THE HUNTING TACTICS OF AN UNSPECIALIZED PREDATOR, PARDOSA VANCOUVERI (ARANEAE; LYCOSIDAE), WITH REFERENCE TO SPATIAL HETEROGENEITY AND THE COMPONENTS OF THE FUNCTIONAL RESPONSE

by

JOHN MICHAEL HARDMAN

B.Sc. Hons., Dalhousie University, 1968

D.I.C., M.Sc. (distinction), Imperial College, 1969

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
in the Department
of
Biological Sciences

SIMON FRASER UNIVERSITY

NOVEMBER, 1972

APPROVAL

Name: John Michael Hardman

Degree: Doctor of Philosophy

Title of Thesis: The Hunting Tactics of an Unspecialized Predator *Pardosa vancouveri* (Araneae;Lycosidae) with Reference to Spatial Heterogeneity and the Components of the Functional Response

Examining Committee:

G. H. Geen, Chairman
Examining Committee

B. P. Beirne
Examining Committee

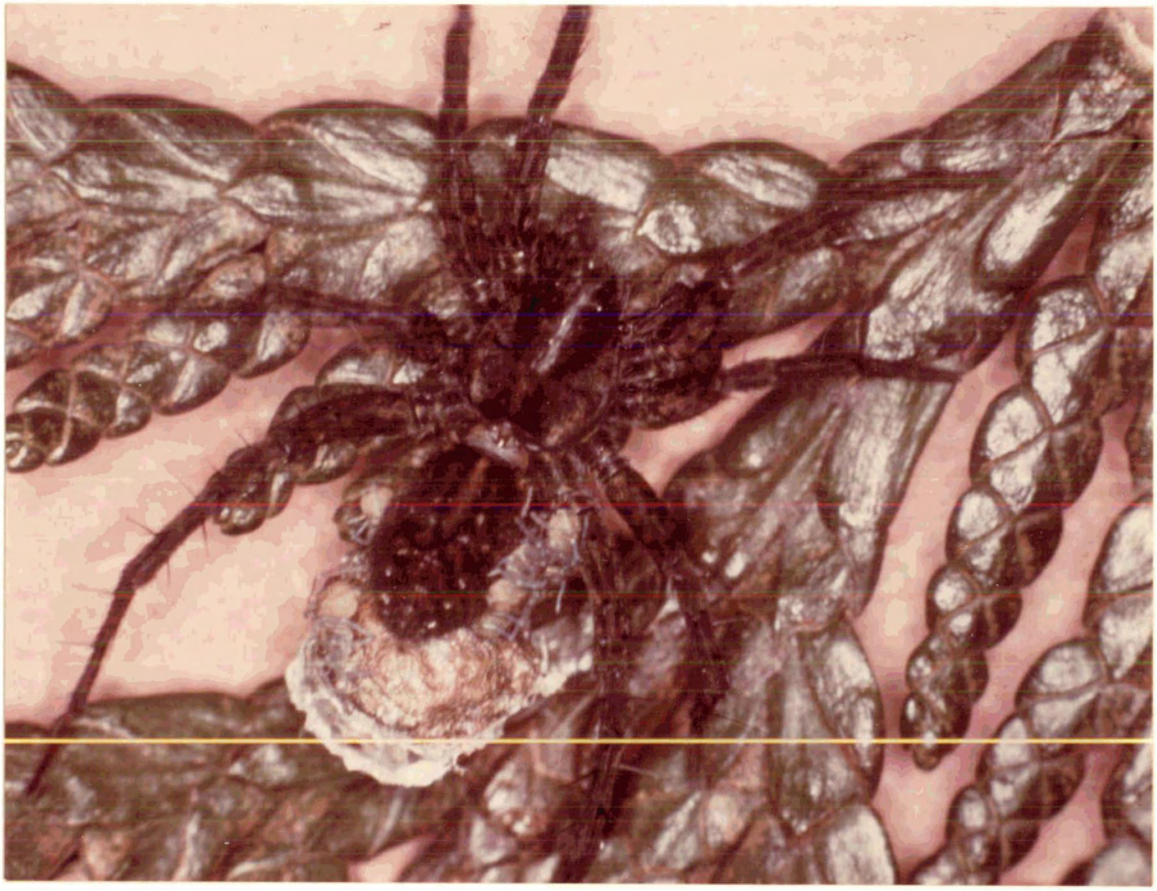
A. L. Turnbull
Senior Supervisor

J. P. M. Mackauer
Examining Committee

C. S. Holling,
External Examiner,
Director,
Institute of Animal
Resource Ecology,
University of British
Columbia,
Vancouver, British Columbia.

R. M. F. S. Sadleir
Examining Committee

Date Approved: November 20, 1972



I E

Title of Thesis/Dissertation:

The hunting tactics of an unspecialized predator, Pardosa vancouveri (Araneae; Lycosidae) with reference to spatial heterogeneity and the components of the functional response

Author:

(signature)

John Michael HARDMAN

(name)

9 April 1973

(date)

ABSTRACT

The polyphagous arthropod predator, *Pardosa vancouveri* (Lycosidae: Araneae) exhibits a well defined functional response to changes in prey density that generally conforms to Holling's (1966) model of the functional response of invertebrate predators. However several anomalies were apparent. In all tests some spiders deprived of food refused to attack prey when prey were presented; a positive linear relationship between the proportion of spiders feeding and time deprived of food was established and used to establish hunger curves. In this spider hunger seems to exhibit two phases: spiders deprived of food for periods up to 10 days conform to Holling's negatively accelerating hunger curve; after 10 days of food deprivation, however, hunger seems to rise steeply once again. The weight of food extracted per prey captured declined as hunger rose. At high hunger levels spiders tended to capture and feed upon several prey at once; this contributed to inefficient extraction of food from each prey captured.

When the attack parameters for the functional response of the spider were placed in the Holling model, the model did not accurately predict the functional response of the spider to prey density. The discrepancy between observed data and the predictions of the model were attributed to deficiencies of the hunger curve to describe the hunger characteristics of this predator.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

I am grateful to Dr. B. P. Beirne, Dr. J. P. M. Mackauer, Dr. R. M. F. S. Sadleir and Mr. R. G. Holmberg of Simon Fraser University and Dr. C. S. Holling of the University of British Columbia for their critical reading and revision of the manuscript.

Financial support was suppled to Mr. J. M. Hardman by the National Research Council of Canada.

INTRODUCTION

One of the main components of any predatory interaction is the functional response to prey density; as prey density increases there is a corresponding change in the number of prey killed by each predator. With most invertebrate predators this relationship is described by a negatively-accelerated rise to a plateau, Holling's (1959a) type 2 functional response.

Using mantids as predators and houseflies as prey, Holling (1966) undertook a comprehensive analysis of the type 2 ("invertebrate") functional response. He first studied mantid hunger _per se_, and the interaction of hunger with rate of successful search, handling time and time available for predation. Each component was divided into subcomponents, hypotheses being devised to explain the action of each subcomponent. Alternative hypotheses were tested experimentally; false ones were rejected. Ultimately Holling obtained a series of equations and attack parameters which faithfully described various parts of the mantid attack system. These components were described in FORTRAN and then synthesised into a computer mode of functional response.

The model centres around the individual attack cycle. Given the attack parameters of the predator, an initial level of hunger for the predator and an initial prey density, the model can generate the durations of successive attack cycles until the total time of the experiment is used up. The number of attack cycles corresponds to the number of prey killed.

The aim of the present study was: (1) to investigate the components of the functional response in a wolf spider, Pardosa vancouveri Emerton, a predator whose hunting tactics differ markedly from those of Holling's mantid, Hierodula crassa; and (2) to test the predictive powers of the Holling model by comparing the predictions of the model with the outcome of an actual functional response experiment.

Pardosa vancouveri, like other wolf spiders, actively chase prey or ambush them (Kirchner 1964, Edgar 1970a). They are polyphagous feeders capturing virtually any arthropod that they can catch and overpower (Bristowe 1958, Edgar 1970b).

They have good frontal and lateral vision (Homann 1930). Their tarsi are sensitive to certain chemicals (Hegdekar and Dondale 1960) and they can detect air-borne sounds (Harrison 1969, Rovner 1967) and vibrations carried by the substrate (Markl 1969). Papi and Tongiorgi (1963) have found that certain wolf spiders can orient themselves by polarized light.

Although learning (sensu Holling 1965) did not appear to play a role in predation experiments conducted with this spider, it must be noted that spiders can be influenced by experience (LeGuelte 1969).

Silk is not used in the capture of prey by lycosids (Richter 1970). However the deposition of drag lines may have had some influence on the course of predation experiments. General observations have shown that the spiders travel most frequently on pathways of silk laid down earlier. This tendency may have influenced spatial relations between spiders and flies.

MATERIALS AND METHODS

Standard Predators

Standard predators, subadult females (spiders from the penultimate stage) collected between the months of September and March 1971 - 1972 were used in all experiments. Spiders were collected from cleared areas colonized by pioneering species of herbaceous ground-layer vegetation on the southern slopes of Burnaby Mountain, British Columbia.

After capture some spiders were placed in wooden cages (described below) in the lab and fed a surplus of flies until their feeding trials. Others were placed in 8-dram cotton stoppered glass vials containing several fruit flies and a piece of wet dental floss. The spiders and flies were refrigerated at 2°C until needed for experiments.

Preliminary trials indicated the great influence that moulting exerted on the feeding levels of P. vancouveri. Many of the subadult spiders underwent their final moult before the experiments were completed. This caused serious difficulties with replication and necessitated the collection of almost double the number of spiders otherwise needed. Moulting also caused unavoidable irregularities in the pattern of replication.

Preliminary feeding trials conducted by Mr. R. G. Holberg indicated that feeding levels of spiders immediately following the penultimate moult differed from those in the midstadial period and these in turn differed from feeding levels for the 3 days preceding the final moult (Holmberg, pers. comm.).

Holmberg's data were based on daily records of the number of flies killed by 8 subadult spiders from the day following their moult into the subadult stage to the day when they moulted into adulthood. Spiders were kept in plastic cages (described later) and provided with 10 adult female D. melanogaster that were replenished daily.

Feeding was highest for the 3 days following the penultimate moult ($\overline{X} = 5.167$, $n = 24$, $SE = .354$), lower for the midstadial period ($\overline{X} = 2.981$, $n = 154$, $SE = .143$) and lowest for the 3 days preceding the final moult ($\overline{X} = .416$, $n = 24$, $SE = .133$). Post moult and midstadial levels were significantly different ($t = 5.722$, 174 d.f., $P < .01$). Midstadial spiders killed more flies per day than premoult spiders ($t = 13.11$, 174 d.f., $P < .01$).

Consequently data for this analysis was taken exclusively from midstadial spiders.

Data from spiders within three days or less of a moult were disregarded.

A further problem with replication was the difficulty in distinguishing subadults and antepenultimates collected during September and October. Stadia were estimated by measuring the width of the carapace. There was overlap in the carapace widths of the two stages of spiders so that some antepenultimates were included with subadult spiders. Data from antepenultimate spiders, i.e., those with incomplete genitalia following a moult, were discarded. The problem with antepenultimates was acute during early autumn, while the problem with spiders moulting into adulthood before completion of the experiments was acute during late February and March.

Preliminary trials indicated that subsequent to experimental treatments spiders had lower appetites than those spiders used for the first time. Thus each predator was used but once in the experiments.

Standard Prey

Adult male and female vestigial-winged (Vg) *Drosophila melanogaster* Meign. were used to feed spiders to satiety prior to a trial. During most trials only male prey were used: F_1 (Vg) adults raised in standard cultures. A standard culture was started as follows: to 2 500 ml autoclaved Erlenmeyer flask were added 100 ml of Instant Drosophila Medium (Barolina Biological Supply Co., Burlington, N.C.), 30 - 50 granules of Baker's yeast, and 75 - 80 ml of water. After the mix had set for 5 minutes, 10 female and 10 male flies were added. The flask was stoppered by a cotton plug covered with cheesecloth and incubated at room temperature (ca. 23°C). Standard flies were taken from 14 - 19 day-old cultures.

Female flies were used as prey in the functional response trials in wooden cages.

Laboratory Conditions

All experiments were carried out under laboratory conditions. Temperature was regulated by an air-conditioner and a thermostatically controlled gas furnace. The mean temperature, based on 5 readings daily for three months of experimentation (Oct. '71, Feb. - Mar. '72) was 23.2 ± 1.2° (SD), with a range from 17.1 - 27.2°C. Ambient relative humidity ranged from 31% to 68%.

Illumination was from two sources, ceiling lights and suspended lights. Two 40 W fluorescent tubes covered by frosted plastic screen were fixed at the ceiling of the laboratory 150 cm above the work benches. Four 40 W naked fluorescent tubes were suspended 70 cm above the bench.

Light was provided 16 hr daily (0800 - 2400 hours P.S.T.). The windows of the laboratory were covered with aluminum foil to exclude natural light.

The behaviour of predators and prey exposed to each other was recorded on videotape (see pg. 12). These experiments were conducted in a room in the Audiovisual Centre. Ambient temperature was thermostatically controlled and was in the range of approximately 19 - 22°C. Lighting is discussed in the section outlining the videotaped trials.

Cages and Arenas

Wooden cages (7.6 x 7.6 x 5.5 cm) with a sliding front panel of clear plastic and a back of plastic mesh served as the arenas for feeding periodicity and functional response experiments. Spiders were also kept in wooden cages prior to experiments and during conditioning that preceded experiments. During times of conditioning moisture was supplied by 4-dram vials filled with water and stoppered with cotton wool. During feeding trials the vials were removed and water was squirted, at least once daily, into the cages through the plastic mesh.

Eight-dram vials containing moistened dental floss and stoppered by cotton served to house spiders prior to trials. During phases of feeding when numerous flies were placed in the vials, the vials were cleaned out every 2 - 3 days. Vials also served for storage of spiders being deprived of food prior to a trial.

Circular arenas were used for the majority of experiments involving components of the functional response. The arena consisted of a plexiglass hoop (11.4 cm ID x 3.7 cm tall) laid over a paper floor divided into quadrants and subdivided into 5 x 5 mm squares. Fluon (Imperial Chemical Industries Ltd., Plastics Division, Welwyn Garden City, Herts., England), an aqueous dispersion of polytetrafluoroethylene, was painted on the inner surface of the plexiglass hoop with a camel hair brush to provide a slippery surface which the spiders and flies could not scale (Ebeling and Wagner 1963, Radinovsky and Krantz 1962, Storch 1968).

Experiments with Feeding Periodicity

Two sets of trials were conducted to detect whether subadult *P. vancouveri* exhibit a diurnal feeding periodicity under laboratory conditions.

First, feeding was compared in light and darkness. Standard predators taken fresh from the field were divided at random into two sets. Ten spiders were placed in cages and exposed to prey for a 24 hr period comprising 16 hr illumination and 8 hr of darkness. This did not correspond to the photoperiod in the field at that time of year. Day length was about 12 hours outdoors; dawn was about 2 hours earlier outdoors than in the laboratory.

Eight other spiders were placed in cages kept in darkness for 24 hours. Inside the cupboard the intensity of light was estimated to be less than that of the laboratory during the hours of darkness. Both sets of spiders were supplied with 20 flies at the beginning of the test period. At the end of the 24 hours period the cages were removed from the cupboard and the living and chewed prey were counted.

In a second series of trials 16 subadult female spiders - which were raised in the laboratory since hatching from an egg-sac - were kept in cages with 20 flies in a regime of 16 hr L - 8 hr D. Every 2 hr from 0800 to 2400 hours flies were counted and losses replenished. A final count of flies consumed was made at 0800 hours on the second day.

Experiments Dealing with Predator Hunger

The general method used by Holling was followed to determine the attack parameters associated with hunger. One hundred and thirty standard predators were fed a surplus of flies for 2 days. The spiders were then deprived of food according to the pattern shown in Table 1. (Not all spiders fed after the various periods of deprivation. The numbers that did feed are recorded in Table 1.)

Experiments were conducted in circular arenas on a work bench in the laboratory, ceiling lights being the only overhead source of light. All trials were carried out in the early afternoon. Twenty standard prey and one standard predator were placed in each arena. Any

TABLE 1

The pattern of replication and the proportion of *P. vancouveri* feeding after varying periods of deprivation from food

Time deprived of food (days)	Number of spiders tested	Number of spiders feeding
0	10	0
1	14	2
2	12	1
3	20	7
4	16	7
5	14	7
7	11	10
10	14	10
16	12	12
21	7	7

prey killed were replaced as quickly as possible. The number of flies captured and the duration of feedings were recorded. Trials terminated when the predator failed to capture a fly for one hour at which point the spiders were considered to be satiated. At the end of the trial prey remains were collected and placed in 1/2 dram glass vials. The vials were placed in an oven at 60°C for at least 48 hours after which the dried flies were weighed to the nearest .001 mg. To compute the dry weight of food required to satiate each predator the sums of the weights of all the prey remains consumed by each spider were subtracted from the weight of an equivalent number of intact dried flies. The mean weight of dried intact flies was 0.255 mg per fly (n = 300).

However the spiders did not ingest the full contents of each fly; after each feeding a "food ball" of fly cuticle was discarded by the spider. The maximum weight ingested from a single fly was 0.221 mg.

The Interaction of Hunger With Other Components of the Functional Response

Prior to this series of experiments standard spiders were fed *ad libitum* for two days and then deprived of food for varying lengths of time.

Trials were conducted in ciruclar arenas in a small windowless room. Initially there were either 5 or 20 flies, and one spider per arena. (See Table 2 for the pattern of replication.) Trials were conducted in the late morning or early afternoon and each spider was tested for 3 minutes. Where there were 5 flies/arena flies were replaced when killed.

TABLE 2

Number of *P. vancouveri* tested (NT) and number feeding (NF) in the videotaped trials

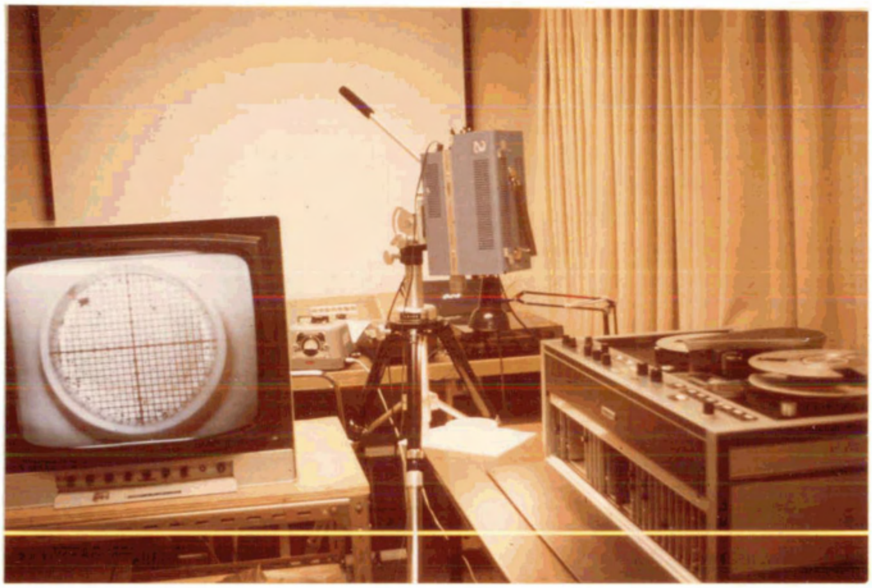
Time deprived of food (days)	Initial No. of Flies Per Arena 5 NT	5 NF	20 NT	20 NF
4	5	0	10	2
7	12	5	8	2
10	10	7	11	8
16	4	0	12	10

To eliminate the possibility of spider movements being influenced by silk or pheromone trials laid down by its predecessor in the arena, a clean paper arena floor was provided for each test.

A television camera (GBC Viewfinder) was mounted on a tripod about 80 cm above the work bench and directed vertically downward onto the arena. The camera was connected to a videotape recorder (Ampex VR 7800) and a T.V. monitor (Fig. 1). Light was provided from two sources: a 40 watt incandescent bulb in a gooseneck lamp connected to a variable voltage box and two 40 watt fluorescent bulbs screened by frosted plastic and suspended from the ceiling. The intensity of light in the arena as measured by a light meter was 6 foot candles.

During the feeding trials the predatory interaction was recorded on 1 inch videotape. Two features of the recorder facilitated analysis when the data were later displayed on the monitor. Firstly it was possible to play the tape backwards or forwards in slow motion, making possible the interpretation of very rapid events. Secondly a built-in timing device indicated the passage of time to the nearest second. Moreover as it was known that each scan takes 0.02 sec to cross the T.V. screen, during slow motion replay it was possible to accurately measure the duration of very rapid events. The monitor permitted accurate observation of events as they occurred. Quadrants and a grid drawn on the paper floor of the arena followed accurate measurement of distances.

Fig. 1. Apparatus used to record feeding trials on videotape including television camera on tripod, gooseneck lamp, arena, videotape recorder and TV monitor.



The Functional Response Experiment

A functional response experiment was carried out to test the predictive power of the Holling model. Forty-five predators were arranged in 5 sets of 9 spiders each. Spiders were placed individually in wooden cages. Prior to the experiment the spiders were fed *ad libitum* for 2 days, then deprived of food for 6 days. Just before the trial the water vials were removed from each cage. Five sets, consisting of 6, 4, 5, 6 and 6 spiders each were exposed to densities of 1, 3, 6, 10 or 20 flies per cage respectivelyq The trials commenced at 1400 hours and continued for 10 hours until midnight. Prey were replenished as soon as kills were noticed. Water was squirted through the plastic mesh of the cages.

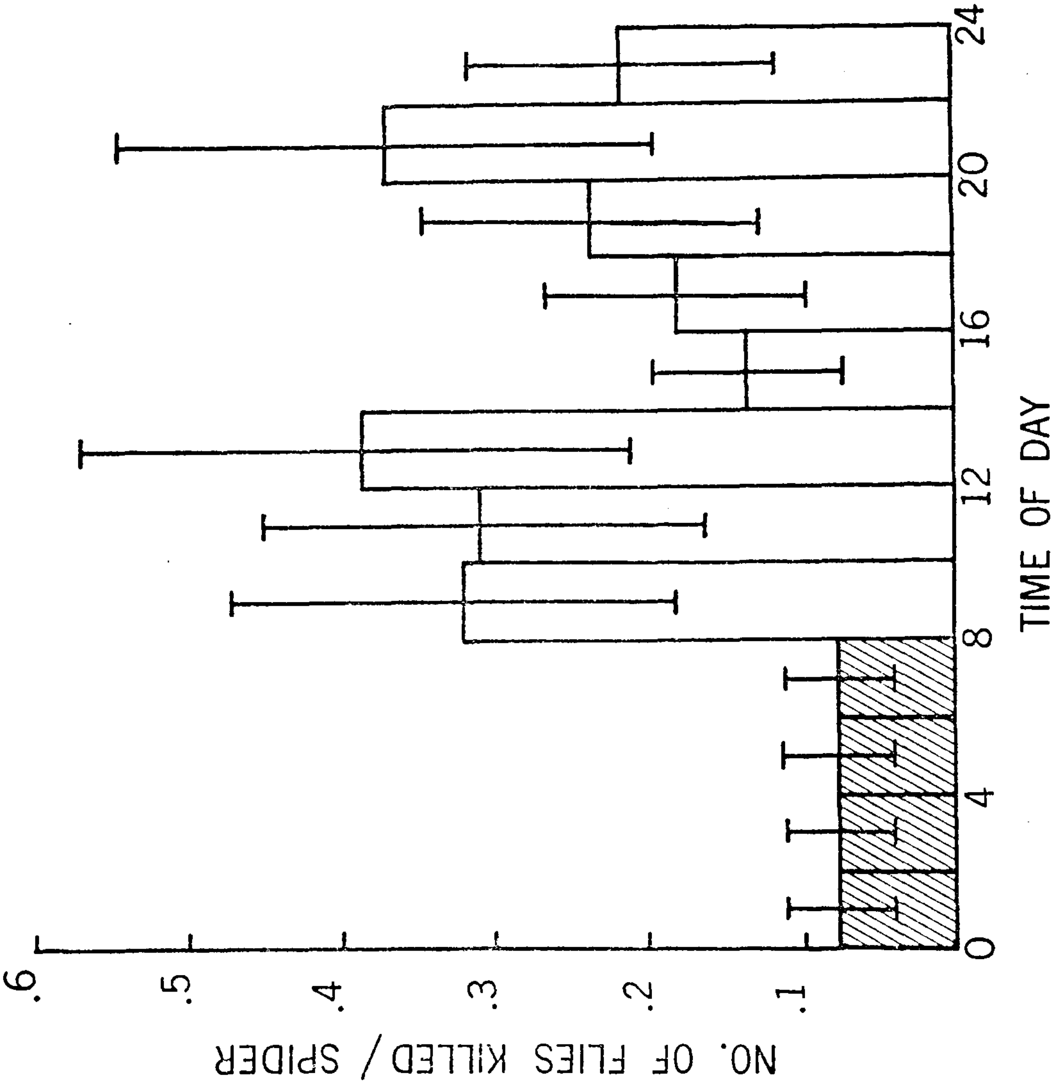
RESULTS

Feeding Periodicty

Mean feeding levels for *P. vancouveri* fresh-collected from the field did not differ significantly ($t = 2.006$ for 15 d. f., $P > .05$) whether spiders were kept in darkness 24 hr ($\overline{X} = 7.625 \pm .885$ SE flies) or exposed to an alternation of 16 hr L - 8 hr D ($\overline{X} = 10.11 \pm .754$ SE flies). Thus hungry, fresh-collected spiders could feed equally well in light or darkness.

The 16 laboratory-raised spiders exposed to a diurnal rhythm of 16 hr L - 8 hr D fed preferentially during daylight hours (Fig. 2). Peaks of feeding were in the late morning and early evening. While

Fig. 2. Dirunal feeding periodicity of laboratory-reared subadult female *P. vancouveri* (average of 16 replicates ± 95% confidence limits). Lined area represents period of darkness.


NO. OF FLIES KILLED / SPIDER
.6
.5
.4
.3
.2
.1
0
4
8
12
16
20
24
TIME OF DAY

extremely hungry spiders could feed in light or darkness, better-fed individuals kept for some time in the laboratory showed a preference for daytime feeding.

Hunger Experiments

Feeding trials were conducted in the early afternoon, when spiders were in the low feeding phase of their circadian rhythm (Fig. 2). Table 3 shows the average weight of food consumed (hunger) by each class of spiders after various periods of fasting. Hunger is defined as the dry weight of prey necessary to satiate the spider, satiation being the point at which the spider fails for at least one hour to kill the feed on prey.

Some of the spiders in these tests did not feed at all, especially those in groups that had fasted only a short time. There is a linear relationship (Fig. 3) between the proportion of spiders feeding (PF) and the average hunger (H) of those spiders which fed:

$$PF = 231\ H - 18.6\ (r = .819 \text{ with } 7 \text{ d. f. and } P < .01).$$

This relationship is shown in Fig. 3.

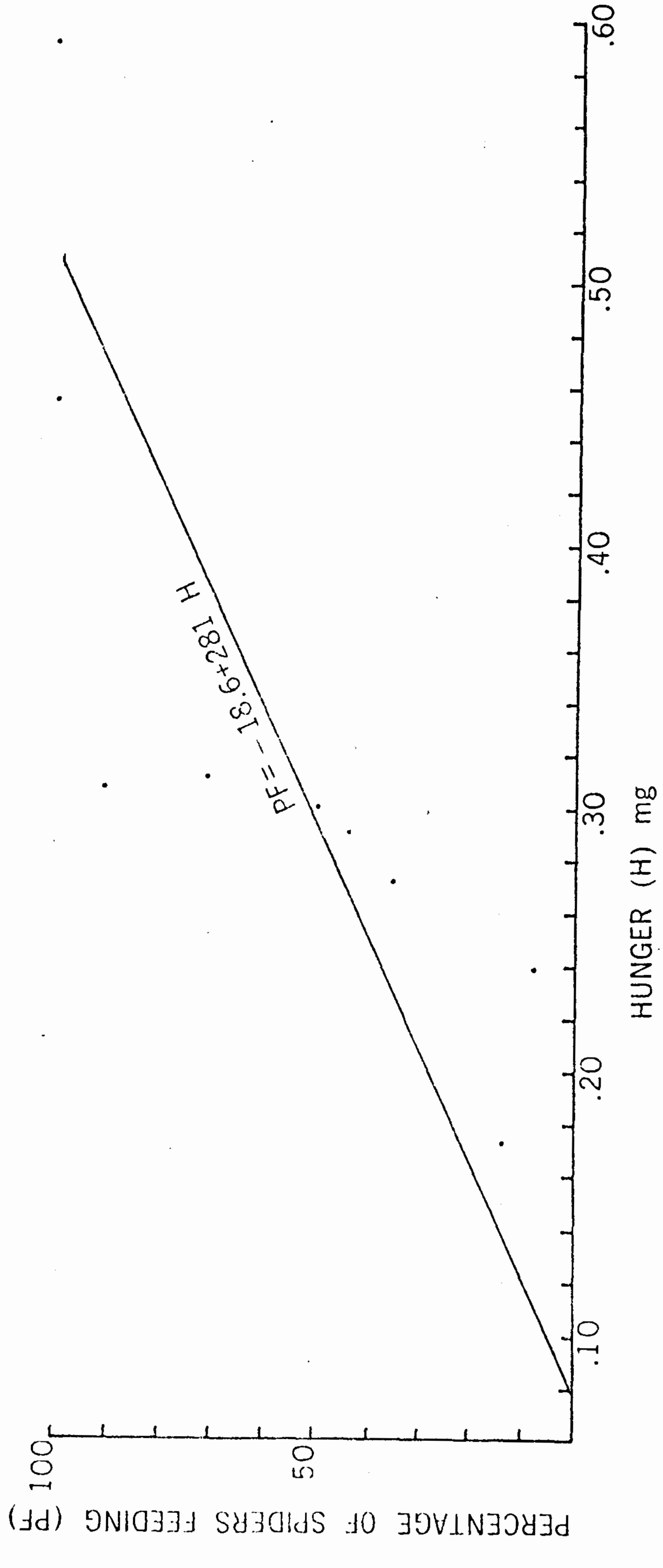
Fig. 4 shows the relationship between the hunger of those spiders which fed and their deprivation from food. For the purpose of simulating the functional response of *P. vancouveri* only data from feeders were considered. Another approach would have been to have included the attack threshold as a probability function, with a mean threshold and a range of values about the mean.

TABLE 3

Average weight of food consumed per spider (hunger) after various periods of fasting

Time deprived of food (days)	Average Hunger (mg)	SE	No. of Observations
1	.0236	.0206	14
2	.0155	.0155	12
3	.0860	.0354	20
4	.1580	.0495	16
5	.1414	.0602	14
7	.2263	.0422	11
10	.2401	.0717	14
16	.4572	.0330	12
21	.5941	.0504	7

Fig. 3. Relationship between the precentage of spiders feeding and the average hunger of those spiders. Points are averages of 1 - 12 replicates.


PF = − 18.6+281 H
PERCENTAGE OF SPIDERS FEEDING (PF)
100
50
.10
.20
.30
.40
.50
.60
HUNGER (H) mg

In his experiment with mantids Holling (1966) obtained a curvilinear relationship between hunger and time deprived of food. To describe the curve he devised a deductive equation with subcomponents including the rate of digestion (AD) and the maximum amount of food the stomach will hold (HK):

$$H = HK\ (1 - e^{-AD(TF)})$$

To determine the value of AD he transformed the hunger curve to the linear form $\ln \frac{HK}{HK-H} = AD(TF)$ and determined the slope of the line. The value of HK that maximized the correlation coefficient was selected by an iterative technique and assumed to be the correct value of the parameter.

For <u>P. vancouveri</u> AD and HK were determined by the same process, with the aid of a digital computer. Values of AD and HK giving the best fit to the data points were used as the parameters. Mean values of hunger were regressed against periods of deprivation of from 1 - 10 days. The correlation coefficient for the curve of best fit was .815 with 5 d.f. The curve of best fit failed to pass through the origin, necessitating the addition of a constant B into the equation to indicate this condition: linearly,

$$\ln \frac{HK}{HK-H} = AD(TF) - \ln B$$

The curvilinear form of the hunger equation becomes

$H = HK\ (1 - Be^{-AD(TF)})$ or more specifically:

$H = .311\ (1 - .264\ e^{-.027(TF)})$.

The curvilinear equation was used only for periods of deprivation up to 10 days. Beyond 10 daysof deprivation hunger appears to rise again (Fig. 4). Whether this apparent increase is due to inadequate experimental replication or represents a real phenomenon can only be resolved by further investigation.

Fig. 5 is a comparison of hunger levels predicted by the equation with observed data for periods of deprivation up to 10 days.

The total weight consumed by each spider (H) divided by the number of prey killed in the experiment (NA) yields the weight of food (WE) derived from each prey (Table 4). Fig. 6 shows a negative linear relation between hunger predicted from the hunger equation and the mean value of WE for each level of hunger: $WE = .28 - .56\ H$ ($r = -.824$, $P < .05$, 5 d. f.). The relationship holds for the period $TF = 1, 10$ days. Beyond 10 days changing hunger physiology altered the relationship between WE and H.

Two phenomena were associated with the decline in WE as H increased. Firstly, the percentage of spiders which captured several prey at once (PMC) increased with hunger in a linear fashion (Fig. 7): $PMC = 206\ H - 25.8$ ($r = 0.825$, $P < .01$, 7 d. f.).

Secondly the percentage of spiders which killed a fly and then quickly abandoned the prey (PQK) also was linearly related to hunger (Fig. 8): $PQK = 226\ H - 24.2$ ($r = 0.730$, $P < .05$, 7 d. f.).

Fig. 4. Effect of time of food deprivation on the hunger of *P. vancouveri* that fed on flies (averages ± SE; pattern of replication seen in Table 1).

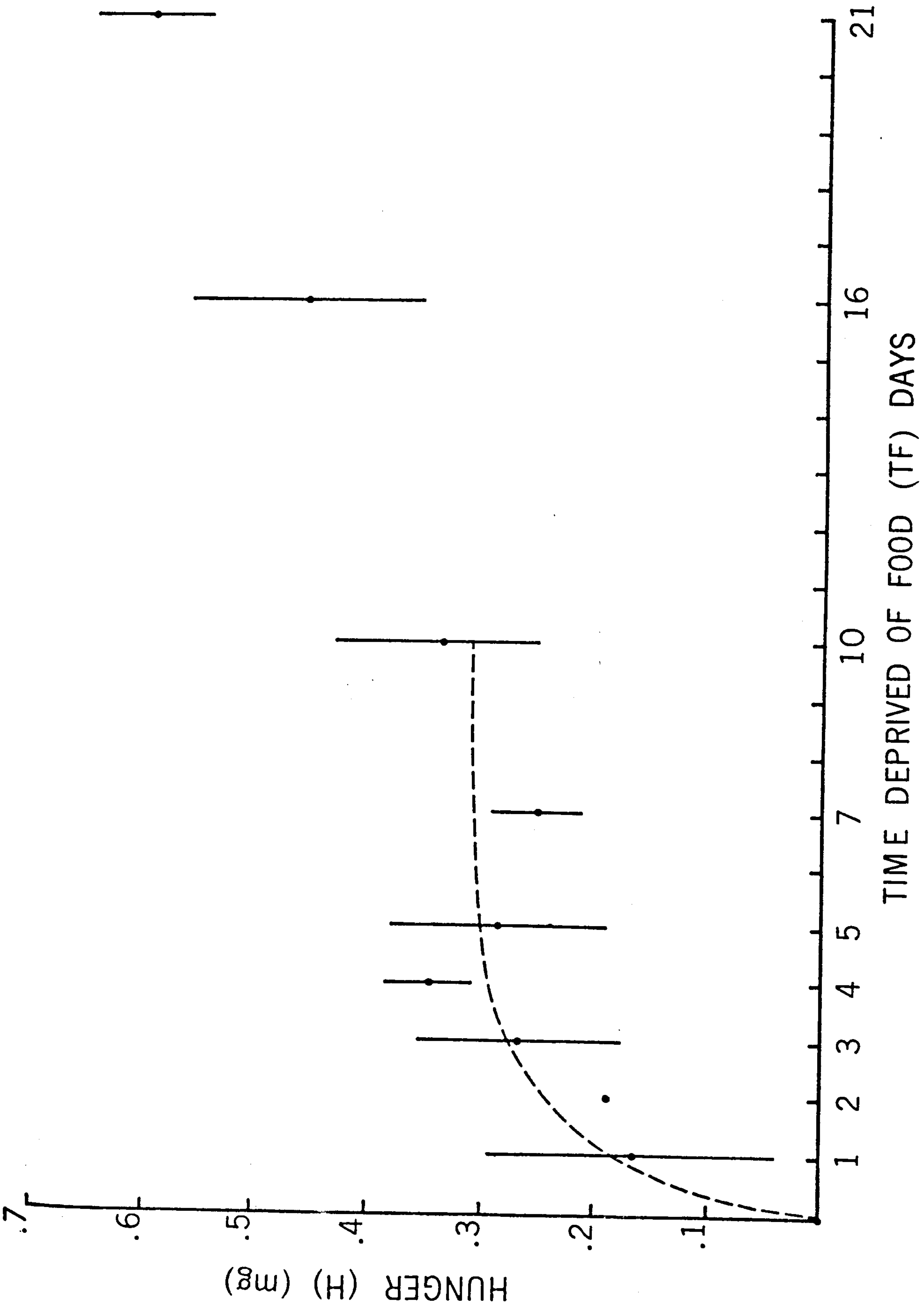

HUNGER (H) (mg)
.1
.2
.3
.4
.5
.6
.7
TIME DEPRIVED OF FOOD (TF) DAYS
1
2
3
4
5
7
10
16
21

Fig. 5. Comparison of observed hunger of *P. vancouveri* (averages ± 1 SE; pattern of replication shown in Table 1) and hunger predicted from the hunger equation. Solid line is curve of best fit. Dotted lines are best fit ± 1 SE.

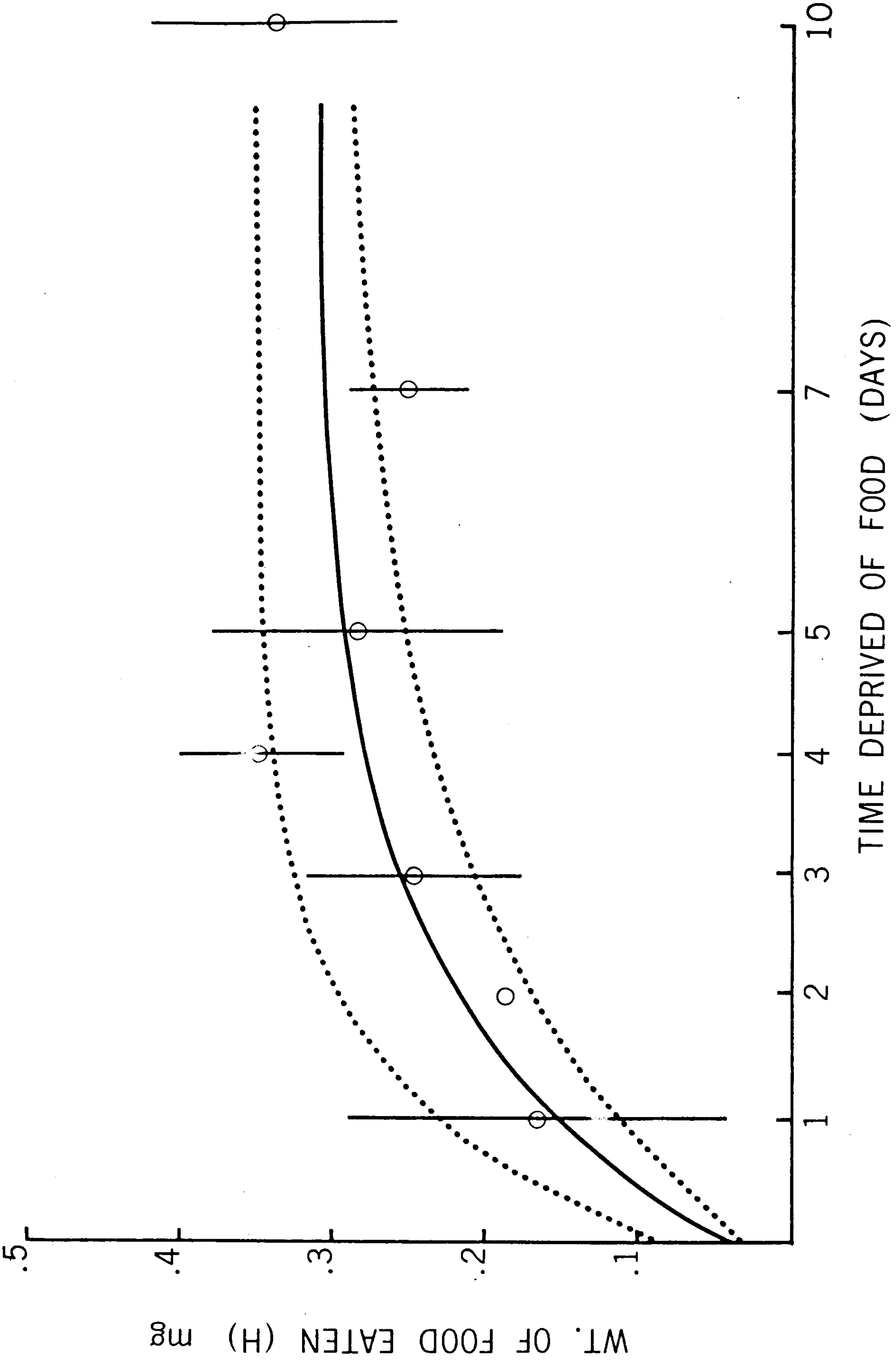

WT. OF FOOD EATEN (H) mg
.5
.4
.3
.2
.1
1
2
3
4
5
7
10
TIME DEPRIVED OF FOOD (DAYS)

TABLE 4

Relationship between mean wt ingested for each prey killed (WE) and the mean hunger (H) of standard *P. vancouveri*

Time deprived of food (days)	Hunger (H)[1] mg	WE (mg)		
		Mean	SE	n
1	.173	.165	.124	2
2	.239	.186	-	1
3	.273	.144	.031	7
4	.291	.121	.018	7
5	.301	.116	.016	7
7	.308	.0958	.027	10
10	.311	.110	.018	10
16	.457	.0925	.022	12
21	.594	.115	.017	7

[1] For periods of deprivation up to 10 days H is calculated from the hunger equation. The hunger equation could not be applied to deprivations of 16 and 21 days; hence for these points mean hunger is taken directly from the data.

Fig. 6. Relationship between the dry weight ingested for each prey killed (WE) and the initial hunger (H) of P. vancouveri (pattern of replication in Table 1). Data is taken only from feeders (see text).

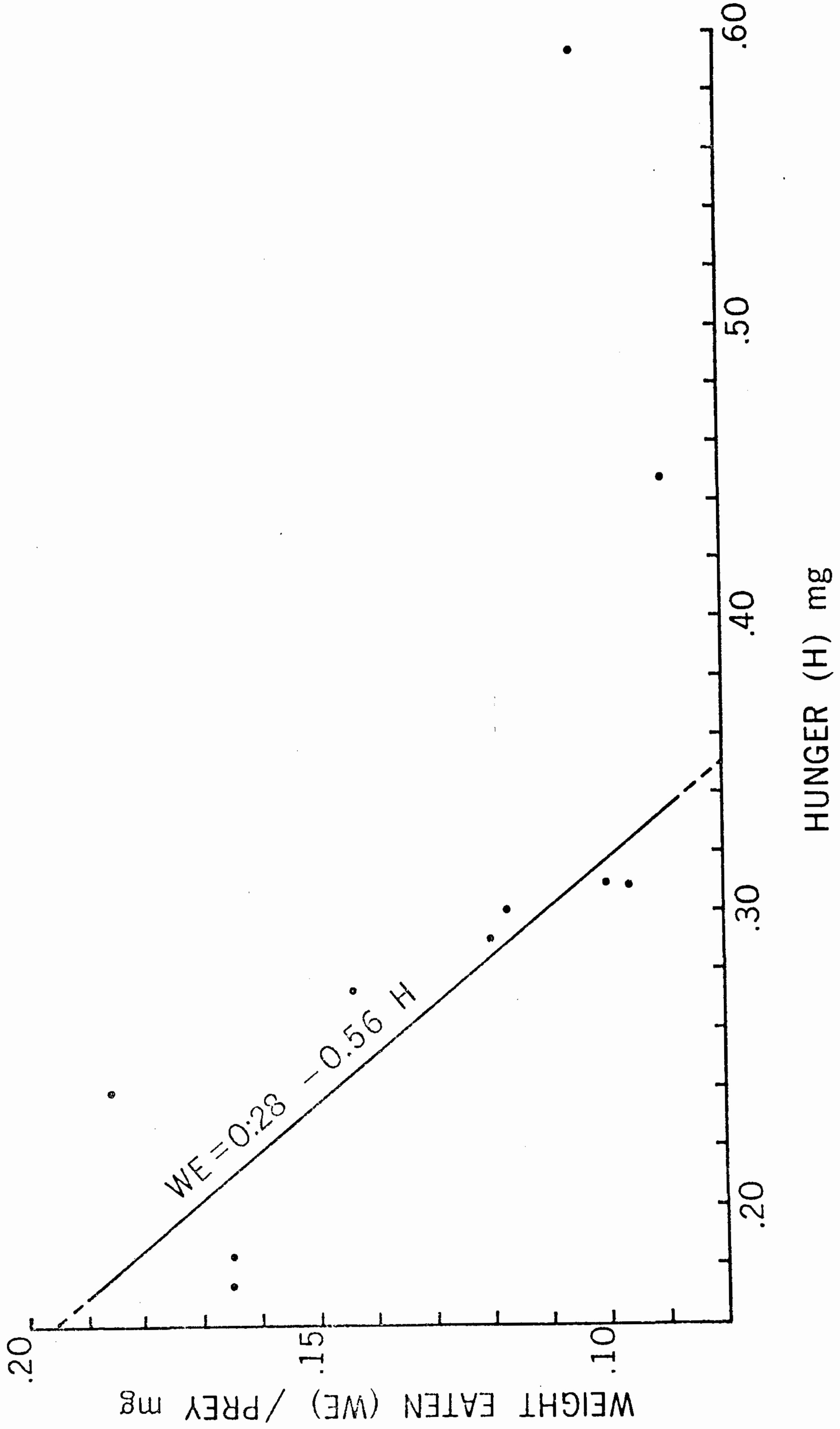

WEIGHT EATEN (WE) /PREY mg
.20
.15
.10
HUNGER (H) mg
.20
.30
.40
.50
.60
WE=0.28 −0.56 H

Fig. 7. Relationship between the percentage of P. vancouveri engaging in multiple prey captures (PMC) and the initial hunger (H) of the spiders. Pattern of replication is shown in Table 1. Data is taken from feeders only (see text).

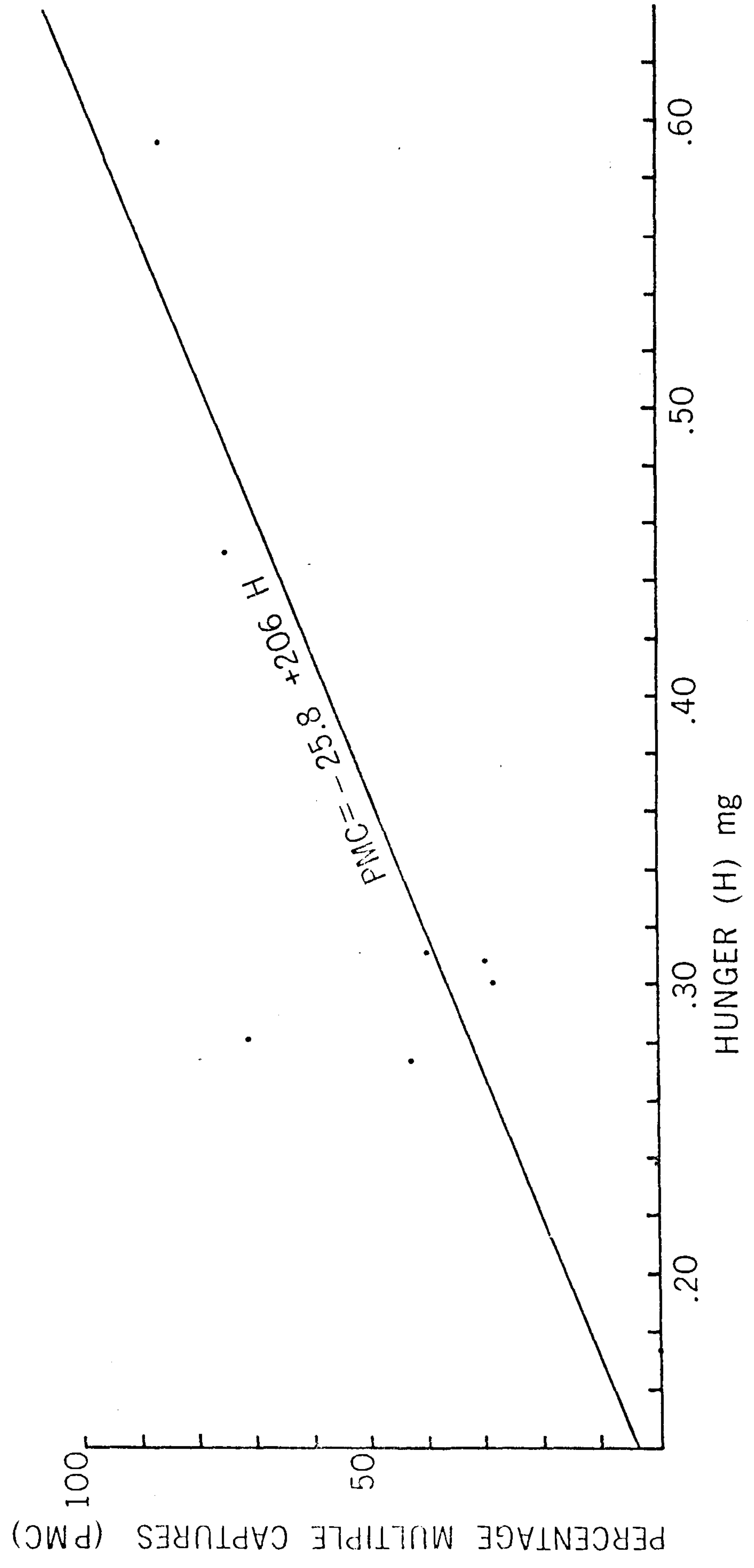
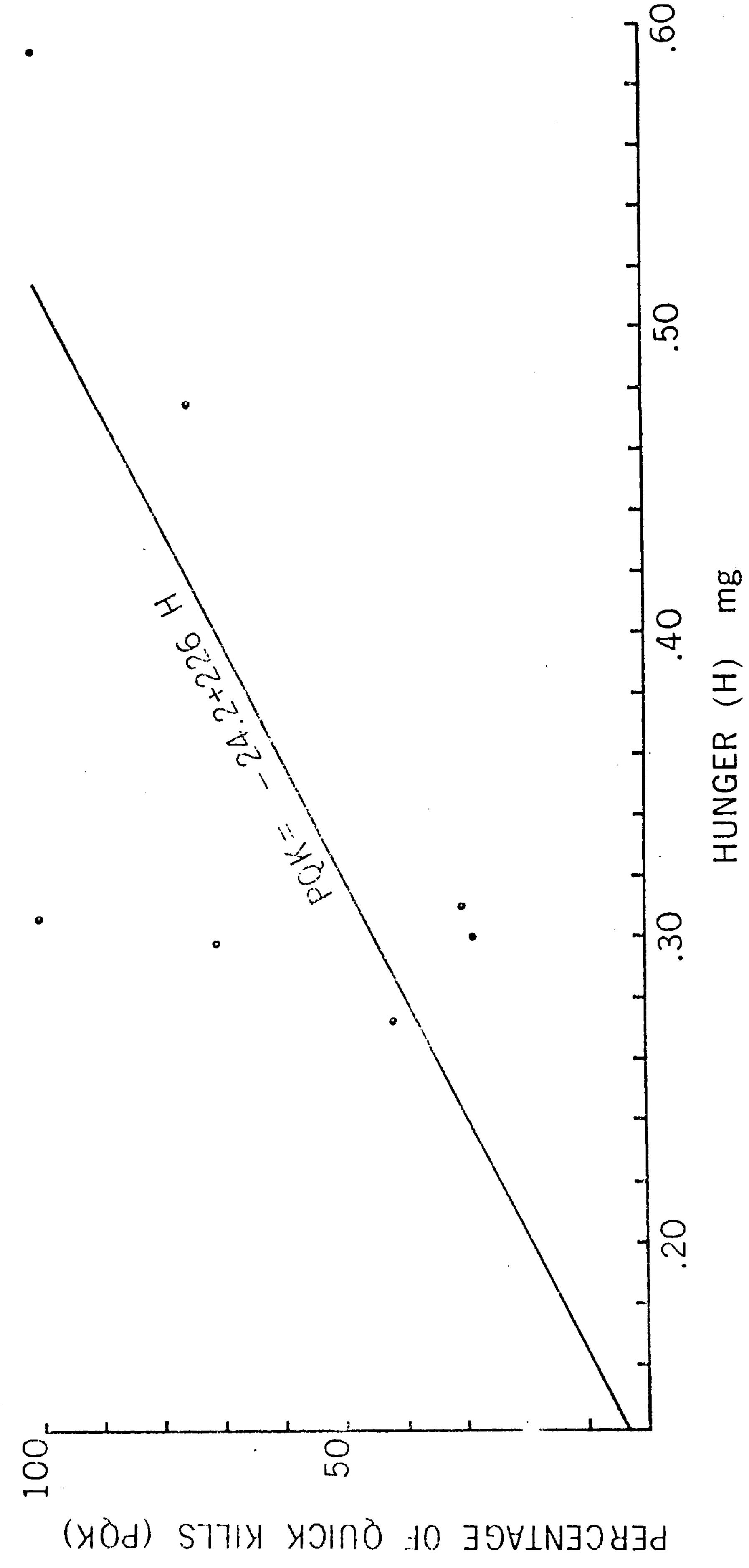

PMC= -25.8 +206 H
PERCENTAGE MULTIPLE CAPTURES (PMC)
100
50
HUNGER (H) mg
.20
.30
.40
.50
.60

Fig. 8. Relationship between the percentage of P. vancouveri that kill and quickly abandon prey (PQK) and the initial hunger (H) of the spiders. Pattern of replication is shown in Table 1. Data from feeders only (see text).


PERCENTAGE OF QUICK KILLS (PQK)
100
50
HUNGER (H) mg
.20
.30
.40
.50
.60
PQK = -24.2+226 H

Hunger Threshold

In *P. vancouveri* a minimal hunger level (HT = hunger threshold) existed below which spiders would not capture and kill prey. Observations showed that the hunger level necessary to cause prey mortality was higher than that which stimulated search and pursuit.

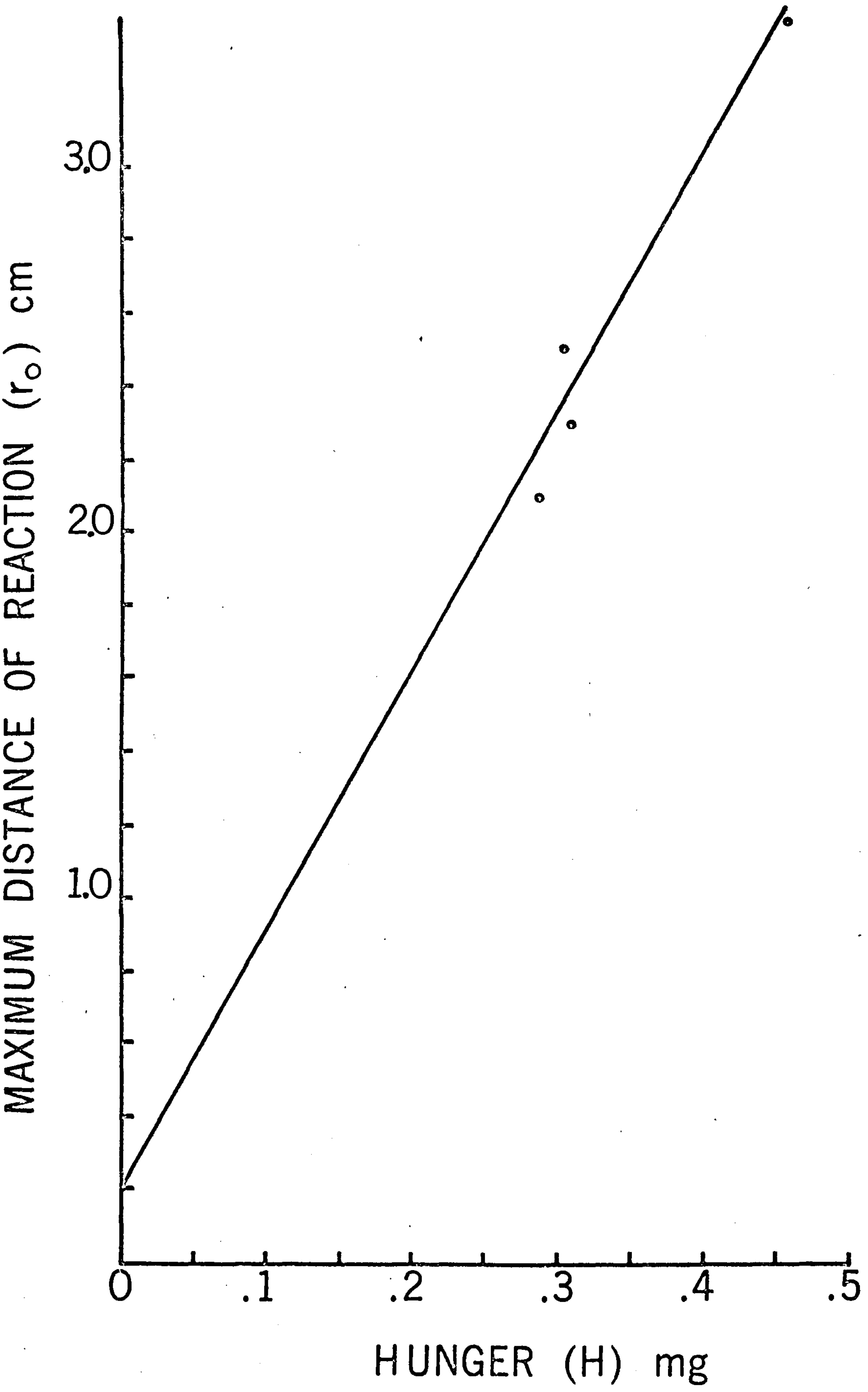
If HT were similar to that of Holling's mantids then it would have been possible to measure hunger threshold in two ways: using the hunger curve (Figs. 4 and 5) and using the data relating maximum distance of reaction is the farthest distance in front of the spider at which it will strike at prey. For each particular level of hunger there is a corresponding maximum distance of reaction.

Using hunger data, HT corresponded to the lowest weights of prey consumed by spiders that were just hungry enough to capture and feed on flies. Because of their high variability, these data could not provide an estimate of HT: the smallest amounts of food eaten were .012, .033, .041 and .060 mg, all other values being above 0.1 mg.

From Fig. 9 it can be seen that the maximum distance of reaction (defined in the next section) approaches zero when hunger approaches zero.

But there is also a third way to estimate HT: it may be defined as that level of hunger below which no spiders (PF = 0) feed.

Fig. 9. Effect of hunger on the maxim distance that *P. vancouveri* attacked flies. Averages of 1 - 3 replicates.


MAXIMUM DISTANCE OF REACTION (r_o) cm
3.0
2.0
1.0
0
.1
.2
.3
.4
.5
HUNGER (H) mg

From the equation in Fig. 3, setting PF = 0 and solving for H, one obtains 0.081 mg as an estimate of HT. This value was used in the Holling model.

The final attack parameter determined from the "hunger curve" trials was the rate of ingestion of food, KE, measured as time (hours) required to consume 1 mg of flies.

This parameter was determined for each spider that fed in the hunger trials using the formula:

$$KE = \frac{TE}{H}$$

where KE is the rate of ingestion, TE is the total time the spider spent feeding and H is the total weight ingested. The average rate of ingestion did not correlate significantly with hunger. Therefore one average rate of feeding 2.37 hr/mg ± .0314 SE (n = 56) was used for all spiders.

Interaction of Hunger With Other Components

Size and Shape of the Reactive Field of Predators for Prey

Wolf spiders depend to a large extent upon vision when seeking prey. Besides having two large eyes that face frontally *P. vancouveri* have a well developed pair of eyes that face laterally, giving the spider a very broad field of vision. As with Holling's mantids, it was found that the size of the spider's reactive field for prey, i.e. the area within which an encountered fly is attacked, is a function of hunger, while the shape of the reactive field corresponds to the shape of the animals's visual field.

As the videotape studies of predatory behaviour were carried out in a 2-dimensional setting, the cirucular arena, only the length and width of the reactive field were considered, its height being ignored. Slow-motion replays revealed both the distance between fly and the snout of the spider and the angle of the fly to the long axis of the spider's body, when the spiders first launched their attacks. Prior to such an attack a spider in motion would momentarily "freeze", rotate to line itself up with the prey and rush after the fly, striking with its forelegs when its jaws were about 4 mm distance from the fly. (The whole operation almost invariably lasted much less than one second.) When the fly was close to the spider but off to one side the spider sometimes leaped sideways on top of the fly, or merely rotated sideways and struck without rushing after it. On certain occasions spiders rotated almost 180° to strike at flies approaching from behind.

Two parameters derived from videotaped attack sequences were the size of the reactive field as related to hunger, and the shape of the reactive field.

For any given level of hunger and any given angle between spider and fly, only the most distant points of attack were used in demarcating the margins of the reactive field. Many records of attack were obtained well within the outer boundaries so defined, but these were considered to be attacks that were not launched until the prey were within the reactive field. The fact that a spider did not attack was not held as proof that a fly lay outside the reactive field. Sometimes spiders passed up several opportunities before attacking a fly. Because of the method of gathering data few replicates were used in the calculation of GM, the parameter relating size of the reactive field to hunger. In Fig. 9, which relates the distance of reaction directly in front of the spiders to hunger, each of the points was based on, at most, 3 replicates (there was only one replicate for the lowest hunger level). The relationship between maximum distance of reaction (r_o) and hunger was significant at the 2% level ($r = .978$) and was described by the equation:

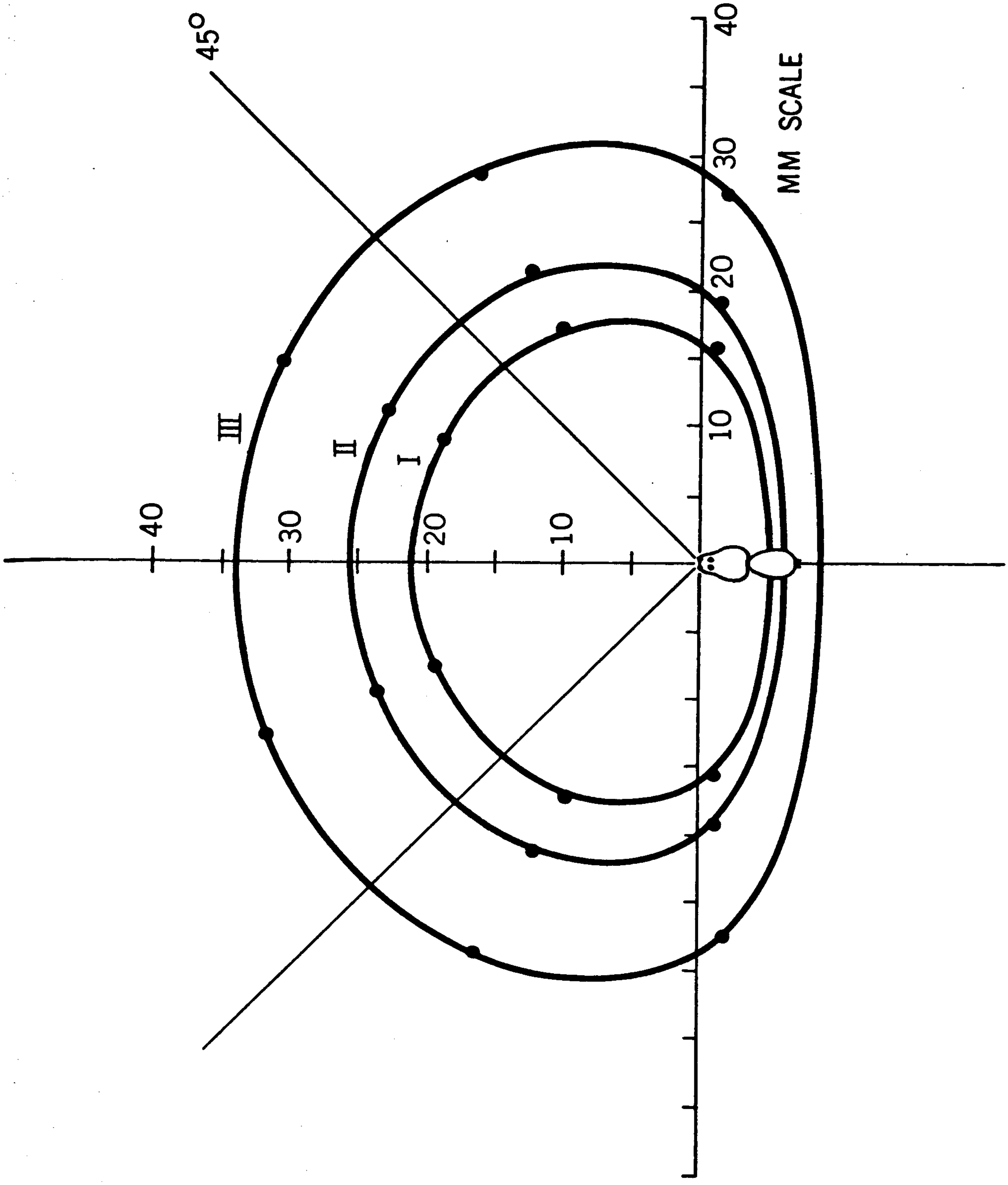
$$r_o = 72.7 \; H + .91$$

giving GM, the slope, a value of 72.7 when r_o is measured in mm.

After determining a value for GM defining the relationship between r directly in front of the predator vs hunger it is necessary to determine another parameter AKR which depends on the shape of the reactive field. AKR is the constant which is multiplied by r_o to determine RD, the radius of a circle which encompasses an area equivalent to the reactive field around the predator. If the reactive field is a circle then AKR is π; otherwise AKR is less than π.

Fig. 10 shows the size and shape of the reactive fields around P. vancouveri where the spiders have fasted 4, 7, 10 and 16 days. The area within each reactive field (A) was measured for each hunger level. (Hunger levels after periods of 7 and 10 days deprivation were very nearly equivalent, so a single reactive field for these two periods of

Fig. 10. Shape of reactive field around P. vancouveri at three levels of hunger, corresponding to 4 (I), 7 or 10 (II), and 16 (III) days of fasting.


45°
40
30
20
10
III
II
I
10
20
30
40
MM SCALE

deprivation is shown in Fig. 10). To estimate the margins of the reactive fields it was necessary to extrapolate maximum distances of reaction for angle to the right and left of centre line from given hunger levels to other hunger levels. Extrapolations were done using the equation relating r_o and H.

Using the equation given below and the data for the four reactive fields corresponding to the four levels of hunger an estimate was made for the areal constant (KA) used to define the shape of the reactive field:

$$KA = \frac{A}{[GM(H-HT)]^2} \qquad \text{(after Holling 1966).}$$

The relevant calculations are shown in Table 5. KA is used in the estimation of AKR, which is the parameter used to relate r_o and RD, the radius of a circle with area A (Holling 1966, p. 82): $AKR - (KA/\pi)$.

Since the areal constant KA was 4.29 (average) for *P. vancouveri*, then AKR, the radial constant was 1.36.

Speed of Movement of Predator and Prey

P. vancouveri exhibited two types of motion-search (*sensu* Holling 1966) which refers to wandering not directly associated with prey capture and pursuit, comprising the phases of "freezing", orientation to the prey, and rushing after a fly until it was within striking distance.

TABLE 5

Calculation of KA, an areal constant relating area of the predator's field of reaction to the distance of reaction directly in front of the predator. For meaning of symbols refer to Appendix II at the back of the text.

TF	H	H-HT	$[GM(H-HT)]^2$	A (cm^2)	$KA = \frac{A}{[GM(H-HT)]^2}$
4	.291	.210	2.33	9.30	3.99
7	.308	.227	2.72	14.90	5.48
10	.310	.229	2.76	12.57	4.55

Search velocities, measured as distance traversed/time spent searching (TS), were measured for those periods of time before and after the periods of pursuit, striking and resting associated with prey capture. Besides being designated according to position within the sequence of attacks (e.g. before 2nd capture, before 3rd, etc.) search velocities were computed over 4 hunger levels and 2 levels of prey density (for the pattern of replication see Table 2). Generally interruptions in the searching of non-feeders were few and infrequent, while feeders had longer and more frequent pauses during their time spent searching. Thus non-feeders had greater search velocities than feeders. It was observed in general observations of caged spiders and spiders used in hunger experiments that spiders deprived a longer period of time, were less restless, and more lethargic than less hungry spiders. Yet field-collected spiders, which behaved as if very hungry, were more active than spiders which had been kept some time in the laboratory. The visibly well-fattened spiders that had spent all their lives in the laboratory (and which were used in the feeding periodicity experiments) were very lethargic.

Only data from feeders were used for the functional response trials. No significant correlation was found between VD and hunger, between VD and prey density, or between VD and position in the attack sequence. Hence only one estimate of search velocity was used for all standard predators: 4053.6 cm/hr ± 889.2 SE (n = 64).

The time spent in pursuit was the interval between the time that an attack was initiated and the time that the prey was seized in the jaws of the predator. Pursuit velocity was computed as the ratio pursuit distance:pursuit time.

The pattern of repliation for pursuit velocity is listed in Table 2. There was no significant correlation with hunger, prey density nor position in the attack sequence. The mean pursuit velocity for all standard predators was 22032 cm/hr ± 1737 SE (n = 49).

Prey speed was measured over three levels of fly density (see Table 6) using the formula:

$$VY = (Nc - \pi r^2 No)/2rt \qquad \text{where}$$

VY is prey speed, Nc is the number of times that flies entered the contact area (explained below), r is the radius of the contact zone swept out by a fly, No is prey density and t is the time available for flies to touch the contact zone.

The contact zone was a linear series of 5 x 5 mm squares adjacent to the median axis (diametre) of the arena floor, an area encompassing 11.05 cm^2. The trials each lasted 3 minutes (t = .05 hr). Half of the sum of the fly's body length and width (measured from wingtip to wingtip) was used as an estimate of r, the radius of contact for one fly (.104 cm). Prey densities (No) were 5, 10 and 20 flies in an area of 99 cm^2 corresponding to densities of .0505, .1010 and .2020 flies/cm^2, respectively. Table 6 shows the mean number of contacts, number of replicates, and the estimates of fly velocity for each of the prey densities. There was

TABLE 6

Mean number of contacts/fly with a portion of the arena floor (Nc), number of replicates, and estimates of fly velocity (VY) over three levels of prey density.

No. of flies per arena	Mean Nc	No. of obs.	SE of mean	VY (cm/hr)
5	4.44	9	.606	150
10	3.25	10	.415	128
20	2.55	7	.262	83.5

a highly significant negative correlation (r = .999, d.f. = 2) for the relation between mean prey velocity and prey density (Fig. 11):

$$VY = 172.4 - 440\ No.$$

Capture Success

The likelihood of a spider capturing a fly entering its reactive field is termed its capture success. Capture success is divided into three parameters, recognition success, pursuit success and strike success. The first parameter, recognition success (SR) is computed from the ratio of number of pursuits initiated:number of encounters. An encounter is said to occur when a fly enteres the reactive field of the predator.

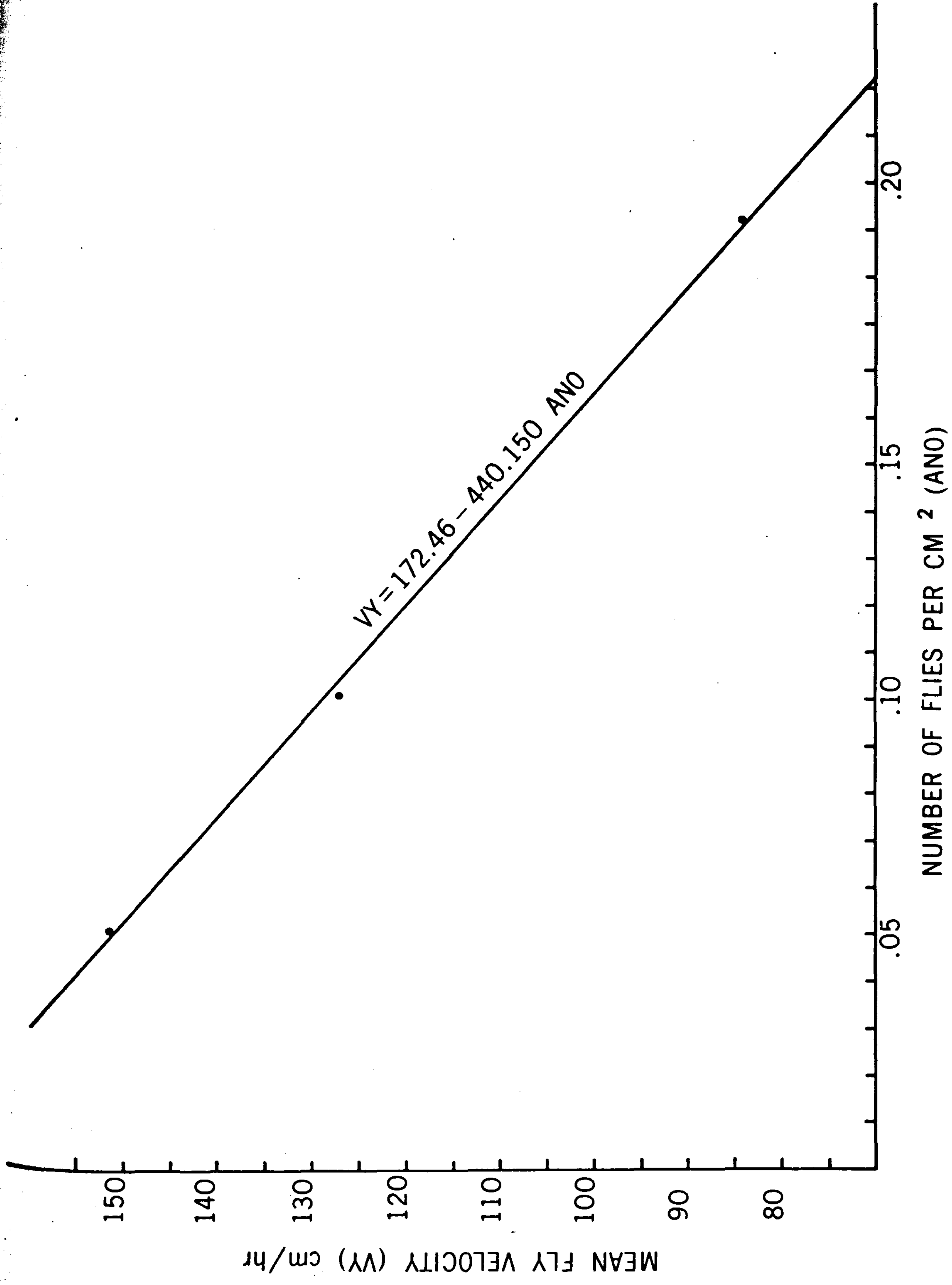
All data for SR were taken from seven spiders that had been deprived of food 10 days and were exposed to 5 flies/arena. Recognition success (SR) was 0.162 ± .075 (SE).

Pursuit success (SP) is the ratio of the number of strikes made: the number of pursuits initiated. It was possible using videotape replays to measure pursuit success directly.

Replication followed the pattern shown in Table 2. There were virtually no departures from an SP of 1.0.

Strike success (SS) is the ratio of the number of successful captures: the number of strikes made. The pattern of replication corresponds to that depicted in Table 2.

Fig. 11. Effect of density of vestigial-winged _D. melanogaster_ on the average velocity of each fly.


VY=172.46-440.150 ANO
.05
.10
.15
.20
NUMBER OF FLIES PER CM 2 (ANO)
150
140
130
120
110
100
90
80
MEAN FLY VELOCITY (VY) cm/hr

There was no significant difference in SS for spiders deprived of food 10 days where prey densities were 5/arena ($\overline{X}$ = .667) and 20/arena ($\overline{X}$ = 0.779, t = 0.631 for 10 d.f. and P > 10%). However there was a significant correlation (P < 1% for r = -.52 with 21 d.f.) between SS and H where there were 20 flies per arena, the line of best fit being:

$$SS = 1.51 - 1.836\ H$$

Note, however, that for any value of H below 0.277 mg, SS is maximal at 1.0, the perfect success ratio.

If all strike success data for both prey densities is pooled than SS does not correlate significantly with hunger (r = -.309 for 27 d.f. giving P > 10%).

For the Holling model the grand average for all individuals was used as an estimate of SS: SS = 0.794 ± .061 SE with n = 29 observations.

Structure of the Attack Cycle

Data from the feeding trials and videotape trials also provided information on the relationship between hunger and the structure of the attack cycle (*sensu* Holling 1966; Fig. 14).

Attack cycles overlapped in cases where there were spiders simultaneously feeding on and attacking several prey. Concerning the duration of the various components of an attack cycle, namely time spent in a digestive pause (TD), time spent searching for prey (TS), time spent in pursuit (TP), and time spent eating (TE), the following observations were made.

In the experiments associated with hunger the time spent in search before the first capture diminished with increasing hunger. At TF = 1 day the single spider that fed had a search time of 5 minutes; at TF = 2 days this was reduced to 2 minutes while at TF = 3 days initial time of search was long in one case - 12 min - but short (< 1 min) with 3 other spiders. Thereafter, with virtually no exceptions, initial time of search was very brief, at most 2 minutes.

Pauses between feedings were shorter (5 min or less) for spiders deprived either for very long periods (> 10 days) or short periods (< 7 days). Some spiders deprived moderate lengths of time (7 - 10 days) had long pauses of 17-43 min between feedings.

These long pauses consist of a digestive pause plus a time spent in search. It is postulated that at higher or lower hunger levels, where pauses are brief (5 min or less), the digestive pause is very short or nonexistent, and this pause actually represents time spent searching and is similar to the duration of searching time exhibited prior to first capture in trials where hunger is low.

At the two longer periods of deprivation (TF = 16 days and TF = 21 days) the spiders were typically engaged in a prolonged bout of feeding from the beginning of the trial to its termination.

Generally speaking the total duration of feeding kept pace with the level of hunger, for a single rate of ingestion was found to be common to all levels of hunger.

Videotape studies showed that even the most voracious spiders had a brief refractory period after capturing a fly when they would neither walk or strike at another fly. This period did not vary in any systematic way with hunger; the mean duration of this rest period was 14.4 ± 2.8 (SE) sec based on 52 observations.

In summary the time spent eating (TE) was by far the largest component of the attack cycle during the hunger-curve trials. In more typical situations where the spiders had a regular food supply, most of the time was spent in a digestive pause or searching. (Unfortunately it was not possible to separate time spent in search (TS) from time spent in a digestive pause (TD). A spider may be receptive or unreceptive to prey whether it is walking or motionless.)

Time spent in pursuit (TP) was typically measured in the span of a fraction of a second. This accorded with Edgar's (1970a) observations with a European lycosid. Similarly TS was short (measured in minutes) in the simple arena stocked with an abundance of prey. TD, the digestive pause was only significant for several spiders that had been deprived of food for moderate periods, e.g. 7, 10 days. On such occasions it lasted up to 20 - 45 minutes.

After the trial, TD became the largest segment of the attack cycle once more. (Recall that the signal for termination of the trial was a TD of 60 min or more.) It was typically several hours at least before the next feeding; subsequently feeding levels remained low if the spider had been deprived for only a short length of time prior to the trial. With hungrier spiders the phase of unusually heavy feeding recurred 1 to several hours after the trial, continued until darkness and resumed the following morning. The spiders typically entered a prolonged phase of lower feeding by late morning of the second day. Apparently the sequence of prolonged deprivation followed by feasting caused the spider to accumulate such a store of reserves that its appetite was influenced for the remainder of its subadult stage.

Functional Response Experiment

The relationship between prey density and mean number of flies killed per spider corresponded to a Holling type 2 functional response curve. In Fig. 12 the lines representing the cumulative functional responses at 2 hour exposure intervals are negatively accelerated curves running roughly parallel to one another. After the flies were exposed to predation for 10 hours, cumulative totals of 0.17, 1.5, 2.6, 3.0, and 2.7 flies/spider were killed at prey densities of 1, 3, 6, 10 and 20 flies/cage, respectively.

Not all spiders fed during the trials (Table 7); the percentage of spiders feeding increased as a function of time and prey density. Thus PF was influenced by two factors in addition to hunger.

Testing the Holling Model of Functional Response

To test the predictive power of the Holling model, the attack parameters characterising the spider were applied to the model and the calculated outcome was compared with an actual functional response

Fig. 12 Functional response of P. vancouveri to prey density following 6 days of fasting. Successive curves are cumulative functional responses after 2 (lowest curve) - 10 (highest curve) hours of exposure to predation.

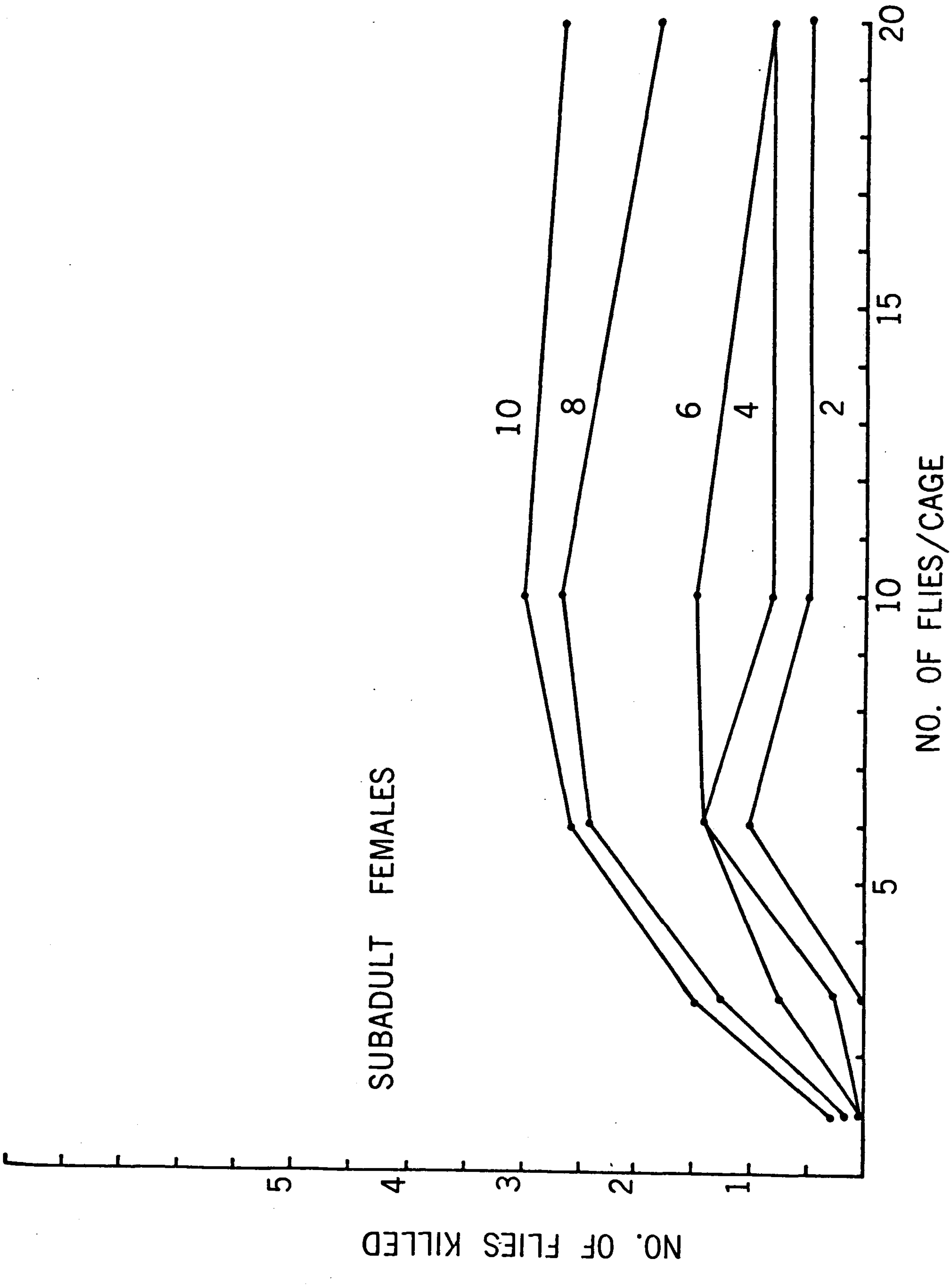

SUBADULT FEMALES
10
8
6
4
2
NO. OF FLIES KILLED
1
2
3
4
5
NO. OF FLIES/CAGE
5
10
15
20

TABLE 7

The influence of duration of the trial (TT) and prey density (ANO) on the cumulative percentage of *P. vancouveri* that fed (PF) in functional response trials in wooden cages.

ANO (flies / cage)	No of spiders tested	Hours exposed to predators				
		0–2	2–4	4–6	6–8	8–10
1	6	0	0	0	16.7	16.7
3	4	0	25	50	75	75
6	5	80	100	100	100	100
10	6	60	67	83	100	100
20	6	33	33	33	83	83

experiment. Table 8 lists all of the attack parameters with the exception of average prey speed VY, which is determined from the equation VY = 172.5 - 440 ANO, where ANO is prey density expressed as number of flies/cm^2. The distance of strike (DS) represents the distance between a fly and the jaws of the spider for the moment when the spider strikes at the fly. Strike distances were measured in slow motion replays of the videotaped feeding trials. DS was typically about 4 mm. The structure of the model is outlined in Fig. 13, and a list of equations is found in Appendix I.

Prior to the functional response trial subadult female spiders were fed to satiation for two days, then deprived of food for 6 days. Average hunger at the start of the trial (HBEG in Table 8) was 0.306 mg from the hunger equation. For the trial the spiders were placed separately in wooden cages with densities of 1, 3, 6, 10 and 20 flies per cage; prey densities (ANO) were .0044, .0132, .0263, .0438 and .0877 flies/cm^2. The mean prey velocities predicted for these densities were 170.5, 166.7, 160.9, 153.2, and 133.8 cm/hr.

Actively feeding spiders attacked newly arrived flies that had been blown into the cage to replace fly losses. This behaviour is in accordance with Edgar's (1970a) comments that lycosids will quickly strike at insects that suddenly land nearby.

Fig. 13. Flow of computations in the Holling model of functional response. Numbers indicate sequence of steps in the program.

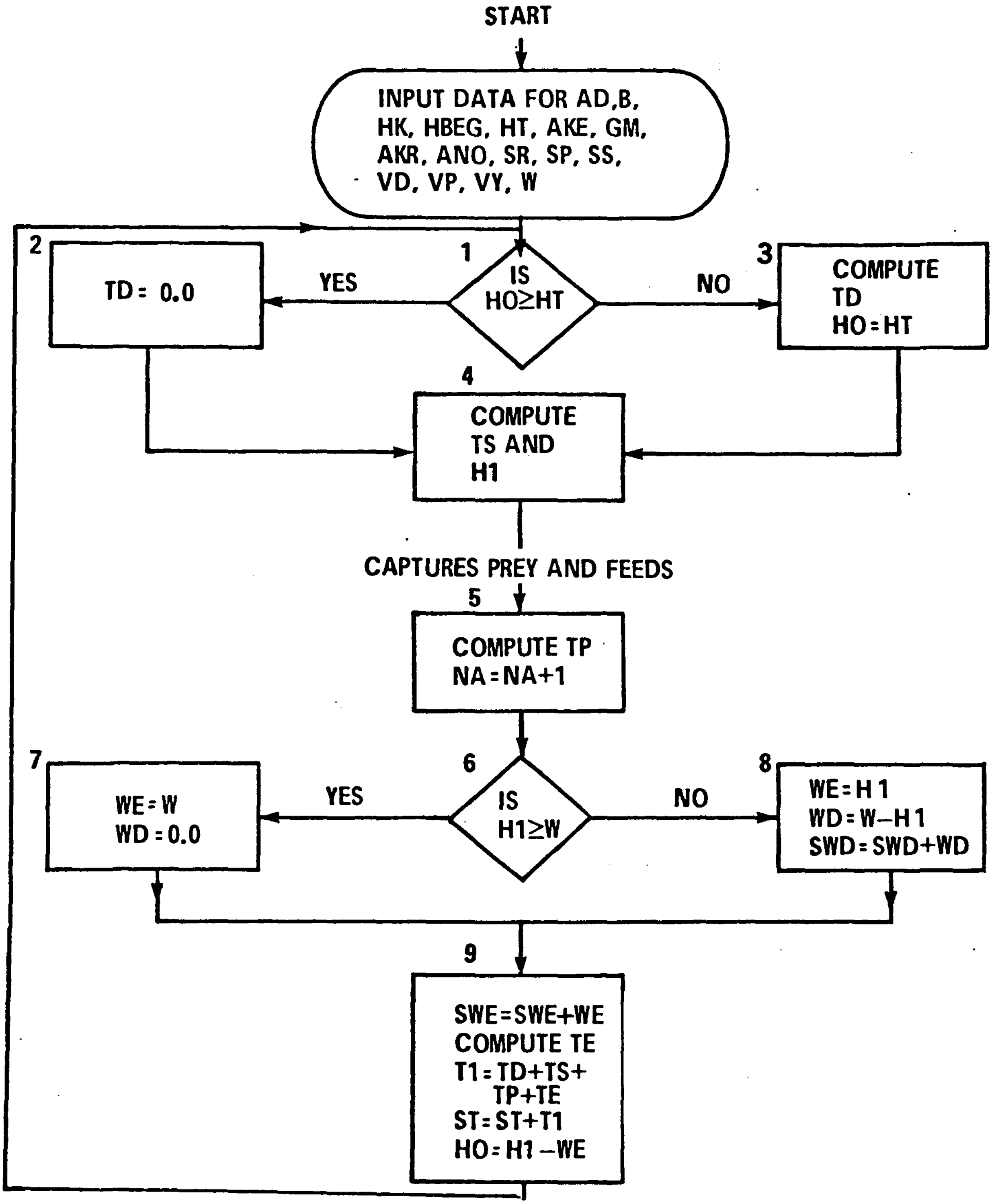

START
INPUT DATA FOR AD,B, HK, HBEG, HT, AKE, GM, AKR, ANO, SR, SP, SS, VD, VP, VY, W
1
IS HO≥HT
YES
2
TD = 0.0
NO
3
COMPUTE TD HO = HT
4
COMPUTE TS AND H1
CAPTURES PREY AND FEEDS
5
COMPUTE TP NA = NA+1
6
IS H1≥W
YES
7
WE = W WD = 0.0
NO
8
WE = H 1 WD = W–H 1 SWD = SWD+WD
9
SWE = SWE+WE COMPUTE TE T1 = TD+TS+ TP+TE ST = ST+T1 HO = H1 –WE

TABLE 8

Values of attack parameters as used in the model for standard subadult female spiders attacking fruit flies[1]

Parameter		Dimension	Value	Source	Page
AD	(C)[2]	mg/hr	0.027	Hunger equation (Figs. 4 and 5)	24, 25
B	(C)		0.264	Hunger equation (Figs. 4 and 5)	24, 25
HK	(C)	mg	0.311	Hunger equation (Figs. 4 and 5)	24, 25
HBEG	(C)	mg	0.306	Hunger equation (Figs. 4 and 5)	24, 25
HT	(C)	mg	0.081	Zero point of Fig. 3	21
AKE	(C)	hr/mg	2.37	Hunger trial data	38
GM	(C)	cm/mg	7.26	Slope of line in Fig. 9	37
AKR	(C)		1.36	Table 5 and text	43, 44
SR	(M)		0.162	Videotaped trials	48
SP	(M)		1.00	Videotaped trials	48
SS	(M)		0.794	Videotaped trials	51
VD	(M)	cm/hr	4053	Videotaped trials	45
VP	(M)	cm/hr	22032	Videotaped trials	46
W	(M)	mg	0.221	Hunger trials	10
TA	(M)	hr	16.0	Feeding periodicity trials (Fig. 2)	15
DS	(M)	cm	0.4	Measured from videotaped trails	58

---

[1] For meaning of symbols refer to Appendix II.

[2] C - calculated with the aid of an equation; M - measured more or less directly from the data.

Fig. 14 is a diagram (after Holling 1966) showing hypothetical changes in the hunger of a predator in the course of a feeding period. The period is divided into successive attack cycles, the duration of each attack cycle being subdivided into a digestive pause (TD) after feeding, a time spent searching (TS), a time spent in pursuit (TP) and a time spent eating (TE).

Such a sequence of attack cycles was predicted for *P. vancouveri* when the unmodified Holling model was used to simulate the functional response experiments carried out in wooden cages. The partitioning of the successive attack cycles for 3 levels of prey density is shown in Fig. 15.

The model predicted that in the time available 2 flies would be killed at all densities tested.

For very low prey densities (1 - 3 flies/cage) the predicted value of two flies was an overestimate. For higher prey densities the error lay in the opposite direction - the predicted number of kills was underestimated by the model.

The initial time spent searching by the spiders in low density cages was greatly underestimated by the model. It was suspected that a faulty estimate of VD caused inaccurate estimates of TS.

Of the parameters going into the equation for TS (see Appendix I) those most in doubt are VD and VY, predator and prey speeds. Of these two parameters, VD is by far the more important since predator speed is many times greater than prey speed and hence has a greater influence

Fig. 14. Hypothetical changes in hunger of a predator over a 16 hr feeding period (after Holling 1966), including details on the partitioning of a single attack cycle. TD - time spent in a digestive pause; TS - time spent searching; TP - time spent in pursuit; TE - time spent eating.

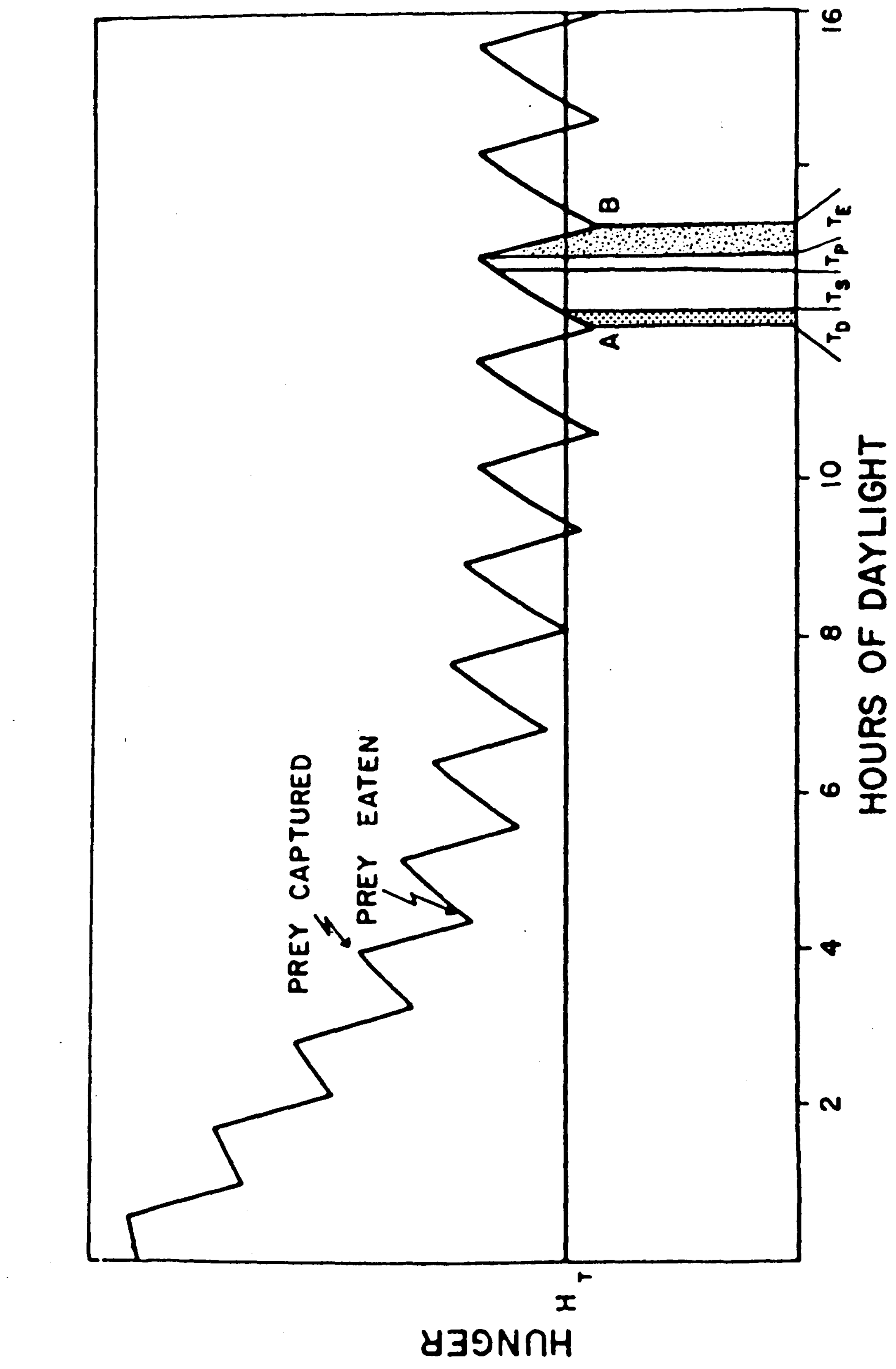
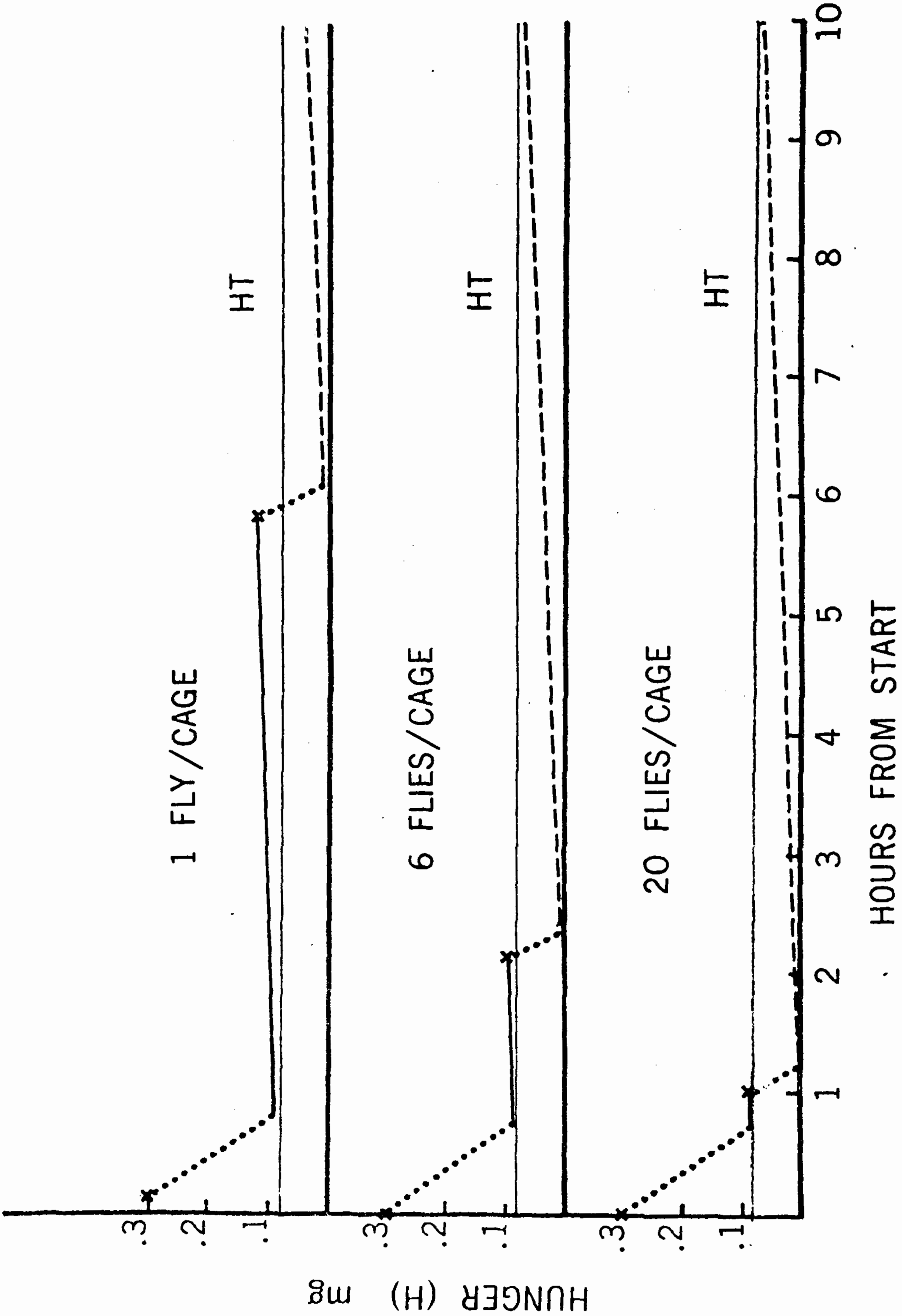

HUNGER
H
T
PREY CAPTURED
PREY EATEN
A
B
T
D
T
S
T
P
T
E
2
4
6
8
10
16
HOURS OF DAYLIGHT

Fig. 15. Changes in hunger of P. vancouveri over consecutive attack cycles where the spiders fasted 6 days and were exposed to varying densities of flies in wooden cages. Kills are indicated by "x", time spent searching by a thick line, hunger threshold by a thin line, time eating by dots and time in a digestive pause by a broken line.


HUNGER (H) mg
1 FLY/CAGE
6 FLIES/CAGE
20 FLIES/CAGE
HT
HT
HT
.3
.2
.1
.3
.2
.1
.3
.2
.1
1
2
3
4
5
6
7
8
9
10
HOURS FROM START

on the number of encounters per unit time than does VY. Any errors in the estimate of VD would lead to an almost directly proportional error in TS. It is quite possible that an estimate of VD based onspider speeds during its first 3 minutes in the arena might not represent the actual mean velocity of search for spiders kept in cages for 10 hours. An overestimate of VD could explain the overestimate of the number of flies killed at low prey densities.

At higher prey densities the model predicted that two flies would be killed in quick succession, after which the spider would enter a digestive pause. The model did not make allowance for the fact that when high hunger levels of spiders and high prey densities coincide the spiders may capture several prey while feeding. When this happens there are characteristically more kills but less feeding on each prey than at lower prey densities and lower levels of hunger. Finally the deterministic nature of the model did not take into account the fact that only a certain proportion of a given group of spiders may be expected to feed, depending upon their average level of hunger.

A second series of simulations was conducted with the Holling model modified so as to include the effects of multiple captures and quick kills on the functional response. In the new model the relationship between WE (weight eaten per prey) and H (for the beginning of the trial) was taken into account.

In the simulations successive prey were captured and a constant weight ingested from each until hunger dropped below HT. TS was assumed to be uniform and short in each of the sequence of multiple captures. Once H dropped below HT the normal sequence of steps in the Holling model (computation of the next TD, TS, TP and TE) was resumed. WE was again computed from the equation. If H after feeding was still above threshold then the model again entered the multiple-capture subroutine. The program stopped when all the time available for predation (TT) was exhausted.

The predictions of these simulations were very close to the results obtained (Table 9) in the hunger trials. (Recall that hunger trials were conducted in circular arenas where prey density was uniformly high (.2020 flies/cm^2) and initial predator hunger (HBEG) was the only variable).

The predictions of the revised model were not accurate for the cage trials. The model consistently overestimated the speed at which flies were killed. Presumably the relationship between WE and H as determined in the arena trials did not apply to the cage situation where there were much lower prey densities.

TABLE 9

Relationship between hunger and the number of flies killed as predicted by the revised Holling model and as obtained from the data. Prey density in the circular arenas was 0.2020 flies/cm^2.

TS (days)	H (mg) from the hunger equation	Mean number of flies killed/spider			
		Observed			Predicted
		$\bar{X}$	N	SE	X
1	.173	1.0	2	-	1
2	.239	1.0	1	-	2
3	.273	2.0	7	.436	2
4	.291	3.0	7	.378	2
5	.301	2.14	7	.553	2
7	.308	3.90	11	.579	3
10	.311	3.10	10	.752	3

DISCUSSION

Experiments concerned with determination of the attack parameters pointed out certain deficiencies in Holling's (1966) concept of hunger, but tended to confirm the other hypotheses expressed in his model. A series of simulations with his model emphasised the deficiencies of the Holling concept of hunger and cast doubt on the validity of Hardman's method of estimating predator search speed. A modified version of the model, taking into account some of the complexities associated with hunger in P. vancouveri (multiple captures, quick kills) still did not describe accurately the sequence of events in functional response trials carried out in the wooden cages. But the simulations did enhance understanding of the complexities of the situation for they led to a thorough second look at the data. Part of the failure of the model was undoubtedly due to the dependence of WE on prey density as well as on predator hunger. Unfortunately the relationship was measured at only one prey density (20 flies/arena). Secondly, Table 7 revealed two pecularities of the cage trials. PF was a function not only of predator hunger but also of time and of prey density. Apparently at low prey densities the capture of prey was a chancy business and generally the first capture came slowly. At the 3 higher prey densities (6, 10, 20 flies/cage) once captures were made the time spent in subsequent searches was less than the times predicted by the model. Why were there such discrepancies?

These two phenomena appeared to indicate that effective prey density was not the same as the number of flies/cm^2. Subsequent observations on flies and spiders placed in cages lent support to this surmise. While flies congregated on the roof of the cage, spiders remained on the plastic mesh. Thus effective prey density was initially lower than predicted. But once the spider discovered the cluster of flies effective prey density rose, because the spider remained in the vicinity of its clumped prey. In the arena effective prey density was invariably higher than predicted for both the flies and the spider generally remained along the margin of the circular arena.

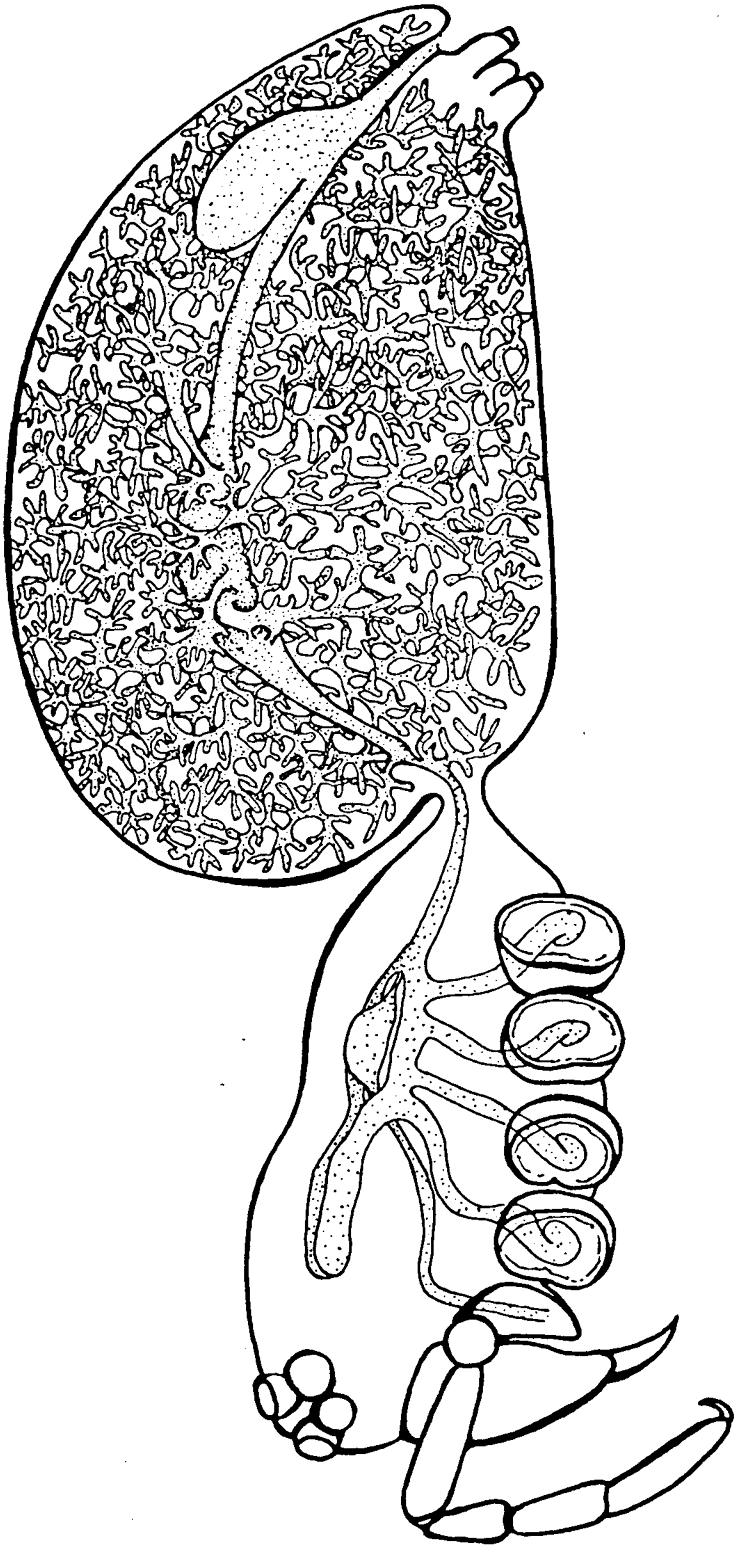
It has been mentioned earlier that the previous feeding history of P. vancouveri, even prior to the periods of satiation and deprivation had an enormous influence on their performance in feeding trials. Moreover, spiders with a whole life of "easy living" were very stout in appearance, light in colouration, and slow in movement compared to individuals taken from the field. In these historical features of hunger spiders seem to differ from mantids, the experimental animals used by Holling. These features of capture are probably associated with the known resistance of wolf spiders to starvation. The ability to lower the metabolic rate when deprived of food and the ability to store enormous quantities of food as adipose tissue have already been cited. Additionally the complex digestive system of wolf spiders represents a sharp digression for the mantid pattern.

The midgut of a spider is elaborated anteriorly into thoracic diverticula and posteriorly into numerous alimentary tubules which together with adipose tissue form most of the mass of the abdomen (Fig. 16). It is postulated that these features of spider anatomy suit it to a feast and famine mode of feeding that characterize the life habits of many spiders species (Grassé 1949, Comstock 1913, Savory 1929). It has been demonstrated that at high prey densities hungrier spiders will engage in multiple captures and quick kills, destroying more flies than is necessary to appease their hunger. Undoubtedly these phenomena are also functions of prey density but their dependence upon prey density has not yet been tested.

Clearly the problems of appetite and food storage in P. vancouveri are complex and should be explored with the same precision as these problems were studied in certain insects (Gelperin 1971, Hill and Goldsworthy 1968, Waldbauer 1968). Until this essential background research is done it will not be possible to devise a predation model for wolf spiders that is (sensu Holling 1966) realistic, precise and general.

This same remark might well be applied to the complexities surrounding the search speed of the predator. The data indicate that long term feeding history and current levels of hunger are in some way determinants of predator search speed. The nature of these relationships requires further investigation.

Fig. 16. The digestive system of a spider: the midgut is elaborated anteriorly into a series of thoracic diverticula and posteriorly into alimentary tubules which, together with adipose tissue, form most of the mass of the abdomen. (Adapted from John Henry Comstock: THE SPIDER BOOK. Copyright, 1912, 1940, by Doubleday, Doran & Company, Inc. Copyright assigned 1948 to Comstock Publishing Inc. Used by permission of Cornell University Press.)



Because of the effect of these additional factors Holling's model of functional response cannot make accurate predictions for predators highly resistant to starvation by virtue of a complex system of food storage, or for predators that engage in multiple captures, or for predators whose speed interacts with hunger and prey density.

SUMMARY

1. Well-fed subadult female P. vancouveri show a well-defined diurnal feeding periodicity in the lab, with peaks of feeding in the late morning and late evening. Hungrier spiders fed in darkness as intensively as spiders exposed to the normal diurnal alternation of light and darkness.
2. Not all P. vancouveri deprived of food fed when exposed to prey. There was a positive linear relationship between the proportion of spiders feeding and their hunger, expressed as the weight of prey ingested.
3. For periods of deprivation up to 10 days there was a negatively accelerated curvilinear relationship between time deprived of food and hunger. It was necessary to add a correction factor to Holling's (1966) hunger equation to describe this relationship. For periods beyond 10 days the relationship was altered and hunger rose steeply.
4. The feeding history of a spider prior to its pretrial treatment (satiation and deprivation) had a large influence on its feeding behaviour in hunger trials.
5. The quantity of food ingested from each prey killed declined as hunger increased; hungrier spiders killed proportionally more flies per mg ingested than less hungry spiders.
6. This increase in kills was partly attributed to a rise in the number of spiders that captured and fed on several flies at once as their hunger increased.

7. Also the proportion of spiders which killed and quickly abandoned flies increased with their hunger.
8. Feeding trials recorded on videotape and played back in slow-motion allowed analysis of the effect of hunger on the attack behaviour of spiders. The size of the reactive field of predators for prey increased with hunger but retained a constant shape over a range of hunger levels.
9. Predator speed of search and pursuit were not influenced by hunger nor by prey density.
10. Mean prey velocity was inversely correlated with their density.
11. The proportion of spider attacks that were successful in capturing prey declined as their hunger increased.
12. *P. vancouveri* exhibited an invertebrate (Holling's type 2) functional response to prey density.
13. When the values of attack parameters for the functional response of the spider were placed in the Holling model, the model did not accurately predict the functional response of the spider to prey density.
14. Discrepancies between observed data and the predictions of the model were attributed to deficiencies in the Holling concept of hunger and to the relationship between spider hunger and capture success.

BIBLIOGRAPHY

Bristowe, W. S. 1958. The world of spiders. Collins. London.

Comstock, J. H. 1913. The spider book. Doubleday, Page and Company, New York.

Ebeling, W. and Wagner, R. E. 1963. Teflon as a barrier to insects. J. Econ. Ent. 56: 715-716.

Edgar, W. D. 1970a. Prey and feeding behaviour of adult females of the wolf spider Pardosa amentata (Clerck). Neth. J. Zool. 29: 487-491.

Edgar, W. D. 1970b. Prey of the wolf spider Lycosa lugubris (Walck.) Entomologists Monthly Magazine 106: 71-73.

Gelperin, A. 1971. Regulation of feeding. Ann. Rev. Ent. 16: 365-378.

Grassé, P. P. 1949. Traité de Zoologie. Vol. VI. Onychophores, Tardigrades, Arthropodes, Tilobiotomorphes, Chélicerates. Masson et C^{ie}. Paris.

Harrison, J. B. 1969. Acoustic behaviour of a wolf spider, Lycosa gulosa. Anim. Behav. 17: 14-16.

Hegdekar, B. M. and C. D. Dondale. 1969. A contact sex pheromone and some response parameters in lycosid spiders. Can. J. Zool. 47: 1-4.

Hill, L. and G. J. Goldsworthy. 1968. Growth, feeding activity, and the utilization of reserves in larvae of Locusta. J. Insect Physiol. 14: 1085-1098.

Holling, C. S. 1959a. The components of predation as revealed by a study of small mammal predation of a European pine sawfly. Can. Ent. 91: 293-320.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Ent. Soc. Can. 45: 1-60.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. Mem. Ent. Soc. Can. No. 48.

Homann, H. 1930. Beiträge zur Physiologie der Spinnenaugen. III. Das Sehvermögen der Lycosiden. Z. verl. Physiol. 9: 40-67.

Kirchner, W. 1964. Bisher Bekanntes über die forstliche Bedeutung der Spinnen. Waldhygiene 5: 161-198.

LeGuelte, L. 1969. Learning behaviour in spiders. Am. Zoologist 9: 145-152.

Markl, H. 1969. Verständigung durch Vibrationssignale bei Arthropoden. Naturwissenschaften 10: 499-565.

Miyashita, K. 1969. Effects of locomotory activity, temperature and hunger on the respiratory rate of Lycosa T-insignita Boes. et Str. (Araneae:Lycosidae) Appl. Ent. Zool. 4: 105-113.

Papi, F. and P. Tongiorgi. 1963. Innate and learned components in astronomical orientation in wolf spiders. Ergebnisse der Zoologie 26: 259-280.

Radinovsky, A. and G. W. Krantz. 1962. The use of fluon to prevent the escape of stored-products insects from glass containers. J. Econ. Ent. 55: 815-816.

Richter, C. 1970. Aspects of silk spinning in wolf spiders in relation to distribution and dispersal (Pardosa, Araneae, Lycosidae). Ph.D. thesis. Free University, Amsterdam.

Rovner, J. S. 1967. Acoustic communication in a lycosid spider (Lycosa rabida Walckenaer). Anim. Behav. 15: 273-281.

Savory, T. H. 1929. The biology of spiders. Sidgwick and Jackson Ltd. London.

Storch, R. H. 1968. Fluoroglide as a barrier to contain non-flying insects in glass containers. J. Econ. Ent. 61: 335-336.

Waldbauer, G. P. 1968. The consumption and utilization of food by insects. Adv. Insect Physiol. 5: 229-288.

Appendix I

Summary of Equations Used in Holling Model

Hunger:

$$H = HK - Ce^{-AD(TF)}$$

Resultant velocity of predator and prey velocities:

$$VR = (VD^2 + VY^2)^{\frac{1}{2}}$$

Area of the reactive field:

$$A = KA[GM(H-HT)]^2, \quad H > HT$$

$$A = 0 \qquad H < HT$$

Speed of movement of spiders:

$$VD = 4053 \text{ cm/hr}$$

Speed of movement of flies:

$$VY = [Nc-\pi r^2(ANO)]/2rt$$

Capture success:

$$SC = (SR)(SP)(SS)$$

Time spent in a digestive pause:

$$TD = \frac{1}{AD} \ln \frac{HK-HO}{HK-HT}$$

Time spent searching for a prey:

$$TS = \frac{1}{2(VR)(AKR)(GM)(HO-HT)(ANO)(SC)} - \frac{\pi(AKR)(GM)(HO-HT)}{2VR}$$

Time spent pursuing each prey:

$$TP = [(AKR)(GM)(HO-HT) - DS]/VP$$

Time spent eating each prey:

$$TE = AKE(WE)$$

Appendix II

Table of Symbols

AD - Rate of food disappearance of digestion

AKE - Feeding rate (time per unit weight of food eaten)

AKR - Equals KA/π

ANA - The number of flies killed by feeding and nonfeeding spiders alike, i.e., NA corrected for the proportion of spiders feeding

ANO - Prey density

B - A constant that is multiplied by the exponential term in the hunger equation

DS - The strike distance

GM - A constant relating distance of reaction to hunger

H - Hunger; dry weight of food needed to satiate the predator

HBEG - Hunger level at the beginning of a trial

HK - Maximum capacity of the gut

HT - The hunger level at which capturing and killing prey begins

KA - An areal constant relating area of predator's field of reaction to the distance of reaction when the angle to the body axis is 0°

NA - Number of prey attacked

No - The number of prey per unit area

PF - Proportion of spiders that feed at a given level of hunger

r - Radius of contact of a standard fly

r_o - Radius of the reactive field directly in front of the predator

SP - The pursuit success or the success of pursuing a prey that is recognized

SR - The recognition success or the success of recognizing a prey that enters the predator's reactive field

SS - The strike success or the success of capturing a prey once a strike is made

ST - The total time elapsed since the start of a trial

SWD - The total weight of prey discarded since the start of the trial

SWE - The total weight of a prey eaten since the start of the trial

t - Time available for flies to touch the contact zone

TI - Total time spent in an attack cycle

TD - Time taken in a digestive pause after a prey is eaten

TE - Time spent eating each prey

TF - Time of food deprivation timed from a condition of complete satiation

TP - Time spent in pursuing each prey

TS - Time spent searching for each prey

TT - Time prey are exposed to predators

VD - Average velocity of predator during searching

VP - Average velocity of predtor during pursuit

VY - Average velocity of prey

W - Weight of one prey

WD - Weight of each prey discarded, uneaten

WE - Weight of each prey eaten

CURRICULUM VITAE

John Michael Hardman Age: 25

Born: 31 October 1947 - Exeter, Ontario, Canada. Married.

University Address: Pestology Centre,
Department of Biological Sciences
Simon Fraser University
Burnaby 2, British Columbia, Canada
Telephone No.: 291-4286 (Area code: 604)

Future Address: Division of Entomology,
Stored Products Section,
C.S.I.R.O.,
P. O. Box 1700,
Canberra City, A.C.T. 2601,
Australia.

Field of Specialization: Arthropod Ecology with particular reference to pest management, aided by systems analysis.

EDUCATION

1952-1963. Elementary schools in Winnipeg, Manitoba; Bedford, Nova Scotia; and Halifax, Nova Scotia.

1963-1964. Grades X and XI at St. Patrick's High School, Halifax, Nova Scotia.

1964-1968. Undergraduate program in Biology at Dalhousie University, Halifax, Nova Scotia, with emphasis on ecology and invertebrate zoology.

Graduated with a B.Sc. First Class Honours (second highest average in graduating biologists; average over 80%).

1968-1969. Master's program in Applied Entomology at Imperial College, University of London, England.

This included extensive course work and lab practicals on the theory and practice of pest control, as well as a summertime research project, "Investigations on the Arthropod Predators of Leafhoppers in an Acid Grassland Field". Graduated first in class with D.I.C., M.Sc. (distinction) in applied Entomology.

1969-1972. Doctoral program in Pestology at Simon Fraser University.

Current training includes courses in the theory of pest control, the use of the digital computer in simulation models of ecological processes, and research toward the thesis-testing Holling's simulation model of invertebrate functional response to prey density, in a wolf spider-fruit fly system.

My investigations on the predatory tactics of the spider should show whether the model for functional response applies to generalists, like the wolf spider, as well as to more specialized predators.

EDUCATION (continued)

1971-1972. Two semester course at the University of British Columbia concerned with mathematical modelling and computer simulation in ecology.

AWARDS, SCHOLARSHIPS

1. 1964. Lieutenant-Governor's Medal for outstanding achievement in the Grade XII Provincial Examinations.
2. 1964. Union Carbide Scholarship of $2,500 for four years of undergraduate study at Dalhousie University.
3. 1968. Deutscher Akademischer Austausch Dienst Scholarship for postgraduate studies in a German University.
4. 1968. National Research Council of Canada (N.R.C.) Scholarship for postgraduate studies in the Pestology Centre of Simon Fraser University.
5. 1968. Commonwealth Scholarship for a Master's program in Applied Entomology at Imperial College, University of London, England.
6. 1969 et seq. N.R.C. Scholarship, renewed annually, for postgraduate study and research towards a Ph.D. from the Pestology Centre, Simon Fraser University.

RESEARCH EMPLOYMENT

Summer 1966. Investigations on the toxic effects of pesticides on salmon and trout in New Brunswick (spruce budworm project) and Prince Edward Island (agricultural uses). Federal Department of Fisheries, Government Building, Bedford Row, Halifax, Nova Scotia.

Summer 1967. Investigations on the influence of light, temperature, and species of prey on the population growth of a unicellular, bioluminescent marine organism. Dr. F. Uhlig, Biologische Meeresanstalt Helgoland, West Germany.

TEACHING EXPERIENCE

Summer 1968. Lab supervisor for an advanced course in marine algae. Dr. L.A. Hanic, Department of Biology, Dalhousie University, Halifax, Nova Scotia.

TEACHING EXPERIENCE (continued)

Autumn 1971. Teaching Assistant for Biology 003, "Human Ecology and the Population Explosion".
Dr. A. L. Turnbull, Department of Biological Sciences, Simon Fraser University.

WORK OBJECTIVES

My main research interests lie in two particular aspects of arthropod population dynamics:

1. The theory and practice of management of insect pests, particularly where this involves the use of biological agents in programs of integrated control.

2. The use of computer simulation models to handle the complexity of those ecological processes which underlie pest control problems.

SOCIETIES

1. Entomological Society of Canada
2. Entomological Society of Ontario
3. Centre International de Documentation Arachnologique
4. British Arachnological Society
5. Arachnologists of the South West
6. American Arachnology

PRESENTATIONS

1. "The deleterious effects of the human population explosion on the well-being of mankind". Presented at a Vancouver High School on invitation of the United Nations Association of Canada.

2. "Predatory tactics of the wolf spider, Pardosa vancouveri Emerton", a progress report on research work given at Simon Fraser University.

3. "Components of the functional response to prey density in an unspecialized predator, Pardosa vancouveri Emerton (Araneae: Lycosidae)". Presented at the 21st Annual Meeting of the Entomological Society of Canada and the 70th Annual Meeting of the Entomological Society of British Columbia, held concurrently at Victoria, B.C., August 24 to 26, 1971.

4. "Predatory behaviour of an unspecialized predator, the wolf spider". Presented before the Zoology Department at the University of British Columbia.