different sizes of <u>Daphnia</u> which was based on differential vulnerability. The model predicted that <u>Chaoborus</u> should include all sizes of <u>Daphnia</u> in its diet for the range of abundances he measured in the field. This was, in fact, the pattern observed.

In general, attempts to measure size selection of prey by in the field have been unsuccessful invertebrate predators (Thompson 1978b, Griffiths 1980, Murtaugh 1981). The range of sizes eaten appears largely to depend on limits set by the mechanics of prey capture, and on differential vulnerability of different sizes. Griffiths (1981) showed that hungry ant-lions would attack small prey for which the energetic costs of capture exceeded the benefits. For predators such as ant-lions, Chaoborus and Thinopinus, which encounter large variations in prey size and abundance, a generalist foraging strategy may be best rule. Morse and Fritz (1982) have suggested that it is the more important for crab spiders to locate good foraging sites than to specialize on certain prey while at a site.

Isopods versus amphipods

frequency-dependent and optimal diet models Both qualitatively predicted the types of prey eaten. The feeding rate on isopods was lower than the rate on all but the smallest Beetles included isopods in their diet at low amphipods. amphipod abundance only and the relationship with abundance appeared to follow a threshold as predicted by the model. In showed that amphipods were highly laboratory experiments I preferred to isopods. Beetles may be more successful in between amphipods and isopods than between distinguishing different sizes of amphipods. Beetles would pick up and drop isopods they could easily capture.

There were also differences between sexes in the frequency with which isopods were included in the diet. Presumably, male beetles were making some kind of "trade-off" between searching for mates and searching for food. Effects of other trade-offs such as between foraging and territorial defence in salamanders (Jaeger <u>et al</u>. 1981) and birds (Kacelnik <u>et al</u>. 1981), or foraging and predator avoidance in fish (Milinski and Heller 1978), have also been shown to reduce attack rates and decrease diet specialization.

Selander (1966) proposed that sexual differences in foraging evolved to reduce intersexual food competition, and that morphological differences in the food-getting apparatus between males and females reflected this competition. Males do have larger mandibles and may be better than females in capturing isopods. However, field data indicated that it was the smaller beetles of each sex which were feeding on isopods. The small isopods used in laboratory experiments could easily have been captured by all beetles.

Morphological differences in mandible size probably resulted from the use of mandibles by male beetles to capture female beetles as well as prey items. Females tended to resist any mating attempt. More than one male sometimes attempted to mate with a female at a given time, leading to male-male fights. Larger males may be more successful in such fights as has been shown for the milkweed beetle (McCauley 1982) and for the dung fly (Borgia 1980).

The difference in prey selection between sexes must be primarily a behavioral response on the part of the beetles rather than a morphological one, and could be accounted for by learning. Male beetles spent more time on the upper beach where isopods were more abundant than did females, and would encounter isopods more frequently. Female beetles may not recognize isopods as prey items.

I have shown that beetles are selective in the sizes and types of prey included in their diet. This selection resulted both from differential vulnerability and from active choice of amphipods over isopods and of larger amphipod sizes. Future studies of foraging should place more emphasis on how invertebrate predators distinguish prey from non-prey items, and how learning and memory affect this process.

CHAPTER 4: HUNGER AND OPTIMAL DIET

Introduction

Models of optimal diet (reviewed by Pyke et al. (1977))assume that predators behave so as to maximize their rate of net energy intake. By knowing the energy values e(i), handling times h(i), relative frequencies f(i) and overall encounter rate R of i potential prey types, it is possible to predict which prey incorporated into the optimal diet (Pulliam 1974, should be Charnov 1976a). These prey should always be eaten, and excluded prey never eaten when encountered - the "always or never" rule. Deviations from the always or never rule typically occur however in experimental tests of the model predictions. They have been explained by the failure of the model to account for other constraints on the foragers such as the need for sampling (Krebs et al. 1978, Davidson 1978, Heinrich 1976), predator avoidance (Milinski and Heller 1978), prey recognition time (Elner and Hughes 1978), nutrient balance (Pulliam 1975, Westoby 1978), and the random nature of encountering prey (Pulliam 1974).

The optimal diet model does not allow for changes in the degree of predator hunger. Increasing hunger is known to affect the predation process by increasing feeding rate (Ernsting 1977, Beukema 1968, McCleery 1977), reaction distance (Holling 1966), predator activity (Beukema 1968, Calow 1974), prey use (Haynes and Sisojevic 1966, Johnson <u>et al</u>. 1975), and size range of prey eaten (Heatwole and Heatwole 1968, Kislalioglu and Gibson 1976). Some of these results may be interpreted in terms of the optimal
diet model if recognition or assessment of food availiability by predators is modified by hunger levels. Then as predators approach satiation, they should behave as if prey were abundant and become more selective (Schoener 1971, Pulliam 1974, Charnov 1976a). Here I describe a two prey model which predicts the opposite result. I show that under certain conditions, predators should expand their diet near satiation to include lower value prey. A predator using this rule is what Heller (1980) has termed an expanding specialist. I then describe an experiment to test whether one predator, the beetle <u>Thinopinus pictus</u>, changes its diet near satiation in the direction predicted by the model.

The model

Consider a time minimizer (Schoener 1971), a predator which attempts to minimize the total foraging time (T) necessary to obtain a fixed food requirement. I make identical assumptions to the optimal diet model with one addition, that the predator can assess the food value D, required from prey to make up its food deficit. Given the evidence cited above for the effect of hunger the predation process, this assumption is not unreasonable. on Maximizing the rate of energy intake over the entire foraging is equivalent to minimizing T. The problem is period to determine which prey types to include in the optimal diet.

For prey types A and B, let A be the more profitable prey, such that e(a)>e(b), and e(a)/h(a) > e(b)/h(b). Then there are three reasonable alternatives:

(1) feed on type A prey only (specialist)

(2) feed on type A and B prey as encountered (generalist)

(3) feed on type A prey if D is less than a given value, otherwise feed on type A and B prey as encountered (expanding specialist).

The model I present here predicts the mean and variance of the total foraging time for a predator following one of the above rules.

First consider the case where $D \le e(a)$. The predator will search for and feed on at most one type A prey, or at most n+1 type B prey. Here n ≥ 0 is an integer such that

 $D = ne(b) + z, \qquad 0 < z \le e(b)$

For the specialist, expected handling time E(H) is the S food requirement divided by the intake rate while feeding on the item. I assume that intake rate, and hence handling time, has zero variance. Expected search time E(S) and its variance V(S) S S S can be derived from the exponential distribution with parameter Rf(a). Here R is the rate at which prey items are encountered (assumed constant), and f(a) is the probability that the encountered item is a type A prey. Hence

f(a) + f(b) = 1

Then expected foraging time is

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

$$S \qquad S \qquad S$$

$$= \frac{Dh(a)}{e(a)} + \frac{1}{Rf(a)}$$

with variance

$$V(T) = 1/[Rf(a)]^2$$

S

For the generalist, the number of items eaten will depend on the order in which type A and B prey are encountered. Expected foraging time is

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

$$G = G$$

$$= \frac{Dh(a)}{e(a)} + \left[\frac{h(b) - h(a)}{e(b)}\right] [D - ne(b)] f(b)$$

$$+ \left[\frac{h(b) - h(a)}{e(b)}\right] e(b) [1 - f(b)]^{n} \frac{f(b)}{f(a)}$$

$$+ \frac{n+1}{e(b)} \frac{n+1}{e(a)}$$

Derivations of E(H) and E(S) are given in Appendix A and G G B respectively. The first term is the handling time for the

specialist. The second term is the extra handling time incurred by the generalist for feeding on an amount z from a type B prey. The third term is the extra handling incurred by the generalist for feeding on type B prey before encountering a type A prey. The fourth term is the search time. Expected handling time is greater for the generalist, while expected search time is greater for the specialist. The generalist will have the lower foraging time when

E(T) < E(T)G S

or when

 $\begin{bmatrix} h(b) - h(a) \\ e(b) \end{bmatrix} \{ z + e(b) \begin{bmatrix} 1 - f(b) \end{bmatrix} \frac{f(b)}{f(a)} \} < \frac{1}{Rf(a)}$

The extra handling incurred by the generalist must be less than the specialist search time.

Foraging time variance for the generalist is given by V(T) = V(H) + V(S) G G Gwhere V(H) and V(S) are derived in Appendix A and B G Srespectively. Search time variance is always greater for the specialist. Hence the generalist will have a lower foraging time variance if

V(H) < V(S) - V(S)G S G

Fig. 16 shows expected foraging times as a function of food requirement. For certain ranges of parameter values, the generalist reaches satiation more quickly than the specialist. Total foraging time increases with D. Increases are discontinuous at the point where D is an exact multiple of e(b), that is, when an additional prey item is required. The discontinuity represents the time spent in searching between successive prey items when foraging time increases, but food intake does not. An increase in e(b), or a decrease in h(b)/e(b) f(a), extends the range of values of D for which the or generalist has the lower total foraging time. Foraging time variance is independent of D for the specialist and increases with D for the generalist, with small discontinuities where an additional prey item is required.

Next consider the general case in which D can take any value. The mean and variance of foraging time can be derived from the gamma distribution as for the restricted case. The

Figure 16. Expected total foraging time for the generalist (solid line), and specialist (dotted line) as a function of the food requirement, D. Error bars represent one standard deviation. Parameter values are R=0.65, e(a)=1 and h(a)/e(a)=20. Other values are given in the figure.



τοτ

specialist will search for and feed on at most m+1 type A prey. Here $m\geq 0$ is an integer such that

 $D = me(a) + y, \quad 0 < y \le e(a)$

Then

$$E(T) = \frac{m+1}{Rf(a)} + \frac{Dh(a)}{e(a)}$$

and

$$V(T) = \frac{(m+1)}{[Rf(a)]^2}$$

Hence foraging time variance for the specialist is a step function of D.

The formula for the generalist is complex, but it can be shown by simulation that for certain parameter values the generalist will have a lower foraging time than the specialist. interesting case however, is for the expanding specialist, The the predator which switches from specialist to generalist after it has consumed m type A prey. That is, at most one type A prey is required for satiation. The mean and variance for total foraging time for the expanding specialist can be obtained from the sum of the mean and variance of foraging time for а specialist feeding on m type A prey and for a generalist feeding on D-me(a) energy units of type A and B prey. This is shown in Fig. 17 which is analogous to Fig. 16b. If the generalist reaches satiation more quickly than the specialist when $D \le e(a)$, then the expanding specialist must have a lower foraging time for the same range of values when D>me(a).

Figure 17. Expected total foraging time for the generalist or expanding specialist (solid lines) and specialist (dashed line) as a function of the food requirement, D. Error bars represent one standard deviation. Parameter values are R=0.65, e(a)=1, h(a)/e(a)=20, h(b)/e(b)=40, e(a)=1, and e(b)=0.25.



A test with Thinopinus

Field data on the predator <u>Thinopinus pictus</u> suggested that <u>Thinopinus</u> preferred large sizes of the amphipod <u>Orchestoidea</u> <u>californiana</u> as prey items. I designed a laboratory experiment to test whether this preference was affected by hunger. Short-term laboratory experiments had shown that on average 2.4 small (8-11 mm) amphipods or 1.0 large (16-19 mm) amphipods were required to satiate a beetle. Mean feeding rates were 1.38 mg/min and 1.99 mg/min on small and large amphipods respectively (Table VII). These values approximately corresponded to those used in Fig. 16a.

Qualitative predictions based on the model were (1) starved beetles prefer large over small amphipods (2) beetles near satiation show no preference. I used densities of 10 small amphipods and 2, 4, 6, 8 or 10 large amphipods. This particular design was chosen so that I could also test the prediction from optimal diet models of frequency-dependent and all prey selection that (3) preference for large amphipods increases with the density of large amphipods.

To obtain two hunger levels I either held beetles without food for 3 d (starvation treatment) or fed them the night prior to the experiment (satiation treatment). For each treatment, 12 male and 12 female beetles were each placed in a glass jar (8 cm diameter, 10 cm deep) containing a 3 cm layer of damp sand and large and small amphipods. Because of this sand layer, a variable number of amphipods were active on the sand surface at any given time, with the remainder of the amphipods in burrows. Beetles also burrowed after feeding, so they did not encounter amphipods continuously. Jars were covered to prevent amphipod escape and were left overnight for 20-22 h under natural photoperiod at laboratory temperatures (16-19°C). I then counted the number of live amphipods in each jar and determined the number eaten by inference. In control jars without beetles I recovered all large amphipods and a mean of 9.3 ± 0.3 (n=8) small amphipods.

separated the effects of sex and amphipod abundance on T the number of amphipods of each size eaten in a 2-way ANOVA for each amphipod size and treatment. There was a weak tendency for male beetles to feed on more small amphipods in the starvation treatment (F=3.57, df=1,110, p=0.06), but other male-female comparisons were not significant (F-tests, df=1,110, p>0.10) and There variances were homogeneous. were no significant differences in the number of small amphipods eaten at different densities of large amphipods in either treatment (F-tests, df=4,110, p>0.10, Fig. 18, white bars), nor were the interaction terms with sex significant (F-tests, df=4,110, p>0.10). The number of large amphipods eaten increased with the number of large amphipods presented (Fig. 18, shaded bars). This effect was more pronounced in the starvation treatment (F=6.22)df=4,110, p<0.0001) than in the satiation treatment (F=2.42, df=4,110, p=0.05), although variances were not homogeneous (Bartlett's test, df=4, p<0.001 and p=0.01 respectively). Again the interaction terms with sex were not significant (F-tests, df=4,110, p>0.10).

Figure 18. The mean ±1SE number (n=24) of large amphipods (shaded bars) and small amphipods (white bars) eaten at densities of 10 small and 2, 4, 6, 8, or 10 large amphipods. (A) starvation treatment and (B) satiation treatment.



I combined results from male and female beetles to test for differences between hunger treatments at each amphipod density. Beetles from the starvation treatment ate more small amphipods than beetles from the satiation treatment when large amphipods were present at densities of 2 and 10 only (t-tests, df=46, p<0.05), and ate more large amphipods at all densities (t-tests, df=46, p<0.01).

Table X. Values of c at different densities of large amphipods for each hunger treatment. Values given are corrected (corr) or not corrected (ncor) for loss of small amphipods.

	stavation		satiation	
density	corr	ncor	corr	ncor
2	1.99	2.78	1.15	0.86
4	2.26	1.68	1.25	0.89
6	1.43	1.02	0.77	0.59
8	1.72	1.25	0.79	0.55
10	0.94	0.75	0.84	0.54

To test for preference I first computed the measure a suggested by Chesson (1978) where preference for large amphipods is given by

 $\alpha_1 = (w_1/x_1)[(w_1/x_1) + (w_2/x_2)]^{-1}$

where w_1 and w_2 are the numbers of large and small amphipods eaten, and x_1 and x_2 are the numbers of large and small amphipods presented. Preference for small amphipods is given by

 $a_2 = 1 - a_1$

This method was chosen because a value for a_1 and a_2 could be obtained when beetles fed on one size of amphipod only. I then starved beetles I used a sign test to compare σ_1 and σ_2 . For found weak preference for large amphipods at densities 2 (n=22, p=0.05) and 8 (n=24, p=0.06), and for small amphipods at density 10 (n=23. p=0.09). For beetles in the satiation treatment, none of the comparisons were significant (n=24, 22, 24, 24 and 19 for densities 2, 4, 6, 8 and 10 respectively, p>0.10) as predicted. I also compared σ_1 for starved beetles and for beetles near satiation using the median test. There was a significant decrease in preference for large amphipods by beetles near satiation at densities 2, 6, and 8 (n=24, p<0.05), and differences at densities 4 and 10 were in the same direction.

To test for changes in preference with density, I computed c (Murdoch 1969) where

$c = w_1 x_2 / w_2 x_1$

I used mean values for w_1 and w_2 from Fig. 18 and repeated the calculations with and without a correction for the mean number of small amphipods lost from control jars. For both treatments, c either showed no trend or decreased with increasing density of large amphipods (Table X). This was opposite to predictions of both frequency-dependent and optimal diet models of prey selection.

Discussion

The optimal diet model (Pulliam 1974, Charnov 1976a) predicts that predators should specialize if

 $\frac{1}{Rf(a)} < e(a)\frac{h(b)}{e(b)} - h(a)$

This condition is met for the parameter values in Fig. 16. Clearly, if predators can assess the food value required from prey, the net rate of food intake does not predict when to specialize. The optimal diet can change in composition such that items of lower value are included as the predator approaches satiation. Essentially this means that if only a portion of a high value item is required, a predator can be satiated more quickly if it accepts the first item it encounters, rather than search for a high value prey.

A range of D values can also be interpreted as a range of food intake requirements to satiate predators of different sizes. For <u>Thinopinus pictus</u> for example, I found a correlation of 0.505 between the weight of food required to satiate a beetle and beetle weight (page 65). Hence, differences in preference are expected for beetles of different sizes. If the encounter rate with the high value prey is sufficiently low, the model predicts switches between specialist and expanding specialist foraging rules with a continuous increase in predator size.

The generalist or expanding specialist may have a

- (1) lower mean and variance of foraging time
- (2) higher mean but lower variance of foraging time
- (3) higher mean and variance of foraging time relative to

the specialist

Whether a predator forages as a generalist, expanding specialist or specialist, will depend in part, on how it responds to variation in encounter rates of the prey types. For outcomes (1) and (3), the generalist or expanding specialist, and specialist strategies respectively are favored. For example, for D=0.20 mean differences in foraging times for the expanding specialist and specialist will be statistically significant (p<0.05) after about 20 foraging bouts (one-tailed z test) using values from Fig. 16b, or after about 6 foraging bouts using values from Fig. 16c. For predators which feed many times during their lifetime, even small time savings may become important.

(2), the generalist or expanding specialist outcome For may be favored by a predator foraging in strategy а risk-aversive manner (Caraco 1980, Caraco et al. 1980). It will have a higher mean foraging time, but will also have a lower probability of taking a much longer time to achieve satiation. For example, Real (1981) has shown that bees and wasps prefer constant over variable food rewards with equal expectations. Conversely, a forager may favor a specialist strategy if it is foraging in a risk-prone manner. It will require a shorter time on average to achieve satiation, but incurs the risk of taking a much longer time.

Rarely will prey be randomly distributed as this model assumes. Heller (1980) developed a model from which he showed that an expanding specialist may also have an advantage when prey are clumped. Hunger was not considered in his model, but profitable prey could be rapidly depleted from a patch and interpatch travel times were long.

It is commonly held that hungry predators accept a wider variety of prey types than do predators near satiation (e.g. Schoener 1971). The best evidence for this comes from the work of Ivlev (1961) who showed that carp became increasingly selective as they approached satiation. In contrast, Akre and Johnson (1979) found a decrease in preference near satiation for damselfly naiads feeding on two prey types. Contrary evidence is given by the experiments reported here.

Thinopinus pictus showed a significant decrease in preference with satiation for large amphipods at most amphipod densities when starved beetles and beetles near satiation were compared. Although this result was in gualitative agreement with model presented here, the quantitative predictions were not the met. Beetles in both treatments fed on small amphipods at all densities. Preference for large amphipods did not increase with density as predicted. The model could account for these from the "always or never rule" if variation among deviations beetles was related to size differences, or if beetles switch specialist to generalist foraging rules as they approach from satiation during an experimental run. There were alternative interpretations of these results, however. Both beetles and damselfly naiads may change their search behaviour near satiation and alter the relative encounter rates of different prey types.

The model presented here is most applicable to predators

near satiation, as other factors likely affect foraging decisions of a predator which has been starved for a substantial period of time prior to experimentation. Future tests must also allow for changes in predator behaviour near satiation. Prey size should be sufficiently large relative to the food requirement, so that changes in preference are measurable. Suitable predators for future tests are anthocorid bugs (Evans 1976) or salticid spiders (Givens 1978), which require a relatively few prey items for satiation.

CHAPTER 5: CONCLUDING REMARKS

staphylinid beetle Thinopinus pictus The lives in а structurally simple environment. Yet, the food supply of Thinopinus varies over a range of spatial and temporal scales. Thinopinus is obviously limited in its ability to assess and respond to this temporal and spatial variation. I have argued that this result is a general one for invertebrate predators. Most of the support for optimal foraging theory with invertebrates has come from active foragers which search for slow-moving or sedentary prey (e.g. crabs (Elner and Hughes 1978), ants (Davidson 1978), and bumblebees (Pyke 1978)). Huey and Pianka (1981) compare various correlates of active and based on studies of desert lizards. ambush foraging modes Species which ambush generally eat fewer, more active prey, have lower metabolic costs, and have a limited learning ability, relative to species which are active foragers. These results can probably be applied to invertebrates as well. One conclusion which emerges is that there are not simple general rules which govern foraging behaviours of all animals. Instead, the rules depend on prey behaviour, on the range of behaviours available to the forager, and on the capacity of the forager to make "correct decisions".

A second conclusion is that the capacities of foragers to respond to prey variation depend on the scale of measurement. Morse and Fritz (1982) suggest that for ambush predators, predictions from optimal foraging theory based on patch choice are more successful than predictions based on diet choice. This was not true for <u>Thinopinus</u>, as <u>Thinopinus</u> showed strong preference for the prey type (amphipod) on which it had the highest feeding rate. However, <u>Thinopinus</u> showed only weak preferences among sizes of amphipods. The difference probably results because a wider variety of cues are available to distinguish among prey types than among sizes of a given prey type.

most successful recent attempts to predict foraging The have been based on simple stochastic rules of behaviours (Hanski 1980), or on assumptions of the memory behaviour capacity of the animal (Pyke 1978, Ollason 1980). For example, in a variety of experiments Caraco et al. (1980), Waddington et al. (1981) and Real (1981) have shown that food preferences depend not only on the expected outcome of a foraging bout, but also on the variance of that outcome. Hence, as is so often true in ecological studies, the distribution is more important than mean. Problems of how foragers learn about and respond to the variation in prey availability will continue to be one exciting and necessary direction for future research.

LITERATURE CITED

- Akre, B.G. and D.M. Johnson. 1979. Switching and sigmoid functional response curves by damselfly naiads with alternate prey available. J. Anim. Ecol. <u>48</u>:703-720.
- Barnard, C.J. and Brown, C.A.J. 1981. Prey size selection and competition in the common shrew (Sorex araneus L.). Behav. Ecol. Sociobiol. 8:239-243.
- Beukema, J. J. 1968. Predation by the three-spined stickleback (<u>Gasterosteus aculeatus</u>): the influence of hunger and experience. Behavior <u>31</u>:1-126.
- Borgia, G. 1980. Sexual competition in <u>Scatophaga</u> <u>stercoria</u>: size- and density-related changes in male ability to capture females. Behavior 75:185-206.
- Bowers, D.E. 1963. Field identification of five species of Californian beach hoppers (Crustacea: Amphipoda). Pac. Sci. <u>17</u>:315-320.
- Bowers, D.E. 1964. Natural history of two beach hoppers of the genus <u>Orchestoidea</u> (Crustacea: Amphipoda) with reference to their complemental distribution. Ecology <u>45</u>:677-696.
- Brooks, J.L. and S. Dodson. 1965. Predation, body size and composition of the plankton. Science 150:28-35.
- Brownell, P. and R.D. Farley. 1979. Prey-localizing behaviour of the nocturnal desert scorpion, <u>Paruroctonus mesaensis</u>: orientation to substrate vibrations. Anim. Behav. <u>27</u>: 185-193.
- Calow, P. 1974. Some observations on locomotory strategies and their metabolic effects in two species of freshwater gastropods <u>Ancylus fluviatilis</u> Mull. and <u>Planorbis</u> contortus Linn. Oecologia 16:149-161.

- Caraco, T. 1980. On foraging time allocation in a stochastic environment. Ecology <u>61</u>:119-128.
- Caraco, T., S. Martindale, and T.S. Whittam. 1980. An empirical demonstration of risk-sensitive foraging preferences. Anim. Behav. <u>28</u>:820-830.
- Charnov, E.L. 1976a. Optimal foraging: Attack strategy of a mantid. Am. Nat. <u>110</u>:141-151.
- Charnov, E.L. 1976b. Optimal foraging, the marginal value theorem. Theor. Pop. Biol. <u>9</u>:129-136.
- Charnov, E.L., G.H. Orians and K. Hyatt. 1976. Ecological implications of resource depression. Am. Nat. 110:247-259.
- Chesson, J. 1978. Measuring preference in selective predation. Ecology <u>59</u>:211-215.
- Connell, J.H. 1975. Some mechanisms producing structure in natural communities. In M.L. Cody and J.M. Diamond (eds.) Ecology and evolution of communities, pp.460-490. Belknap Press, Cambridge, Mass.
- Cook, R.M. and B.J. Cockrell. 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. J. Anim. Ecol. 47:529-547.
- Cowie, R.J. 1977. Optimal foraging in Great Tits (<u>Parus major</u>). Nature 268:137-139.
- Craig, P.C. 1970. The behavior and distribution of the intertidal sand beetle, <u>Thinopinus pictus</u> (Coleoptera: Staphylinidae). Ecology <u>51</u>:1012-1017.
- Craig, P.C. 1971. An analysis of the concept of lunar orientation in <u>Orchestoidea</u> <u>corniculata</u>. Anim. Behav. <u>19</u>: 368-374.

- Craig, P.C. 1973a. Orientation of the sand-beach amphipod, Orchestoidea corniculata. Anim. Behav. <u>21</u>:699-706.
- Craig, P.C. 1973b. Behaviour and distribution of the sand-beach amphipod Orchestoidea corniculata. Marine Biology 23: 101-109.
- Crowley, P.H. 1979. Behavior of zygopteran nymphs in a simulated weed bed. Odonatologica 8:91-101.
- Davidson, D.W. 1978. Experimental tests of the optimal diet in two social insects. Behav. Ecol. Sociobiol. <u>4</u>:35-41.
- Draper, N. and H. Smith. 1966. Applied regression analysis. John Wiley and Sons, Inc., New York
- Eggers, D.M. 1977. The nature of prey selection by planktivorous fish. Ecology 58:46-60.
- Elner, R.W. and R.N. Hughes. 1978. Energy maximization in the diet of the shore crab, <u>Carcinus maenas</u>. J. Anim. Ecol. <u>47</u>:103-116.
- Enders, F. 1975. The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae, and Salticidae). Am. Nat. <u>109</u>: 737-763.
- Ernsting, G. 1977. Effects of food deprivation and type of prey on predation by <u>Notiophilus biguttatus</u> F. (Carabidae) on springtails (Collembola). Oecologia <u>31</u>:13-20.
- Evans, H.F. 1976. The role of predator-prey size in determining the efficiency of capture of <u>Anthocoris nemorum</u> and the escape reactions of its prey, <u>Acyrthosiphon pisum</u>. Ecol. Entomol. 1:85-90.
- Everson, P. 1980. The relative activity and functional response of <u>Phytoseiulus</u> <u>persimilis</u> (Acarina: Phytoseiidae) and <u>Tetranychus urticae</u> (Acarina: Tetranychidae): The effect of temperature. Can. Entomol. <u>112</u>:<u>17-24</u>:.

- Gardner, M.B. 1981. Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. Ecology <u>62</u>: 571-578.
- Givens, R.P. 1978. Dimorphic feeding strategies of a salticid spider (Phidippus audax). Ecology 59:309-321.
- Goss-Custard, J.D. 1977. Optimal foraging and the size selection of worms by redshank (<u>Tringa totanus</u>). Anim. Behav. <u>25</u>: 10-29.
- Greenwood, J.J.D. and R.A. Elton. 1979. Analyzing experiments on frequency-dependent selection by predators. J. Anim. Ecol. <u>48</u>:721-737.
- Griffiths, D. 1980. The feeding biology of ant-lion larvae: prey capture, handling and utilization. J. Anim. Ecol. <u>49</u>: 99-125.
- Griffiths, D. 1981. Sub-optimal foraging in the ant-lion Macroleon guinguemaculatus. J. Anim. Ecol. <u>50</u>:697-702.
- Grum, L. 1971. Spatial differentiation of the <u>Carabus</u> L. (Carabidae, Coleoptera) mobility. Ek. Pol. <u>19</u>:1-34.
- Hanski, I. 1980. Movement patterns in dung beetles and in the dung fly. Anim. Behav. <u>28</u>:953-964.
- Hassell, M.P., Southwood, T.R.E. 1978. Foraging strategies of insects. Annu. Rev. Ecol. Syst. <u>9</u>:75-98.
- Hayes, W.B. 1970. The accuracy of pitall trapping for the sand-beach isopods Tylos punctatus. Ecology <u>51</u>:514-516.
- Haynes, D.L., and P. Sisojevic 1966. Predatory behavior of <u>Philodromus</u> rufus Walckenaer (Araneae:Thomisidae). Can. Entomol. <u>98</u>:113-133.
- Heatwole, H., and A. Heatwole 1968. Motivational aspects of feeding behavior in toads. Copeia <u>4</u>:692-698.

- Heinrich, B. 1976. The foraging specializations of individual bumblebees. Ecol. Monogr. <u>46</u>:105-128.
- Heller, R. 1980. On optimal diet in a patchy environment. Theor. Pop. Biol. 17:201-214.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. <u>91</u>:385-398.
- Holling, C.S. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. <u>48</u>: 1-86.
- Huey, R.B. and E.R. Pianka. 1981. Ecological consequences of foraging mode. Ecology <u>62</u>:991-999.
- Hughes, R.N. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. Am. Nat. <u>113</u>:209-221.
- Inouye, R.S., G.S. Byers and J.H. Brown. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. Ecology <u>61</u>: 1344-1351.
- Ivlev, V.S. 1961. Experimental feeding of fishes. Yale University Press, New Haven.
- Jaeger, R.G. and D.E. Barnard. 1981. Foraging tactics of a terristial salamander: Choice of diet in structurally simple environments. Am. Nat. 117:639-664.
- Jaeger, R.G., K.C.B. Nishikawa, and D.E. Barnard. 1981. Foraging tactics of a terrestial salamander: Effect of a competitor on choice of diet. Am. Nat. in press.
- Johnson, D.M., B.G. Akre, and P.H. Crowley. 1975. Modelling arthropod predation: wasteful killing by damselfly naids. Ecology 56:1081-1093.

Kacelnik, A., A.I. Houston, and J.R. Krebs. 1981. Optimal foraging and territorial defence in the great tit (<u>Parus</u> <u>major</u>). Behav. Ecol. Sociobiol. <u>8</u>:35-40.

ŧ,

- Kislalioglu, M., and R.N. Gibson. 1976. Prey 'handling time' and its importance in food selection by the 15-spined stickleback, <u>Spinachia</u> <u>spinachia</u> (L.). J. Exp. Mar. Biol. Ecol. 25:151-158.
- Krebs, J.R., A. Kacelnik, and P. Taylor. 1978. Test of optimal sampling by foraging great tits. Nature 275:27-31.
- Krebs, J.R. 1978. Optimal foraging decision rules for predators. Behavioral ecology: an evolutionary approach (Ed. by J.R. Krebs and N.B. Davies), pp. 23-63. Sinauer, Sunderland, Mass.
- Maynard Smith, J. 1978. Optimization theory in evolution. Annu. Rev. Ecol. Syst. 9:31-56.
- McCauley, D.E. 1982. The behavioural components of sexual selection in the milkweed beetle <u>Tetraopes</u> tetraophthalmus. Anim. Behav. 30:23-28.

McCleery, R.H. 1977. On satiation curves. Am. Nat. 25:1005-1015.

- Milinski, M., and R. Heller 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (<u>Gasterosteus</u> <u>aculeatus</u> L.). Nature <u>275</u>:642-644.
- Morse, D.H., and R.S. Fritz. 1982. Experimental and observational studies of patch choice at different scales by the crab spider Misumena vatia. Ecology 63:172-182.
- Murdoch, W.W. 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. Ecology 39:335-354.
- Murdoch, W.W. and A. Oaten. 1975. Predation and population stability. Adv. Ecol. Res. <u>9</u>:1-131.

- Murtaugh, P. 1981. Size-selective predation on <u>Daphnia</u> by <u>Neomysis mercedis</u>. Ecology <u>62</u>:894-900.
- Ollason, J.G. 1980. Learning to forage optimally? Theor. Pop. Biol. <u>18</u>:44-56.
- Paloheimo, J.E. 1979. Indices of food preference by a predator. J. Fish. Res. Board Can. 36:470-473.
- Parker, G.A 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. <u>45</u>:525-567.
- Parker, G.A. and R.A. Stuart. 1976. Animal behavior as a strategy optimizer: Evolution of resource assessment strategies and optimal emigration thresholds Am. Nat. <u>110</u>: 1055-1076.
- Pastorok, R.A. 1981. Prey vulnerability and size selection by Chaoborus larvae. Ecology <u>62</u>:1311-1324.
- Polis, G.A. 1980. Seasonal patterns and age-specific variation in the surface activity of a population of desert scorpions in relation to environmental factors. J. Anim. Ecol. <u>49</u>:1-18.
- Pulliam, H.R. 1974. On the theory of optimal diets. Am. Nat. 108:59-74.
- Pulliam, H.R. 1975. Diet optimization with nutrient constraints. Am. Nat. <u>109</u>:765-768.
- Pyke, G.H. 1978. Optimal foraging: Movement patterns of bumblebees between inflorescences. Theor. Pop. Biol. <u>13</u>: 72-98.
- Pyke, G.H., H.R. Pulliam, and E.L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. Quart. Rev. Biol. 52:137-154.

- Real, L.A. 1981. Uncertainty and pollinator-plant interactions: the foraging behavior of bees and wasps on artificial flowers. Ecology <u>62</u>:20-26.
- Richards, L.J. and J.H. Myers. 1980. Maternal influences on size and emergence time of the cinnabar moth. Can. J. Zool. <u>58</u>: 1452-1457.
- Rogers, D. 1972. Random search and insect population models. J. Anim. Ecol. 41:369-383.
- Schlager, G. 1960. Sperm precedence in the fertilization of eggs in <u>Tribolium</u> <u>castaneum</u>. Ann. Entomol. Soc. Amer. <u>53</u>: 557-560.
- Schoener, T.W. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369-404.
- Schulter, D. 1981. Does the theory of optimal diets apply in complex environments. Am. Nat. <u>118</u>:139-147.
- Selander, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor <u>63</u>:29-86.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., New York
- Smith, R.L. 1979. Repeated copulation and sperm precedence: paternity assurance for a male-brooding water bug. Science 205:1029-1031.
- Thompson, D.J. 1978a. Towards a realistic predator-prey model: the effect of temperature on the functional response and life history of the damselfly, <u>Ischnura</u> <u>elegans</u>. J. Anim. Ecol. <u>47</u>:757-767.
- Thompson, D.J. 1978b. Prey size selection by larvae of the damselfly, <u>Ischnura elegans</u> (Odonata). J. Anim. Ecol. <u>47</u>: 769-785.

- Toft, C.A. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. Oecologia <u>45</u>: 131-141.
- Turnbull, A.L. 1964. The search for prey by a web-building spider <u>Achaearanea</u> <u>tepidariorum</u> (C.L. Koch) (Araneae, Theridiidae). Can. Entomol. <u>96</u>:568-579.
- Waddington, K.D., A. Tracy and B. Heinrich. 1981. Floral preferences of bumblebees (<u>Bombus</u> <u>edwardsii</u>) in relation to intermittent versus continuous rewards. Anim. Behav. 29:779-784.
- Westoby, M. 1978. What are the biological bases of varied diets? Am. Nat. 108:290-304.
- Wiens, J.A. 1976. Population responses to patchy environmnets. Annu. Rev. Ecol. Syst. <u>7</u>:81-120.
- Zach, R. and J.B. Falls. 1976. Ovenbird (Aves: Parulidae) hunting behavior in a patchy environment: an experimental study. Can. J. Zool. <u>54</u>:1863-1879.
- Zach, R. 1978. Selection and dropping of whelks by northwestern crows. Behavior 67:134-148.

APPENDIX A

Expected handling time for the generalist can be expressed as

$$E(H) = \sum_{i=0}^{n} [iP+W]f(a)f(b) + Xf(b)$$

where
$$P = h(b)-e(b)h(a)/e(a)$$

$$W = Dh(a)/e(a)$$
 and $X = Dh(b)/e(b)$

The term in square brackets is the time to feed on i type B prey, and then to complete feeding on a type A prey. This term is multiplied by the probability that such a sequence of events will occur. The second term gives the time to reach satiation for feeding on type B prey only, times the probability that no type A prey are encountered.

The mean and variance can be derived from the moment generating function

$$M_{H}(t) = f(a) \sum_{i=0}^{n} f(b) + e f(b)$$

$$= \frac{Wt}{f(a)[1-e} (n+1)Pt + n+1 Pt -1]$$

$$= t e f(a)[1-e f(b)][1-e f(b)]$$

$$= \frac{Xt}{f(b)}$$

Then

$$E(H) = M'(0)$$

$$G = H$$

$$= P[nf(b) - (n+1)f(b) + 1]f(b)/f(a)$$

$$+ W[1-f(b)] + Xf(b)$$

and

Ś

$$V(H) = M''(0) - [E(H)]^{2}$$

$$G = H = G$$

$$= [X-W]^{2} [1-f(b)]f(b)$$

$$- 2P[X-W][nf(b)] - (n+1)f(b)] + 1]f(b) / f(a)$$

$$- 2P[X-W][nf(b)] + 2n]f(b)$$

$$+ P[n(1+f(b)] + 2n]f(b)$$

$$+ P[2nf(b)] - (2n+1)f(b)] + f(b)$$

$$- f(b)^{n} + 1]f(b) / f(a)^{2}$$

.

APPENDIX B

The moment generating function of search time for the generalist is given by

$$M(q) = \sum_{\substack{f(a)f(b) \\ i=0}}^{n} \int_{e}^{i} \int_{e}^{\infty} qt - Rt \quad i+1 \quad i \quad -1} f(a)f(b) \int_{e}^{\infty} R \quad t \quad [i!] \quad dt$$

$$+ f(b) \int_{0}^{\infty} qt - Rt \quad n+1 \quad n \quad -1 \\ + f(b) \int_{0}^{\infty} e \quad R \quad t \quad [n!] \quad dt$$

The integration term describes the moment generating function of the gamma distribution, the distribution of waiting times to obtain exactly i+1 prey items. It is multiplied by the probability that exactly i+1 prey items are eaten, and summed over all values of i. After performing the integrations and summations this becomes

$$M_{S}(q) = \frac{Rf(a)}{Rf(a)-q} \{1-[Rf(b)/(R-q)]^{n+1}\} + f(b)^{n+1} \{R/(R-q)\}$$

The expected value of search time is given by

$$E(S) = M'(0)$$

$$G = S$$

$$= [1-f(b)^{n+1}][Rf(a)]^{-1}$$

ith variance

$$V(S) = M''(0) - [E(S)]^{2}$$

$$G = S = G$$

W

$$= [1-2(n+1)f(b) + 2(n+1)f(b) - f(b)][Rf(a)]$$