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SELECTIVE PREDATION IN A POLYPHAGOUS INVERTEBRATE PREDATOR, *Pardosa vancouveri* (ARACHNIDA, ARANEAE)

by

Robert George Holmberg

B.A.(Hons.), University of Saskatchewan, 1970

M.Sc., University of Saskatchewan, 1971

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

SIMON FRASER UNIVERSITY

July 1978

Frontispiece. Adult female *Pardosa vancouveri* feeding on a "small" *Tenebrio molitor* larva (X 11).

APPROVAL

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Selective predation by a generalized invertebrate predator, *Pardosa vancouveri* (Arachnida Araneae)

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ABSTRACT

Selective predation (i.e., non-random feeding) was studied in a laboratory system that allowed individual lycosid spiders, *Pardosa vancouveri*, to feed on prey populations consisting of one or two kinds of insects. Various combinations of male and female fruit flies (*Drosophila melanogaster*), 'small' and 'large' beetle larvae (*Tenebrio molitor*), and nymphal milkweed bugs (*Oncopeltus fasciatus*) were used as prey. Spiders of both sexes and two age classes were used as predators. In 14 experiments, the spiders showed strong selection in six, moderate to weak selection in five, and very weak or no selection in three. Generally, fruit flies were selected by the spiders over mealworms or milkweed bugs, and 'small' mealworms over 'large' ones. Very weak or no selection occurred between male and female flies and between beetle larvae and milkweed bugs. Subadult and adult spiders always showed similar selective tendencies. Prior feeding experiences did not alter feeding selections, but changes in the physical complexity of the environment did. Thus, by adding tree leaves to the cages, the number of flies eaten by the spiders decreased significantly.

Potential benefits to the spiders which were measured included percent maturing, percent surviving, rate of weight gain, size gain, and production of false egg-sacs. In prey combinations that produced moderate to strong selection, 7 out of 28 benefit measurements statistically favored the spiders. Prey combinations that produced weak selection tendencies gave no benefit measurements (N = 26) that statistically favored the spiders. Spiders fed the less-selected prey exhibited no benefits that were superior to those fed the more-selected prey. Spiders fed the more-selected prey did just as well as spiders fed both prey. It is hypothesized that this particular selective predation process involves prey sampling, memory of prey attributes, and selection of prey that possess certain attributes. Selected prey seem to confer certain benefits to the predator. As most benefits were associated with increased biomass within time limits, *P. vancouveri* tends to be more an energy maximizer than a time minimizer.

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INTRODUCTION

1. General Introduction

Before we can predict population changes accurately or learn how to manage populations efficiently, we must first understand which processes regulate them. The actual causes of natural population changes have been vigorously debated since the beginning of this century. Though most ecologists now agree that many environmental factors influence the number of organisms that exist at any given time or place, they conclude that, for animals, food relations are an important part of this process. Some ecologists go further and claim that only the constantly changing balance between food and feeders provides the necessary feedback relationships that maintain the peculiar combination of stability and variability that is characteristic of animal populations.

In order to live, all animals must feed on organic molecules which are obtained from other organisms. Animals have thus been classified as to what they eat (e.g., carnivores, herbivores, insectivores, omnivores), where they eat (e.g., endoparasites, ectoparasites, arboreal feeders), and how they eat (e.g., filter-feeders, grazers, predators).

Animals can also be classified according to their range of acceptable food items. This range varies considerably.

Some animals feed only on one species (i.e., monophagy) or a very limited number of species (i.e., oligophagy); most feed on many species (i.e., polyphagy).

While an animal may obtain food from a number of sources, some acceptable sources are used more frequently than others. This non-random feeding processs is called selective feeding. Though selective feeding is often called food preference or food choice, it may not be clear whether active preference or choice is actually being carried out. Observed differences in feeding frequencies may simply reflect differences in the number of encounters between the food and the feeders or the ability of the feeders to obtain and ingest the food. Furthermore, even if it is proven that a feeder actively selects certain foods, the question still arises as to why it selects these foods and not others.

This thesis is concerned with (a) whether a polyphagous predator (a predator is defined here as an animal that kills and eats other animals - - its prey) is capable of certain forms of selective feeding and (b) whether the selective feeding benefits the predator in terms of its survival and reproduction.

The predator used in this research was the wolf spider Pardosa vancouveri (Emerton). The method of detecting selective predation compared the numbers of each kind of prey eaten in environments where only one kind of prey was

was available with those eaten in environments containing two kinds of prey.

2. Significance of Selective Predation to Biology

Selective predation is important to a number of theoretical aspects of ecology, behavior and evolution, as well as to the applied areas of population management and biological control.

In the area of ecology, observations that animals do not use all of the potential foods in their environments have led to:

(a) the concept of the trophic niche (Elton 1927);

(b) much of competition theory including the competitive displacement principle (De Bach 1966);

(c) the theory that predators help maintain species polymorphism (Lees and Creed 1975) and community diversity (Paine 1966, MacArthur 1972, Schoener 1974);

(d) the suggestion that the food selection processes can be used to determine which populations are limited by food resources (Emlen 1966);

(e) the idea that these processes can be used to discover how energy is partitioned within food webs (O'Neill 1969); and

(f) the concept that when the relative abundance of prey species changes, the predators will 'switch' from feeding on certain prey to feeding on other prey and so maintain stability of prey populations (Elton 1927, Murdoch 1969, Murdoch and Oaten 1975).

It should also be noted that, in mathematical modeling of predator-prey systems, the numerical, functional and developmental responses of predators to their prey (Holling 1965) and the optimization of energy resources (Cody 1974) will be affected when more than one kind of prey is available to a predator.

In the area of behavior, selective predation supposedly has led to certain methods of prey recognition (Tinbergen 1960) as well as to certain hunting and escape tactics (Holling 1966).

Though all of the above points relate directly or indirectly to evolution, workers in this area of biology are especially concerned with how selective predation affects character displacement and sympatric speciation (Brown and Wilson 1956), the existence of mimics of unpalatable species (Holling 1965), and the development of defensive-offensive structures and mechanisms (Eisner and Meinwald 1966).

Various individuals and institutions associated with agriculture, fisheries, forestry, hunting and medicine are also concerned in one way or another with selective predation. They have to deal with such questions as:

(a) are coyotes going to continue to feed upon small rodents when sheep are available?,

(b) if we introduce trout into a stream, will there be enough suitable insects for them to eat?,

(c) will native birds turn from their normal diets to those that include large numbers of an introduced forest pest?,

(d) do wolves kill more 'non-trophy' than 'trophy' moose?, and

(e) does the mosquito-fish really feed on disease-carrying mosquitoes and not on harmless crustaceans?

Selective predation is also important in the area of biological control. Before a predator is released to control a pest, work must be done to ensure that the predator does in fact feed on the pest and not on a beneficial species, that it can survive on alternative prey when the pest population is low, and that it can compete with native predators. Raising predatory animals for biological control purposes may also cause problems. For example the food that the predators initially eat in captivity (i.e., 'pre-feeding') may affect the predators' later feeding behavior when they are confronted with other kinds of prey.

3. Components of Selective Predation

Hutchinson (1959) stated "It has long been realized that the presence of two species at any [trophic] level, either of which can be eaten by a predator at a level above, but which may differ in palatability, ease of capture or seasonal and local abundance, may provide alternative foods for the predator." This quote summarizes the major factors that affect selective predation. In most studies of this process, however, the factors are not clearly defined. This has led to some confusion about the meanings of such words as selection, preference and palatability.

Selective predation is here defined as occurring when a predator that is exposed to a mixture of possible prey feeds on certain kinds of prey more frequently than would be expected from the relative abundance of each prey kind. In other words, selective predation means non-random feeding; prey are selected on some basis other than the chances of predator-prey encounters. Selective predation can be produced by a number of factors, including such things as availability, catchability and preference. These factors are considered below.

a. Availability Factors

The factors that influence prey availability to predators fall into three groups: (i) coexistence in time and space, (ii) density and (iii) distribution.

Before any predator-prey contacts are possible, both animals must coexist in time and space. If this condition is not met, the availability of the prey is zero. Coexistence in time relates to migration, both seasonal and daily, and to life cycle strategies. Coexistence in space involves such abiotic factors as temperature, light, moisture and substrate. It is also related to the tolerance limits of the animals and the role these factors play in determining micro- and macrohabitats.

If the above conditions of coexistence are met, then the degree of availability may depend upon the density of both prey and predators. Normally, as prey density increases, the number of contacts between prey and predators also increases. This in turn results in increased predation. The amount of predation continues to increase with increases in prey density until a point is reached where predation rates tend to be constant, even if prey density increases further. This relationship was called a functional response by Solomon (1949).

Note that if the relative frequency of encounters is the only factor affecting the number of prey captured, then predation is non-selective. Selection exists, however, if there is a prey density below which prey are not eaten even though predator-prey contacts do occur, or if there is a prey density above which prey are eaten at a higher rate than would be expected from their relative density.

Solomon (1949) also described a numerical response that is related to predator density. Numerical response includes the long term consequences of functional response which affect the survival, reproduction and migration patterns of the predators. Further, it should be remembered that increases in predator density usually cause increases in competition for prey. An exception is found in social predators where a minimum number of animals is necessary for the benefits of cooperative hunting.

With respect to distribution, organisms are classified as being distributed in a random, uniform or clumped manner. The availability of a prey to a predator will depend on the conformity of the predator's searching behavior wth the distribution of the prey. For a randomly dispersed prey, the best search pattern for a predator is a random traverse of the environment; for an evenly dispersed prey, a systematic traverse; and for a clumped prey, a random traverse until a prey is detected, then a systematic search in the vicinity of that prey.

b. Catchability Factors

Catchability, a term used by Rapport and Turner (1970), refers mainly to the aspects of morphology and behavior of both predators and prey that are involved when a predator stalks, captures and consumes a prey.

Prey possess a wide variety of defensive structures and mechanisms for use against predators. These include: spines, armor plating, teeth and claws; urticating hairs, stingers and obnoxious odors and tastes; cryptic forms, colors and behaviors; autotomy; rapid escape movements, schooling behavior, flash alarm displays and warning colors; and forms, colors and behavior that mimic dangerous animals. All prey have some of these devices, but no prey has them all.

On the other hand, predators have an equally diverse array of structures and mechanisms useful for capturing prey: sharp teeth or mandibles; grasping legs; claws; protective integuments; venoms; silk snares; cryptic colors and forms; ambush and pursuit tactics; and rapid attack and capture movements. As with the prey, all predators have some of these devices, but no predator has them all. As a result of these adapations, a predator may overcome some of the prey defences some of the time, but not all of the defenses all of the time.

Size is also important in determining whether a predator does or does not capture a certain prey. Prey that are too small or too large may be physically unavailable to a predator because of the nature and size of its food acquisition apparatus. Also, for any given predator, there is an optimal size of prey. As prey depart from the optimal size, they become less and less catchable (Holling 1965, Brooks and Dodson 1965, MacArthur 1972, May 1974, Schoener 1974, O'Brien et al. 1976, Hall et al. 1976, Goss-Custard 1977). As prey become less catchable, they may require too much of the predator's time and energy per unit of prey obtained to be worth eating.

Finally, the state of health (i.e., the amount of physical injury, disease, parasitism, pesticide poisoning and malnutrition) of both the predators and prey affects the catchability of any prey.

c. Preference Factors

'Preference' is often used as a catch-all term to include the factors involved in availability and catchability as well as all the physiological and possibly psychological factors that influence a predator's decision to eat or reject an available and catchable prey. Here <u>preference</u> is defined as the innate or learned attributes of an animal that predispose it to expend relatively more time and energy to locate and ingest certain food items than it would expend on other available and catchable food items. Preference can be detected in predators that take more of certain kinds of prey when a number of other prey items are both available and catchable. It is possible that preference is expressed only when a surplus of food is available.

Palatability is defined here as the extent to which a food item is 'agreeable', in terms of its taste, odor and texture, to a feeder. It is not equivalent to, but is a part of, preference. Palatability is influenced by the kinds of 'short range' sense receptors on the ingestion organs of the feeder as well as by the structural and chemical characteristics of both the external and internal features of the food. What is palatable to one feeder may or may not be palatable to another. What is palatable to a feeder at one time may or may not be palatable to the same feeder at another time (Holling 1965).

The digestive capability of predators is a factor of preference that does not come into play until after ingestion. It may act as a delayed palatability factor in organisms, such as birds, that do not have very sensitive odor and taste receptors (Brower et al. 1968).

It must be remembered that:

(a) high palatability is not necessarily associated with a high degree of preference (i.e., a food may taste

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'good' but may not be preferred or it may be preferred but tastes 'bad'), and

(b) high palatability is not necessarily associated with a highly nutritious food (i.e., it may taste 'good' but may provide little or no food value to the feeder).

Hunger is a major factor affecting preference. As hunger increases, predators start to feed on prey which were previously not extensively used for food (Young 1945; Ivlev 1961; Holling 1965, 1966; Pritchard 1964; Emlen 1966).

The physiological ages of both the predators and the prey are important in preference. At different times in its life cycle, a predator may require different kinds of foods. For example, it may require a diet high in protein only at times of egg laying. Another point is that the usefulness of a prey to a predator may change as the prey ages and the relative proportions of potential nutrients change.

In summary, the most preferred prey is not necessarily eaten most often by a predator. Preference as a criterion of food selection is always compromised by the factors of availability and catchability. If the density of the most preferred prey is low, or the prey is very difficult to catch, the predator may not even attempt to search for it.

4. Past Studies of Selective Predation

The close relationships between the populations of a predator and its prey have long intrigued both biologists and mathematicians. Since the 1920s, many mathematical models have been produced (see Royama 1971, Hassel 1976) which try to predict, at any moment in time, the number of the prey (which is constantly reduced by predation) and the number of the predators (which is restricted by the number of prey).

Though these models have formed the basis of many of our present concepts about population regulation by predation, they have a number of deficiencies. As they are largely deductive mod~~els~~ based on a few simple assumptions that can be readily fitted into simple mathematical equations, ~~they~~ fall short of describing the observed behavior of animals. Most of these models also assume that the frequency of predation is based on random encounters between predators and prey and that predators are strictly monophagous. If there is more than one kind of prey available, then it is tacitly assumed that the only difference between them is their frequency of occurrence. None of the prey species supplies more worth to the predator than any other, and costs of capturing all prey are the same. These assumptions severely limit the usefulness of the mathematical models so far produced. A recent exception to this is a model produced by Krebs et al. (1977) that incorporates prey with different energy values.

Elton (1927), when speculating on the reason predators seldom over-exploit their prey, concluded that "... most carnivores do not confine themselves rigidly to one kind of prey; so that when their food of the moment becomes scarcer than a certain amount, the enemy no longer finds it worthwhile to pursue this particular prey and turns its attention to some other species instead." Though this idea has been around for 50 years, very little has been added to it (Murdoch 1969).

To state Elton's idea a little more precisely - he proposed two (or more) kinds of prey populations, say Prey 1 and Prey 2, and one kind of predator population that initially feeds almost exclusively on Prey 1, the more abundant prey. Partly because of predation, Prey 1 declines in numbers to the point where the predator no longer obtains enough food from it. Instead of the predator declining in numbers because of starvation, as is usually proposed in mathematical models, the predator stops feeding on Prey 1 and 'switches' to another prey such as Prey 2. This indicates that Prey 2 is an acceptable food source and raises the question of why Prey 2 was not part of the predator's diet previously. There are several answers to this question.

One answer is supplied by Tinbergen (1960). He suggested that a predator normally will form a 'search image' for a particular prey and will confine much of its feeding to that prey as long as the prey remains above a certain threshold density. This theory implies that there is an advantage to the predator of confining its search and capture activities to a limited number of prey types at any one time. If switching to other prey in itself requires expenditure of resources, then switching should be minimized. Thus in the above example, the predator had a search image for Prey 1 and would not feed on Prey 2 until Prey 1 failed to meet the predator's food requirements.

A second possible answer is that predators have preferences for certain kinds of prey and will select the preferred prey as long as they are available. This mechanism implies that preferred prey give more benefits to the predator than non-preferred prey. In the Elton model, the predator preferred Prey 1 and continued to eat it until it was unavailable. Then the predator switched to feeding on the less preferred Prey 2.

Holling (1965) has brought these two explanations together in vertebrate predators by explaining Tinbergen's search image in terms of 'learned preferences' based on the 'palatability' of the prey. He proposed that at a high level of hunger, a predator will sample any potential prey item.

When any prey is eaten, its degree of palatability-unpalatability will be associated with some recognizable feature of the prey and will be remembered for a certain length of time. As long as encounters with known palatable prey are frequent enough (i.e., high prey density) to keep the hunger level low, the predator forms a search image and predominantly feeds on known palatable prey. However, when encounters are infrequent (i.e., low prey density), the palatability of the previously preferred prey is forgotten, the prey is dropped from the predator's diet, and as hunger increases, the predator becomes more polyphagous. This continues until the predator discovers a new kind of palatable prey and begins concentrated feeding on it.

This outcome is similar to Emlen's (1966) model in which he assumed that predators ought to adapt a feeding strategy that gives a maximum amount of energy per unit of time. Emlen argued that when prey are abundant, the best strategy is to select only 'preferred' prey, but when prey are scarce, the best strategy is to exploit all available prey.

Murdoch (1969) has also examined the process of selective predation from the aspect of predators (i.e., snails) switching from one prey to another. He concluded that switching occurs rarely and only under certain circumstances. These circumstances occur when the degree of selective predation is weak or absent or when the predators feed on only one kind of prey for a time before other prey become available to them. One of the difficulties with Murdoch's experiments is that the predators, when released from starvation conditions, ate less than predators that were fed regularly. This raises the following problem. If the snails were not stimulated to feed even after a month without food, there would not be any (hunger induced) reason for the predators to switch from the 'preferred' to less 'preferred' prey when the 'preferred' prey were still available at low densities. Remember that Elton's model requires a shortage of 'preferred' prey to stimulate feeding on alternative prey and that Holling's model requires an increase in hunger caused by a shortage of 'preferred' prey to stimulate attacks on alternative prey.

5. Economic Models

Recently, economic models have been used to describe biological phenomena, including predator-prey relationships (Schoener 1971, Cody 1974, Covich 1976, Rapport and Turner 1977). In general, models concerned with predation attempt to predict how predators allocate their resources (e.g., time, energy) to obtain certain amounts and kinds of prey. These economic-ecological models fall into three categories: consumption models, production models and producer-consumption models (Rapport and Turner 1977). As there are definite analogies, and perhaps even homologies, between these economic models and selective predation, I have briefly outlined their similarities and differences below.

a. Consumption Models

In economics, the goal of an optimal consumer is to maximize utility within budget or income constraints. Schoener (1971) described an ecological model to determine the utility of maximizing energy intake per unit time versus the utility of minimizing time needed to obtain a specific amount of energy - all within the constraints of such things as the time and energy available to a foraging animal.

Cody (1974) presented a model for maximizing the utility of certain measures of biological fitness (e.g., reproduction) within the restraints of time and energy expended in searching for food. He concluded that when prey types are available that can result in maximum fitness, a predator will feed only on those prey, that is, the predator acts as a specialist. As the number of these 'preferred' prey declines, it becomes more economical for the predator to be a generalist (cf. Emlen 1966).

b. Production Models

In the production area, the economist is concerned with the amounts and costs of inputs such as capital, labor and land and the amounts and revenues of outputs such as goods and services. The ecologist is concerned with the amounts and costs of time and energy that are expended to produce offspring which, in turn, vary in numbers and viability. Reproduction, in predators, can occur only when the costs of obtaining the prey are less than the benefits derived from the prey. In the economist's terms, the revenue must be greater than the cost. The amount of benefits derived and the rate at which they are derived help determine whether the organism produces many small batches or one big batch of offspring (Gadgil and Bossert 1970).

c. Producer and Consumer Models

This is the realm of supply and demand curves. The economist deals with such things as the amounts and costs of goods and services available to the consumer (i.e., supply) as opposed to those purchased by the consumer (i.e., demand). The ecologist deals with such things as the amounts of prey available to predators at certain times as opposed to the rates at which the prey are eaten. These factors lead to feedback relationships. In economics, increased consumption stimulates further production. In ecology, consumption first leads to a loss in the number of prey capable of reproduction. However, in the long run, increased predation may promote increases in the number of young produced by the prey because of the reduction of intraspecific competition within the prey population. Also, in evolutionary time scales, both the predators and the prey tend to evolve structures and/or mechanisms to increase, respectively, the facilities to hunt and to escape.

Another example of an attribute of supply and demand curves that does not (at first) seem to apply to predator-prey systems is the area of "brand loyalty". It is well known that humans will often continue buying a certain trade name of merchandise even if they are provided with evidence that other brands are cheaper and have the same or even more utility. This situation may be similar to predators that do not switch to alternative prey when it seems to human observers that it is to their benefit to do so.

There are differences, however, between economics and ecology with respect to these models. In economics, producers normally compete to have their products consumed. Obviously, prey do not normally compete to be consumed.[1] Another difference is the mechanism for measuring revenues and costs. In economics, money, which has no intrinsic value in itself, is usually used to produce equivalent units. In ecology, energy, which is of use to the organisms concerned, is the usual standard of measurement.

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[1] Possible exceptions to this are birds that 'advertise' themselves as potential prey by calling and feigning broken wings when predators come too close to their nests.

One common problem with economical-ecological models that are concerned with supply and demand curves is the assumption that the consumer has complete information about the selection situation. This is, of course, not the case. A predator about to pursue a prey does not have knowledge about the quantity or quality of the next prey that may or may not be just "coming 'round the corner". Nor does it know the exact probability of the prey escaping or the potential of the prey to inflict physical injury. The predator can only deal with the limited pieces of information that it has about past and present events. However, it is usually assumed that the net result of a number of selection situations is the same as if each predator had complete information about each situation.

6. Utility of the Prey Selection Process to Predators

All models concerned with food selection processes assume that the result of selection is associated with food quality. In other words, animals 'like' those foods that are 'good' for them and 'dislike' those foods that are less nutritious or harmful. This assumption follows from conventional evolutionary theory. That is, most of the traits associated with catchability and preference are genetically controlled and are selected for according to the degree of reproductive advantage the traits supply to the individuals who possess them. Thus, the traits that lead to acquisition of superior foods are retained in the population and the traits that lead to inferior foods are eliminated.

Figure 1 is a model of the factors that affect a predator's 'decision' to eat or not to eat a certain prey. The model centers around a utility function that is influenced by the factors of availability, catchability and preference (as discussed in the last section) as well as such factors as the predator's 'fitness strategy'.

To the predator, the utility of any prey is the difference between the 'revenues' and 'costs' associated with capturing, ingesting and digesting that prey. That is, revenues - costs = utility. Revenues include the increases of energy and nutrients that the prey will confer to the predator. Costs include the losses of time, energy and nutrients associated with the act of predation. Encounters with noxious chemicals and physical injury resulting from capture are two examples of costs.

If the above equation results in a positive utility (i.e., benefit), motivational drives in the predator, such as hunger, are reduced. The resources gained are usually first used in maintaining body functions for survival while the rest go for maturation (i.e., growth and development), reproduction (i.e., gamete production, mating, care of

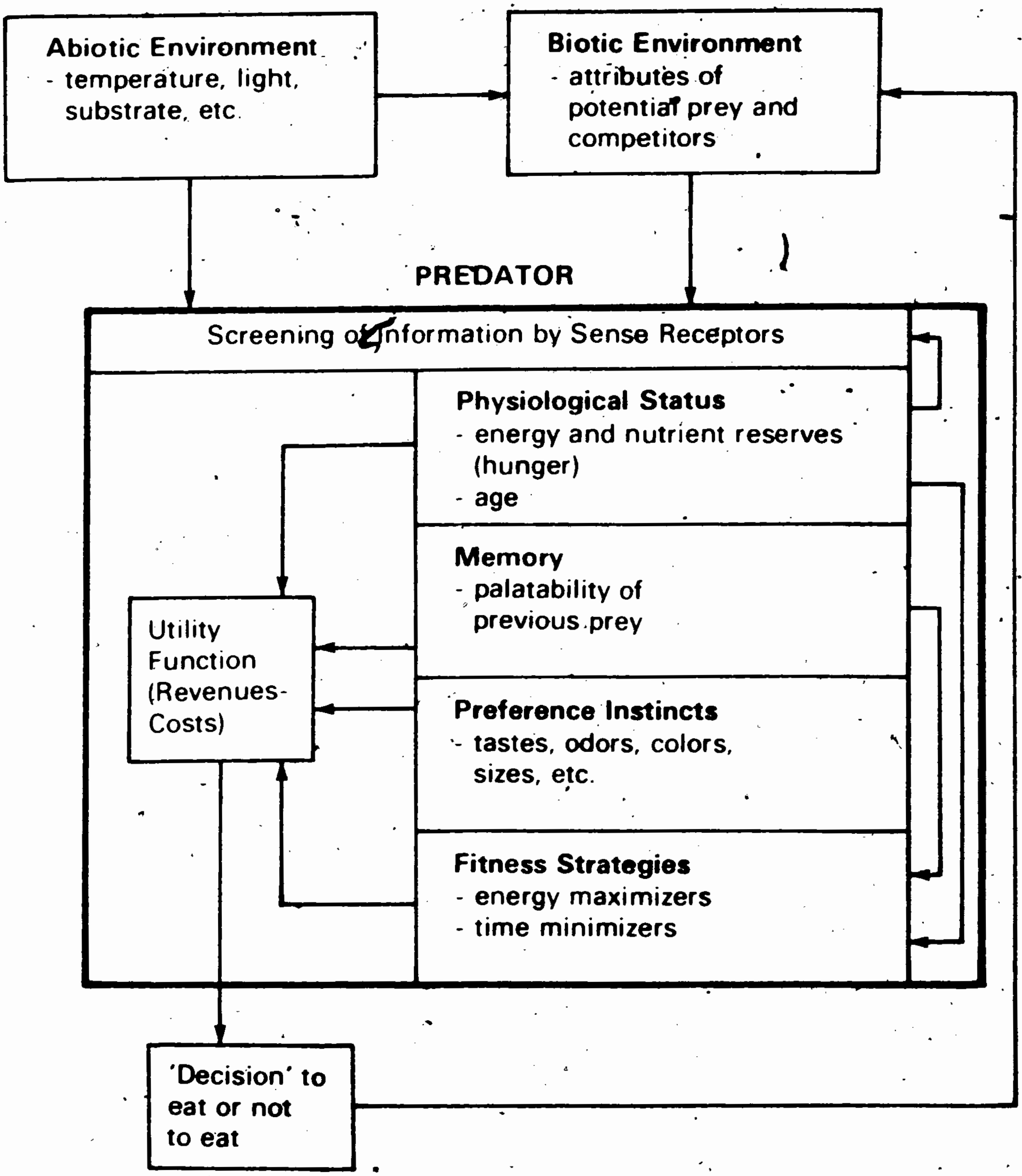

Figure 1. Factors that affect the 'decision' about whether a predator does or does not eat a certain prey.

offspring) and dispersal (i.e., exploitation of new or under-exploited habitats).

The utility function can also result in a negative utility (i.e., loss). For example, this may happen when a predator encounters an unfamiliar prey or when a predator eats a prey that is highly palatable but non-nutritious. However, if the predator persists in this line of activity, it will eventually die of starvation.

How an organism apportions the use of its benefits from feeding between survival, maturation, reproduction and dispersal is often called its fitness strategy. It is generally assumed that organisms tend to increase fitness by maximizing potential benefits.

Schoener (1971) described two extremes of fitness strategies. The energy maximizers are one extreme. "These are animals whose fitness is maximized when net energy is maximized for a given time spent feeding." Animals following this strategy exhibit a relatively fixed age of maturation. However, the number of offspring that they produce varies directly with the amount of energy that they have accumulated during a fixed time interval. For example, passerine birds tend to mature at the same time but their clutch sizes vary with their nutritional histories. The time minimizers are the second extreme. "These are animals whose fitness is maximized when time spent feeding to gather a given energy requirement M is minimized..." Schoener goes on to say, "...no reproductive output is achieved until M energy units are gathered, and energy beyond M gathered during [time period] P does not further increase expected reproductive output..." This strategy tends to minimize development time and may lead to increases in the number of generations produced per season. It is advantageous to those animals that produce a fixed number of offspring per clutch, have a variable number of clutches per year, are parthenogenic, or do not need synchronous maturation of the two sexes.

Schoener's work leads to a number of criteria for describing predators, which select prey from a number of alternatives available to them, as either energy maximizers or time minimizers. Energy maximizers should have the following characteristics:

(a) synchronous maturation of local populations,

(b) increase in body size and/or weight of adults is correlated with increases in number and/or vigor of offspring produced, and

(c) survival of young increases with increases in parental care.

Time minimizers, in order to fully exploit available energy supplies, should have the following characteristics:

(a) variable age of maturation,
(b) variable rate of growth, and
(c) maturation after achieving a threshold weight or size.

If the adults of time minimizers are capable of reproduction after the first clutch of eggs is produced, there are two more characteristics that can be measured. These are:

(i) a varying duration of adult survival after maturity, and
(ii) a varying number of clutches produced after maturity.

7. Objectives, Approach, and Limitations of Present Study

The first major objective of this study was to determine whether a common type of polyphagous invertebrate predator, a wolf spider, was capable of selective predation when the factors of availability and catchability were greatly reduced. The second major objective, providing that the predator was found to be capable of selection, was to determine whether the prey selected benefited the predator in terms of improving its chances of maturing and reproducing.

Though naturalists have long recognized the concept of selective predation, it has only recently been studied in a quantitative way. Manly et al. (1972) reviewed four basic approaches to the measurement of selective predation. The first method compares the number of prey sampled from an environment by a predator with the number of prey sampled from the same environment by an investigator. The second method analyzes differential predation by the use of mark and recapture techniques. The third method repeatedly offers prey in alternative pairs and the frequency of each prey eaten is compared with the frequency with which they were presented. In the fourth method, sample populations of two test prey are presented to predators and after a certain fraction of the total number of prey is eaten, the experiment is stopped and the numbers of each prey eaten are compared.

The first two methods are suitable for estimating selective predation of natural or field populations. However, these methods have major difficulties associated with obtaining accurate estimates of: the relative abundance of each prey species, the numbers of prey eaten, emigration and immigration, and non-predator mortality of prey. The last two methods are suitable for laboratory experimentation but possess difficulties in presenting prey in ways that do not prejudice the choices made by the predators, and in dealing with changing proportions and densities of the prey species as predation depletes their numbers. Both methods are suitable only for short term experiments and thus are of little value in estimating any benefits that might accrue to the predators from the selections made.

Though each method has its own advantages and disadvantages, all have a common problem. All are based on the assumption that if the proportions of the various kinds of prey eaten by the predators differs from the relative density of each kind of prey in the environment, the predator is discriminating between the prey types. That is, the predator 'prefers' certain prey over others. It is my view that this assumption is not necessarily justified because of the possible, but perhaps unknown, differences in the availability and catchability of various prey that may greatly exceed the differences related to preference.

Rapport and Turner (1970) proposed a method of assessing selective predation that attempts to overcome most of the complicating issues of availability and catchability. Basically, their method estimates the feeding rates of predators in situations where only one prey type is available to situations where many prey types are available at one time. This method was used in the present study and is described in detail in the next section.

As stated above, the term 'benefits' refers to any feature of growth and/or development that results in a gain of usable energy, time and/or nutrients. These gains are assumed to increase the chances of survival and reproduction of the feeder. It is difficult to predict on an *a priori* basis what constitutes a benefit to *P. vancouveri*. However, keeping Schoener's (1971) ideas on energy maximizers and time minimizers in mind, the following are tentatively consider[illegible] as possible benefits:

(a) anything that increases the probability of the predator surviving to the reproductive stage;

(b) anything that reduces the time required by the predator to reach sexual maturity;

(c) anything that increases the size and vigor of the adult predator; and

(d) anything that increases the number and viability of the offspring.

The actual characteristics tha[illegible]ere measured are described more fully in the next section.

MATERIALS AND METHODS

1. Predator

Adult and subadult wolf spiders, Pardosa vancouveri (Emerton) (Lycosidae), were used as predators.[1] This spider species is commonly found near or on short herbaceous vegetation in open areas of forests of coastal British Columbia, Washington and Oregon. It does not spin webs, but does produce drag-line silk. It captures prey by a combination of ambush and stalking. Because spiders ingest only liquid food, they produce food balls or 'rejectamenta' made of unconsumed remains of their prey. The rejectamenta were used to help estimate the number of prey eaten.

P. vancouveri has a one year life cycle. The immatures overwinter and moult into adults in the spring.[2] Immature spiders that were suitable for experimentation were available between September and May and the adults between May and July. For most selective predation experiments, immatures were collected in September or October.

Specimens were collected with mechanical aspirators

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[1] See Vogel (1970) for taxonomic characteristics.

[2] For examples of the life histories of other lycosid spiders, refer to Englehardt (1964), Eason and Whitcomb (1965), Vlijm and Kessler-Geschiere (1967), Eason (1969), Edgar (1971), Van Dyke and Lowrie (1975) and Humphreys (1976).

(Husbands 1958) from cleared areas in a second growth forest on the south slope of Burnaby Mountain, British Columbia (latitude 49° 16'N, longitude 122° 55'E). The cleared areas contained patches of bare ground and clumps of pioneering plants. Spiders were either used immediately or, more usually, stored in individual containers at ca. 2 °C until required. The storage containers were 36 ml glass shell vials stoppered with cotton. Water was supplied by means of cellulose sponges or dental rolls.

2. Prey

For these experiments the ideal prey should have the following characteristics: 1) acceptable to the predator, 2) easy to rear and handle in large numbers, 3) not cannibalistic, 4) not predacious on nor detrimental to other prey, and 5) able to survive without food for at least two days in the experimental cages. It was desirable to keep prey without food during the spider feeding experiments because spiders can ingest non-living food, that is, food meant for the prey (Peck and Whitcomb 1968).

Five types of test prey were used: male and female fruit flies, two sizes of beetle larvae, and one size of nymphal bug. Though not all of these prey completely fulfilled the above criteria (see Part 1 of the Results section), they were satisfactory for my purposes. The rearing, separation and handling methods of the test prey are outlined below.

a. *Drosophila melanogaster*

Adult male and female vestigial-winged fruit flies, *Drosophila melanogaster* Meig. (Drosophilidae), served as two types of prey. Flies were reared in the laboratory in sterilized 500 ml Erlenmeyer flasks stoppered with cotton and cheesecloth plugs. The medium consisted of ca. 30 g Carolina Instant *Drosophila* Medium No. 67-5002 (Carolina Biological Supply Co.), ca. 23 mg dry yeast and 75 ml tap water. Ten female and 10 male flies were added to start new cultures. The first generation started to emerge after 14 to 15 days under laboratory conditions. Each culture produced about 1000 flies within 20 days. 'Standard' flies were adults that had emerged from cultures that were 14 to 21 days old. Only standard flies were used for test prey and to start new cultures. 'Non-standard' flies (i.e., adults from cultures that were older than 21 days) were occasionally used to feed spiders prior to the actual experiments.

b. *Tenebrio molitor*

Two sizes of mealworms, larval *Tenebrio molitor* L. (Tenebrionidae), also served as prey. The beetles were reared in 10 l plastic buckets kept at 20 to 25 °C. Bran, occasionally supplemented with fresh slices of apple, was used as food. The larvae were sized by allowing them to crawl down through a series of four sieves. The openings were 1.52 x 1.64 mm for the first sieve, 1.08 x 1.36 mm for the second, 0.88 x 0.96 mm for the third, and 0.32 x 0.32 mm for the fourth. After one to two hours, 'large' larvae were removed from the second sieve and 'small' larvae from the fourth. Larvae not eaten by spiders within two days were put in holding containers with bran until needed again. These larvae were allowed to feed at least one day before being re-sieved and re-used. Because the strength of the cuticle of _T. molitor_ may have been an important factor in their catchability by the spiders, only larvae with fully sclerotized and pigmented cuticles were used.

c. _Oncopeltus fasciatus_

Nymphal milkweed bugs, _Oncopeltus fasciatus_ (Dallas) (Lygaeidae), served as the fifth prey type. The bugs were reared in the laboratory in 3.5 l glass jars. Cracked seeds of sunflower, _Helianthus annuus_ L., were used as food. Dental rolls, partially inserted into 125 ml Erlenmeyer flasks, acted as wicks to supply water to the bugs. Cotton balls served for oviposition sites. Nymphs were sized by the same sieves used for _T. molitor_ but the sequence of sizes was reversed as the nymphs tended to move upwards. Sunflower seeds and wet sponges, placed on the top sieve, stimulated upward movement through the sieves, separation taking place overnight. Nymphs used in the experiments came from the same size sieve as the small T. molitor. Nymphs not eaten by the spiders within two days were re-sieved and re-used only after at least one day of feeding by the bugs.

3. Handling Methods, Cages and Laboratory Conditions

The spiders and D. melanogaster were handled with aspirators; T. molitor and O. fasciatus with flexible microdissection forceps. Fluon (an aqueous dispersion of polytetrafluoroethylene, Imperial Chemical Industries Ltd., Welyn Garden City, England) was applied to the inner surfaces of holding containers to minimize the number of escapes of spiders, flies and bugs. Fluon produces a surface on which arthropods find it difficult to climb (Radinovsky and Krantz 1962, Ebeling and Wagner 1963, Storch 1968).

Two kinds of cages were used, plastic and wooden. The plastic cages were transparent 'Lustoware Refrigeration Dishes' (Bordon Chemical Co., Columbus Plastic Products Division) modified by removing 6 x 6 cm pieces of the lids and covering the resulting holes with plastic screen (maximum size of openings 0.32 x 0.32 mm). Inside dimensions were 7.2 x 7.5 x 9.3 cm. The wooden cages had a back of plastic screen (maximum size of openings 0.52 x 0.56 mm) and a sliding front panel of clear plastic. Inside dimensions were 5.5 x 7.6 x 7.6 cm (Nicholls, 1970). Unless otherwise noted, plastic cages were used in the experiments.[1] The wooden cages were mainly used in 'pre-feeding' spiders (i.e., feeding the spiders in the laboratory with prey before the actual experiments).

Temperature was regulated in the laboratory by a thermostatically controlled gas furnace and an air conditioner. The mean temperature was ca. 23 °C.

Relative humidity outside of the cages ranged between 33% and 68%. Water was supplied in the cages with 8 cm^3 pieces of cellulose sponge each of which held 5 to 7.5 ml. The sponges were re-wetted every second day. When spiders were kept for a week or more before or after experiments, water was supplied in 20 ml glass vials stoppered with cotton.

Most illumination came from two banks of four 40 W cool white fluorescent lamps suspended above the cages. These were turned on for 16 hr daily (08:00 to 24:00 local time) and provided a minimum of 200 to a maximum of 1200 lux inside the plastic cages and a minimum of 10 to a maximum of 600 lux inside the wooden cages. Light intensity varied due to the position of the cages with respect to the lamps. Supplemental light was periodically provided during working

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[1] Experiment 6 (see Results section) used wooden cages.

hours by similar ceiling lamps covered with frosted plastic. They increased the light intensity by about 20%. Natural and other external light was excluded by covering the laboratory windows with aluminum foil.

4. General Information on the Various Predator and Prey Classes

All linear measurements of predators and prey were done with a dissecting microscope fitted with an ocular micrometer. Measurements were recorded in eyepiece scale-units under 6X to 50X magnifications, and later converted to the nearest 0.01 mm. The length, width and height of the prey were measured at the largest part of their bodies but excluded the lengths of their antennae, legs and wings.

Mature spiders have fully developed palps or epigyna. Immature stadia were determined by measuring the width of the cephalothorax with a microscope and a simplified version of Seligy's holding apparatus (Seligy 1970). The apparatus consisted of a plastic cylinder, 25 mm in diameter and 30 mm tall, that was closed on one end by a circular glass coverslip cemented on with hot paraffin. A piston of plastic foam was used to hold the spider in place against the coverslip. A paired t-test performed on data derived from replicated cephalothorax measurements of adult female P. vancouveri showed no significant differences between repeated measurements ($P = 0.76$, $t = 0.31$, $df = 36$). Spiders that were considered to be prepenultimates (i.e., two moults from maturity) and that moulted once, were labeled as 'subadults'. Subadult males could be distinguished from subadult females by their expanded, but not fully developed, palps. The sexes of spiders younger than the subadult stage could not be distinguished consistently.

'Wet' weighings were done on live or freshly killed (with solid carbon dioxide) animals. 'Dry' weighings were done after more than three days of drying at 60 °C. A Mettler H20T balance (Mettler Analytical and Precision Balances, Zurich, Switzerland) was used for samples weighing more than 10 mg; and a Cahn Gram Electrobalance (Ventron Instruments Corp., Paramount, California) for samples weighing less than 10 mg.

Some general behavioral observations were made on the predators and prey in the cages to determine the availability of the various prey to the predators and any difficulty experienced by the predators in capturing a particular prey type. Prior to the selective predation experiments, the test prey were checked for the amount of mortality not caused by spiders and, to a limited extent, for compatability with other prey. Behavioral data on the prey and predators were obtained by observing the same animals once a day over a period of a number of days. A set of observations made on one cage, which contained one or more animals, is called an 'observation-day'. For example, observations made for 20 days on 10 cages with five *T. molitor* in each gave 200 observation-days. Details of the measurements, weights and behavioral information on the various predator and prey types are given in Tables A-I to A-V of Appendix I.

5. Test for Selective Predation

The general experimental design used to test for selective predation was a modification of that proposed by Rapport and Turner (1970). In essence, Rapport and Turner's method compares the numbers of each kind of prey eaten in environments containing only one prey kind with the numbers eaten in environments containing mixtures of these same kinds of prey. For instance, if a predator eats three of Prey 1 per day from an environment containing only Prey 1, and five Prey 2 per day from an environment containing only Prey 2, then, if the predator does not discriminate between the two kinds of prey on any basis and if all other factors are kept constant, the Rapport-Turner method assumes than in an environment containing both Prey 1 and Prey 2, the ratio of prey eaten is expected to be 3:5. If the observed ratio of the numbers of Prey 1 and 2 eaten deviates significantly from the expected ratio, it is taken as evidence that the predator differentiates between the various kinds of prey.

The method used to test for selective predation in this work differed from that reported by Rapport and Turner (1970) and Rapport et al. (1972) in the following points: 1) Densities of each prey in the two prey treatments were the same, rather than one-half the densities of the single prey treatments. This meant that, as long as there were no overcrowding effects, the amount eaten would be more comparable in all treatments. 2) The mean feeding rates of individual predators, rather than the relative discrimination coefficients (see Equation 6 below), were used to calculate the probability that selective predation occurred. This was done because of the uneven and limited number of replicates. Also, Rapport and Turner distinguished between catchability of prey and preference for prey, and claimed that their method can discriminate between these two elements of the selective predation process. It is my view that it cannot make this distinction completely, but that it is a valid method of testing whether or not selective predation occurs. This matter is elaborated upon in the Discussion.

In the experiments described here, prey types were tested individually and in pairs to determine whether predators differentially selected for either one of a pair of prey. For each pair of prey tested, three treatments were applied. One predator group was supplied Prey 1 alone at a density of D1, (i.e., Treatment 1) a second predator group was supplied with Prey 2 alone at density D2, (i.e., Treatment 2) and a third predator group was supplied a mixture of Prey 1 at density D1 plus Prey 2 at density D2 (i.e., Treatment 3). Density D1 did not necessarily equal D2.

Densities D1 and D2 were set at levels such that at all times more prey were available than the predators could catch in the time interval allowed, but below levels where inhibition of feeding, because of overcrowding, occurred. Previously, these densities were found to be 10 per cage per day of male and female *D. melanogaster* and *O. fasciatus* and 5 per cage per day for small and large *T. molitor*. It had also been determined that the predators could capture each of these kinds of experimental prey.

The three treatments gave four feeding rates (i.e., the number of prey eaten per spider per day): u_1 for Prey 1 alone, u_2 for Prey 2 alone, u^*_1 for Prey 1 when both prey were present, and u^*_2 for Prey 2 when two prey were present.

In the absence of selection, the number of prey eaten in the two prey situation (u_{1+2}) should equal one-half the number eaten in the two single prey situations. That is:

$$u_{1+2} = \frac{u_1}{2} + \frac{u_2}{2} \qquad (1)$$

or $$u_1 = u^*_1 \times 2 \qquad (2)$$

and $$u_2 = u^*_2 \times 2. \qquad (3)$$

Equations (2) and (3) serve as the null hypotheses for the selection tests. If selection occurs, equations (2) and (3) are not true.

It is convenient to express the relative degree of selection in terms of a single number. I have called it the 'relative discrimination coefficient' (cf. Rapport and Turner 1970, Rapport et al. 1972). It is calculated as follows:

$$c_1 = \frac{u^*_1 \times 2}{u_1} \qquad (4)$$

and $$c_2 = \frac{u^*_2 \times 2}{u_2} \qquad (5)$$

and $$c_{1,2} = c_1 - c_2. \qquad (6)$$

The symbol c_1 is associated with the amount of selection for Prey 1; and c_2, for Prey 2. The relative discrimination coefficient, $c_{1,2}$, is the difference between c_1 and c_2.

Theoretically, the coefficient varies between -2 and +2 for complete selection for Prey 2 and Prey 1, respectively. In the absence of selection, the coefficient equals 0.

The spiders used for the selective predation experiments included at least one of the following types: 1) adult females, 2) adult males, 3) subadult females, 4) subadult males. These four main types were further subdivided into 'pre-fed' spiders (i.e., spiders that were fed flies in the laboratory before the actual experiments) and 'field' spiders (i.e., spiders not pre-fed in the laboratory) as well as into types based on their subadult moulting histories. If the date when the spiders moulted to the subadult stage was known, they were placed in one group; if this date was unknown, they were placed in another group.

In order to observe feeding from the beginning of the subadult stage, the following procedure was followed for most of the experiments. Immature spiders were collected, identified and measured. Only those that were judged to be in the prepenultimate stage were retained. These spiders were then fed with (usually non-standard) flies for up to two weeks. The spiders that moulted[1] within this period were then randomly assigned to one of the three treatment regimes. Each spider in each treatment was then observed daily until it matured or until 70 days had elapsed since it had reached the subadult stage. Even though feeding data were obtained for up to 70 days on each subadult spider,

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[1] These spiders were assumed to have moulted into the penultimate stage but are labeled here as subadults.

only the first 20 days were used to estimate the mean feeding rates. Most of the spiders which matured within this 70 day period were then observed for an additional 20 days. Thus, unless otherwise indicated, selective predation data on adult spiders were derived from spiders that had been fed the same diet as both subadults and adults.[1]

It should also be noted that in order to reduce the number of spiders that had to be collected and maintained, two selective predation experiments were often run concurrently. This involved five treatments with one single-prey treatment being used for both experiments. For example, in the case of testing female *D. melanogaster* with small *T. molitor* and female *D. melanogaster* with *O. fasciatus*, the five treatments were as follows: #1 *D. melanogaster* alone, #2 *T. molitor* alone, #3 both *D. melanogaster* and *T. molitor*, #4 *O. fasciatus* alone, and #5 both *D. melanogaster* and *O. fasciatus*. In this case, treatment #1 was used as the single prey treatment for both the *D. melanogaster* - *T. molitor* and the *D. melanogaster* - *O. fasciatus* tests. However, even with using this method of reducing the required number of spiders, not all possible combinations of five types of prey were treated because of the difficulty in obtaining enough

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[1] Though 20 and 70 days are arbitrary cutoff points, most subadult feeding took place within the first 20 days after moulting, most subadults moulted into adults after 20 days but before 70 days, and most adults produced an egg-sac somewhere between 10 and 20 days after reaching maturity.

spiders of the proper stage and sex. For example, if 100 immature spiders were collected, about 30 would be too young (small) or too old (large), about 20 would not moult within the defined period into the required stage, and half would be of one sex. Thus, only about 25 spiders of one predator type could be obtained for every 100 collected. Coupled with this problem were the difficulties of rearing large enough numbers of prey to feed much more than 100 spiders per day.

The following variables were recorded daily for each cage: date; time; number of live, dead and rejectamenta of each prey type; and presence of spider exuviae and egg-sacs. Wet weights and cephalothorax measurements of spiders were recorded periodically.

When the above information was recorded, all rejectamenta, dead prey, and exuviae were removed. Unless otherwise noted, prey were completely replaced with fresh prey every second day (i.e., 'renewal' days) and enough fresh prey were added on alternative days (i.e., 'replenishment days') to restore the prey densities to the initial levels.[1] On renewal days the sponges were also re-

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[1] Though prey were usually renewed every two days, an early attempt was made to run the experiments on a weekly basis, i.e. with three renewal and four replenshment days each week. However, because of high mortality rates after two days, this was stopped. The observations affected by this procedure are Experiments 8 and 9 in Table V and the experiments related to Table A-V.

wetted. Most observations were made between 14:00 and 17:00 hours, the time of least daytime feeding activity for *P. vancouveri* (Hardman 1972).

In all selective predation experiments, one spider feeding for 20 consecutive days equaled one replicate (e.g., 10 cages with one spider each observed over 20 days gave 10 replicates). About 10 subadult spiders were used per treatment, but because some of the spiders failed to mature and others died, the number of spiders involved in the adult calculations were fewer than the number of subadult spiders.

Two experiments were done to determine whether pre-feeding caused a change in selection of prey. Each experiment included three treatments. The first group of spiders was fed with *D. melanogaster* alone, the second with small *T. molitor* alone, and the third with both prey. After about one week (see Results for exact times), spiders in all three treatments were fed both prey.

One experiment was performed to test whether increasing the physical complexity (i.e., 'spatial heterogeneity') of the cages would affect selection. This was done with two treatments, both using subadult female spiders supplied with female *D. melanogaster* and small *T. molitor*. One treatment had three flattened red alder (*Alnus rubra* Bong.) leaves added. The leaves increased the surface area within the cages by 62% (i.e., from 385 to 624 cm^2 per cage) and created a number of refugia for the prey and predators. The second treatment, that is the control, had no additional material.

6. Utility of the Prey to the Predators

Up to 12 factors that were potentially beneficial to the spiders were monitored in most of the selective predation experiments. These characteristics were:

1) Maturation

   a) Percentage of subadult spiders which reached maturity within 70 days from the time they moulted into the subadult stage.

   b) Mean time (days) for the subadult spiders to reach maturity.

   c) Percentage of spiders that produced 'extra' (i.e., more than one) exuviae before reaching maturity or within 70 days from the start of the experiment.

2) Mortality

   a) Percentage of subadults that died before reaching maturity or before the 70 day limit.

   b) Percentage of adults that died within the 20 day period that adult spiders were observed.

3) Weight and Size Gain

   a) Mean weight gain (excluding exuvia) between subadult weight and adult weight (= subadult weight gain).

b) Mean weight gain between time of moulting into an adult (day '0') and ten days later (day '+ 10').

c) Mean rate of weight gain between initial subadult and adult weights. Rate of weight gain = Subadult weight gain divided by time (in days).

d) Mean size increase of cephalothorax width between subadult and adult stages.

4) Potential Number of Offspring

a) Percentage of mature spiders that produced a 'false egg-sac'[1] within 20 days of reaching maturity.

b) Mean time (days) for the production of the first false egg-sac.

c) Mean dry weight of false egg-sacs.

One experiment was done to determine if subadult feeding affected the benefits that were monitored in the adult spiders. Two groups of subadult female spiders were used. The first group was fed female D. melanogaster, and the second was fed large T. molitor. When the spiders matured, all were fed large T. molitor.

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[1] The term 'false egg-sac' is used because the females produced abnormal egg-sacs that contained a mass of yolk rather than separate eggs. Probably this was the result of the spiders not being mated or fertilized. I found it impossible to have the spiders mate in captivity.

7. Statistical Analysis

The data were recorded on coding sheets and then transferred to computer punch cards for statistical analysis.

The number of prey eaten could not be estimated by simply counting the number of rejectamenta because (a) there was not a simple one-to-one relationship of prey eaten and rejectamenta produced and (b) the *T. molitor* occasionally fed on both rejectamenta and dead prey (see Part I of the Results section). For these reasons, the following two equations were used to calculate the number of prey eaten per spider per day. If there were no rejectamenta of prey species 1, the estimated number of Prey 1 eaten (Ep_1) was zero.

That is, $Ep_1 = 0$ (7)

If rejectamenta were present, $Ep_1 = |Ip_1 - (Lp_1 + Dp_1)|$ (8)

where Ip_1 = initial number of Prey 1, Lp_1 = number of Prey 1 alive, and Dp_1 = number of Prey 1 dead from causes other than spider predation.

It was assumed that errors associated with calculating the number of prey eaten were minimized by the use of these two equations. The dead prey in equation 8 were readily separable from prey killed by spiders (i.e., those that were formed into rejectamenta).

Feeding rates were calculated for each prey type for each spider for each day over a certain period of time (usually 20 days) and used to calculate a mean number of prey eaten per spider. These means were then compared statistically (see below).

Before any variables were statistically analyzed, the replicates (i.e. the cages) within each treatment were first checked for independence of positional effects by a runs test.[1] Note: No treatments showed trends (i.e. non-randomness).

Secondly, the data were tested as to whether or not they were normally distributed. This was done by means of the Kolmogorov-Smirnov test (D-maximum test) as described in Sokal and Rohlf (1969) but with tables given by Lilliefors (1967).

If the data were normally distributed or could be transformed to the normal (see below), the following procedures were performed before comparing means. Homogeneity of variances was checked with Bartlett's test or the F maximum-test. If the variances were not heterogeneous (i.e., homogenous), t-tests or one-way analyses of variance were performed. If the variances were heterogeneous, an

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[1] Unless otherwise indicated, Sokal and Rohlf (1969) and their associated tables (Rohlf and Sokal, 1969) were used for the statistical tests.

approximate test of equality of means or an approximate t-test was used.

If the data did not meet the requirements for parametric tests (e.g., not transformable to the normal distribution), the following non-parametric tests were used to compare means: the non-paired Mann-Whitney U-test for two treatments (used to test for selective predation), the Wilcoxon two sample test when $N > 20$, the Kruskal-Wallis test for more than two treatments (= non-parametric single analysis of variance), and an a posteriori simultaneous test procedure. Fisher's exact test was used to test whether two percentages were equal.

The results of observation-days were not independent because they involved the use of the same organisms for more than one day in succession. Thus, they could not be tested statistically with the usual parametric tests. In all cases these results are simply expressed as percentages.

The means of normally or near normally distributed variables are followed by their standard errors (SE). Means of variables that were transformed are followed by the lower and upper 95% confidence limits, with all three values changed back to the original scale. The number of observations (N) that were used to estimate each mean is also listed.

Except for the Kruskal-Wallis test and the test of equality of means with heterogeneous variances, all probabilities given are two-tailed. Though all probabilities are stated, probabilities between 0.05 and 0.01 are regarded as 'statistically significant' and are marked with one asterisk (*). Probabilities less than 0.01 are regarded as 'highly statistically significant' and are marked with two asterisks (**).

Statistical analyses were done on a IBM 370 model 155 computer using programs listed in Sokal and Rohlf (1969) and version 5.0 of the Statistical Package for the Social Sciences (Nie et al. 1970, Nie and Hull 1973).

RESULTS

1. General Information on Calculating Feeding Rates

Consider the following situation. An experimenter places a single predator in a cage with ten specimens of a potential prey species. He then leaves for a period of time. When he comes back, he observes that five prey are still alive, two are dead and some prey remains are strewn about the cage. If he concludes that the predator killed five prey and ate three of them, he could easily be wrong. It is possible that the predator killed nothing, that the dead prey were the result of natural mortality, and that the missing prey were the result of cannibalism, escape or simple counting errors. This example, even though hypothetical, helps to illustrate that in any predator-prey situation involving non-continuous observation, the predator and prey themselves may confound the evidence relating to the number of prey eaten by the predator. It is therefore important that, before presenting the main results of the thesis, I summarize here some general information on the problems involved in calculating feeding rates, and hence in determining whether or not selective predation occurred.

First of all, even in the absence of spiders, there was some prey mortality. The mean rates of non-predator mortality for each prey class were:

O. fasciatus 0.04,
female *D. melanogaster* 0.31,
small *T. molitor* 0.35,
large *T. molitor* 0.42, and
male *D. melanogaster* 0.75 dead animals per
cage per day.[1] The mortality was relatively low in *O. fasciatus*, high in male *D. melanogaster* and moderate in the remaining prey.[1]

The relative importance of the factors that caused non-predator mortality are indicated below (1 = least important, 3 = most important):

Factor	Prey affected		
	O. fasciatus	*D. melanogaster*	*T. molitor*
Starvation	2	3	1
Drowning	1	1	3
Moulting	2	Nil	2
Accidental mechanical injury	2	2	1
Cannibalism	2	Nil	1

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[1] For details, see Tables A-V and A-VI in Appendix I.

Secondly, there were interactions between the various kinds of prey that affected the calculation of feeding rates. These were mainly confined to *T. molitor* because it has chewing mouth parts. *D. melanogaster* does not have mouth parts that are capable of killing or completely ingesting the dead or rejectamenta of any of the prey types. *O. fasciatus* has piercing and sucking mouth parts that can be used to feed on body fluids of other animals. Though there was no evidence that *O. fasciatus* harmed *D. melanogaster* or *T. molitor*, it did kill members of its own species when they were in the process of moulting. These corpses were easily distinguished from those produced by *P. vancouveri*.

By supplying *T. molitor* with live, dead and spider rejectamenta of *D. melanogaster*, it was found that the beetle larvae:

(a) did *not* feed on live flies;

(b) did feed on dead flies; and

(c) did feed on the rejectamenta produced by spiders.[1]

From these results, it was assumed that *T. molitor* also fed on the dead and rejectamenta of *O. fasciatus* as well as on the dead and rejectamenta of other beetle larvae.

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[1] For details, see Tables A-VII, A-VIII, and A-IX in Appendix I.

Thirdly, the spiders themselves contributed to the problem of estimating how much they ate. One problem was prey consolidation. Usually, P. vancouveri killed one prey and fed upon it until only a ball of chitinous remains was left (i.e., one prey, one rejectamentum). However, when the spider was very hungry (as when it was just brought in from the field or just after moulting), it often fed on more than one prey at a time and so produced only one rejectamentum that consisted of two or more prey. This phenomenon occurred with O. fasciatus and D. melanogaster but not with T. molitor. A second problem was with fragmentation of rejectamenta. That is, one prey could be formed into more than one rejectamenta. This was far more common with T. molitor than with any other species of prey. There was no evidence to indicate that the spiders killed any prey on which they did not feed.

For the reasons given above, equations (7) and (8) (see Part 7 of the Materials and Methods section) were used to estimate the number of prey eaten by the spiders. The kind, direction and size of the errors inherent in using these equations are outlined below:

Errors	Prey affected (in order of increasing importance from left to right) [1]	Direction of error	Estimate of relative size of error
Counting live prey	D.m.,O.f.,T.m.	±	1
Counting dead prey	D.m.,O.f.,T.m.	±	1
Counting rejecta	O.f.,D.m.,T.m.	±	1
Cannibalism	O.f.,T.m.	+	1
Prey escape from cage	O.f.,D.m.	+	2
T.m. burrowing into sponge	Small T.m.	+	2
Consolidation of rejectamenta	O.f.,D.m.	-	1
Fragmentation of rejectamenta	T.m.,D.m., O.f.	+	1
T.m. eating dead prey	D.m., O.f.	+	2
T.m. eating rejectamenta	D.m., O.f.	-	2

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[1] Hereafter, D.m. = *D. melanogaster*, T.m. = *T. molitor*, O.f. = *O. fasciatus*.

Counting errors were judged to be small and, being both positive and negative, tended to cancel each other out. Cannibalism was a very minor factor. As mentioned above, cannibalism in *O. fasciatus* usually occurred when an individual moulted but the results could be easily distinguished from the rejectamenta formed by *P. vancouveri*. Cannibalism in *T. molitor* was also rare and could be distinguished from spider predation. Escape of *O. fasciatus* and *D. melanogaster* from the cages and the burrowing of small *T. molitor* into sponges, which supplied water to the animals, were greater problems. However, except in the case of *O. fasciatus*, these errors were small. Estimates of the size of escape errors for the various prey classes were as follows:

large *T. molitor*	0.00%,
female *D. melanogaster*	0.19%,
both male and female *D. melanogaster* combined	0.51%,
small *T. molitor*	2.92%, and
O. fasciatus	8.54%.[1]

The effect of escape errors were minimized by the use of the single and the two prey method of calculating selective

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[1] For details, see Table A-I in Appendix I.

predation. It was assumed that equal proportions of prey escaped in both single and two prey treatments; thus the ratios of the numbers of each kind of prey in each treatment were only minimally affected. Consolidation and fragmentation of rejectamenta had little effect on the estimates of the number of prey eaten because the rejectamenta were scored only as being present or absent. There were no problems in differentiating between the rejectamenta of each prey species. However, it was not possible to distinguish between rejectamenta of male and female D. melanogaster. Finally, the problem of T. molitor eating dead prey (+ error) and rejectamenta (- error) also tended to cancel each other out. Thus, even though the method for estimating the number of prey eaten was judged to give results slightly higher than the actual amount, it was considered satisfactory.

2. Selective Predation Experiments

Selective predation was tested by comparing the numbers of prey taken when only one kind of prey was present with the numbers taken when two kinds of prey were present. In total, 14 experiments were done. The results are given below in Figures 2 through 5 and in Table I.

Figures 2, 3, 4 and 5 illustrate the feeding rates of the selective predation experiments that involved subadult

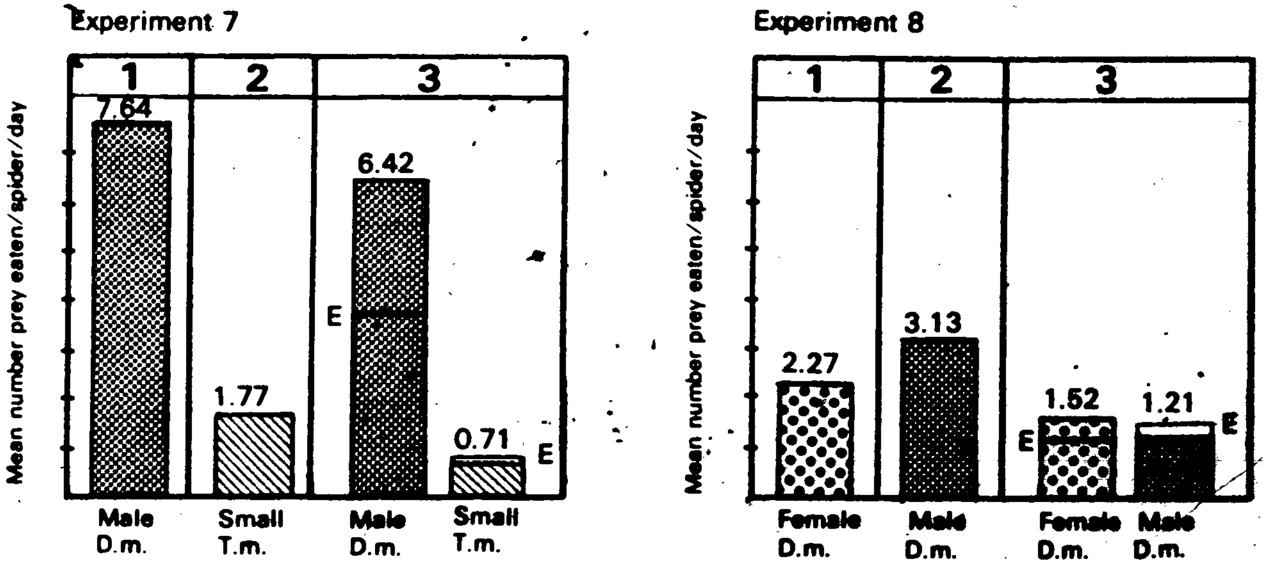

Figure 2. Feeding rates of subadult male spiders in one and two prey treatments. Explanation in text.

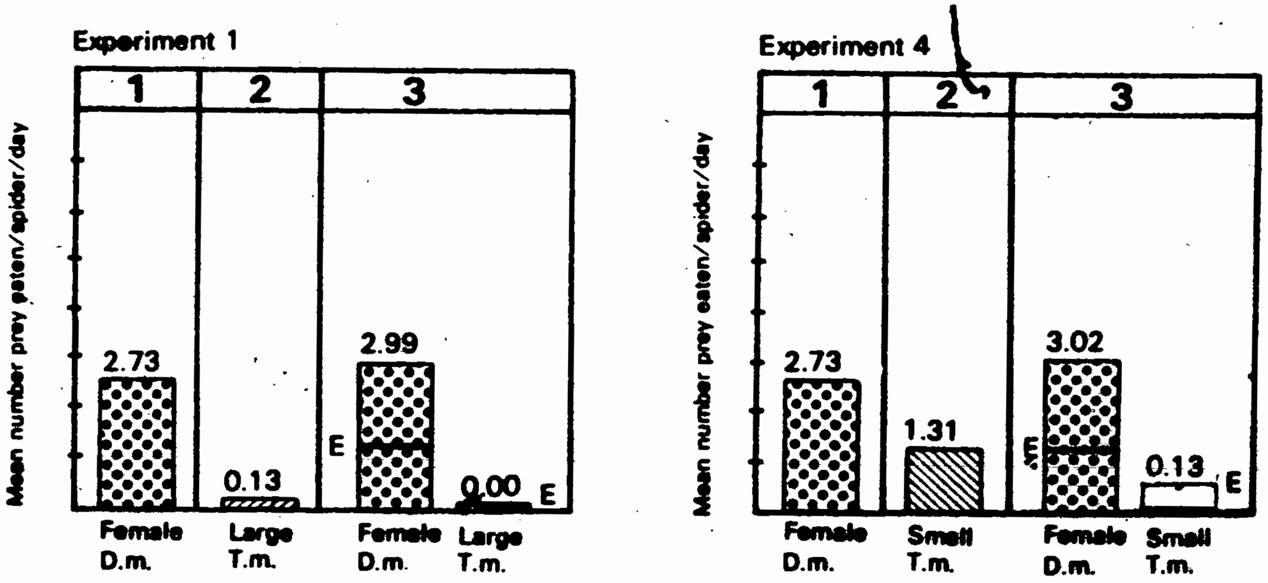

Figure 3. Feeding rates of adult male spiders in one and two prey treatments. Explanation in text.

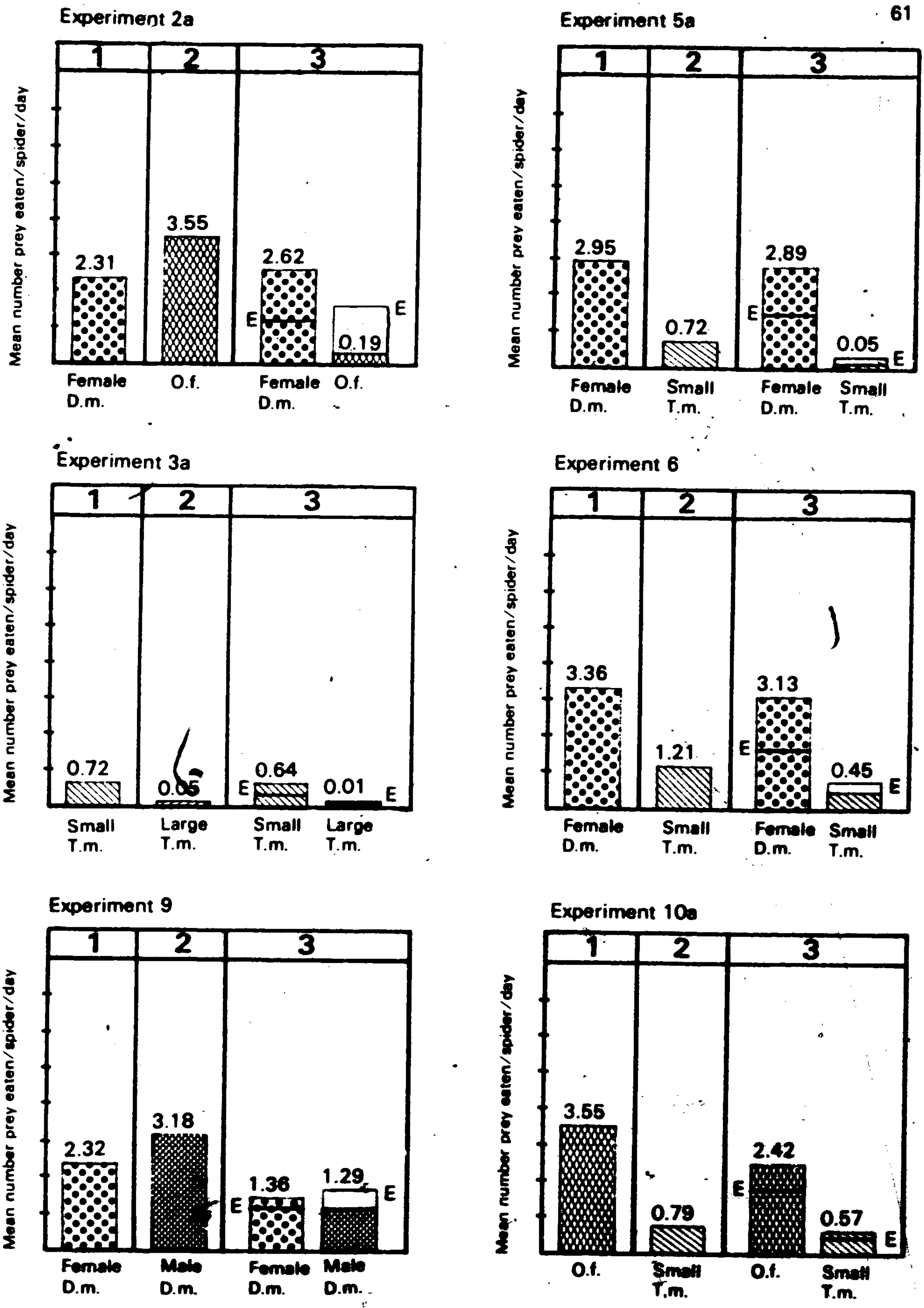

Figure 4. Feeding rates of subadult female spiders in one and two prey treatments. Explanation in text.

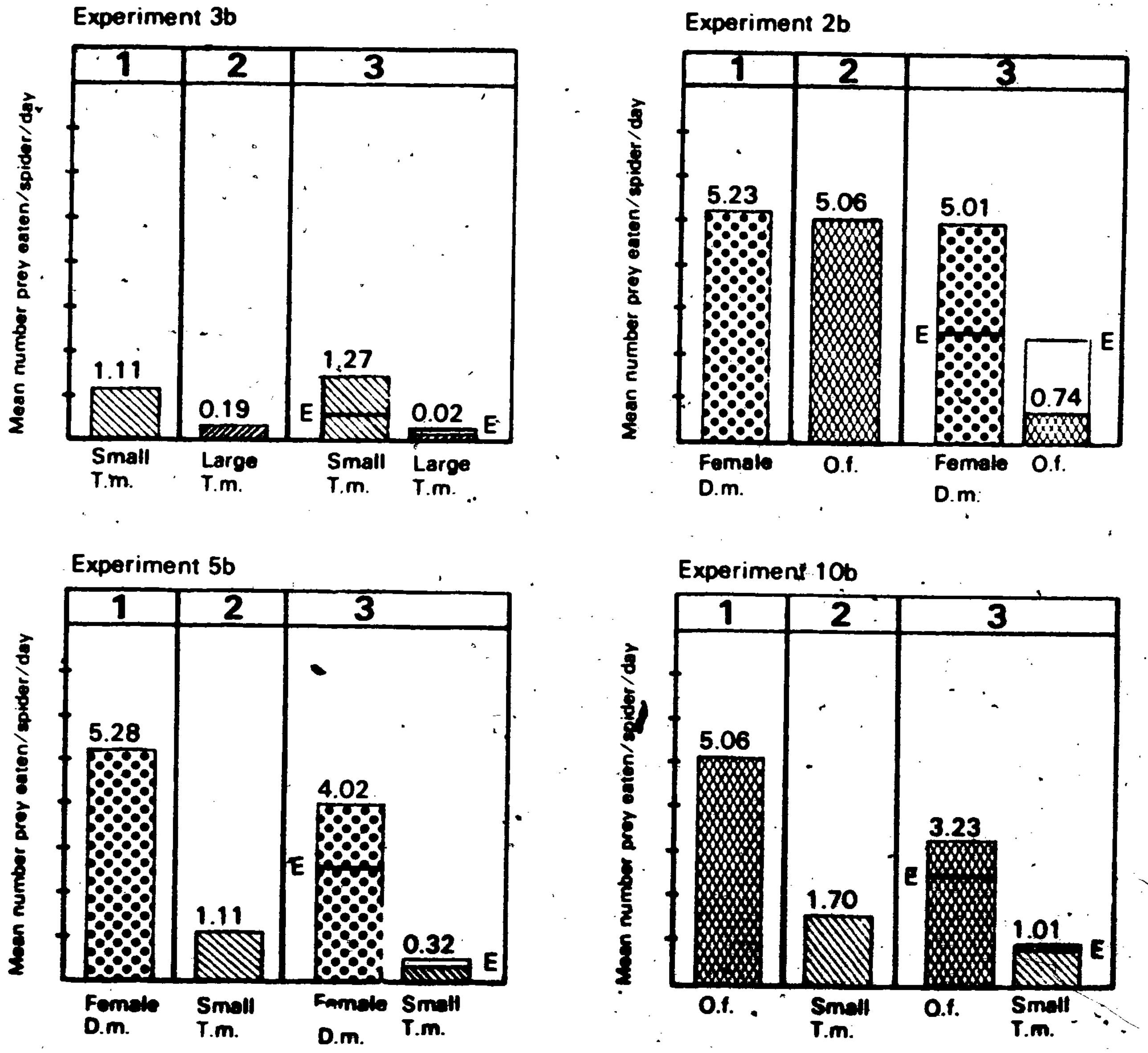

Figure 5. Feeding rates of adult female spiders in one and two prey treatments. Explanation in text.

male, adult male, subadult female and adult female spiders, respectively. The 'a' and 'b' parts of the experiment labels link the experiments that were done with the same spiders. For example, in Experiment 2a of Figure 4, I used the spiders that matured from Experiment 2b of Figure 5. For each experiment, the first bar indicates the mean number of Prey 1 eaten per spider per day (i.e., u_1). The second bar indicates the mean number of Prey 2 eaten per spider per day (i.e., u_2). The third bar indicates the feeding rate on Prey 1 when both prey were present (i.e., u^*_1) and the fourth bar, u^*_2. The letter E on the third and fourth bars are the estimated feeding rates - assuming there was no selection (i.e., the first E equals one half of u_1 and the second E equals one half of u_2). For example, in Experiment 7 of Figure 2, u_1 = 7.64 male D. melanogaster per spider per day, the observed u^*_1 = 6.42, and the expected u^*_1 (or E) = 3.82. Note that the bars are arranged so that the more-selected prey is illustrated on the left, and the less-selected prey on the right. Feeding rates are not necessarily comparable between experiments because of differences in procedures. For example, in Experiments 7 and 8 (Figure 2) the feeding rates for subadult male spiders feeding on male D. melanogaster are 7.64 and 3.13 flies per spider per day, respectively. This is due to differences in pre-feeding and length of observation periods. For information on exceptions, replicates, probabilities, etc., see below.

Table I summarizes the parts of the results of the selective predation experiments not presented in Figures 2 through 5. The first column of the table uses the same labels for the experiments as described above. The second, third and fourth columns refer, respectively, to the stage, sex, and numbers of spiders used in each experiment. In the fourth column, there are three numbers related to the experiment described in that row. Of these three numbers, the first refers to the number of spiders that were fed the more-selected prey, the second to the number of spiders fed both prey, and the third to the number of spiders fed the less-selected prey. For example, in Experiment 2a, there were 8 subadult female spiders fed only female _D. melanogaster_, 10 fed both female _D. melanogaster_ and _O. fasciatus_, and 12 fed only _O. fasciatus_. The more-selected prey is placed first for the convenience of having all the relative discrimination coefficients come out positive.

The probability that no selection occurred is given in column seven. The probabilities are usually stated as less than a certain figure because the method of calculating selection actually involved two probabilities, one comparing mean numbers of Prey 1 eaten in single and two prey treatments, and the other comparing mean numbers of Prey 2

Table I. Summary of 14 selective predation experiments ranked according to the relative discrimination coefficient. See text for further explanation.

Experi-ment	Spider			Prey		Prob. of no selection	Relative discrimination coefficient	
	Stage	Sex[1]	N	More-selected	Less-selected			
1	Adult[2]	M	8,14,14	Female D.m.	Large T.m.	<0.002**	2.19	Strong selection
2a	Subadult	F	8,10,12	Female D.m.	O.f.	<0.002**	2.17	
3b[3]	Adult	F	4,5,9	Small T.m.	Large T.m.	<0.02*	2.08	
4	Adult[2]	M	8,15,14	Female D.m.	Small T.m.	<0.002**	1.98	
5a	Subadult	F	12,14,12[4]	Female D.m.	Small T.m.	<0.002**	1.82	
2b	Adult	F	4,9,6[4]	Female D.m.	O.f.	<0.01**	1.62	
3a	Subadult	F	12,14,11[4]	Small T.m.	Large T.m.	<0.10	1.38	Moderate selection
6	Subadult[5]	F	14,16,14	Female D.m.	Small T.m.	<0.05*	1.12	
5b	Adult	F	9,8,4	Female D.m.	Small T.m.	<0.05*	0.95	Weak selection
7	Subadult[5]	M	20,22,21	Male D.m.	Small T.m.	<0.20	0.88	
8	Subadult	M	9,7,12[4]	Female D.m.	Male D.m.	<0.10	0.57	
9	Subadult	F	7,9,9	Female D.m.	Male D.m.	>0.20	0.36	Very weak or no selection
10b	Adult	F	6,8,6	O.f.	Small T.m.	>0.20	0.09	
10a	Subadult	F	10,12,10	O.f.	Small T.m.	<0.20	0.08	

[1] M = Male, F = female.

[2] Spiders with unknown moulting histories and observed for only 10 days (not 20) after maturing.

[3] Treatment of subadult spiders fed on only large *T. molitor* did not mature. Another group of spiders with unknown moulting histories was used to calculate adult feeding rates.

[4] Total number of observation-days slightly less than (Number of spiders x 20) because one or more spiders matured in less than 20 days.

[5] Freshly caught spiders without previous laboratory feeding and with unknown moulting histories. Observed for only 7 or 8 days (not 20) as spiders started to mature.

eaten in single and two prey treatments.[1] Only in six of the 14 experiments were the probabilities the same. In this table, the higher of these two probabilities is presented. For example, in Experiment 3a the probability of '<0.10' is recorded in this table, but the probability that more small *T. molitor* were eaten in the two prey treatment was actually between 0.002 and 0.01, and the probability that fewer large *T. molitor* were eaten was between 0.05 and 0.10. Note that the first set of probabilities are statistically significant while the second set are not. Results that were statistically significant with one prey and not with the other, also occurred in Experiments 7 and 8. The probabilities given in Table I are therefore very conservative.

Column 8 gives the relative discrimination coefficient associated with each experiment. The results are ordered so the experiments that showed the strongest selective tendencies are listed first. The experiments are further categorized by grouping them into those that showed strong selection (i.e., with a relative discrimination coefficient above 1.5), moderate selection (i.e., 1.0 to 1.5), weak selection (i.e., 0.5 to 1.0) and very weak or no selection (i.e., 0.0 to 0.5).

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[1] For details, see Table A-XI in Appendix II.

From the results in Table I, one can make several generalizations. First, some experiments showed that _P. vancouveri_ may or may not be highly selective in what it eats, depending on the circumstances. Second, subadult and adult spiders tended to select the same kinds of prey (i.e., Experiments 2a and 2b, 3a and 3b, 5a and 5b). Third, the degree of selection in subadults and adults was not consistent. For example, in Experiments 2a and 2b, the relative discrimination coefficient was 2.17 for subadults and _decreased_ to 1.62 for adults, while in 3a and 3b, the coefficient was 1.38 for subadults and _increased_ to 2.08 for adults. Fourth, there was no indication that male and female spiders selected for different prey (i.e., Experiments 4 and 5b, 8 and 9). Fifth, as the relative discrimination coefficient decreased, the probability increased that selection did not occur. Sixth, the relative discrimination coefficient sometimes exceeded the theoretical limit of 2.

There was little or no evidence that pre-feeding the spiders for seven to eight days with one prey species influenced their subsequent selection of prey when they were given access to both the pre-fed prey and another prey. The results of the experiments designed to test for the influence of pre-feeding are given in Table II. In the first experiment, female spiders were pre-fed with either female _D. melanogaster_ or small _T. molitor_ or both. After eight days, the spiders were all fed both prey for another eight

Table II. Feeding rates of *P. vancouveri* in two prey systems consisting of *D. melanogaster* and *T. molitor* after being pre-fed with one of these prey.

----Spiders---- Stage	Sex	N	Pre-feeding treatment	Mean number of prey eaten/spider/day (SE) after pre-feeding treatment	
				Female D.m.	**Small T.m.**
Sub-adult to adult[1]	F	18	Female D.m.	3.38 (3.340)	0.44 (0.127)
		14	Small T.m.	3.54 (2.797)	0.57 (0.454)
		16	Both prey	3.74 (3.697)	0.58 (0.212)
				Male D.m.	**Small T.m.**[3]
Sub-adults[2]	M	20	Male D.m.	2.34 (1.597)	0.10 (0.029-0.161)
		21	Small T.m.	3.04 (1.525)	0.16 (0.055-0.272)
		22	Both prey	2.16 (1.896)	0.09 (0.041-0.152)

[1] These spiders had eight days of pre-feeding before eight days of post-feeding on both prey. During this time, the spiders started to moult into adults. Data from Experiment 6.

[2] These spiders had seven days of pre-feeding before seven days of post-feeding on both prey. Data from Experiment 7.

[3] Means transformed with log (x+1) with 95% confidence limits in parentheses.

days. A Kruskal-Wallis test revealed no significant differences ($0.50<P<0.90$, $H = 0.117$). In the second experiment, using male spiders, a Kruskal-Wallis test was significant ($0.01<P<0.025$*, $H = 7.744$) but a subsequent test (i.e., the a posteriori simultaneous test procedure) to determine which of the three treatments were statistically different was not significant ($P>>0.05$). In general, the tests indicated that the selection in favor of *D. melanogaster* was not changed by pre-feeding with either prey species, or a mixture of the two.

Table III was based on subadult female *P. vancouveri* feeding for six days in a two prey system of female *D. melanogaster* and small *T. molitor*. By increasing the physical complexity of the cages (i.e., by adding three tree leaves), the number of *D. melanogaster* eaten decreased significantly. Though the number of *T. molitor* eaten increased in the treatments with leaves, it was not statistically different from the controls. It was concluded that changing the physical complexity of the cages did affect the relative amounts of prey eaten by the spiders.

3. Utility of the Prey to the Predators

When the null hypothesis, that spiders fed the less-selected prey did just as well as those fed the more-selected prey, was tested, seven out of 54 tests (i.e., 13%)

Table III. Results of increasing the physical complexity of the cages by adding three alder leaves.

Factor	Treatment	Mean[1]	SE	U-Statistic	Probability[2]
Number *D. melanogaster* eaten	Leaves[3]	3.05	0.179	305.5	0.01<P <0.001**
	No leaves[4]	3.74	0.150		
Number *T. molitor* eaten	Leaves	0.68	0.084	233.5	0.2<P <0.4
	No leaves	0.54	0.078		

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[1] Mean number of prey eaten per spider per day.

[2] Probability that means were equal.

[3] N = 21 spiders.

[4] N = 19 spiders.

did not uphold this hypothesis (i.e., $P < 0.05$). In these cases (see Table IV) the differences between the spiders always benefited (i.e., greater and faster weight gains, less mortality, faster production of and heavier false egg-sacs) those that fed on the more frequently selected prey. In all other cases (i.e., 87%) no significantly different benefits were achieved from either of the prey. But in no case did the less-selected prey provide any significant benefit.[1]

When the null hypothesis, that spiders fed the more-selected prey did just as well as those fed both prey, was tested, only two of the 62 tests (i.e., 3.2%) did not substantiate this hypothesis (i.e., $P < 0.05$). In other words, in 97% of the tests where spiders were supplied with only the more frequently selected prey, the spiders fared *at least as well* as the spiders provided with two prey species. In one of the two exceptional cases, subadult female spiders fed only small *T. molitor* matured sooner than spiders fed both small and large *T. molitor* (i.e., 28.8 days vs. 48.0 days, $P = 0.040$*). In the second of the two cases, adult female spiders fed *O. fasciatus* gained less weight than those fed both *O. fasciatus* and small *T. molitor* (i.e., 5.81

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[1] For details, see Column A=C in Tables A-XII to A-XVII of Appendix III.

Table IV. Benefit criteria that were statistically significant in favor of those spiders that ate the more-selected prey.

Experiment	Prey		Benefit Criteria (Means or percentages for more- and less-selected prey)	Probability of no difference
	More-selected	Less-selected		
2b	Female D.m.	O.f.	Days to first false egg-sac (13 vs. 19.5 days)	0.004**
			Adult day 0 to +10 weight gain (11.45 vs. 5.81 mg)	0.038*
			Dry weight false egg-sac (4.93 vs. 1.04 mg)	0.040*
3a	Small T.m.	Large T.m.	Mortality before maturity or 70 days (0% vs. 75%)	<0.001**
5a,b	Female D.m.	Small T.m.	Subadult to adult weight gain (17.16 vs. 10.26 mg)	0.002**
			Adult day 0 to +10 weight gain (20.06 vs. 11.43 mg)	0.019*
			Subadult to adult rate of weight gain (0.68 vs. 0.40 mg/day)	0.035*

g vs. 9.76 g, $P = 0.025$*).[2]

Table V summarizes the benefit criteria examined in Experiments 2, 3, 5, 8, 9 and 10. It excludes Experiments 1, 4, 6 and 7 because in these experiments the spiders were not observed from the beginning of the subadult stage. This table shows which prey combinations that produced relative discrimination coefficients of about 1.4 to 1.9 (i.e., moderate to strong selection) gave a relatively high proportion of benefit criteria (i.e., 25% of 28 tests) that favored the predators. On the other hand, those combinations that gave a coefficient of about 0.1 to 0.6 (i.e., weak selection) showed no differences in the benefit criteria that were measured (i.e., 0% of 26 tests).

Table VI indicates that a group of spiders supplied with prey that were more-selected (i.e., female *D. melanogaster*) fared better in the subadult stage, in terms of four out of seven benefit criteria, than another group of spiders supplied with prey that were less-selected (i.e., large *T. molitor*). But when the adults produced by these two feeding treatments were all supplied with a common prey (i.e., large *T. molitor*), no differences in the adult benefit criteria could be detected. In other words, benefits accruing in the sub-adult stage from a prey that was more-

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[2] For details, see Column A=B in Tables A-XII to A-XVII of Appendix III.

Table V. Percentage of benefit criteria that favored the more-selected prey.[1]

Experiment	Prey		Approx. relative discrim. coeffic.	Total number of benefits measured	Percentage benefits better for more-selected prey
	More-selected	Less-selected			
2a,b	Female D.m.	O.f.	1.9	12	25
3a,b	Small T.m.	Large T.m.	1.7	4[2]	25
5a,b	Female D.m.	Small T.m.	1.4	12	25
8	Female D.m.	Male D.m.	0.6	7[3]	0
9	Female D.m.	Male D.m.	0.4	7[4]	0
10a,b	O.f.	Small T.m.	0.1	12	0

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[1] Only those criteria that had a probability greater than 0.95 than the more-selected prey gave greater weight and size gains, higher maturation rates, or less mortality than less-selected prey are included.

[2] Subadult spiders did not mature on large T. molitor so some subadult and all adult benefit criteria could not be measured.

[3] Male spiders. Adult data not collected.

[4] Adult data not collected.

Table VI. Benefit criteria for female *P. vancouveri* in one prey systems involving large *T. molitor*. Results are expressed as means (SE, N) per spider or as percentages (N) of all spiders.

Benefit Criteria	Treatments[1] A	Treatments[1] B	Probability A = B
Subadult Spiders			
Subadult to adult weight gain(mg)	14.81 (0.910,15)	7.30 (0.974,10)	<0.002**
Subadult to adult rate of weight gain (mg/day)	0.55 (0.049,15)	0.20 (0.033,10)	<0.002**
Subadult to adult size increase(mm)	0.35 (0.027,15)	0.23 (0.031,10)	0.010*
Days for maturation	30.1 (3.17,15)	41.1 (4.13,10)	0.020*
Maturation within 70 days	94% (16)	67% (15)	0.144
Mortality before maturity or 70 days	0% (16)	20% (15)	0.202
Extra moults	7% (16)	6% (15)	1.000
Adult Spiders			
Adult day 0 to +10 weight gain(mg)	4.48 (1.380,15)	6.44 (1.342,9)	0.200
Spiders producing false egg-sacs	7% (14)	22% (9)	0.762
Adult mortality within 20 days	0% (16)	0% (15)	1.000
Days to first false egg-sac	18.0 (0.657,2)	14.0 (0.00,1)	ca. 1.000

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[1] Treatment A was first fed female *D. melanogaster* until maturity. Treatment B was fed large *T. molitor* until maturity. After maturity, both treatments were fed large *T. molitor*.

selected did not improve the performance of the adult spiders.

DISCUSSION

1. Detection of Selective Predation

a) Critique of the Experimental Design

Though selective predation is commonly estimated by comparing the densities of each kind of prey in an environment with the number of prey taken by predation within that environment, Rapport and Turner (1970) rightly pointed out a serious flaw in this method - different kinds of prey are not equal alternatives to predators. In other words, prey vary in such features as availability, catchability and preferableness.

Rapport and Turner's method of detecting 'preference' was to remove the complicating aspects of catchability and availability by presenting a group of predators with many kinds of prey and comparing their feeding rates with groups of predators fed only single kinds of prey. Whatever selective tendencies were left, with regard to predators feeding on some prey more frequently than what was expected, were lumped under the term 'preference'.

When a polyphagous predator is restricted to feeding on a single kind of prey, its degree of selection is reduced to two choices: to eat or not to eat. Under these circumstances, the predator will tend to take as many prey as it can within the time and mechanisms available to it to search, stalk, attack, subdue, ingest, store and digest the prey as well as to eliminate the resulting wastes. The kind and extent of these limitations are not essential to the present work because the same limitations exist in both the one and two prey systems. The only difference is that, in the two prey systems, the predator has more choices: not to eat, to eat only Prey 1, to eat only Prey 2, and to eat both Prey 1 and Prey 2 in equal or unequal proportions.

Generally, the method used in this study to test for selective predation was satisfactory. It allowed long term familiarity of the predators with the different prey, more than adequate time for prey capture and ingestion, ready access by the predators to the prey, limited disruption by the experimenter, 'acclimatization' to the laboratory conditions, and feeding during a period when the physiology of the predators changed with age and moulting condition. It also required few replicates to demonstrate strong selection even though strong selection biased the results towards the less-selected prey as the density of the more-selected prey was reduced by feeding.

The method was unsatisfactory in that the relative discrimination coefficient sometimes exceeded the theoretical maximum of 2.0, the two probabilities within one selective predation experiment were not always the same, and the use of single prey treatments did not completely rule out the factor of differing catchability.

Though the relative discrimination coefficient theoretically cannot be greater than 2.0, it exceeded this value in three of the 14 selection experiments. Coefficients greater than 2.0 meant that in the two prey treatments, the feeding rates increased as a result of either synergism or normal variation. Since the differences in the feeding rates were neither consistent nor statistically different, it was concluded that the increases were a result of normal variation and not synergism. Rapport et al. (1972) had relative preference coefficients ranging up to 5.9. My results were closer to the theoretical maximum (i.e., the largest value was 2.19).

The second problem, that of unequal probabilities within the selective predation experiments, is also best explained by normal variation in the feeding rates.

The third problem concerned the elimination of the catchability factor. Most likely, the large *T. molitor* were not selected because of their large size, their possession of a strong cuticle and their active resistance to predation. Most spiders caught and killed large *T. molitor* only after several days of starvation but a few spiders never fed on this prey. Thus, large *T. molitor* were not equally catchable to all the predators. With this experimental method, the single prey treatments eliminate the possibility that certain prey are totally uncatchable. However, the method is not completely satisfactory in borderline cases where the prey may be catchable to only a certain percentage of the predators. Similar problems could arise if the prey were slightly obnoxious in taste.

The procedure used could be improved by increasing replication, by changing the source of water so that it was accessible but did not contribute to prey mortality (e.g., drowning of _T. molitor_ and escape of small _T. molitor_ into the sponges), and by using larger cages with a physical complexity approaching the natural habitat. The use of artificial leaf litter (Martin 1969) may be useful in bringing laboratory systems closer to natural situations.

b) Selective Predation in _Pardosa vancouveri_

The results indicated that _P. vancouveri_ are capable of selective predation under laboratory conditions. Of 14 selective predation experiments, six showed strong selection, two showed moderate selection, three showed weak selection, and three showed _very_ weak or no selection.[1]

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[1] In this study, experiments with relative discrimination coefficients less than 0.5 were classified essentially as showing no selection. This result will not necessarily be the case in other experiments. It should be possible to obtain true instances of selection with relative coefficients less than 0.5. That is, weak selection but with high probabilities that the single and two prey treatment feeding rates are different.

Spiders are often assumed to be polyphagous predators that feed upon all suitably sized animals that chance their way (Savory 1928). However, this work shows that they may be somewhat selective in what they eat. Bristowe (1941) stated that spiders were selective, at least to the extent of rejecting 'distasteful' organisms. However, as Bristowe's experiments lacked controls and were inadequately replicated, his conclusions are questionable. Turnbull (1960) observed that a web-building spider sometimes accepted and sometimes rejected certain prey. He speculated that this might be due to a learned selection process, but was unable to support this idea.

Thompson (1951) suggested that most predators are more specific in their feeding habits than is realized. He seems to have meant that few predators feed randomly, taking prey indiscriminately on an opportunistic basis. But food discrimination by a predator does not necessarily mean that the predator is a specialist. Specialization implies innate or genetically fixed feeding behaviors. It is likely that spiders, as other polyphagous predators, while exploiting very many kinds of prey are still capable of discriminating between them. This may be especially true when resources are abundant (Cody 1974).

Some of the prey pairs used in these experiments were chosen so that, on an _a priori_ intuitive basis, no selection was expected (e.g., male and female *D. melanogaster*). Other pairs were chosen so that a high degree of selection was expected (e.g., *D. melanogaster* and large *T. molitor*). Still other pairs were chosen with no *a priori* expectations (e.g., *O. fasciatus* and small *T. molitor*).

The *a priori* expectations were largely substantiated. No discrimination between male and female *D. melanogaster* could be shown even though females were considerably larger and therefore perhaps 'more profitable' to the spiders. High discrimination did occur between the smaller prey (i.e., *D. melanogaster*, small *T. molitor*) and the largest prey (i.e., large *T. molitor*). This was expected because large *T. molitor* were known to approach the maximum size of prey that the spiders could handle.

In the experiments with no *a priori* expectations, it was found that *D. melanogaster* was selected over all other experimental prey and that there was very weak or no selection between *O. fasciatus* and small *T. molitor*.

Though not all of the combinations of prey pairs were tested, there was a hierarchy of selection similar to that found in seastars by Landenberger (1968). By combining the results of subadults and adults, the hierarchy for male *P. vancouveri* was:

Female *D.* Male *D.* Small *T.* Large *T.*
melanogaster = *melanogaster* > *molitor* > *molitor*

Similarily, for female *P. vancouveri* it was:

Female *D.* Male *D.* Small *T.* *O.* Large *T.*
melanogaster = *melanogaster* > *molitor* = *fasciatus* > *molitor*

It is possible that hierarchies may be useful to predict selection in untested prey combinations. For example, if Prey 1 is selected over Prey 2 and Prey 1 is equally selected when paired with Prey 3, Prey 3 may be selected over Prey 2.

If polyphagous predators, like *P. vancouveri*, are shown to be more selective than is commonly believed, there are a number of hypotheses that can be predicted. For example, in two ecosystems with the same species diversity, the one that is older, and therefore has had more time to establish stable interspecific relationships, should have the following characteristics:

(a) simpler food webs (i.e., less variety in kinds of foods eaten),

(b) more efficient transfer of food energy between trophic levels (i.e., increased chances for specialized digestive systems and enzymes),

(c) more prey with highly elaborate defensive mechanisms (i.e., specific prey defenses evolve against specific kinds of predators), and

(d) more predators with highly elaborate offensive mechanisms (i.e., specific predation weaponry and

tactics arise for specific kinds of prey).
Another example is more practical. If selective predation is common under field conditions, there is an increased potential for controlling pest species with predators.

2. Transient Nature of the Selective Predation Process

In the section above, the hierarchies of selection were taken as being fixed. But it is not that simple. Selection seems to be a transient phenomenon and may change for many reasons (Rapport 1972).

Though the sex and age of the spiders and their pre-feeding did not seem to make a difference in their selective tendencies,[1] the physical complexity of the cages did. When a few leaves were added to the cages, the degree of selection between D. melanogaster and small T. molitor changed. This may have been the result of a number of factors such as changes in the escape reactions of the prey, increased shelter for the prey and/or predators, and changes in the efficiency of prey capture. Thus, with changing environmental conditions (both abiotic and biotic), the degree of selection or even the selected prey may change.

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[1] Even though these were negative results, they do not rule out the possibility that factors such as age, sex and pre-feeding may affect food selection under different circumstances with different predators.

Different diets fed to larval flies have been shown to affect taste responses of adult flies (Dethier and Goldrich 1971). Also, changes in selective predation have been shown to occur with differences in the number of prey choices available (Landenberger 1968), geographical location (Dix 1968), relative food frequencies (Murdoch 1969, Manly et al. 1972) and hunger (see references in Introduction).

Though hunger is usually thought of in terms of energy and carbohydrates, it is possible that there are several kinds of hunger (e.g., hunger for protein-rich foods, hunger for specific amino acids, and hunger for certain vitamins). If this is true, it is possible that the hunger results from certain physiological needs that are in turn related to some aspect of growth and/or reproduction. This is then a possible mechanism for inducing changes in patterns of food selection. For example, Ross and Bras (1975) have shown that rats select different ratios of carbohydrates or protein at different ages and that these selections affect the longevity of the rats. McNeill (1971) noted that a mirid bug fed on the leaves of its host plant during its early stages, but then fed on the flower heads when the bug reached maturity. However, it is not clear from McNeill's paper if this shift of feeding occurred only when the flower heads formed and thus became available to the bugs (i.e., the problem of availability vs. preference). Also, Rodgers and Qadri (1977) have demonstrated that the calorific values of aquatic invertebrates vary significantly from season to season and House (1972) has shown that the food value of a diet may change with temperature. This means that the cost-revenue balance may not be static, even with one kind of predator and one kind of prey.

3. Benefit Criteria

In order to detect whether the selective predation process resulted in any positive utility (i.e., benefit) to the spiders, twelve measurable criteria were selected that intuitively were expected to be closely associated with achievement of maturation and reproduction of _P. vancouveri_. These benefit criteria were monitored over an extended period of time for most of the spiders used in the selective predation experiments (i.e., up to 70 days for spiders that were in the subadult stage and, for those that matured, another 20 days while they were adults). For example, for close to three months some spiders were only fed female _D. melanogaster_, others only small _T. molitor_, and still others both female _D. melanogaster_ and small _T. molitor_.

Of the 12 benefit criteria used, four did not shown any statistical differences between any of the feeding treatments.[1] All four of these were measured as percentages. As statistical methods for detecting differences between percentages with few replicates are not sensitive,[1] it was concluded that these criteria may still be appropriate for measuring benefits, but not for these experiments.

Of the remaining eight criteria that showed statistical differences only four (i.e., subadult to adult weight gain, subadult to adult rate of weight gain, days for maturation, and adult weight gain between moulting and 10 days later) were significantly different more than once.[2]

Of these eight criteria, two were related to maturation (i.e., percentage of subadults that matured within 70 days, and days for maturation), four were related to weight and size gain (i.e., subadult to adult weight gain, subadult to adult rate of weight gain, adult weight gain between moulting and 10 days later, and increase of cephalothorax size), and two were related to increasing the potential number of offspring (i.e., time to produce first false egg-sac and weight of first false egg-sac).

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[1] For subadults, these were the percentages of spiders that matured within 70 days and that produced extra exuvia. For adults, these were the percentages of spiders that produced false egg-sacs and that died within 20 days of reaching maturity.

[1] Only one criterion measured as a percentage was statistically significant (i.e., percentage of subadult mortality within 70 days.)

[2] Tables IV and VI.

In the experiment where a more-selected prey was fed during the subadult stage and a less-selected prey in the adult stage, there was no evidence of a carry-over of benefits from the subadult to adult stages. This supports the idea that benefits obtained in the subadult and adult stages can be treated independently. For example, benefits measured in the subadult stages were not derived from the (unknown) prey that were captured in the previous stadia.

Having shown that P. vancouveri are capable of making selections between two kinds of prey, and having commented on the benefit criteria used, the question now arises - "Do the attributes that were measured really benefit the spiders?" My answer, with some reservations, is "Yes".

All of the criteria measurements were directly or indirectly related to increasing the spiders' chances of surviving to maturity and reproducing successfully. The ability to reach maturity is an obvious advantage, but the advantages of the criteria connected with weight-size gain and increasing the potential number of offspring are less obvious. All of the criteria connected with increasing the weight and size gains are mutually related. That is, in lycosid spiders, weights have been directly and positively correlated with carapace size (Hagstrum 1971) and carapace size similarily has been correlated with the numbers of eggs produced (Peterson 1950). Minimizing time to produce the first egg-sac is regarded as an advantage because lycosid spiders tend to produce more than one egg-sac and if a spider can produce a second egg-sac, its total egg production is increased. Finally, the size of the false egg-sacs are assumed to be correlated with the number or at least the weight of the eggs that would have been produced if they had been fertilized. In all of these cases it is assumed that more eggs will increase the likelihood of more offspring and help ensure the continuation of the species.

Whereas Slobodkin (1964) has advocated that the best criterion to judge evolutionary fitness is long term survival of the species, the advantages or benefits that were measured in this study were all short term factors directly or indirectly related to either maximizing the longevity of the individual spiders (taken as samples of a population) or maximizing potential number of offspring. These factors have the following problems:

(a) excessive numerical increases in the predator population may lead to severe competition and overexploitation of the prey;

(b) adult survival past reproductive requirements may lead to cannibalism;

(c) an excessive increase in physical size may increase rates of predation and parasitism; and

(d) an excessive shortening of the life span may result in losses of potential food supplies and problems in synchronizing the time of maturation of both sexes.

Factors (a) and (b) are potential problems for both energy maximizers and time minimizers. Factor (c) is a problem of energy maximizers and (d) of time minimizers.

In the words of Cody (1974): "... optimal and maximal reproductive effort are likely to differ, and overall fitness is maximized by a reproductive effort that is less than all out". Also what is optimal varies "...with respect to the given constraints of history and a variety of simultaneous selective forces" (Cody 1974). As it was assumed that the spider population, from which the individual predators were taken, had not fully exploited their natural habitat, and as very long term studies (i.e., over many generations) were not possible in order to determine optimal sizes and maturation times, it was concluded that the kinds of criteria used in these experiments were the best available for measuring survival and reproductive success.

4. Relationship Between Selection and Benefit in *Pardosa vancouveri*

The single prey experiments could have led to the following possible outcomes:

(a) the spiders that were fed the more-selected prey exhibited a *greater* expression of the benefit criteria than those fed the less-selected prey;

(b) the spiders that were fed the *less-selected* prey exhibited a *greater* expression of the benefit criteria than those fed the more-selected prey; or

(c) there was no relationship between the selected prey and the benefit criteria.

The results showed that outcome (a) was slightly favored when all experiments, ranging from strong selection to weak or no selection, were considered (i.e., 13% of 54 tests were statistically significant) but was moderately favored when only strong to moderate selections were considered (i.e., 25% of 28 tests). Prey combinations that gave only weak selections (i.e., male and female *D. melanogaster*, *O. fasciatus* and small *T. molitor*) produced no benefit criteria that were detectibly different (i.e., 0% of 26 tests). Outcome (b) was not supported by any tests (i.e., 0% of 54 tests). Thus, these results conform to the idea that benefits, at least when they were detected, arose from the process of feeding on the more-selected prey.

A possible consequence of discovering that increased benefits are associated with a high degree of selection is a simplified method of detecting selective tendencies in predators. That is, based on the prey species that, when fed alone, gives the most benefits to a predator, one may be able to predict which of two or more prey will be selected for most frequently. This might be useful as a fast screening device for selecting potentially useful predators for biological control work.

There was a second set of possible outcomes from the selective predation experiments. That is, the spiders that fed on the _more-selected_ prey did (a) '_better_' than, (b) '_worse_' than, or (c) as well as those fed both prey. The results indicated that in 97% of 62 tests, (c) held true. It was concluded that there was no major difference between spiders fed the more-selected prey and those fed both prey because in the two prey systems the spiders had access to and fed more extensively on the prey that provided the most utility. In other words, even if the spiders had two prey to choose from, they fed mostly on, say, Prey 1 and so the benefits derived were not significantly different than those spiders fed only Prey 1.

There were two exceptions to the above conclusion. In one case, outcome (a) was supported when spiders fed small _T. molitor_ matured sooner than those fed both small and large _T. molitor_. The best explanation for this is that in the two prey system the large _T. molitor_ interfered in some way with the normal feeding process of _P. vancouveri_. In the second case, outcome (b) was favored. In this situation, adult spiders fed both _O. fasciatus_ and small _T. molitor_ gained more weight than those fed only O. fasciatus. However, this might be expected because there was little or no selection between these two prey species and because neither prey species, when tested with other prey, were highly favored. These exceptions may also be the result of random events.

5. Mechanisms Behind the Selective Predation Process

So far, I have tried to avoid suggesting why the spiders selected the prey that they did. I was especially concerned about suggesting that the spiders selected certain prey because they 'preferred' these prey.

There are five major categories of reasons why predators may discriminate between different kinds of prey when they are given alternatives from which to select. They are:

(a) differences in the availability of the prey,

(b) differences in the catchability of the prey,

(c) differences in the energy and/or nutrient content of the prey,

(d) differences in the palatability and/or digestability of the prey, and

(e) innate and/or learned preferences of the predator.

In these experiments, the variables of availability (i.e., coexistence of predators and prey in time and space, differences in density, and distribution of prey) were eliminated by the use of the one and two prey treatments and by the selection of suitable prey densities. Thus, availability [i.e., category (a)] was not a reason why some prey were selected over others.

The one and two prey treatment method does remove most of the variability due to differences in prey catchability [i.e., category (b)]. However, it is possible that the reason why a predator selected certain prey was that they were easier to capture - in terms of less energy expenditure or less risk of physical injury. Large T. molitor larvae probably were not selected because they approached the maximum size that the spiders could handle, and they violently twisted from side-to-side when they were attacked. For P. vancouveri, feeding on large T. molitor is an energy consuming and 'risky' business.

Category (c) includes the possibility that predators selected prey that have the greatest amounts of energy and/or nutrients. Certainly large prey contain more gross nutritional units than small prey. Also there may be qualitative differences in the nutritional values of different kinds of prey. For example, a prey may be highly favored because it contains essential minerals, amino acids or vitamins.

Another possibility is that selection occurred due to a combination of ease of capture and the amount of energy available [i.e., a combination of categories (b) and (c)]. Whether a predator is an energy maximizer or a time minimizer, the best feeding strategy is to utilize the greatest possible amount of energy from each prey captured. That is, maximum utility results from the greatest _net_ energy gain. Thus, the most-selected prey may not be the one that yields the greatest amount of food or is easiest to capture, but is the one that results in the greatest positive utility (i.e., after costs are deducted from revenues).

Category (d), that is, palatability, tries to explain selective predation in terms of the predators taking more prey that taste "good" and less prey that taste "bad". Palatibility may have played a role in the experiments that used the brightly colored Q. _fasciatus_. Gelperin (1968) observed that mantids may avoid O. _fasciatus_ after attacking one, and Jackson (1977) observed that jumping spiders rejected them. Thus, it is possible O. _fasciatus_ were not readily eaten by P. _vancouveri_ because of their taste. However, this possibility is slight for the following reasons:

(1) O. _fasciatus_ was readily accepted by P. _vancouveri_ when it was supplied alone, and the spiders successfully matured;

(2) when O. _fasciatus_ was presented with T. _molitor_ (which

has no record of being obnoxious to arthropod predators), P. vancouveri showed no selective tendencies that were statistically significant;

(3) the most probable active components that repel predators (i.e., cardiac glycosides), are not present in O. fasciatus reared on sunflower seeds (Duffey and Scudder 1974); and

(4) O. fasciatus has been observed being eaten by other arthropod predators including spiders (Andre 1934, Sauer and Feir 1972).

As mentioned in the introduction and as discussed below, foods that are highly palatable and/or digestable may or may not be highly selected. Also, though it is usually assumed that foods that are highly palatable should be highly nutritious, this may not always be so.

Category (e) is concerned with the innate and/or learned attributes of the predator that predispose it to select certain kinds of prey over others - that is, preference. The possible kinds of attributes that could be used by the predator to detect preferred kinds of prey include such things as size, form, color, odor and taste. If preference for certain prey is based on taste, some recognition character of the prey probably will be associated with highly palatable foods. There are possible exceptions however. An example of a highly preferred food that is not highly palatable may be one associated with a preference for a very important mineral, such as iron in humans, that tastes "bad" but is taken because it is needed for maintaining a good state of health. However, as with palatability, strong preferences may or may not be associated with highly nutritious food.

If palatability and preference are associated with high quality prey, their effects cannot be separated, by the experiments used here, from those conferred by categories (b) and (c). However, if palatability and preference are associated with low quality prey, one would expect that the more-selected prey (i.e., the one more palatable or more preferred) would yield fewer benefits than the less-selected prey. It is also possible that palatability and preference do not play more than a minor role in selection of prey. These factors may be completely overshadowed by other features of the selective predation process.

One or more of categories (b) through (e) could have caused the strong selections observed. In cases of no selection, either all contributing factors were equal or the factors that influenced the predator to select, say, Prey 1 were effectively cancelled by equally important factors that influenced the predator to select, say, Prey 2.

Though it is not possible, with these experiments, to indicate exactly why the spiders chose the prey that they did, the results do show that the test prey varied in terms of the degree of utility that they conferred to the spiders, and that the spiders were able to detect these differences and use the information obtained to provide themselves with benefits. That is, the selections made by the spiders tended to be the optimal ones for maximizing individual fitness with respect to survival and reproduction. Thus, I hypothesize that the ultimate reason that certain selections were made was to maximize fitness.

In this hypothesis, I do not suppose that a spider makes a conscious decision, every time it encounters a certain prey, about whether that prey will provide it with more benefits than some alternative prey. The choice at any one time may be made for more immediate reasons such as availability, catchability, or palatability and the many subcomponents that comprise these factors.

Neither do I suppose that every selection a predator makes is necessarily an optimal selection. Young (1945) showed that rats, while capable of switching from sugar to casein, did not do so when deprived of protein. Gelperin and Dethier (1967) demonstrated in the laboratory that a species of blow fly selected certain sugars that were deleterious to it. Gill and Wolf (1975) found that sunbirds tended to feed on open rather than closed flowers even though the latter potentially provided more benefits. These discrepancies may arise because natural selection is not an instantaneous process. Several or even hundreds of generations may be required for a population to respond genetically to an environmental change. New, advantageous, traits are slow to become established and old, now disadvantageous, traits are slow to be removed. Thus, a new superior food for which a predator has not evolved selective mechanisms may remain unexploited, and a currently held innate 'taste' may lead a predator to take a disadvantageous food. Man's reluctance to use new nutritious foods such as algal cultures may be an example of a 'taste' that has not evolved, and our innate 'taste' for sweetness, which once led our ancestors to select fruits that supplied energy and vitamins, may now lead us to overuse of refined sugars. Also, just because a superior food exists, it does not necessarily mean that the food will be selected. If no individual eats it, its superior characteristics will remain unrecognized and no selective advantage can occur. Further, even if the trait to use the food does arise in some individuals, but the population as a whole is not nutritionally limited, the food will confer no or little advantage and the tendency to use it will have little chance of increasing.

Thus, some feeders in a population may 'err' in their selections of certain foods or 'err' at certain times or under certain circumstances. However, the majority of the selections will be associated with foods that experience has shown to provide high utility to the feeders in terms of their fitness for their environment. If they constantly 'erred', they would lose out in the competitive struggle for survival.

The results of these experiments tend to agree with this hypothesis. They clearly show that P. vançouveri does discriminate between some kinds of prey. Of the prey presented, some were selected significantly more frequently than their alternatives. Usually no prey was selected to the total exclusion of the alternative prey, indicating that both of the alternatives were at least sampled. In only one case[1] was any kind of prey not fed upon because it was unavailable, uncapturable, or because the spiders were "ignorant" of its qualities. The results also show that when the spiders discriminated between two prey, the prey selected more frequently provided greater benefits than the one selected less frequently. When no discrimination between prey pairs could be demonstrated, the benefits accruing from each of the two prey were about equal.

Having stated that selection is based on fitness, the next problem is to explain how this selection might be implemented by the spiders. First of all, the spiders must

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[1] Exception: Experiment 1 when adult male spiders did not eat on large T. molitor when both the larvae and D. melanogaster were available.

be able to detect what kinds of nutrients (i.e., prey) are available. Though it is possible that this could be done at a distance (i.e., with visual and odorous clues), it is more probable that the spider uses more direct contact (i.e., clues gained by taste and ingestion). The latter implies that the spiders will tend to sample all available and catchable prey. A part of this detection process is the question of whether the spiders use palatability or some other mechanism to discover the presence of nutritious foods. Though I have repeatedly stated that palatability need not be associated with highly favored foods, taste is probably the easiest way for discovering which prey are valuable as food. Of course the relationship between what is palatable and what is nutritious must have evolved through the process of natural selection. If palatability is not the mechanism, the next probable means is the use of chemical receptors that are associated with the digestive tract and are stimulated by such things as carbohydrates, proteins, fats, amino acids or minerals.

The next part of the problem concerns how the spider uses the information about nutrition to select its prey. The simplest explanation is that the spiders, through natural selection, possess innate behaviors that cause them to eat certain prey that commonly inhabit their environment and that possess certain recognizable characteristics (i.e., color, size, form, texture, and/or chemical attributes).

Thus when a prey is encountered, the predator instinctively knows its qualities. This model minimizes the errors of attacking dangerous, toxic, or nutritionally inferior prey and would restrict, but not eliminate, exploitation of new and possibly superior prey. Also the qualities of several hundred, perhaps thousands, of potential prey types would have to be genetically coded and available for use.

A second model assumes that each predator learns, by sampling, the qualities of each prey type that it encounters. This model assumes some risk involved with sampling dangerous, toxic, or nutritionally inferior prey, but allows exploitation of new kinds of prey and little expenditure for genetically coded information.

It is very unlikely that any of the prey types used in these experiments are encountered by P. vancouveri in nature.[1] It is therefore unlikely that the spiders had any a priori or innate knowledge of the qualities of the experimental prey. Thus it is the second model that was tested. That is, there is a learning process that is associated with the trial and error sampling of the various

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[1] Attempts were made to discover the natural prey, but of the 500+ spiders collected in the field, only three had food in their chelicerae - a collembola, a lepidopterous larva, and another lycosid spider. After this study was well under way, it was found that other lycosid spiders feed heavily on Diptera, Hemiptera and other Araneae (Edgar 1969, 1970a, 1970b; Hallander 1970).

potential prey (cf. Holling 1965).

6. Why Eat More Than One Kind of Prey?

In all cases, except where *D. melanogaster* was paired with large *T. molitor*, the predators in the two prey treatments ate at least some of the less favored prey. The question then arises - why should the predators eat any alternative prey when a favored prey was available? The seven possible reasons are discussed below.

One reason is that the density of the favored prey was reduced as the predator fed. This meant that as the predator fed on the favored prey, there were fewer contacts between the predator and the favored prey and relatively more contacts between the predator and the less-favored prey. This in effect reduced the catchability of the favored prey and so the less-favored prey was eaten.

A second reason is related to the spider's unfamiliarity with the prey. In order to determine which of two or more prey kinds is superior, a predator may first have to sample the range of what is available. During this sampling period, the predator will try prey that it may reject in the future. To fully assess the quality of a prey, a predator must not only taste it, but also ingest and probably digest at least some of it. Also, the memory function associated with this practise may last for only a few days and so sampling may have to be repeated on a regular basis.

A third reason is that the prey are eaten in a ratio that is optimal with respect to energetics. Under certain conditions, it may be more energy efficient for a predator to actively go and search for certain kinds of prey, while under other conditions it may be more efficient for the predator to sit and wait for the various prey to come to it. The former will lead to active selection, while the latter will lead to prey taken in proportion to those prey that approach the predator.

A fourth reason is related to nutrition. A certain mixture of two prey may provide a better diet than either prey alone. That is, the prey complement one another nutritionally.

A fifth reason, in opposition to the first reason, is that there was an excess of food. This may be best illustrated with an anthropocentric example. Given the choice between steak and hamburger, I much prefer steak. But I eat hamburger much more frequently because of the greater cost of steak. I select hamburger, but prefer steak. However, I occasionally purchase steak even though I am aware that it yields less nutritional units per dollar than hamburger. This is done only when I have a small surplus of income and can afford to pay extra for the palatability.

Similarly, when a predator has an excess of food it may occasionally select a more palatable prey even if it yields a smaller net energy gain.

A sixth possibility is that monophagy may cause monotony. If there is an excess of food available, a predator may sample another prey just because it is different, not necessarily better. An example of this in humans is found in a once popular song - "Once you've been eating steak a long time, beans, beans, beans, taste fine".

A seventh possibility is that predators have some innate mechanism to allow some highly favored prey to escape. Possibly, this would allow the prey to reproduce and provide more prey to the predator or the predator's offspring.

Of these seven possibilities, I suggest that the first one tended to be important only during the first few days of the 20 day feeding tests. During the beginning of these periods of time, the spiders were very hungry because they had recently moulted and so fed on all available prey. As the spiders fed, their hunger decreased and the number of less-favored prey that were eaten also decreased. Though the effects of the second factor (i.e., the need to sample the various possible prey) cannot be distinguished from the effects of reasons five, six, and seven, it probably played a role throughout the selection experiments. The third and fourth reasons (i.e., energy and nutrition) are probably the most important factors because of the relationship between selection and increased benefits. Reasons five, six and seven are possible but, in my opinion, improbable.

7. *Pardosa vancouveri* as an Energy Maximizer

On Schoener's (1971) continuum of energy maximizers and time minimizers, I place *P. vancouveri* towards the side of the energy maximizers because relatively more of the benefit criteria that were statistically significant sided with increasing biomass, rather than reducing time limitations.

The biology of this spider also conforms to this conclusion - an animal that maximizes its energy intake in a fixed period of time. The spider hatches from the egg about the middle of June and is carried around on its mother's back for a few days until it can fend for itself. From then until about October it has to accumulate enough energy to supply it through the winter. Then, within a matter of a few weeks during late April or early May, the spiders mature, mate and produce the next generation of young. The factors of parental care, a constant time of maturation (regulated by the seasons), and the probability of a correlation between size or body weight and the number of eggs produced (Petersen 1950), all point towards energy maximization. However, there are two factors that side towards time minimization. These are: 1) a high percentage of the adult females survive after producing the first egg-sac and 2) the tendency for the production of a second egg-sac.

Having thus classified _P. vancouveri_ as mainly an energy maximizer, I must point out one thing. That is, if the energy intake becomes excessive it may lead to obesity and diminished fitness. Perhaps energy maximizers would be better defined as those organisms that maximize energy gain per unit time _up to an optimal amount_. Normally, most predators probably do not find enough prey for the optimal limit to be reached, much less exceeded.

In contrast to _P. vancoueri_, _Linyphia triangularis_ tends to be time minimizing spider. Turnbull (1962) found that by increasing feeding rates, the spider's developmental period could be reduced from about 300 to 70 days. There were no differences between the number of eggs produced by the spiders fed the minimal or maximal rates and the total food consumed per life-time was nearly constant at all feeding rates. _L. triangularis_ is, however, a bit of an energy maximizer because though the number of eggs produced is constant, the weight per egg is increased with increased food intake. The differences in size are due to increases in the amount of yolk, and this presumably increases the chances of survival of the offspring produced.

Probably most animals will be found to combine both energy maximizing and time minimizing strategies.

CONCLUSIONS

The following is a summary of the conclusions derived from this work:

1. P. vancouveri, a polyphagous invertebrate predator, is capable of selective predation.
   (a) When the factors related to availability and, to a lesser extent, catchability were removed, P. vancouveri showed a range of discrimination from high selection to no selection.
   (b) A hierarchy of selection did occur with D. melanogaster being most-selected and large T. molitor being least-selected. This hierarchy was stable under certain conditions but may change when conditions are altered.
      (i) The kind of selection did not change with the sex or age of the spiders. Neither did it change by pre-feeding the spiders with certain prey.
      (ii) Selection did change with changes in the physical complexity of the test environments.
2. The test prey varied in their degree of utility to P. vancouveri. The spiders were able to detect and use this information to increase their survival rate and potential number of offspring.
   (a) Prey combinations that led to moderate to strong selection produced most of the benefit criteria

that were statistically superior.

(b) Prey combinations that led to weak selection produced no observable differences in the benefits that could have accrued to the spiders.

(c) The spiders that were fed the less-selected prey exhibited no benefits that were superior to those spiders fed the more-selected prey.

(d) Spiders fed the more-selected prey tended to do just as well as those fed both prey.

(e) It is hypothesized that the ultimate cause of this selective predation process is associated with maximizing fitness.

(f) It is hypothesized that in this selective predation process the predator samples the available prey, determines their attributes, remembers these attributes, and then selects prey that possess certain attributes. Attributes selected seem to be related to prey characteristics that confer benefit to the predator.

(g) _P. vancouveri_ tends to be more of an energy maximizer than a time minimizer.

APPENDIX I, Specific Information on the Various Predator and Prey Classes

This appendix presents some specific information about the measurements, weights and behavior of the various kinds of predators and prey used in the experiments.

Table A-I gives cephalothorax widths, live weights, and dry weights of the exuviae of the various predator types. Data were derived from prepenultimate spiders collected in the field and raised to maturity on *D. melanogaster*. All the measurements of female spider types were larger than those of the same male types. However because the means were so close, none of these measurements, whether used alone or together, were as useful as morphological characteristics for separating the sexes.

Tables A-II and A-III summarize the physical dimensions and the mean weights of the test prey. Very little overlap occurred between any two prey types of the same species. Infrequently, large *T. molitor* had a few smaller larvae mixed in with them because of incomplete separation. The standard errors of the dry weights of test prey were very low because more than one individual was used per sample. The smallest to largest prey, based on size and weight, were: *O. fasciatus* < male *D. melanogaster* < female *D. melanogaster* < small *T. molitor* < large *T. molitor*. (The large *T. molitor* weighed nearly as much as the subadult spiders.)

Table A-IV shows the usual resting places of predators and prey at their normal densities in the plastic cages. These positions are a measure of the accessibility of the animals to the various parts of the cages. In general, though the distribution patterns of the various prey types varied, the spiders had access to all parts of the cages and, hence, access to all types of prey.

Except for the predator, the resting positions were obtained from experiments with only one kind of animal present. The predator results came from an experiment in which five large T. molitor were also present. The exact number of individual prey observed was not known because some prey were observed for more than one day. The usual resting place of P. vancouveri was the floor of the cage. Often the vertical plastic surfaces were accessible to the spiders only after one to two days of occupancy, by which time some drag-line silk had been deposited. O. fasciatus and D. melanogaster had access to all surfaces within the cages but T. molitor was restricted to the floors. The flies collected mainly on the sides of the cages. The bugs aggregated on the ceilings. Even though the T. molitor often crawled under or into the sponges (that supplied water to the animals), most were still accessible to the spiders as potential prey as only their head regions were covered.

Similar observations were obtained in the wooden cages except that T. molitor had access to the sides and the screen back. Also P. vancouveri rested more often on the screen back than on the floor.

Generally, P. vancouveri would kill one prey and feed upon it until completion. However, when it was very hungry it often fed on more than one prey at a time (see Hardman 1972). Also, when feeding on T. molitor, a spider would often stop feeding, drop the partially eaten larva, and return later to resume feeding. The latter phenomenon was not observed when the spiders were fed on D. melanogaster or O. fasciatus.

The prey species that showed the greatest struggle when captured was T. molitor. When attacked by a spider, a larva usually twisted violently from side to side. This sometimes resulted in the larva being released by the spider.

Table A-V gives the non-predator (i.e., starvation-drowning) mortality of D. melanogaster one, two, and three days after flies were initially placed in the cages. In this experiment flies were the only animals in the cages and were renewed (i.e., totally replaced) three times and replenished (i.e., only dead flies replaced) four times each week. In the column labeled "1", the 0.23 refers to the mean number of male flies that were dead one day after they were renewed. The dead flies were then replenished. In the next column, 1.57 is the mean number of flies that were dead two days after renewal but one day after being replenished. Similarly, the mean of 2.77 refers to the mortality three days after renewal, but includes two replenishment days (i.e., days 1 and 2). The grouped means are mean results for the same cages 1 and 2 days after initial renewal and 1, 2 and 3 days after initial renewal, respectively. In general, the results indicated that mortality rose considerably after two days. Thus, for most experiments[1] dealing with selective predation, prey were renewed every two days and the attempt to use weekly schedules was abandoned.

The statistical tests (see bottom of Table A-V) compare the non-predator mortality rates found in *D. melanogaster* in the one day renewal-one day replenishment cycle that was done for most selective predation experiments. The tests indicate significant mortality differences between the males and females, but no differences within the same sex. That is, about twice as many males died as females but there was no change in mortality when the two kinds of flies were placed together.

Table A-VI gives the non-predator (i.e., starvation-drowning-cannibalism) mortality of *O. fasciatus* and the two sizes of *T. molitor*. The densities of the prey were the same

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[1] Exceptions were Experiments 8 and 9 in Table V.

as in the selective predation experiments with the spiders. In _O. fasciatus_, mortality was low; in _T. molitor_, moderate. The mortality of large _T. molitor_ increased with time, as occurred in _D. melanogaster_. However, mortality in _O. fasciatus_ and small _T. molitor_ mainly occurred during the first day and did not increase on the following day.

Table A-VII indicates that when small and large _T. molitor_ were placed with live _D. melanogaster_ there was no increase in mortality over the controls (P > 0.9 for small _T. molitor_ and >0.5 for large _T. molitor_). This, coupled with direct observations, indicated that neither small or large _T. molitor_ kill _D. melanogaster_. Though it was observed that _T. molitor_ larva sometimes fed on dead flies, the numbers of dead flies in the cages with _T. molitor_ were not significantly less than the controls (P>0.1). However, there was a significant difference between the estimated number of dead flies eaten by the small and large _T. molitor_ - the small larvae ate more (P>0.01*).

Table A-VIII gives the feeding rates of large _T. molitor_ on cold-killed _D. melanogaster_. Notice that the density of both the beetle larvae and the dead flies were much higher than what occurred in the selective predation experiments (i.e., 10 vs. 5 larvae per cage and 10 vs. about 2 dead flies per cage). Thus, the feeding rate of 0.465 dead flies per larva per day is much higher than what occurred in the selective predation experiments.

Table A-IX gives the feeding rates of both small and large _T. molitor_ on rejectamenta of _D. melanogaster_. Again, note that the densities of both the larvae and rejectamenta were higher than the usual circumstances found in the selective predation experiments. The rates work out to be 0.090 rejectamenta per larva per day for large _T. molitor_ and 0.015 rejectamenta per larva per day for small _T. molitor_. These feeding rates are very different statistically ($P < 0.001$**, $U = 2057$).

Table A-X lists the escape rates (plus counting errors) of the various prey types. The escape rates were calculated in the same manner as the number of prey eaten per spider per day, except of course, that there were no spiders and no rejectamenta. There were no escapes of large _T. molitor_. Some, 2.92%, of the small _T. molitor_ were lost when they burrowed into the sponges. Escape of _D. melanogaster_ was less than 0.2% when the density was 10 flies per cage but climbed to two and a half times that value when there were 20 flies per cage (i.e., 10 males plus 10 females). The escape rate of _O. fasciatus_ was the highest at 8.54%. This was due to their ability to move through the small cracks that resulted from the imperfect fit of the lids and bases of the plastic cages. The Results section comments on how these errors were taken into account when the feeding rates of the predators were calculated.

Table A-I. The mean cephalothorax widths, live weights, and dry weights of exuviae of male and female *P. vancouveri* (SE,N).

	Male spiders		
	Antepenultimate	Subadult	Adult
Cephalothorax width (mm)	1.79 (0.004,170)	2.05 (0.004,170)	2.36 (0.007,23)
Live weight at moulting (mg)	....	15.58 (0.324,80)	21.44 (1.018,39)
Dry weight of exuvia (mg)		0.28 (0.010,44)	0.56 (0.015,29)

	Female spiders		
	Antepenultimate	Subadult	Adult
Cephalothorax width (mm)	1.81 (0.004,140)	2.06 (0.005,140)	2.51 (0.006,93)
Live weight at moulting (mg)	....	16.61 (0.262,177)	31.11 (0.513,99)
Dry weight of exuvia (mg)		0.31 (0.012,39)	0.58 (0.023,26)

Table A-II. The mean (mm) length, width and height of test prey (SE). N = 30 individuals of each prey type.

	O. fasciatus	*D. melanogaster*		*T. molitor*	
		Male	Female	Small	Large
Length	1.85 (0.126)	2.64 (0.010)	2.73 (0.011)	5.59 (0.187)	10.08 (0.302)
Width	0.88 (0.061)	0.78 (0.003)	0.87 (0.004)	0.85 (0.010)	1.62 (0.013)
Height	0.58 (0.043)	0.94 (0.003)	1.02 (0.003)	0.71 (0.010)	1.32 (0.016)

Table A-III. Mean weights (mg) of test prey (SE).

	O. fasciatus	*D. melanogaster*		*T. molitor*	
		Male	Female	Small	Large
Wet Weights[1]	0.46 (0.038)	0.80 (0.016)	1.23 (0.030)	2.41 (0.222)	12.66 (0.731)
Dry Weights[2]	0.238 (0.0002) [33x10]	0.253 (0.0004) [29x100]	0.354 (0.0003) [27x100]	1.008 (0.0024) [12x20]	6.350 (0.0100) [13x20]

[1] Wet weights were based on 30 individual weights.

[2] Dry weights were based on a number of samples of more than one individual. This is expressed as [number of samples x number of individuals per sample].

Table A-IV. Resting positions of *P. vancouveri* and test prey in plastic cages.

Animal	Resting positions (%)[1] 1	2	3	4	5	Total number observations	Number of animals observed
Subadult female *P. vancouveri*	0.0	5.1	54.5	20.1	20.1	154	18
O. fasciatus	6.2	8.9	5.3	21.6	57.8	415	>120[2]
Female *D. melanogaster*	0.0	30.4	7.8	37.1	24.6	601	>300[2]
Small *T. molitor*	9.2	5.6	85.1	0.0	0.0	141	>50[2]
Large *T. molitor*	13.0	5.2	81.7	0.0	0.0	115	>50[2]

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[1] Resting positions expressed as percentages of total amount of observations. Code for resting positions: 1 = under or within sponge, 2 = on surface of sponge, 3 = on cage floor (excluding sponge), 4 = on cage walls, 5 = on cage ceiling.

[2] Observations were taken over more than one day and more than once on each animal.

Table A-V. Non-predator mortality of *D. melanogaster*. Results are expressed as mean number of dead flies observed per cage per day (95% confidence limits). Transformation = square root (X + 0.5).

Prey (number prey per cage)	Number of days after prey renewal[1]			Grouped means	
	1	2	3	1+2	1+2+3
Male (10)	0.23 (0.015-0.253)	1.57 (1.225-2.085)	2.77 (1.946-3.714)	0.75 (0.516-1.003)	0.98 (0.729-1.250)
Female (10)	0.03 (0.0-0.067)	0.65 (0.417-0.918)	3.17 (2.566-3.834)	0.31 (0.193-0.473)	0.59 (0.417-0.783)
Male (with female) (10+10)	0.14 (0.008-0.286)	2.18 (1.687-2.732)	3.89 (1.740-5.317)	0.99 (0.707-1.292)	1.31 (0.990-1.652)
Female (with male) (10+10)	0.07 (0.009-0.133)	1.03 (0.721-1.374)	2.26 (2.192-4.517)	0.49 (0.335-0.662)	0.78 (0.565-1.012)
Number of observation-days	54	54	18	108	126

STATISTICAL TEST (U values)[2]

	Male	Female	Male (with Female)	Female (with male)
Male				
Female	304**			
Male (with Female)	186	309**		
Female (with male)	271**	226.5	286**	

---

[1] Flies were 'renewed' every two or three days, as indicated, and 'replenished' once each day.

[2] The statistical test was the *a posteriori* nonparametric simultaneous test procedure and was used on the data for days 1+2. Number of treatments = 4, number of means per treatment = 18, number of observation-days per mean = 6. $P<0.01$** Note: For $P = 0.01$, the critical value of $U = 260.4$; for $P = 0.05$, $U = 243.2$.

Table A-VI. Non-predator mortality in *O. fasciatus* and *T. molitor*. Results are expressed as mean number of dead prey observed per cage per day (95% confidence limits)[number of observation-days]. Transformation = square root (X + 0.5).

Prey (number of prey/cage)	Number of days after prey renewal[1] 1	2	Grouped mean 1+2
O. fasciatus (10)	0.08 (0.0-0.425) [24]	0.00 (0.0-0.343) [24]	0.04 (0.0-0.277) [48]
Small *T. molitor* (5)	0.36 (0.209-0.509) [16]	0.34 (0.214-0.459) [16]	0.35 (0.256-0.434) [32]
Large *T. molitor* (5)	0.40 (0.199-0.604) [14]	0.45 (0.183-0.696) [14]	0.42 (0.272-0.574) [28]

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[1] Prey were 'renewed' every two days and 'replenished' once each day.

Table A-VII. Feeding rates of *T. molitor* larvae on dead female *D. melanogaster*. Results are expressed as mean numbers observed per cage per day (SE).

T. molitor (10/cage)	Number of observation-days	Initial density (N) (10 live *D. melanogaster* /cage)		
		Number live (L)	Number dead (D)	Estimated number Eaten (N-(L+D))
Small	48	8.42 (0.268)	0.94 (0.196)	0.38 (0.106)
Large	72	8.13 (0.248)	1.11 (0.173)	0.32 (0.110)
None (Control)	120	8.33 (0.189)	1.65 (0.190)	----

STATISTICAL TESTS

Treatments compared	U. Stat.[1]	Probability that means are equal
Number Live - Small T.m. vs. Control	2907.5	>0.9
Number Live - Large T.m. vs. Control	4547	0.5<P<0.9
Number Dead - Small T.m. vs. Control	3315.5	0.1<P<0.2<P
Number Dead - Large T.m. vs. Control	4767.5	0.2<P<0.4
Estimated Number Eaten - Small T.m. - vs. Large T.m.	1544	0.01<P<0.02*

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[1] Mann-Whitney U-test.

Table A-VIII. Feeding rate of large *T. molitor* on dead (frozen) female *D. melanogaster*. Results are expressed as mean number observed per cage per day (SE).

T. molitor (10/cage)	Number of obs.-days	Initial density (N) (10 dead *D. melanogaster* /cage)		
		Number un-eaten (UE)	Number partially eaten	Estimated number eaten (N-UE)
Large	72	5.35 (0.362)	0.67 (0.088)	4.65[1] (0.362)

---

[1] Number eaten per 10 larvae per day.

Table A-IX. Feeding rates of *T. molitor* on *D. melanogaster* rejecta. Results are expressed as mean number per cage per day (SE).

T. molitor (10/cage)	Number of obs.-days	Initial density (N) (5 *D. melanogaster* rejectamenta per cage)	
		Number rejectamenta (R)	Number eaten (N-R) [1]
Large	48	4.10(0.112)	0.90(0.112) [2]
Small	48	4.85(0.051)	0.15(0.051) [2]

---

[1] Number eaten per 10 larvae per day.

Table A-X. Escape rates of prey from plastic cages. Results are expressed as percentages of the total number of prey counted.

Prey	Density (initial number per cage)	Total initial number of prey	Estimate of size of escape rates[1]
Large *T. molitor*	5	240	0.00%
Female *D. melanogaster*	10	1080	0.19%
Both male female *D. melanogaster*	10+10	2160	0.51%
Small *T. molitor*	5	240	2.92%
O. fasciatus	10	480	8.54%

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[1] Escape rate = (Initial Density) - (Number of Live + Number of Dead). The escape rates include counting errors and errors due to small *T. molitor* burrowing into sponges.

APPENDIX II, Details of the Selective Predation Experiments

The detailed results of the 14 selective predation experiments are given in Table A-XI. A shortened version appears in Table I. The layout of Table I and Table A-XI is the same except that the four feeding rates and the two probabilities that are derived from the three treatments are given in the expanded table. For example, in Experiment 2a. there were three treatments of subadult female spiders. One group of 8 was fed only female *D. melanogaster* and these gave a grand mean feeding rate of 2.31 flies per spider per day (i.e., u_1). Another group of 12 spiders was fed only *O. fasciatus* and gave a feeding rate of 3.55 bugs per spider per day (i.e., u_2). The third group was fed both female *D. melanogaster* and *O. fasciatus* together. They gave two feeding rates; 2.62 flies per day (u^*_1) and 0.19 bugs per day (u^*_2). The 'x2' is there as a reminder that the means that made up the grand means in the two prey treatment were each multiplied by two (see Equations 2 and 3 in Materials section) before they were used to calculate the Mann-Whitney statistic 'U'. In this case, the probability that the mean feeding rates of 2.31 and (2.62 x 2) are equal, is less than 0.002. The relative discrimination coefficient was calculated by the Equations 4 to 6 given in the Materials and Methods section. For example, in Experiment 2a:

$$c_1 = \frac{u^*_1}{u_1} \times 2 = \frac{2.62}{2.31} \times 2 = 2.28$$

$$c_2 = \frac{u^*_2}{u_2} \times 2 = \frac{0.19}{3.55} \times 2 = 0.11$$

$$c_{1,2} = c_1 - c_2 = 2.28 - 0.11 = 2.17$$

Table A-XI. Results of 14 selective predation experiments ranked according to the relative discrimination coefficient. See text for explanation.

	Spider								
Experiment	Stage	Sex	Number of obs. days	N	Prey presented	Mean no. prey eaten /spider /day	Mann Whitney stat. (U)	Prob.	Relative discrim. coefficient
1	Adult[1]	M	10	8	Female D.m.	2.73	112	<0.002 **	2.19
				14	Female D.m. (+ Large T.m.)	2.99x2			
				14	Large T.m.	0.13	175	** <0.002	
				14	Large T.m. (+ Female D.m.)	0.00x2			
2a	Subadult	F	20	8	Female D.m.	2.31	80	<0.002 **	2.17
				10	Female D.m. (+ O.f.)	2.62x2			
				12	O.f.	3.55	120	<0.002 **	
				10	O.f. (+ Female D.m.)	0.19x2			

(Table continued)

Table A-XI continued

3b	Adult	F	20	4	Small T.m.	1.11	20	0.02 *	2.08
				5	Small T.m. (+ Large T.m.)	1.27x2			
				9[3]	Large T.m.	0.19	44	0.002 **	
				5	Large T.m. (+ Small T.m.)	0.02x2			
4	Adult[1]	M	10	8	Female D.m.	2.73	121.5	<0.002 **	1.98
				15	Female D.m. (+ Small T.m.)	3.02x2			
				14	Small T.m.	1.31	209.5	<0.002 **	
				15	Small T.m. (+ Female D.m.)	0.13x2			
5a	Subadult	F	20	12[4]	Female D.m.	2.95	167	<0.002 **	1.82
				14	Female D.m. (+ Small T.m.)	2.89x2			
				12[4]	Small T.m.	0.72	167	<0.002 **	
				14	Small T.m. (+ Female D.m.)	0.05x2			

(Table continued)

Table A-XI continued

2b	Adult	F	20	4	Female D.m.	5.23	36	<0.01 **	1.62
				9	Female D.m. (+ O.f.)	5.01x2			
				6*	O.f.	5.06	54	<0.002 **	
				9	O.f. (+ Female D.m.)	0.74x2			
3a	Subadult	F	20	12*	Small T.m.	0.72	137	0.002< P <0.01 **	1.38
				14	Small T.m. (+ Large T.m.)	0.64x2			
				11	Large T.m.	0.05	111	0.05< P <0.10	
				14	Large T.m. (+ Small T.m.)	0.01x2			
6	Subadult[2]	F	8	14	Female D.m.	3.36	208	<0.002 **	1.12
				16	Female D.m. (+ Small T.m.)	3.13x2			
				14	Small T.m.	1.21	161	0.02< P <0.05 *	
				16	Small T.m. (+ Female D.m.)	0.45x2			

(Table continued)

Table A-XI continued

5b	Adult	F	20	9	Female D.m.	5.28	72	<0.002 **	0.95
				8	Female D.m. (+ Small T.m.)	4.02x2			
				4	Small T.m.	1.11	28	0.05 *	
				8	T.m. (+ Female D.m.)	0.32x2			
7	Subadult[2]	M	7	20	Male D.m.	7.64	409	<0.001 **	0.88
				22	Male D.m. (+ Small T.m.)	6.42x2			
				21	Small T.m.	1.77	294.5	0.10< P <0.20	
				22	Small T.m. (+ Male D.m.)	0.71x2			
8	Subadult	M	20	9[4]	Female D.m.	2.27	54	0.02 *	0.57
				7[4]	Female D.m. (+ Male D.m.)	1.52x2			
				12[4]	Male D.m.	3.13	65.5	0.05< P <0.10	
				7[4]	Male D.m. (+ Female D.m.)	1.21x2			

(Table continued)

Table A-XI continued

9	Subadult	F	20	7	Female D.m.	2.32	41.5	>0.20	0.36
				9	Female D.m. (+ Male D.m.)	1.36x2			
				9	Male D.m.	3.18	51	>0.20	
				9	Male D.m. (+ Female D.m.)	1.29x2			
10b	Adult	F	20	6	O.f.	5.06	34	>0.20	0.09
				8	O.f. (+ Small T.m.)	3.23x2			
				6	Small T.m.	1.70	27.5	>0.20	
				8	Small T.m. (+ O.f.)	1.01x2			
10a	Subadult	F	20	12	O.f.	3.55	82	0.10< <0.20	0.08
				10	O.f. (+ Small T.m.)	2.42x2			
				10	Small T.m.	0.79	70.5	0.10< P <0.20	
				10	Small T.m. (+ O.f.)	0.57x2			

(Table continued)

Footnotes for Table A-XI

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[1] Spiders with unknown subadult moulting histories.

[2] Freshly caught spiders without previous laboratory feeding (i.e., no pre-feeding) and with unknown subadult moulting histories.

[3] Subadult spiders with unknown moulting histories raised to maturity on large *T. molitor* but not tested concurrently.

[4] Total number of observation-days slightly less than (Number of spiders x 20) because one or more spiders matured in less than 20 days.

APPENDIX III, Details of the Utility of the Prey to the Predators

Tables A-XII to A-XVII summarize the benefit criteria that were measured in the selective predation experiments. All tables, except Table A-XVI, refer to female spiders. Results are expressed as means (SE, N) per spider or as percentages (N) of all spiders.

In these tables column 'A' refers to the benefit criteria that were associated with the spiders that ate the more-selected prey; column 'B', both prey; and column 'C', the less-selected prey. The hypotheses tested in the 'Probability' columns are: 1) the utility of feeding on the more-selected prey equals the utility of feeding on both prey (i.e., A = B) and 2) the utility of feeding on the more-selected prey equals the utility of feeding on the less-selected prey (i.e., A = C). The rows of the tables are arranged from top to bottom by increasing probabilities of the last column. Because the maximum limit for observations was 85 days, a few spiders which matured late (i.e., after 65 days) were not observed for all 20 days after reaching maturity. This gives a few inconsistencies in the replication of the results for adult spiders.

Significant differences (i.e., 2) for column "A = B" occur in only Tables A-XIII and A-XVII. Significant differences (i.e., 7) for column "A = C" occur in Tables A-

XII, A-XIII and A-XV. Notice that in Table A-XIII most of the spiders died when they were fed only large _T. molitor_. This greatly reduced the number of statistical tests that could be made.

Table A-XII. Benefit criteria for female *P. vancouveri* in one and two prey systems using female *D. melanogaster* and *O. fasciatus*. Data from Experiments 2a and 2b.

Benefit	Treatment A Female D.m.	Treatment B Both Prey	Treatment C O.f.	Probability A=B	Probability A=C
Days to first false egg-sac	13.0 (0.58,3)	11.8 (3.12,5)	19.5 (0.50,4)	0.784	0.004 **
Adult day 0 to +10 weight gain(mg)	11.45 (1.947,4)	14.03 (2.674,9)	5.81 (0.854,4)	0.559	0.038 *
Dry weight (mg) false egg-sacs	4.93 (0.746,3)	3.18 (1.488,5)	1.04 (0.871,4)	0.429	0.044 *
Extra moults	0% (8)	40% (10)	31% (13)	0.137	0.239
Spiders producing false egg-sacs	50% (4)	56% (9)	67% (6)	1.000	0.266
Days for maturation	43.3 (7.87,4)	38.8 (3.74,9)	31.5 (6.79,4)	0.567	0.301
Subadult to adult weight gain (mg)	13.55 (2.702,4)	16.44 (1.657,9)	10.68 (0.900,4)	0.358	0.353
Subadult to adult rate of weight gain (mg/day)	0.33 (0.060,4)	0.44 (0.038,9)	0.44 (0.165,4)	0.172	0.562
Subadult to adult size increase(mm)	0.36 (0.005,4)	0.45 (0.002,9)	0.32 (0.002,4)	0.404	0.780
Mortality before maturity or 70 days	38% (8)	10% (10)	23% (13)	0.415	0.819
Maturation within 70 days	50% (8)	90% (10)	31% (13)	0.695	1.000
Adult mortality within 20 days	0% (4)	0% (9)	0% (6)	1.000	1.000

Table A-XIII. Benefit criteria for female *P. vancouveri* in one and two prey systems using small and large *T. molitor*. Data from Experiments 3a and 3b.[1]

Benefit	Treatment			Probability	
	A Small T.m.	B Both Prey	C Large T.m.	A=B	A=C
Mortality before maturity or 70 days	0% (12)	0% (14)	75% (12)	1.000	<0.001 **
Maturation within 70 days	33% (12)	43% (14)	8% (12)	0.928	0.320
Adult mortality within 20 days	0% (4)	0% (5)	100% (1)	1.000	0.400
Extra moults	17% (12)	21% (14)	0% (12)	1.000	0.621
Subadult to adult weight gain (mg)	10.26 (0.409,4)	12.10 (2.006,6)	0.80 (0.000,1)	0.487	....
Subadult to adult size increase(mm)	0.34 (0.010,4)	0.35 (0.013,6)	0.24 (0.000,1)	0.890	....
Days for maturation	28.8 (6.03, 4)	48.0 (5.01, 6)	58.0 (0.00, 1)	0.040 *	....
Subadult to adult rate of weight gain (mg/day)	0.40 (0.076,4)	0.26 (0.025,6)	0.01 (0.000,1)	0.058	....
Days to first false egg-sac	15.0 (1.00,2)	16.5 (0.50,2)	....	0.312	....
Adult day 0 to +10 weight gain(mg)	11.43 (1.393,4)	12.33 (1.367,6)	....	0.672	....
Dry weight (mg) false egg-sacs	1.54 (0.804,2)	2.14 (1.908,2)	....	0.800	....
Spiders producing false egg-sacs	50% (4)	40% (5)	....	1.000	....

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[1] The only spider that matured on large *T. molitor* died in moulting. Thus, probabilities for some A = C tests and comparison data for adults are missing.

Table A-XIV. Benefit criteria for female *P. vancouveri* in one and two prey systems using female *D. melanogaster* and small *T. molitor*. Data from Experiments 5a and 5b.

Benefit	Treatment A Female D.m.	 B Both Prey	 C Small T.m.	Probability A=B	 A=C
Subadult to adult weight gain (mg)	17.16 (1.084,9)	15.63 (0.674,9)	10.26 (0.409,4)	0.249	0.002 **
Adult day 0 to +10 weight gain(mg)	20.06 (1.962,9)	18.27 (2.176,9)	11.43 (1.393,4)	0.549	0.019 *
Subadult to adult rate of weight gain (mg/day)	0.68 (0.070,9)	0.50 (0.056,9)	0.40 (0.076,4)	0.052	0.035 *
Dry weight (mg) false egg-sacs	3.11 (0.299,9)	2.53 (0.406,8)	1.54 (0.804,2)	0.505	0.059
Maturation within 70 days	75% (12)	64% (14)	33% (12)	0.592	0.100
Spiders producing false egg-sacs	100% (9)	100% (8)	50% (4)	1.000	0.154
Days to first false egg-sac	12.8 (1.04,9)	12.4 (0.68,8)	15.0 (1.00,2)	0.757	0.364
Subadult to adult size increase(mm)	0.38 (0.001,9)	0.41 (0.001,9)	0.34 (0.001,4)	0.368	0.473
Days for maturation	27.0 (2.71, 9)	34.3 (3.63, 9)	28.8 (6.03, 4)	0.125	0.762
Extra moults	8% (12)	14% (14)	17% (12)	1.000	1.000
Mortality before maturity or 70 days	8% (12)	0% (14)	0% (12)	1.000	1.000
Adult mortality within 20 days	0% (9)	0% (8)	0% (4)	1.000	1.000

Table A-XV. Benefit criteria for female *P. vancouveri* in one and two prey systems using female and male *D. melanogaster*. Data from Experiment 8.[1]

Benefit	Treatment			Probability	
	A Female	B Both Prey	C Male	A=B	A=C
Subadult to adult weight gain (mg)	10.37 (1.001,6)	12.18 (1.304,7)	13.05 (1.033,8)	0.306	0.094
Subadult to adult rate of weight gain (mg/day)	0.32 (0.060,6)	0.32 (0.045,7)	0.38 (0.026,8)	0.968	0.318
Subadult to adult size increase (mm)	0.40 (0.001,6)	0.38 (0.001,5)	0.42 (0.001,8)	0.716	0.408
Days for maturation	35.2 (3.75,6)	39.1 (3.07,7)	34.1 (1.77,8)	0.425	0.789
Maturation within 70 days	86% (7)	78% (9)	88% (9)	1.000	1.000
Mortality before maturity or 70 days	0% (7)	0% (9)	0% (9)	1.000	1.000
Extra moults	0% (7)	0% (9)	0% (9)	1.000	1.000

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[1] Spiders were not raised past maturity, so no adult benefits were measured.

Table A-XVI. Benefit criteria for male *P. vancouveri* in one and two prey systems using female and male *D. melanogaster*. Data from Experiment 9.[1]

Benefit	Treatment			Probability	
	A Female	B Both Prey	C Male	A=B	A=C
Subadult to adult size increase(mm)	0.34 (0.001,8)	0.33 (0.002,7)	0.32 (0.001,11)	0.777	0.224
Days for maturation	25.2 (1.82,9)	26.7 (2.49,7)	26.3 (2.73,12)	0.626	0.757
Subadult to adult rate of weight gain (mg/day)	0.33 (0.060,9)	0.29 (0.036,7)	0.31 (0.052,12)	0.618	0.806
Subadult to adult weight gain (mg)	7.66 (0.864,9)	7.26 (0.447,7)	7.47 (1.000,12)	0.710	0.892
Maturation within 70 days	100% (9)	100% (7)	100% (12)	1.000	1.000
Mortality before maturity or 70 days	0% (9)	0% (7)	0% (12)	1.000	1.000
Extra moults	0% (9)	0% (7)	0% (12)	1.000	1.000

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[1] Spiders not raised past maturity, so no adult benefits were measured.

Table A-XVII. Benefit criteria for female *P. vancouveri* in one and two prey systems using *O. fasciatus* and small *T. molitor*. Data from Experiments 10a and 10b.

Benefit	Treatment A O.f.	 B Both Prey	 C Small T.m.	Probability A=B	 A=C
Adult day 0 to +10 weight gain(mg)	5.81 (0.845,4)	9.76 (0.987,7)	8.00 (0.784,6)	0.025 *	0.102
Days for maturation	31.5 (6.79,4)	34.0 (4.72,7)	43.8 (5.91,6)	0.763	0.214
Maturation within 70 days	31% (13)	73% (11)	67% (9)	0.100	0.220
Subadult to adult rate of weight gain (mg/day)	0.44 (0.165,4)	0.40 (0.023,7)	0.28 (0.044,6)	0.737	0.410
Days to first false egg-sac	16.3 (1.93,4)	14.0 (1.16,3)	18.3 (1.59,3)	0.406	0.586
Subadult to adult weight gain (mg)	10.68 (0.900,4)	12.42 (1.112,7)	11.65 (2.414,6)	0.317	0.762
Extra moults	31% (13)	27% (11)	44% (9)	1.000	0.833
Dry weight (mg) false egg-sacs	1.06 (0.398,4)	1.94 (1.003,3)	1.02 (0.069,2)	0.399	0.960
Subadult to adult size increase(mm)	0.32 (0.002,4)	0.37 (0.002,7)	0.32 (0.002,6)	0.600	1.000
Mortality before maturity or 70 days	23% (13)	9% (11)	0% (9)	0.749	1.000
Spiders producing false egg-sacs	67% (6)	43% (7)	67% (6)	1.000	1.000
Adult mortality within 20 days	0% (6)	0% (3)	0% (6)	1.000	1.000

Appendix IV, Guide to the Important Terms Used in the Text

Availability (of prey to predators) - includes factors related to coexistence in time and space, density and distribution of both prey and predators.

Benefit - positive result of the utility function, e.g., gain in usable energy, time and/or nutrients.

Catchability - the aspects of morphology and behavior that are involved when a predator stalks, captures and consumes a prey.

Costs - outlay (e.g., energy, time, nutrients) used by a feeder to obtain its food.

Density - number of organisms per unit area or unit volume.

False egg-sacs - infertile egg sacs produced by spiders that had not mated; false-egg sacs were incompletely formed or abnormally shaped and the eggs formed a mass of yolk rather than separate spheres.

Fitness - the degree to which an organism is successful in terms of its survival maturation, reproduction and dispersal; ability to transmit its genetic material to the next generation.

Fitness strategy - how an organism apportions its resources such as time and energy between survival, maturation, reproduction and dispersal.

Functional response - relationship between the density of a prey and the number that are killed by a predator;

usually the amount of predation increases with increases in prey density until a plateau is reached where predation rate remaining constant even if prey density increases further.

Hunger - a physiological drive (i.e., 'desire' or 'need') for food that normally increases with time since the last meal.

Loss - negative result of the utility function, e.g., decrease in usable energy, time and/or nutrients.

Monophagy - feeding on only one species or kind of food.

Non-standard flies - adult D. melanogaster that were from cultures more than 21 days old.

Numerical response - relationship between changes in the density of prey and the changes in the survival, reproduction and migration patterns of their predators.

Nutrition - relative value of a food to sustain survival and promote growth.

Observation-day - a set of observations made on the animals in one experimental cage; observations made over a series of days were often made on the same animals, thus observation-days were not independent and cannot be compared statistically.

Oligophagy - feeding on only a few species or kinds of food.

Palatability - extent to which a food item is agreeable to a feeder, in terms of its taste, odor and texture.

Polyphagy - feeding on many species or kinds of food.

Predator - an animal that kills and eats other animals (i.e., its prey).

Pre-feeding - the feeding of an organism on a certain diet before it is fed another diet.

Preference - innate or learned attributes of an animal that predispose it to expand relatively more time and energy to locate and ingest certain food items.

Prey - an animal that is killed and eaten by another animal (i.e., a predator).

Rejectamenta (singular = rejectamentum) - aggregation of unconsumed remains of prey fed upon by a spider.

Renewal days - all prey replaced with fresh prey; sponges also re-wetted.

Replenishment days - dead and eaten prey removed and only enough fresh prey added to restore the prey densities to the initial levels.

Revenue - income (e.g., energy, time, nutrients) to a feeder from its food.

Selective feeding - feeding in a non-random manner; feeding on certain items, when more than one kind is available, more frequently than would be expected from the relative abundance of each kind of food.

Standard flies - adult D. melanogaster that emerged from cultures that were 14 to 21 days old; i.e., the adults had emerged from their pupal cases less than 7 days previously.

Strategy - how an organism apportions its resources towards some goal; see 'fitness strategy'.

Subadult spiders - immature spiders that were judged (by size) to be in the prepenultimate stage and that moulted within a two week period during which they were fed D. melanogaster; these spiders were assumed to be one moult away from being adults, i.e., in the penultimate stage.

Utility function - the difference between revenues and costs; positive utility results in benefits, negative utility results in losses.

APPENDIX V, List of Non-Standard Abbreviations

* - statistical probabilities between 0.05 and 0.01, statistically significant.

** - statistical probabilities less than 0.01, highly statistically significant.

approx. - approximate(ly)

ca. (*circa*) - about, approximately

cf. (*confer*) compare

c_1 - amount of selection for Prey 1

$c_{1,2}$ - relative discrimination coefficient

D.m. - adult, vestigial-winged fruit flies, *Drosophila melanogaster* Meig. of the Family Drosophilidae

discrim. coeffic. - relative discrimination coefficient

D1 - density of Prey 1

df - degrees of freedom

Dp - number of Prey 1 dead

e.g. (*exempli gratia*) - for example

et al. (*et alii*) - and others

Ep_1 - estimate of number of Prey 1 eaten

etc. (*et cetera*) - and so forth

F - female

i.e. (*id est*) - that is; that is to say

Ip_1 - initial density of Prey 1

Lp_1 - number of Prey 1 alive

M - male

N - number of observations

obs.-day - number of observation-days

O.f. - nymphal milkweed bugs, *Oncopeltus fasciatus* (Dallas) of the Family Lygaeidae

P - probability

Prey 1 - population of one kind of prey

Prob. - probability

SE - standard error of the mean

T.m. - bettle larvae or mealworms, *Tenebrio molitor* L. of the Family Tenebrionidae; two sizes, "large" and "small"

u_1 - feeding rate on Prey 1 with only Prey 1 present

u^*_1 - feeding rate on Prey 1 with Prey 1 and another prey present

APPENDIX VI, Curriculum Vitae

NAME:

HOLMBERG, Robert George

BORN:

25 December 1946, Canada

EDUCATION:

Primary schools: Hyas, Sturgis, and Yorkton, Saskatchewan. 1952-1960.

Secondary school: Sturgis Composite High School, Sturgis, Saskatchewan. 1960-1964.

B.A. received 1967. University of Saskatchewan, Saskatoon, Saskatchewan. Major in Biology with emphasis on invertebrate zoology. 1964-1967.

Honours degree in Biology received 1970. University of Saskatchewan, Saskatoon, Saskatchewan. 1967-1968.

M.Sc. received 1971. University of Saskatchewan, Saskatoon, Saskatchewan. Thesis topic: "The odoriferous glands of some Palpatores Phalangida (Opiliones) (Arachnida)". Supervisor: Dr. T.H.J. Gilmour. 1968-1970.

Since 1971. Ph.D. program at the Department of Biological Sciences, Simon Fraser University. Thesis topic: "Selective predation in a polyphagous invertebrate predator, _Pardosa vancouveri_ (Arachnida, Araneae)".

Senior supervisor: Dr. A.L. Turnbull.

AWARDS, SCHOLARSHIPS:

Government of Saskatchewan University Entrance Scholarship, 1964.

Teaching Assistantship Award from the University of Saskatchewan, 1969.

Teaching Assistantship Unit Scholarship from the University of Saskatchewan, 1970.

Simon Fraser University Graduate Scholarship, 1972.

Graduate Student Stipend from Simon Fraser University, 1973.

TEACHING EXPERIENCE:

1) Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan:

a) Laboratory Demonstrator in Biological Sciences 100. Supervisor: Dr. F. Turrel. 1965-1966.

b) Teaching Assistant in Biology 203. Supervisor: Dr. T.H.J. Gilmour. 1968-1969.

c) Teaching Assistant in charge of the Biology 203 laboratory. Supervisor: Dr. T.H.J. Gilmour. 1969-1970.

d) Laboratory Instructor for a 6 week Summer School session of Biology 203. Supervisor: Dr. T.H.J. Gilmour. 1970.

2) Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia:

a) Teaching Assistant and occasional lecturer for Biological Sciences 409. Supervisor: Dr. R.M. Sadlier. 1971.

b) Teaching Assistant for Biological Sciences 316. Supervisor: Dr. R.M. Sadleir. 1972.

c) Teaching Assistant and occasional lecturer for Biological Sciences 409. Supervisor: Dr. R.M. Sadleir. 1973.

d) Teaching Assistant in Biological Sciences 102. Supervisor: Dr. B.P. Beirne. 1974.

3) Environmental Sciences, Athabasca University, Edmonton, Alberta:

a) Course Coordinator for World Ecology: The Scientific Context 201. Supervisor: Dr. T.S. Bakshi. 1974 to present.

b) Instructor for Field Ecology Workshops associated with World Ecology. Co-Instructors: Dr. T.S. Bakshi, Dr. L. Fenna. Summers 1975 to present.

c) Course Coordinator and Instructor for Introductory Biology 100. Supervisor: Dr. T.S. Bakshi. 1976 to present.

LECTURES AT SCIENTIFIC MEETINGS:

"The odoriferous glands of some Palpatores Phalangida (Opiliones) (Arachnida)". Presented at a joint meeting of the Entomological Society of Canada and the Entomological Society of British Columbia in Victoria, British Columbia. 1971.

"Prey preference in a general invertebrate predator, *Pardosa vancouveri*, (Arachnida, Araneae)". Presented at a joint meeting of the Entomological Society of Canada and the Entomological Society of Alberta in Banff, Alberta. 1973.

"Selective predation by a spider". Poster presentation at the XV International Congress of Entomology, Washington, D.C., 1976.

RESEARCH EMPLOYMENT:

Student Assistant working on identifying, collecting and rearing mosquitoes for a Western Encephalitis virus study. Supervisor: Dr. J.R. McLintock, Canada Agriculture Research Station, Saskatoon, Saskatchewan. 1966-1968.

Research Assistant working on spider ecology. Supervisor: Dr. A.L. Turnbull, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia. 1971.

PUBLICATIONS:

Holmberg, R.G. and D. Troffimenkoff. 1968. Aedes melanimon in Saskatchewan. Mosquito News 26:651-652.

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MEMBERSHIP IN PROFESSIONAL SOCIETIES:

American Arachnological Society
Arachnological Society of East Asia
British Arachnological Society
Canadian Society of Zoologists
Centre International de Documentation Arachnologique
Entomological Society of Alberta
Entomological Society of Canada

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