STUDIES ON THE FORAGING BEHAVIOUR OF DAMSELFLY LARVAE (ODONATA; ZYGOPTERA)

by

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ABSTRACT

A series of experiments, based on the functional response, was designed to test alternative hypotheses regarding the change in diet breadth of a polyphagous predator, faced with a reduction in prey abundance due to competitive exploitation. Experiments on the damselfly species *Pyrrhosoma nymphula* (Sulzer) and *Coenagrion puella* (Linnaeus) feeding on *Aedes aegypti* (Linnaeus) and *Daphnia magna* (Straus) revealed irregular and variable functional responses.

Investigations into the effects of the experimental conditions on damselfly predatory behaviour showed that the starvation period prior to experimentation and the experimental arena size both affected the variance and mean numbers of prey eaten. Damselfly age within the ultimate instar was also shown to significantly influence the number of each prey type eaten. Sit and watch experiments revealed that the functional response parameters themselves may vary with prey density, although such variations need not always result in irregular functional response curves.

Mixed prey experiments showed that both predators prefer *Aedes aegypti* to *Daphnia magna*, and neither predator switches. Both damselflies contract their diets in response to a reduction in prey density, although *Pyrrhosoma*'s diet is narrowest when *Coenagrion*'s effect on it is greatest, while the reverse is true for *Pyrrhosoma*'s effect on *Coenagrion*. Mechanisms are suggested which may operate to reduce the intensity of competition between these two predators in the field, and a mathematical model, formalizing one of these hypotheses, is constructed.

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1. Introduction

1.1. Summary

It was the original intent of this project to test a hypothesis against an alternative hypothesis, by means of controlled laboratory experiments (see section 2.4.3.a)). The question under consideration was this: does a polyphagous predator broaden or narrow its diet, when faced with increased competition for prey? A literature survey revealed two apparently conflicting outcomes to this situation, predicted by two branches of ecological theory. Sections 1.3. and 1.4. in this introduction trace the logic behind each of these two alternative hypotheses. The last section in this chapter reviews evidence culled from the ecological literature which supports each hypothesis.

The practical work undertaken in this study was designed to test these alternative hypotheses in one particular situation. Only with knowledge of the individual predator's responses to single and mixed prey, could the competitive mixed prey situation be fully understood. The functional response of a single predator to one prey type was hence chosen as the experimental unit in this study. This model for predator-prey interactions is reviewed in the next section of this introduction.

1.2. The Functional Response

The term 'functional response' was first coined by Solomon, in 1949, who distinguished between the 'functional response' of a predator individual and the 'numerical response' of a predator population. He defined the functional response of a predator to an increase in prey density, as an increase in the number of prey eaten per predator, over a fixed period of time. This relationship is usually represented by a graph of the number of prey eaten per predator against the number of prey available. The time period, the arena size, and the number of predators must be constant for all prey densities. The three basic types of functional response, type 1, type 2, and type 3, were described by Holling (1959a), and are illustrated in Figure 1.1. In general, they have been observed to apply to spiders, insects, and vertebrates, respectively (Holling, 1965), although type 3 responses have also been documented for arthropod predators (Hassell, Lawton and Beddington, 1977).

The effects of many factors on predator functional responses, and the mathematical models describing them, have been discussed in the literature. Perhaps the most important of these are: learning (Tinbergen, 1960; Gibb, 1962; Murdoch, 1969 and 1973; Taylor, 1974; Murdoch, Avery and Smyth, 1975), predator age structure and other age-related effects (Holling, 1966; Murdoch, 1971 and 1972; Fox and Murdoch, 1974; Thompson, 1975), hunger (Watt, 1959; Holling, 1965 and 1966; Sandness and McMurtry, 1972; Glen, 1975; Johnson, Akre and Crowley, 1975; Curry and De Michele, 1977), confusion (Holling, 1961 ; Mori and Chant, 1966; Mori, 1969), spatial and temporal heterogeneity (Griffiths, 1969; Hassell and May, 1974; Oaten and Murdoch, 1975; Murdoch and Oaten, 1975), interference (Hassell, 1971a; Hassell and Rogers, 1972; Rogers and Hassell, 1974; Hassell and May, 1973; Beddington, 1975), and predator size and geometry (Holling, 1973; Werner, 1974). The above list is not exhaustive, and a number of comprehensive reviews discuss this subject in detail (Holling, 1961, 1965 and 1966; Royama, 1971; Rogers, 1972; Krebs, 1973; Murdoch, 1973; Murdoch and Oaten, 1975; Hassell, Lawton and Beddington, 1976).

The experimental section of the current study was designed to eliminate the influence of most of the above factors, in order to both simplify analysis, and minimize confounding. Consequently, the data have been analyzed using only the simplest, and most widely accepted, functional response model. This model, developed by Holling (1959b), and modified by Rogers (1972), has been applied with success to a wide variety of invertebrate predators (Hassell, Lawton and Beddington, 1976). The original equation derived by Holling (1959b) is usually termed the 'disc equation', since it was developed from the study of a human 'predator', 'searching' for sand-paper discs on a table. The type two functional response which resulted (Figure 1.1.) shows that as the number of prey offered increases, the number eaten increases too, but at a decreasing rate. At high prey densities the number of prey eaten levels off to an asymptote, determined by the limit to the time available for search set by the increasing time spent in handling prey.

If we assume that the handling time for each prey item captured, *Th*, and the attack rate of the predator, *a* (arena units searched/time), and the number of prey available in the arena, *No*, remain constant during the length of the experiment, *Tt*, then the time spent searching, *Ts*, and the number of prey eaten, *Ne*, can be described by:

$$Ts = Tt - Th\ Ne, \text{ and } Ne = a\ Ts\ No.$$

$$\text{Therefore:} \quad Ne = \frac{Tt\ a\ No}{1 + a\ Th\ No}.$$

The values of *a* and *Th* can be estimated from experimental data by calculating the linear regression of $\frac{Ne}{No}$ on *No*. The intercept will give a value for *Tt a*, and the slope for - *a Th*.

Royama (1971) and Rogers (1972) pointed out that the above set of equations applies only to predator prey interactions in which there is no depletion of prey due to predator exploitation, and the probability of a predator finding a prey during a given period of time is proportional to prey density. They both modified the 'disc equation' to include exploitation effects. The equation which resulted is known as the 'random predator equation':

$$Ne = No\ (1 - e^{-a\ (Tt\ -\ Ne\ Th)}).$$

a and Th can again be estimated by fitting a linear regression to the relationship between $\ln \frac{No - Ne}{No}$ and Ne; the resulting intercept giving an approximation for $-Tt\ a$, and the slope for $a\ Th$. Cock (1977), has pointed out that in many cases, functional response experiments do not satisfy the assumptions of the linear regression technique: that for any given prey density, the numbers of prey eaten are independently and normally distributed, and that the variance around the regression line is constant, and independent of prey density or the number of prey eaten. He has proposed that under these circumstances, an unbiased least squares best fit method should be used to estimate a and Th.

This model has been further developed by Lawton, Beddington and Bonser (1974), and Cock (1977), to apply to situations in which a predator is feeding on a mixture of two prey types, when the functional responses of the predator on each prey type are known. If the attack rates, a_1 and a_2, and the handling times, Th_1 and Th_2, for prey types 1 and 2 have been estimated using the 'random predator equation', then the numbers of prey eaten of type 1, Ne_1, and type 2, Ne_2, from a mixture of prey offered, No_1 and No_2, can be predicted by:

$$Ne_1 = No_1\ (1 - e^{-(a_1\ (Tt\ -\ Th_1\ Ne_1\ -\ Th_2\ Ne_2))})$$

and

$$Ne_2 = No_2\ (1 - e^{-(a_2\ (Tt\ -\ Th_2\ Ne_2\ -\ Th_1\ Ne_1))}).$$

These equations assume that the parameters a and Th are the same for the mixed prey situation as for the single prey case, and are not altered by learning or the presence of an alternate prey. Again, a multivariate best fit method can be used to estimate a_1, a_2, Th_1, and Th_2 instead of the regression technique. To estimate parameters a_1 and a_2, and Th_1 and Th_2, from mixed prey experimental data, a multiple regression of $\ln \frac{No_1 - Ne_1}{No_1}$ on Ne_1 and Ne_2, and of

$\ln \frac{No_2 - Ne_2}{No_2}$ on Ne_1 and Ne_2, will yield intercepts of $-a_1\ Tt$ and $-a_2\ Tt$ respectively, and slopes of $a_1\ Th_1$ and $a_1\ Th_2$, and $a_2\ Th_1$ and $a_2\ Th_2$, respectively.

Ultimately, any model of a predator's functional response is just a formalization of the feeding behavior of that predator, using the abstract parameters a and Th. It is very important to identify the behavioral determinants for any changes in the predator's attack rate and handling time. Holling (1963) divided each of the parameters of the disc equation into sub-components. He considered the attack rate, a, to be a function of: 1) the speed of movement of the predator relative to that of the prey; 2) the reactive distance of the predator to a prey (i.e. the maximum distance at which a predator will react by attacking a prey); 3) the capture success of the predator. He considered the handling time, Th, to be a function of: 1) the time spent in pursuing and subduing a prey; 2) the time spent in eating a prey; 3) the time spent in digestive pause after eating a prey. The experimental period, Tt, he divided into: 1) the time spent in activities related to feeding; 2) the time spent in activities not related to feeding. A change in any one of these behavioural subcomponents will alter the corresponding functional response parameter.

Both the Holling (1959b) disc equation and the Rogers (1972) random predator equation, and their two-prey extensions, assume that the predator's attack rate and handling time are constant, for all prey densities and levels of predator hunger. However, it has long been recognized that this is not usually the case. Holling (1959b) presented data from his artificial predator experiments, indicating that a decreased with increasing prey density, though Th did not appear to change in this way. The capture success of the mite *Typhlodromus occidentalis* (Nesbitt) and of the nematode *Prionchulus punctatus* have also been shown to decline as the prey density increases (Fransz, 1974; Nelmes, 1974), although Haynes and Sisojevic (1966) found that the overall attack rate a increased with prey density for male *Philodromus rufus* (Walkenaer) spiders. A number of other studies indicate that handling time, or the proportion of each prey utilized, decreases with increasing prey density (Turnbull, 1962; Haynes and Sisojevic, 1966; Mori and Chant, 1966; Glen, 1973; and Johnson, Akre and Crowley, 1975).

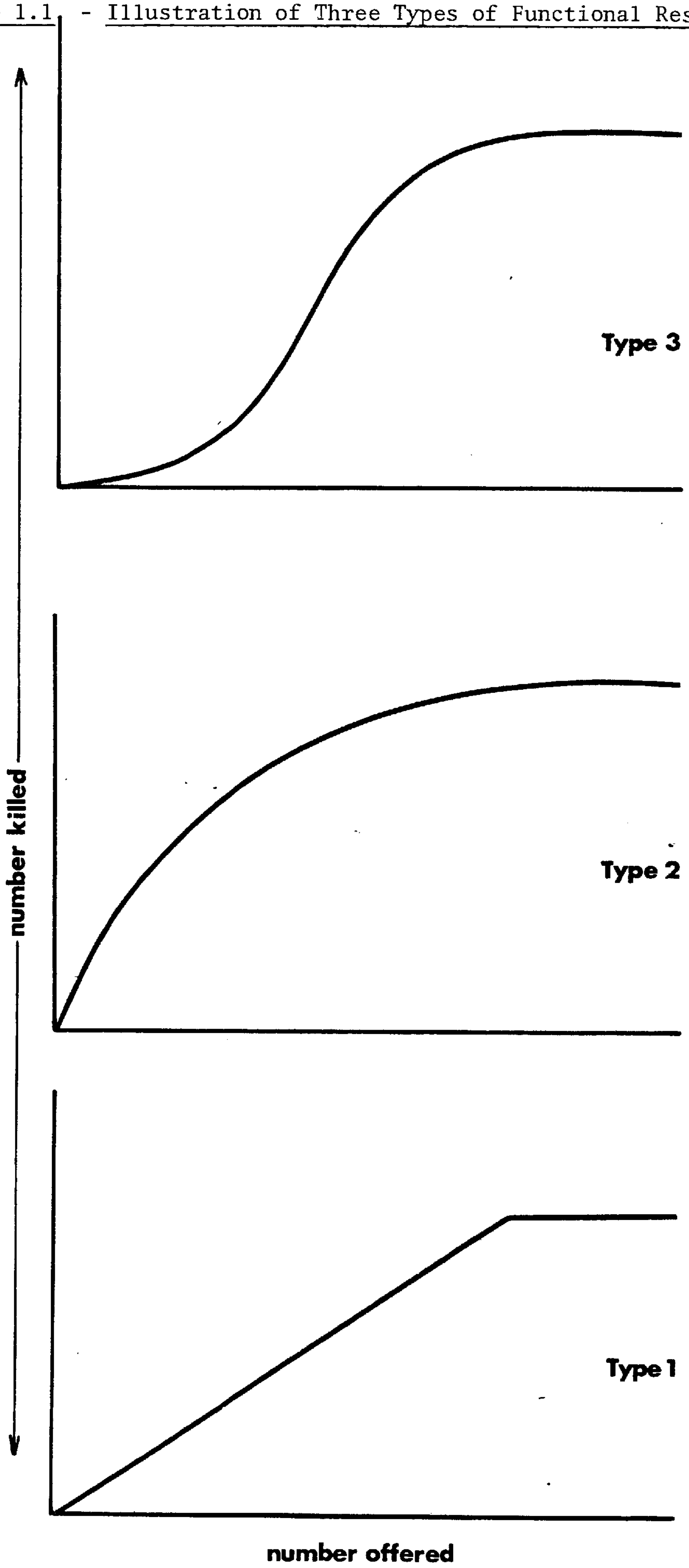
Haynes and Sisojevic (1966), studying the spider Philodromus rufus, Sandness and McMurtry (1970) working on Phytoseiidae mites, and Johnson, Akre and Crowley (1975), studying the damselfly Ishnura ramburii, proposed that wasteful killing of prey at high densities resulted in an apparently anomalous 'double plateau' in the predator response curve. More prey were killed at high prey densities than was predicted by the functional response equation. These results indicated that the predator attack rate rose at high prey densities, while the handling time declined, as prey were captured, but not wholly consumed.

Mori and Chant (1966), and Mori (1969), working on Phytoseiid mites, and Tostawaryk (1972), studying the pentatomid Podisus modestus, all reported that these predators' functional responses turn over at high prey densities, resulting in a 'dome-shaped' functional response. Mori and Chant (1966), attributed this to the abandonment of captured but alive prey, due to disturbance by other prey at high prey densities, though Mori (1969) later argued that the predatory mites wasted more time when their movement was restricted by prey aggregations at high prey densities. Both these explanations would result in a decrease in a with increasing prey density. Tostowaryk (1972) claimed that more effective defense reactions by the sawfly larvae prey, resulting in an increase in Th were the cause of the turnover in Ne at high prey densities.

Werner (1974) and Werner and Hall (1974) reported that sunfish (Lepomis macrochirus and L. cyanellus) handling times were an increasing function of predator satiation, and Thompson (1975) suggested that this relation held for the damselfly Ishnura elegans as well. However, Sandness and McMurtry (1972) suggested that this relationship was the reverse for the mite Amblyseius largoensis (Muma) feeding on adult Oligonychus. Holling (1966) found that the reactive distance of the preying mantid Hierodula crassa increased with hunger, and Thompson (1975) described how the damselfly *Ishnura elegans* left its fishing site and stalked prey when it was hungry, thus increasing its reactive distance, and hence, its attack rate *a*. Glen (1975) documented a similar case in which the mirid bug *Blepharidopterus angulatus* became less active immediately after feeding, and then more active, after a critical period of prey deprivation. Thomas (1974) described a rather different situation, whereby the stickleback *Gasterosteus aculeatus* (L.) tended to search more intensively in the area of recent predatory success, after acceptance of a prey, whereas, after rejection of a prey, it searched less intensively, and tended to move away from the area of prey rejection.

Hassell, Lawton and Beddington (1976) reviewed examples of such variability in the functional response parameters, while concluding that the Rogers (1972) random predator equation remained a remarkably good approximation to the feeding behavior of many predators.

Figure 1.1 - Illustration of Three Types of Functional Responses



1.3. Foraging Theory

1.3.1. Summary

Foraging theory is a new field, which has developed rapidly over the past ten years. There is no central hypothesis, or theory, as such (Covich, 1976); the field represents a new approach to feeding behaviour in particular, and to trophic relations in general. Interactions between ecology, and more theoretically sophisticated disciplines such as economics, have resulted in the quantification of feeding behaviour in cost-benefit terms.

Predation, in particular, lends itself to such analysis, since time and energy partitioning appear to be the major considerations in the process. Other less easily quantifiable factors, such as food quality, are not so important, since the tissue that predators consume is very similar in chemical composition to their own. Particular nutritional requirements are thus not expected to affect their choice of prey. This assertion is especially valid when applied to a fresh water system. In this case, the majority of available prey are detritus feeders, and do not sequester toxins and distasteful substances from their food plants, as do many terrestrial herbivores (Brower, Ryerson, Coppinger and Glazier, 1968).

If there is any unifying principle in foraging theory, it is that of natural selection. Evolution produces reproducing machines, and any attribute which results in a greater number of viable offspring per parent will, a posteriori, be adaptive. Therefore feeding behaviour will only be modified in evolutionary time if it allows the feeder to leave a greater number of viable progeny behind. Two contrasting ways of achieving this increased fitness have been suggested: 1) maximizing the energy gained in feeding, and 2) minimizing the time spent in feeding, leaving as much time as possible free for other necessary activities. In his excellent review, Schoener (1971) discusses possible optimal strategies balancing these two opposing forces, and the circumstances likely to accompany them.

As a consequence of this reflection of predator fitness in the energy gained and time spent in feeding, most models of foraging theory attempt to maximize, or optimize, a measure of the net energy gain per unit time spent feeding. The techniques used derive largely from economics, operations research, and probability theory. Due to a dearth of relevant quantitative data on predator feeding behaviour, most foraging theory models are explanatory in nature. Rather than attempting to mimic actual predator responses, they try instead to provide a rigorous mathematical basis for foraging theory. Predictions of prey choice in given situations are generated, and these hypotheses can then be tested experimentally, providing a direct measure of the realism of the prey choice logic incorporated in the model.

1.3.2. Review of General Models

J.M. Emlen (1966, 1968) developed a probabilistic model describing the behaviour of a wise predator in an arena with constant proportions of two prey types. Assuming random search and sequential encounter of prey items, he argues that a predator will consume a certain prey item if the energy gain per time would be higher, having taken that item, than having ignored it. Based on the probability of this criterion being satisfied, he predicts the proportions of the two prey types that would be eaten. Depletion effects on absolute and relative prey abundances are ignored. Net energy gain and time spent in capture and consumption of prey items are assumed to be independent of prey density. This model predicts that some prey of each type will be eaten, though predators will tend to be more selective when prey are abundant. Selection of prey types is not solely dependent on the efficiency of their exploitation. A very abundant, but poor and less efficiently exploited prey type may be taken disproportionately more than a richer, but rarer, prey type. Emlen and Emlen (1975) tested the above model with experiments on mice. The predictions generated by the model were not supported by the experimental results, except when allowance was made for poor judgement on the part of the predator!

MacArthur and Pianka (1966) developed a model describing predation on a number of equally abundant prey species, in a fine-grained environment. The total time spent feeding is divided into pursuit time and search time, the latter total being constant, and independent of the number of prey species included in the diet. The prey species are ranked in order of decreasing harvest per unit time, and it is argued that when a new prey species is added to the predator's diet, the mean search time per prey species will decrease, since the total search time is constant. The mean pursuit time, however, may increase, as more evasive and less efficiently captured prey species are added to the diet. If the increase in mean pursuit time is less than the decrease in mean search time due to the addition of a new prey species to the diet, then this prey species will be included in the diet of the predator. Increased productivity is predicted to result in decreased predator search time, and hence a more specialized predator diet.

Another prediction generated by this model (perhaps not entirely consistent with the prediction just stated), called the 'Compression Hypothesis', suggests that competition should decrease the number of patches visited, but not alter the variety of prey taken by a predator. The argument emphasizes that although prey depletion due to competition will increase mean search time and possibly mean pursuit time for the predator, prey types whose inclusion in the diet was advantageous before competition should have the same effect after competition. This prediction was later slightly modified (MacArthur, 1972) to accommodate the possibility of an introduced generalist competitor reducing the abundance of a whole segment of a resident specialist's diet, thereby causing a subsequent increase in the breadth of the resident predator's diet. (See section 1.4. for discussion of 'niche breadth'.)

There are several grounds on which this model can be criticized. It incorporates the crucial assumption that a ranking system based on decreasing net harvest per unit time is equivalent to one based on increasing pursuit time. No allowance is made for a case such as a small, slow prey which provides a low net harvest per unit time due to its size, but also has a low pursuit time, due to its sluggishness. Similarly, it is assumed that a competitor will usually deplete the available prey in such a way as to increase the original predator's mean search time and mean pursuit time. A competitor whose prey ranks do not correspond to those of the original predator could increase that predator's mean search time and mean pursuit time differentially. This would have the probable result of increasing the diet breadth of the original predator, since mean search time is more likely to be increased by a reduction in prey abundance than is mean pursuit time.

Schoener (1969a, 1969b) developed a far more sophisticated model for predator feeding strategies. He divides predators into two broad classes: The pursuers and the searchers. The pure pursuer (which is roughly analagous to MacArthur and Pianka's (1966) predator) expends no time or energy specifically in searching, but searches for prey while it carries on other essential activities. Prey are divided into size classes for each distance, $\underline{r}$, from the predator, and they are ranked in order of the net energy gained per time spent for each size-distance class. The pursuer eats succesive prey classes in order of decreasing net energy gain per time spent, until its energy requirement is satisfied, and it stops feeding. The pure searcher spends no time or energy in pursuit, but must set aside time for prey search which can be used for no other simultaneous activity (as does Emlen's (1966) predator). It is assumed that the environment is fine-grained and the prey proportions are constant. The model determines the most profitable range of prey sizes for the predator, such that its energy requirement is satisfied in the minimum search time.

For both categories of predator, rather complex expressions incorporating all the various energy and time costs are developed. Although this complexity has frustrated empirical testing of the models, the detailed itemization of the energetic components in the predation process has done much to clarify predator behaviour. Among the many predictions Schoener derives from these models, he proposes that a decrease in prey abundance should favour predator diet expansion. As in the model of MacArthur and Pianka (1966), Schoener's models predict that a prey type will be always taken, or always ignored, regardless of the densities of alternate prey types. He does, however, point out (Schoener, 1969a) that this prediction may not always be realistic.

Pulliam (1974) reviews the previous models predicting optimal diets, and describes a new model of his own. He assumes that prey are randomly distributed, and the predator searches for them systematically. Prey density, $\underline{di}$, distribution, caloric content, $\underline{ci}$, and pursuit and handling time, $\underline{ti}$, are specified as important prey characteristics governing predation. A criterion for diet expansion is developed which minimizes the expected total time spent in finding a certain energy requirement, or maximizes the expected rate of caloric return.

This model leads to the prediction that the introduction of a generalist competitor will favour expansion of the original predator's diet, whereas the introduction of a specialist competitor (which feeds on the original predator's non-preferred prey), will not. Pulliam points out that this predicted diet will only be realistic during conditions of low prey abundance, or predator energy stress. Again, the relative densities of the different prey species are unimportant. Only the absolute densities of the preferred prey affect the predator's diet breadth. Similarily, prey species are accepted into the predator's diet sequentially. In a later paper, Pulliam (1975) modifies these predictions to allow predation on proportions of different prey types, when there are nutritional restraints on the predator.

In a more recent series of papers on this subject, Charnov (1976a, 1976b; Ryan, Krebs and Charnov, 1974) has proposed and tested yet another model for optimal foraging. He assumes that prey are encountered one at a time, and that the predator energetics are the same for all parts of the foraging process. A prey type is included in the optimal predator diet if the net energy gain provided per handling time spent is greater than some critical value. The assumptions and conclusions of this model are very similar to those of MacArthur and Pianka (1966). Individuals of a prey type are either all taken or all ignored, and the decision to include a prey type in the predator's diet is independent of the abundance of the particular prey type, but is based on the abundances of the more desirable prey types. Data provided by Holling (1966) are used to test the model, and although the predicted behavior is supported, several possible alternative explanations for the data are discussed. As usual, a decrease in prey abundance leads to an increase in predator diet breadth. Krebs, Erichson, Webber and Charnov (1977) later used great tits to test the model prediction that increased abundance of a more profitable prey type would result in reduced predation on a less profitable prey type, regardless of its abundance. They found that while this prediction was supported, the birds did not suddenly become more selective at a critical abundance of profitable prey, but did so gradually. It is conjectured that this gradual change permitted continual sampling of the profitability of all the available prey types.

Estabrook and Dunham (1976) develop a model based on the assumptions that prey individuals are encountered sequentially, that the predator has a constant pursuit time (included in the measure of prey type handling time), and that the prey types have independent distributions. Prey are ranked in terms of 'food value' per unit time, and a criterion for diet expansion is derived. As in all the previous models, decreased prey abundance leads to increased predator diet breadth, and, as in most of the previous models, the ranking system is absolute. Although the absolute prey abundance is the most important factor in determining optimal diet, this algorithm is unusual in incorporating the relative prey abundances of the different prey types. As a consequence, alternate prey density does affect prey choice.

All of the models described above except that of Emlen (1966), are based on the total acceptance or rejection of each prey type. Although such prey ranking systems have been documented (F.D. Williams, personal communication), absolute acceptance or rejection of all prey individuals in each prey species is highly unlikely. This type of foraging would require the predator to either: 1) feed on prey types in order of their preferences, including a new prey type only when the previous one is exhausted, (no supporting evidence for this alternative has been found), or 2) know in advance what range of prey must be accepted to satisfy its energy demands. In the latter case, either learning, or an instinctive (evolutionarily determined), assessment of the necessity of each prey type must be assumed.

Hunger, the most likely behavioural determinant of diet breadth, is ignored in foraging theory (though not entirely in the work on the functional response; see section 1.2.). It is likely that a foraging theory model averaging the effects of hunger determined predation over an extended time period could provide a biologically realistic simulation of changes in diet breadth and the operation of prey preference. A submodel describing the operation of hunger at updated times could incorporate a decline in hunger associated with each successful capture, different hunger thresholds for attempted captures on each prey type, and a gradual increase in hunger following satiation.

1.3.3. Review of Economic and Dynamic Optimization Models

Tullock (1971) suggested that an organism may behave just as efficiently (though for different reasons) as a human consumer. This logic has led to the development of foraging theory models which apply economic principles to ecological interactions.

Rapport (1971) and Covich (1972a, 1974) independently developed very similar models of foraging theory based on predator 'indifference curves' and 'consumption frontiers' (or linear 'budget lines' in Covich (1972a, 1974)). The economic ideas used are in fact very similar to the 'fitness sets' proposed by Levins (1962). Each predator has a characteristic set of 'indifference curves' (plotted on a graph where each axis indicates the number of each prey type eaten), representing the combinations of two prey types to which it is indifferent. Points on a curve provide roughly similar energy benefits, and curves farther from the origin provide more energy than those closer to the origin. The consumption frontier represents the maximal prey combinations that can be consumed by a predator exposed to a given prey mixture for a limited time period. This consumption frontier intersects the indifference curves, and the highest (farthest from the origin) indifference curve which is tangential to the consumption frontier defines the prey combination which will be eaten. Using these concepts, predictions regarding predator behaviour under altered prey densities can be derived. Generally, the shape of the predator's set of indifference curves (i.e. the predator's prey preferences) determines how changes in the absolute or relative abundance of the prey affect predator diet. Alternate prey densities are of great importance in determining the numbers of preferred prey eaten. When preference is strong, increased numbers of alternate prey may lead to increased consumption of preferred prey as well (Covich, 1974). When preference is weak, switching (see section 1.3.5.) may occur (Rapport, 1971).

These two models directly contradict most of those discussed in the previous section. Whereas for the most part, foraging theory models predict that prey will be taken sequentially, these models assume that prey types can always be substituted for each other. Problems arise in the application of these two models to experimental situations. As revealed in Covich (1972a), indifference curve data is likely to be extremely variable. Also, unfortunately, several data points are necessary to determine the exact shape of the curve, which is critical for predicting changes in both numbers and proportions of prey eaten.

Another model of foraging theory uses a 'dynamic optimization' approach to predict optimal predator behavior. Marten (1973) assumes that a predator has a particular 'search mode' and 'desired level of consumption' for each prey type. All prey types are considered to be equally rewarding, and the total of all the 'desired levels of consumption' for each prey type represents the total quantity of food 'desired'. This probabilistic model generates optimal predator behavior, producing a range of possible solutions including all three types of functional response and 'switching' (see section 1.3.5.). However, the assumptions incorporated in this model are both inconsistent and biologically unreasonable. If all prey types were equally rewarding, they could be substituted for each other. Then no prey type could have a fixed 'desired level of consumption', and the total quantity of food 'desired' could be composed of any combination of the prey types available.

1.3.4. The Foraging Theory Hypothesis

The preceding group of models, though differing in their implicit assumptions and mathematical techniques, are similar in general form. Assumptions are made regarding predator wisdom, environmental homogeneity, and the simplicity of the feeding process. Prey are ranked according to some measure of predator preference, and a criterion is proposed for diet expansion. Alternatively, a probabilistic equation predicts the optimal combination of prey types in the diet. Evidence broadly supporting the assumptions and conclusions of these models is presented in several general reviews (Schoener, 1971; Morse, 1971; Pulliam, 1974, Covich, 1974; Pyke, Pulliam and Charnov, 1977; amongst others).

With the possible exception of the models proposed by Rapport (1971) and Covich (1972a), all the above models predict that a decrease in prey abundance will broaden the predator's diet. As Pulliam (1974) states: "This leads to the conclusion that competition, if it affects the diets of competitors at all, will tend to cause greater generalization". This hypothesis will be called the "Foraging Theory Hypothesis" in this study.

1.3.5. Switching

Murdoch (1969) proposed the 'switching hypothesis' to predict predator feeding behaviour when two prey types are available. He suggests that "the number of predator attacks upon a species is disproportionately large when the species is abundant relative to other prey, and disproportionately small when the species is relatively rare". Switching is consistent with those foraging theory models which permit non-sequential selection of prey types: the probabilistic optimizing models (Emlen, 1966; Marten, 1973), the models based on economic theory (Rapport, 1971; Covich, 1972a), and the model proposed by Estabrook and Dunham in 1976. Ivlev (1961) first suggested that such a mechanism might operate for fish eating non-preferred prey. In their discussions of a 'specific searching image' Tinbergen (1960) and Gibb (1962) suggested that a predator could learn to recognize a particular prey species, if it were encountered often enough. At moderate densities, the predator would be likely to remove a disproportionate number of individuals from that prey population. Turnbull (1960) found evidence supporting this hypothesis in his work on spiders, and Tullock (1970) confirmed the economic sense of the switching hypothesis, under qualified conditions.

In a series of papers on the subject, Murdoch and others (Murdoch, 1969 and 1973; Murdoch and Marks, 1973; Murdoch, Avery and Smyth, 1975; Oaten and Murdoch, 1975), develop criteria for the determination of 'switching' from experimental data, and list the situations most likely to produce it. Perhaps the most common natural mechanism resulting in 'switching' is the selection of feeding habitats with aggregations of particular prey types (Royama, 1970a). Switching is said to operate if a preference index increases as the ratio of the two prey species available increases. Murdoch defines a preference index, $\underline{c}$, equal to the ratio of the two prey species in the diet divided by the ratio of the two prey species available (Murdoch, 1969), or equal to the ratio of the attack rates on the two prey species (Murdoch, 1973). Lawton, Beddington and Bonser (1974) and Cock (1973) make the important qualification that the null case ought to be defined by the mixed prey extensions of the random predator equation (Rogers, 1972), and not by the constancy of <u>c</u> , which represents only a slice through the three dimensional surface relating the numbers of prey eaten to the density of each prey species.

The 'switching' hypothesis makes no predictions regarding changes in predator diet breadth following an increase or decrease in absolute prey abundance. Nevertheless, the mixed prey extensions to the random predator equation do provide a null case for testing the 'Foraging Theory Hypothesis'.

1.4. Niche Theory and the Competitive Exclusion Principle

The term 'niche' was coined more or less simultaneously by Joseph Grinnell and Charles Elton in the 1920's. Grinnell used the term to denote the distribution of a species subject only to its physical and climatic limitations, whereas Elton used the same term to mean the position occupied by a species with respect to the other organisms in the community. In 1957, G.E. Hutchinson clarified these rather vague definitions with a set theory approach, and this provided the foundation for modern niche theory. Hutchinson (1957) defined a species 'niche' as "an n-dimensional hyper-volume...every point in which corresponds to a state of the environment which would permit the species...to exist indefinitely". His model involves allocating an axis to every ecosystem parameter, and mapping the maximum and minimum tolerances for each parameter on the consequent n-dimensional graph. The volume enclosed by all these points represents the species' fundamental, or pre-interactive, niche. The realized, or post-interactive, niche is that subset of the fundamental niche actually occupied by a species after the interactions with all the other organisms present in the community have been taken into account (Hutchinson, 1957; Vandermeer, 1972). The implications and shortcomings of niche theory are discussed in detail by Hutchinson (1957), MacArthur (1968), Levins (1968), Vandermeer (1972), and Kroes (1977).

Closely related to the concept of the niche is that of 'niche breadth' or 'niche width'. In his excellent paper developing this idea, Roughgarden (1972) states that: "given...a resource axis, niche width with respect to that axis is the length of the interval from which the population obtains most, say 95%, of its resources. The actual niche width of a population reflects the abundance of resources at each position on the resource axis, the regime of interspecific competition, and something about natural selection". In other words, the niche width of a species, or population, describes the degree to which it is a generalist in its use of a particular resource. Roughgarden (1972) makes the important distinction between the B.P.C. or the between phenotype component of niche breadth, and the W.P.C. or the within phenotype component of niche breadth. The former represents the degree of variability in resource use among the phenotypes in the population, and the latter indicates the variety of resources used by each phenotype.

The niche theory framework described above can be extended to apply to the interaction of two species using the same resource. The problem of competition for a common resource was originally studied analytically by Volterra (1926) and Lotka (1932), who demonstrated that under constant conditions, two species limited by the same finite resources cannot coexist. Gause (1934, 1935) and others (Levin, 1970; Stewart and Levin, 1973; Schoener, 1974), have confirmed and extended this general conclusion, which has become known as the 'Competitive Exclusion Principle' (Hutchinson, 1957; Hardin, 1960). The principle is circular, since apparent coexistence of two species with identical niches can always be explained by the existence of a crucial but as yet unmeasured niche dimension separating the two species (Hutchinson, 1957; Hardin, 1960; MacArthur, 1968; Peters, 1976). Hence the Competitive Exclusion Principle is impossible to disprove directly, or to test by observation. Nevertheless, a large body of ecological data does lend general support to this principle, and despite its tautological nature, the Competitive Exclusion Principle is recognized as being fundamentally important to ecological theory.

If we accept the set theory terminology used by Hutchinson (1957), and define N1 and N2 as the fundamental niches of two members of a community, then the intersection set N1.N2 is the area of niche overlap. Hutchinson (1957) defined the realized niche for species 1 as N1 - N1.N2 plus that portion of N1.N2 in which species 1 persisted. On this basis, he rephrased the Competitive Exclusion Principle as "realized niches do not intersect" (Hutchinson, 1957), again an untestable hypothesis. This has been further refined by MacArthur and Levins (1964, 1967), May and MacArthur (1972) and May (1974) who suggest that, although the niches of members of a community do not have to be exclusive, there is nevertheless a theoretical limit to the amount of niche overlap which is tolerable, particularily in variable environments.

In an attempt to overcome the circularity of the Competitive Exclusion Principle, ecologists have derived falsifiable corollaries to the set theory definition proposed above by Hutchinson (1957). Predictions regarding niche breadth and overlap, expected on the basis of the above formulation of the principle, can then be tested directly with field data. The alternative hypothesis examined in this study was developed in this way by Colwell and Futuyama (1971) and Roughgarden (1974): "a population incurs a smaller total niche width as...the number of competing species increases". This hypothesis will be referred to as the Niche Theory Hypothesis, in the following sections of this thesis.

Evidence supporting the Niche Theory Hypothesis had been derived primarily from the estimation of niche breadths of individual species, and of niche overlaps between pairs of species, based on data from field observation. Levins (1968) and Schoener (1974) integrated these studies with the laboratory competition studies by developing an equation which measures the Lotka-Volterra competition coefficients in terms of the actual resource use of the species in the field. Such 'species packing' studies have been conducted by Root (1964), Rand (1964), Pico, Maldonado and Levins (1965), Cody (1968), Pianka (1969), Orians and Horn (1969), Lanciani (1969), Culver (1970), Kohn (1971), Colwell (1973), and Ulfstrand (1977), amongst others. In all cases, the niche theory model is supported and coexistence is explained. However, in most cases, the crucial evidence indicating that the resources under consideration are limiting, has been difficult to establish. Only in a very few cases (Ward, 1965; Gibb, 1960; for example) has it been possible to deduce that a particular resource is limiting, and that its reduction is therefore likely to intensify competition. Furthermore, even if two species do not compete directly, they may harm each other while independently acquiring resources. Competition may be by interference, rather than by exploitation (Schoener, 1974). In this way, the circularity of the Competitive Exclusion Principle is reaffirmed; active competition is very difficult to detect. Yet another complication arises from the possibility that many communities are in non-equilibrium states (Connell, 1978; Wiens, 1977). If environmental variability gives alternate advantages to competing species, then competitive exclusion may never take place, and competing species may persist in an unstable state of apparent coexistence. In a later section (1.5.2.) of this thesis, comparative studies examining the altered niche breadth of a species when subjected to different intensities of competition (or to a gradient of productivity) are reviewed and discussed. These investigations, by choosing to observe 'before and after' situations, largely avoid the shortcomings of the species packing studies.

1.5. Test Cases from the Literature

1.5.1. Summary

There are four types of ecological investigation which attempt to test the outcome of competition for prey between polyphagous predators: 1) studies of comparable sets of predators in environments which differ either in prey abundance or in numbers of competing predators; 2) studies of long-lived predators in environments with varying productivity over time; 3) studies of predators with varying energy demands throughout their life histories; 4) experimental studies in which prey abundance and/or the number of competing predators are manipulated by the experimenter.

The first type of study constitutes a direct test of the Foraging Theory Hypothesis and the Niche Theory Hypothesis, while avoiding the pitfalls (see section 1.4.) of non-comparative 'species packing' studies. The second and third categories provide an indirect test of these hypotheses. These studies record changes in the diet resulting from variations in productivity or in predator energy demand, but for only one predator species. In these cases, the effect of decreased prey abundance on the predator diet was judged (as cited in Roughgarden, 1974) to be similar enough to the effect of increased competition for prey (with consequent reduction in prey density due to prey removal by the competitor) to make the comparison worthwhile. The fourth class of investigation represents the experimental approach to this problem, whereby competition and productivity effects are isolated, and then measured.

Tables 1.1. and 1.2. summarize the evidence provided by the first two types of investigation.

Table 1.1. Evidence Supporting the Foraging Theory Hypothesis

Reference	Organism Studied	Interval Separating Compared Observations	Latitude	Niche Breadth Components Measured	Comments
Type 1 Investigations					
Kohn, 1968	gastropods	evolutionary	tropical	WPC & BPC	*Conus* diet breadth was greatest in the most hospitable habitat, with the highest number of congeneric predators.
Powell and Stage, 1962	robberflies	less than predator life-span	subtropical	WPC & BPC	smaller, faster, less conspicuous prey were taken in dryer areas
Orians, 1966	nestling blackbirds	less than predator life-span	temperate	WPC & BPC	smaller, faster, less conspicuous prey were taken in a less productive area.
Goss-Custard, 1977	redshank	less than predator life-span	temperate	WPC	a higher proportion of preferred prey was eaten when their absolute abundance was greater.
Type 2 Investigations					
Holmes and Pitelka, 1968	sandpipers	seasonal	arctic	WPC & BPC	diet overlap was maximal when insect abundance peaked, *but* during the period of declining insect abundance, there was a staggered schedule of sandpiper migratory departures.
Fenton and Morris, 1976	bats	very brief - less than an hour	temperate	WPC & BPC	bats feeding near a light trap, where there was a high concentration of insects, selected the larger ones as prey.

Reference	Organism Studied	Interval Separating Compared Observations	Latitude	Niche Breadth Components Measured	Comments
Pulliam and Enders, 1971	finchs	seasonal	temperate	WPC & BPC	declining seed abundance in late winter resulted in almost total diet overlap but finch population sizes and seed abundance were correlated.
Orians and Horn, 1969	blackbirds	-	temperate	WPC & BPC	diet overlap between species was almost total but habitat overlap was much lower.
Ulfstrand, 1977	passerine birds	seasonal	north temperate	WPC & BPC	niche overlap was lowest in summer, when prey abundance was highest but niche breadths did not change;total guild niche size was greatest in summer.
J.L. Menge, 1974	snails	diurnal	temperate	WPC	as search time increased, less preferred prey were taken more readily.
Orians, 1966	nestling blackbirds	diurnal	temperate	WPC & BPC	smaller prey were consumed in the evening, when larger prey were less available.

Reference	Organism Studied	Interval Separating Compared Observations	Latitude	Niche Breadth Components Measured	Comments
Lack and Owen, 1955	swifts	seasonal	temperate	WPC & BPC	smaller prey were consumed in poor weather
Buchler, 1976	bats	seasonal	temperate	WPC & BPC	smaller prey were consumed when larger prey were less available.
B.A. Menge, 1972a	starfish	seasonal	temperate	WPC	diet was broadest during late winter and early spring, when prey were least abundant.

Type 1 Investigations = studies of comparable sets of predators in environments which differ either in prey abundance or in numbers of competing predators.

Type 2 Investigations = studies of long-lived predators in environments with varying productivity over time.

WPC = within phenotype component of niche breadth

BPC = between phenotype component of niche breadth

Table 1.2. Evidence Supporting the Niche Theory Hypothesis

Reference	Organism Studied	Interval Separating Compared Observations	Latitude	Niche Breadth Components Measured	Comments
Type 1 Investigations					
Grant, 1966 and 1968	birds	evolutionary	tropical	BPC	bill length variability was greater on islands than on the mainland.
Schoener, 1965	birds	evolutionary	tropical	BPC	bill size variability was greater for sympatric congeners feeding on more abundant prey.
Diamond, 1970	birds	evolutionary	tropical	WPC	hunting habitats and techniques of solitary predators were expanded to include those of their erstwhile competitors.
Kohn, 1966	gastropods	evolutionary	subtropical	WPC & BPC	solitary *Conus* in California had much broader diet than did *Conus* species occurring together in Hawaii.

Reference	Organism Studied	Interval Separating Compared Observations	Latitude	Niche Breadth Components Measured	Comments
Roughgarden, 1974	lizards	evolutionary	tropical	BPC	jaw size variability was greater for solitary species than for those with many sympatric congeners.
Schoener, 1967 and 1968	lizards	evolutionary	tropical	BPC	sexual dimorphism with respect to prey size was greater for solitary species.
Soulé, 1966	lizards	evolutionary	subtropical	BPC	body size was inversely proportional to the square root of the number of sympatric Iguanid lizard species.
Pulliam, 1973	birds	evolutionary	tropical	WPC	island birds were much less stereotyped in their seed type choice than were mainland birds.
Rothstein, 1973	jays	evolutionary	temperate	BPC	bill size variability and sexual dimorphism were inversely related to an index of sympatry.
Ross, 1967 and 1971	dragonflies	brief - less than seasonal	temperate	WPC	dragonflies in an experimental arena with few prey selected large prey more than those in an arena with higher overall prey abundance.

Reference	Organism Studied	Interval Separating Compared Observations	Latitude	Niche Breadth Components Measured	Comments
<u>Type 2 Investigations</u>					
Zaret and Rand, 1971	fish	seasonal	tropical	WPC & BPC	fish diets were most specialized, with minimum diet overlaps during the dry season, when prey abundance was lowest.

Type 1 Investigations = studies of comparable sets of predators in environments which differ either in prey abundance or in numbers of competing predators.

Type 2 Investigations = studies of long-lived predators in environments with varying productivity over time

WPC = within phenotype component of niche breadth

BPC = between phenotype component of niche breadth

1.5.2 Type 1 Investigations

Most examples of comparable sets of predators in environments which differ either in prey abundance, or in number of competing predators, are provided by studies of island faunas. Comparisons between islands which differ in productivity (and possibly size), but which have the same number of competing predators, represent two points on a gradient of increasing productivity. Alternatively, two islands which are comparable in size and productivity, but which differ in the number of sympatric predator species, represent points on a gradient of increasing predator competition. The interdependence of these two factors has resulted in some confusion. An unusually productive island will probably have an exceptional number of top predators. This confounding of the contrary effects of increased productivity, and increased numbers of sympatric predators, has resulted in conflicting predictions regarding the likelihood of increased diet breadth on small islands, when compared with larger islands, or the mainland. Grant (1968), though aware of this confusion, argued that competition is likely to be more intense on smaller, relatively depauperate islands. On the other hand, MacArthur (1968) discussing the phenomenon of 'competitive release', predicted that competition is likely to be more intense on larger islands, with more predator species, or on the mainland. Van Valen (1965), in his 'niche variation' hypothesis, proposed that such a release would favour increased variability in the island population.

Most of the type 1 examples support the Niche Theory Hypothesis (Table 1.2., Type 1 Investigations). In situations of reduced, or even non-existent, competition for food, predator species have been shown to broaden their diets through relaxed prey selectivity (Pulliam, 1973), the adoption of foraging techniques normally used by other species (Diamond, 1970), or by increased sexual dimorphism (Schoener, 1967 and 1968; Rothstein, 1973). Divergence, commonly called 'character displacement', occurs between sympatric species (Grant, 1965, 1966 and 1968), enabling this diet expansion to occur without increased competitive stress. General comparative studies reveal a correlation between diet specialization and the number of competitors for prey (Kohn, 1966; Soule, 1966; Rothstein, 1973; Roughgarden, 1974). Consideration of the three counter examples supporting the Foraging Theory Hypothesis (Table 1.1., Type 1 Investigations) reveals some ambiguity in their results. Although a predator may be forced to expand its diet in areas where prey are scarce, as predicted by foraging theory, this may have as much to do with relative prey abundance, as with absolute prey abundance. In fact there may be no overall change in diet breadth, merely a shift from one predominant prey type to another. This must necessarily be a diet adjustment which can be accomplished by an individual predator in a short period of time. Only the within phenotype component of niche breadth is concerned. These results are in accordance with the 'compression hypothesis' (MacArthur and Pianka, 1966) (see section 1.3. for discussion). In contrast, the island studies are primarily concerned with differences in population characteristics. These changes in the between phenotype component of niche breadth are the result of long-term adaptation to a specific area with relatively constant selective pressures. As pointed out by Roughgarden (1972), such changes in the variability of a population characteristic will take longer, evolutionarily, than a comparable change in the mean of such an attribute.

1.5.3. Type 2 Investigations

A number of studies have been conducted on the effects of seasonal variations in prey abundance on predators' diets. It is presumed that during periods of drought, or cold weather, small numbers of available prey will result in more intense predator competition. These findings, while broadly supporting the Foraging Theory Hypothesis, are often confused by the existence of some strategy for avoiding competition, at times when the diet overlap of sympatric predators is greatest. Some of these strategies are listed in Table 1.1. (Type 2 Investigations).

For the last four examples in the table, the apparent diet expansion during certain seasons, times of the day, or weather conditions, may represent a change in diet composition, and not in diet breadth. As mentioned in section 1.5.2., this could result from a change in the pattern of prey availability, rather than from an overall reduction in prey density. Under these circumstances, competition (if operating at all), would not be intensified unless all the sympatric predators shifted their diets in the same direction at the same time. If, instead, the total predator guild niche breadth increased at these times (Ulfstrand, 1977), then each predator's diet breadth could increase, but its diet overlap would not.

The fish studied by Zaret and Rand (1971) represent a genuine anomaly (Table 1.2., Type 2 Investigations). If food was limiting during the dry season, it is very surprising that the fish diets were most specialized at this time. It seems likely that mortality during this period must have reduced the fish population to the point where food was no longer limiting, and specialists were not penalized. It is possible that in this case, competition was by interference (rather than by exploitation), and this mechanism enforced diet specialization on the competing predator species.

Thus it appears that the short-term strategy of diet expansion on the part of an individual predator is often prevented from causing excessive competitive stress by an adjustment in the use of other resources, or by the niche expansion of the whole predator guild, at this time.

1.5.4. Type 3 Investigations

All the examples of predators with variable energy demands derive from comparing the diet of parent birds with the food they bring to their young. Insectivorous birds are able to bring only one prey at a time back to their nestlings (Royama, 1970b). More time, and energy, must be spent in transit from the feeding area to the nest, and hence it has been suggested (Royama, 1970b) that parent birds forage more efficiently when they are feeding young. If this situation of increased energy demand can be considered as roughly analagous to that of decreased prey abundance, then the Foraging Theory Hypothesis is supported by Cottam (1939), Mendall (1949), Collias and Collias (1970), and Bryant (1973). Bellwood and Fenton (1976) also report similar observations for lactating bats. These authors show that when energy demands are greatest, a broader range of prey taxa is consumed. However, prey distribution in the diet is most different from that available at this time, since there appears to be marked selection for large prey in the nestling's diet. Therefore these results are somewhat ambiguous; diet expansion occurs simultaneously with an increase in the exercise of prey choice.

1.5.5. Type 4 Investigations

Four short-term experiments have been reported, in which the prey choice of an individual predator was monitored under a variety of conditions. Swamy and Rao (1974) reported that dytiscid beetles were less selective after a period of starvation, than at times when they had not been starved (see also J.L. Menge (1974), Table 1.1.). Werner and Hall (1974) related how sunfish sequentially dropped the smaller size classes of Daphnia from their diet, as overall prey abundance increased. Ivlev (1961), in his classic study of fish feeding, also found that the less preferred prey types were dropped from the predator's diet when the prey density was increased. Popham (1941) reported similar results, in which a fish ate a larger proportion of prey of a colour contrasting with the background, when the densities of both contrasting and cryptic prey were increased.

All these experiments on the short term feeding strategy of an individual predator appear to support the Foraging Theory Hypothesis. The one experimental study which does not, was conducted by Neill (1975) on herbivorous crustacea. He found that as competition between the herbivores was reduced by predation, their diets became more generalized with respect to prey size, and their diets overlapped more. However, this study was a much longer term investigation than those described above. Furthermore, both of the components of niche breadth were included in the estimates of herbivore diet breadth. The diet changes reported were not merely the tactical responses of individuals, but were general population responses, and possibly even evolutionary changes. As pointed out by Roughgarden (1974), asexually reproducing populations such as these can effect a rapid release in their between phenotype component of niche breadth. Consequently, a rapid increase in overall niche breadth would have been possible in this particular situation. In the four other type 4 studies, competitors were absent from the experimental arenas, and hence short-term increases in individual predator diet breadths had no adverse effects.

1.5.6. Discussion

Examination of the evidence presented in the preceding four sections of this chapter reveals that, in general, studies reporting short-term changes in diet are likely to support the Foraging Theory Hypothesis, while studies dealing with long-term changes are more likely to concur with the Niche Theory Hypothesis.

With the exception of the work reported by Zaret and Rand (1971), all the studies comparing the same (or interbreeding) predator individuals, under different conditions, provide evidence that increased competition is likely to cause diet expansion. Most of the predators under investigation in these studies originate in temperate areas, where both environmental heterogeneity and seasonal changes in prey availability are likely. Some plasticity in feeding behaviour and diet breadth becomes advantageous under these conditions, and hence the within phenotype component of niche breadth is very important in these studies.

Conversely, studies comparing different sets of predators which have been genetically isolated for a long time, indicate that a decrease in predator diet breadth is likely to accompany any increase in the number of similar predators in the community. With the exception of the work reported by Diamond (1970), and Pulliam (1973), this increased specialization is the result of a decrease in the variability of the population as a whole, rather than an increase in the exercise of prey selection by each individual predator. Such modifications in the mean or variance of a populations characteristic are exceedingly slow (Roughgarden, 1974), and consequently much more likely in the tropics, where the biological communities have enjoyed climatic stability. Despite recent suggestions that tropical communities may be less stable than had previously been thought (Connell, 1978; Wolda, 1978), the rich and relatively unperturbed tropical environment still renders stereotyped behavioural responses less of a disadvantage than in the temperate zones.

This latitude effect on species packing has been attributed not only to the obvious increases in productivity and predictability, but also to an increase in the tolerable niche overlap between coexisting species (Klopfer and MacArthur, 1961), an increase in the number of top predators, which act to prevent single prey species from monopolizing limiting resources (Paine, 1966), and an increase in the types and degree of specialization possible in the tropics (Colwell, 1973).

2. Experimental Studies

2.1. General Introduction

2.1.1. Experimental Design

This study was designed to test the Foraging Theory Hypothesis against the Niche Theory Hypothesis, in one particular experimental situation. However, in order to determine whether an increase in competition, and a reduction in prey abundance results in expansion or contraction of the predator's diet, the null case of the original predator diet breadth must be known. Therefore, three series of experiments were designed, whereby the results of each series of experiments could be used to generate a null hypothesis against which the results of the next series of experiments could be tested: 1) the response of each predator type to a range of densities of each prey type would be measured; 2) the response of each predator type to various combinations of both prey types would be measured; and, time permitting, 3) the response of both predators together in an arena of mixed prey would be measured. In this way, a Rogers (1972) model of the functional response experiments could be extended, using the technique developed by Lawton, Beddington and Bonser (1974), to generate a null hypothesis of unaltered predator behaviour in an arena of mixed prey.

Clearly, this technique for hypothesis testing depended on conventional predator behaviour in the initial series of experiments; it relied upon the Rogers (1972) model providing a reasonable approximation to the functional response data. However, the functional response experiments on the four principle predator-prey interactions yielded curves which were rather dissimilar to the expected type 2 functional response, and only in the case of *Coenagrion puella* (L.) eating *Daphnia magna* (Straus) did the Rogers (1972) model provide a significant fit to the data (Figures 2.2., 2.3., Tables 2.3., 2.4.).

During the total period of single predator-single prey functional response experiments, some 59 individuals of Pyrrhosoma nymphula (Sulz) and some 47 individuals of Coenagrion puella (L.) were observed (sometimes concurrently) for 11760 and 15624 hours respectively with Aedes aegypti (L.) as prey, and for 11592 and 10920 hours respectively with Daphnia magna (Straus) as prey. (See Table 2.1.) In total, therefore, the number of observations was considerable; that the data did not support the Rogers (1972) model could have been due to two factors: 1) the high variability of the data might have masked the actual type 2 functional responses; or, 2) these data might have represented a real departure from the type 2 functional responses. In an attempt to distinguish between these two alternatives, a thorough breakdown of the components of variability in the damselfly predatory response was undertaken. The effects of predator age and hunger, and experimental photoperiod, prey distribution, and arena size were controlled and tested. It was hoped that in this way, the predatory variability could be examined, traced, and perhaps reduced by further controls on the experimental predators. The resulting distilled data might then reveal the extent of the predator's conformity to the type 2 functional response.

Furthermore, the sources of predator variability might in themselves be interesting. While many laboratory tests have supported the random predator model (Hassell, Lawton, Beddington, 1976), the experimental conditions used are often rather unlike the field situation. The practical work conducted in this study incorporated large predatory arenas, more natural photoperiods and perching sites, and a greater proportion of the damselflies' ultimate larval instar than has been the case in many comparable series of experiments. Some of the consequent variability in the data reported here may thus mimic the field situation, and provide some insight into the natural mechanisms for effective predation and predatory coexistence.

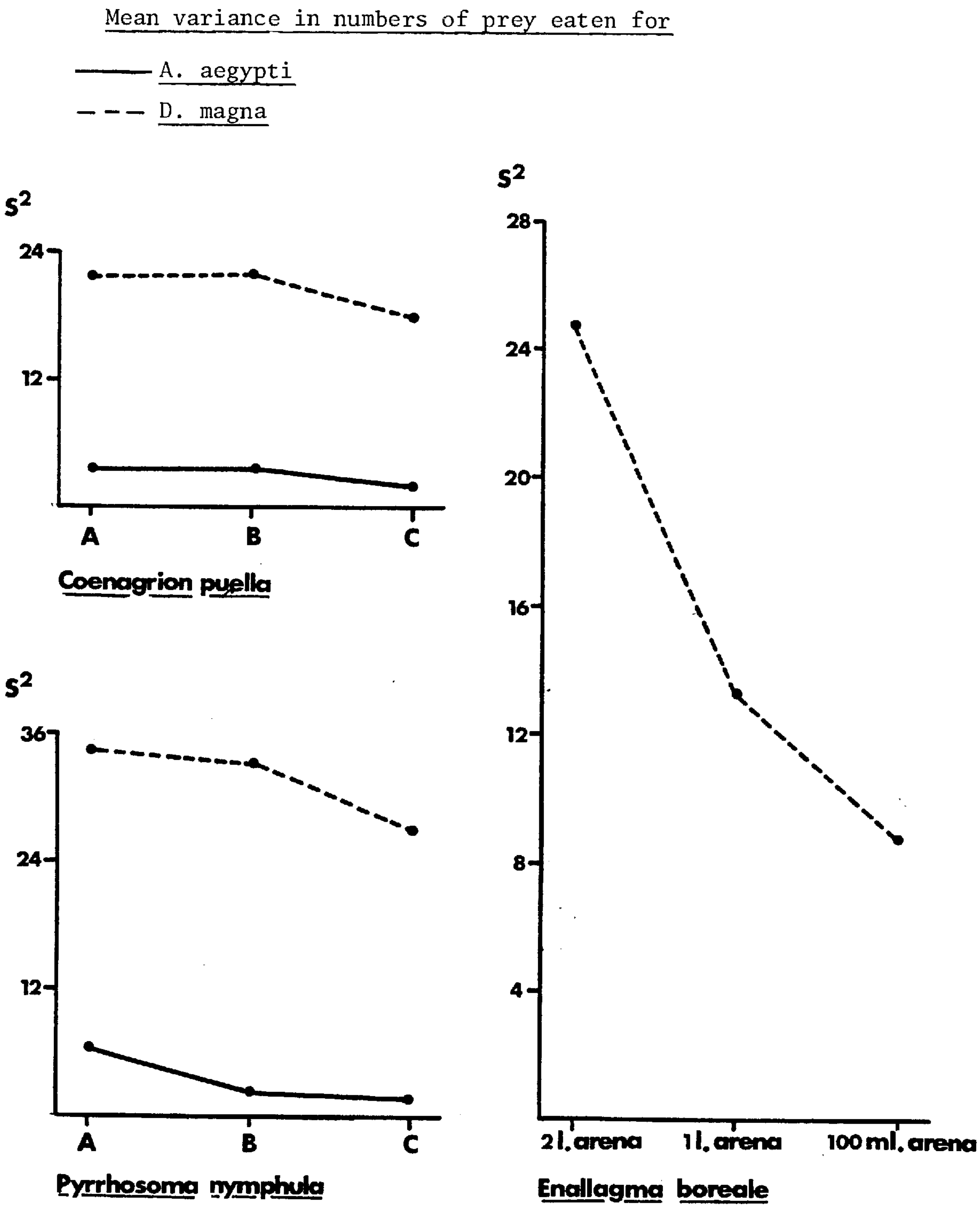
The detailed examination of a number of possible components of damselfly predatory variability is described in the following sections 2.2.1. to 2.2.7. Section 2.2.8. is devoted to the discussion of this analysis, and its bearing on the fit of the Rogers (1972) model to the experimental data. The general results of these investigations are presented in Figure 2.1. and Table 2.2.

In section 2.3., changes in the functional response parameters, and their possible effects on the Rogers (1972) model are documented and discussed. Sections 2.4. and 2.5. document the mixed prey experiments, predicted changes in damselfly predatory behaviour with age, and the model of damselfly predation in the field.

TABLE 2.1. - Practical Work on *Pyrrhosoma nymphula* and *Coenagrion puella*

Predator	Prey	year	no. of preds	total number expts.	number discarded	number available for analysis
L. sponsa	*A. aegypti*	1974	31	43	13	30
L. sponsa	*D. magna*	1974		32	5	27
L. sponsa	*A. aegypti*	1975	36	46	17	29
P. nymphula	*A. aegypti*	1974				
C. puella	*A. aegypti*	1974				
P. nymphula	*A. aegypti*	1975	35	38	12	26
P. nymphula	*D. magna*	1975		69	17	52
P. nymphula	*A. aegypti*	1976	24	32	22	10
C. puella	*A. aegypti*	1975	35	72	32	40
C. puella	*D. magna*	1975		65	9	56
C. puella	*A. aegypti*	1976	12	21	9	12
P. nymphula	mixed	1976	23	34	17	17
P. nymphula	mixed	1977	6	22	9	13
C. puella	mixed	1976	13	19	7	12
C. puella	mixed	1977	38	46	6(+19)	40(-19)
C. puella	*A. aegypti*	1977	8	8	0	8
	D. magna	1977	8	8	0	8

Figure 2.1. - Components of Variability in the Damselfly Functional Responses



A: Data collected throughout ultimate instar

B: Data for pre-metamorphosis individuals only

C: Data for pre-metamorphosis individuals corrected for age

Table 2.2. - *Sources of Variability in the Predator Response: mean of the variances for Ne, for all prey densities*

predator-prey interaction	n(number of experiments on which mean s^2 is based)	data collected throughout the predator instar	data for non-metamorphosing individuals only	n(number of experiments on which mean s^2 is based)	data for non-metamorphosing individuals corrected for age
P. nymphula eating *A. aegypti*	71	6.56	2.49	36	2.02
P. nymphula eating *D. magna*	68	34.35	33.54	51	27.10
C. puella eating *A. aegypti*	94	3.88	4.08	53	2.83
C. puella eating *D. magna*	65	22.14	22.30	56	18.18
L. sponsa eating *A. aegypti* (2-day starvation)	46	17.41	12.50	31	

Continued....

Table 2.2. - Sources of Variability in the Predator Response: mean of the variances for *Ne*, for all prey densities

predator-prey interaction	n (number of experiments on which mean s^2 is based)	data collected throughout the predator instar	data for non-metamorphosing individuals only	n (number of experiments on which mean s^2 is based)	data for non-metamorphosing individuals corrected for age
L. sponsa eating *A. aegypti* (1-day starvation)	42	84.28	57.15	28	
L. sponsa eating *D. magna* (1-day starvation)	32	69.91	43.37	20	

predator-prey interaction	n (number of experiments on which mean s^2 is based)	arena size is 2 l.	n (number of experiments on which mean s^2 is based)	arena size is 1 l.	n (number of experiments on which mean s^2 is based)	arena size is 100 ml.
Enallagma boreale eating *Daphnia magna*	87	24.74	77	13.23	99	8.72

2.1.2. Experimental Procedure

In accordance with the experimental design explained in the previous section, four functional responses were measured; one for each of *Pyrrhosoma nymphula* and *Coenagrion puella* eating each of *Aedes aegypti* and *Daphnia magna*. Based on the calorific equivalents determined for the two prey types (Section 2.4.1.), standard training diets of twenty *A. aegypti* or fifty *D. magna* were used. The experimental predators were fed in the morning when the lights came on, on the day after an experiment, day 1, and on day 4. All prey were removed when the lights came on, on day 5, and the next experiment was started when the lights came on, on day 7.

An experimental period of six hours was chosen, following a preliminary experiment in 1974 on the feeding rate per hour of starved damselfly larvae (see Appendix 1). These results indicated that the damselfly feeding rate declined and became less variable, after four hours exposure to prey, and that it was lowest, and most uniform, during the fifth and sixth hours. After prolonged exposure to prey, the variability resulting from random prey encounter had diminished, and a six hour period appeared to be sufficient for predator satiation.

After each experiment, the number of prey remaining was subtracted from the number offered, to give the number eaten by the predator. For experiments on *D. magna*, the numbers of both live and dead prey remaining after six hours were recorded. A control experiment on *D. magna* mortality, conducted in 1974, revealed a natural death rate, over the six hour experiment, of 3.54 + 2.92%. (n = 32) (see Appendix 2). Mean experimental *D. magna* mortality in early 1975, was 9.89 + 7.21% (n = 62) for *P. nymphula*, and 7.41 + 6.44% (n = 20) for *C. puella* (see Appendix 3). Since these figures were substantially greater than the control mortality, Kruskal-Wallis one way analysis of variances were conducted to determine whether experimental *D. magna* mortality was independent of *D. magna* density. The results were significant at the 90% level for *P. nymphula* and at the 50% level for *C. puella*. Consequently, experimental *D. magna* mortality was judged to be independent of *D. magna* density, implying that each damselfly species was killing and not eating a more or less constant proportion of the available prey. Hence, for the sake of consistency, dead D. magna were counted as uneaten.

The remaining prey were removed and the experimental prey type and density to be used in the following experiment on each predator was determined, using a random number table. Each predator was retrained on the appropriate prey type, allowance being made for the calorific value of the prey eaten in the immediately prior experiment. For example, if six A. aegypti had been eaten in the prior experiment, and the predator was to be tested on D. magna in the following week, then:

$$50 - (2.5 \times 6) = 35 \text{ D. magna}$$

would be placed in the bucket with the damselfly. In this way, the number of calories made available to each predator during the entire training period was standardized.

For each experimental trial, the identification number of the particular predator, the date, the number of prey offered, No, and the number eaten, Ne, were recorded (for definitions of all symbols used in this thesis, see Appendix 4). Later, the sex, exuvium dry weight, adult dry weight, number of days from the previous moult (when known), and number of days to emergence, were also recorded, for each experimental trial (see Appendices 5-14).

In all cases, results of Kolmogorov-Smirnov tests on sex differences in the number of prey of each type eaten by each predator species (using both the original and the age-corrected data; see Section 2.2.2.c)), were not significant at the 5% level (see Appendix 15). Consequently, Ne data from both sexes were pooled, for each predator type.

The bulk of the functional response experiments was conducted during the spring of 1975, but checks on numbers of prey eaten at selected prey densities were carried out in 1976. Mann-Whitney U tests on the two-tailed differences between the numbers of prey eaten (corrected for age; see Section 2.2.2.c)) by each year class from each prey density offered, yielded non-significant results (at the 5% level) in all cases (see Appendix 15). Hence, the different year classes of damselflies were considered to have the same functional responses.

2.1.3. Initial Results of the Functional Response Experiments

The experiments described in the previous section provided the results displayed in Figures 2.2. to 2.4. and Tables 2.3. to 2.5. For each predator-prey interaction, the number of replicates, $\underline{n}$, the prey densities used, $\underline{No}$, and the mean, $\underline{Ne}$, standard error of the mean, $\underline{s_x}$, and variance, $\underline{s}^2$, of the number of prey eaten at each prey density are listed. The predicted numbers of prey eaten, $\underline{Nep}$, were calculated recursively from the random predator equation (Rogers, 1972), using the Newton-Raphson technique (Sutton, 1954). $\underline{a}$ and $\underline{Th}$ were estimated using the linear regression method described in Section 1.2., and the statistic $\underline{F}$ provided a measure of the fit of the data to this linear regression. (Application of the non-linear least squares method to be data resulted in similar predicted values (see Appendix 2 1.).) Symbols are all as defined in Appendix 4, and will be used in subsequent sections of this thesis without further explanation.

It is apparent from Figures 2.2. to 2.3. that the raw data do not conform to the smooth type 2 functional responses which had been expected. In addition, the standard errors for each mean $\underline{Ne}$ (Figures 2.2. and 2.3., and Tables 2.3. and 2.4.) are large, and do not inspire confidence in these results.

For all of the functional responses, except for that of C. puella eating D. magna, the significance of the $\underline{F}$ statistics exceed the 10% level, indicating that the Rogers (1972) model does not provide an adequate fit to most of these data sets. The resulting $\underline{Nep}$'s are therefore quite different from the raw data which they simulate.

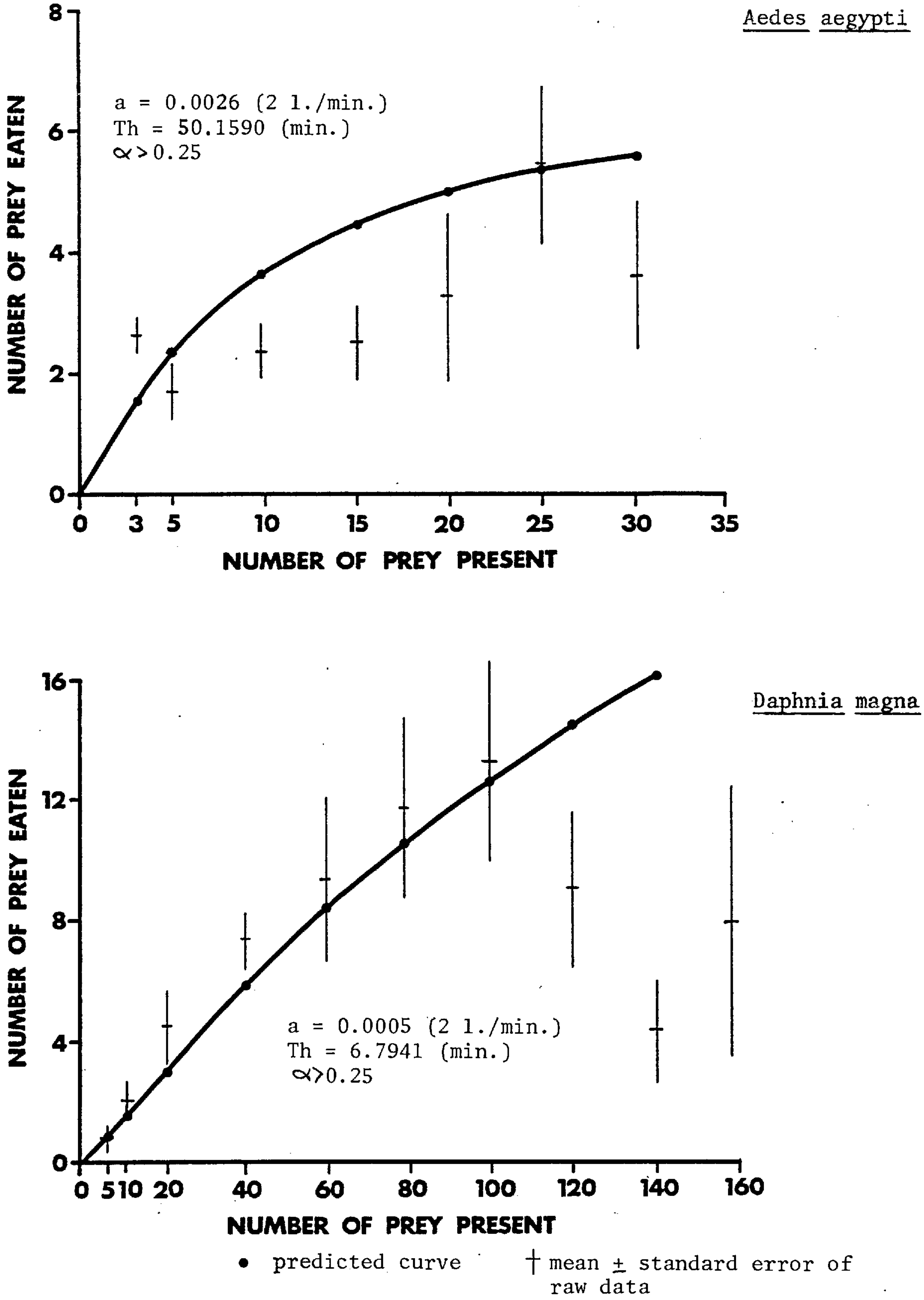


Figure 2.2. - Predicted and Observed (Raw Data) Functional Responses of *Pyrrhosoma nymphula*

Table 2.3. - Functional Responses of *Pyrrhosoma nymphula* (raw data)

a) with *Aedes aegypti* as prey

No	3	5	10	15	20	25	30	35
n	3	18	16	17	7	4	6	0
$\bar{x} \pm s_x$	2.67±0.33	1.72±0.46	2.38±0.45	2.53±0.65	3.29±1.44	5.50±1.35	3.67±1.26	
s^2	0.34	3.87	3.23	7.19	14.49	7.25	9.56	
Nep	1.56	2.34	3.67	4.47	4.98	5.34	5.59	5.79

Tt = 360 minutes; a = 0.0026 (2 l./minute); Th = 50.1590 minutes; $F_{1.5}$ = 0.2299; $\alpha > 0.25$;
mean variance = 6.56

b) with *Daphnia magna* as prey

No	5	10	20	40	60
n	7	9	7	5	7
$\bar{x} \pm s_x$	0.71±0.36	2.00±0.75	4.43±1.29	7.40±0.93	9.43±2.70
s^2	0.90	5.00	11.62	4.32	50.95
Nep	0.81	1.60	3.12	5.91	8.43

Table 2.3. - Functional Responses of *Pyrrhosoma nymphula* (raw data) (continued)

b) with *Daphnia magna* as prey (continued)

No	80	100	120	140	160
n	6	6	9	9	3
$\bar{x} \pm s_{\bar{x}}$	11.83±3.00	13.33±3.40	9.11±2.60	4.33±1.69	8.00±4.51
s^2	54.00	69.36	60.61	25.75	61.02
Nep	10.70	12.77	14.65	16.37	17.95

Tt = 360 minutes; a = 0.0005 (2 l./minute); Th = 6.7941 minutes; $F_{1,8} = 0.2789$; $\alpha > 0.25$; mean variance = 34.35

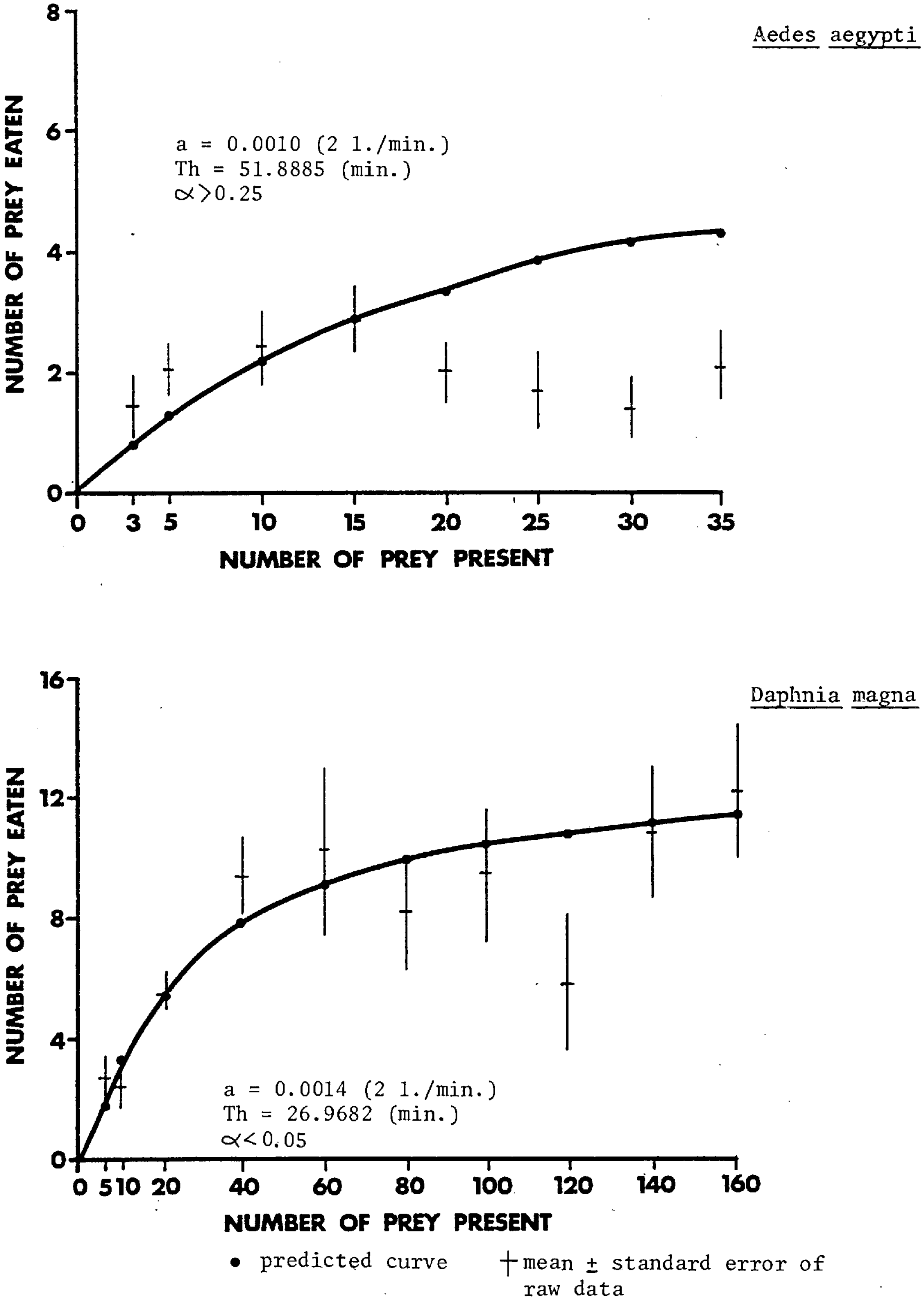


Figure 2.3. - Predicted and Observed (Raw Data) Functional Responses of *Coenagrion puella*

Table 2.4. - Functional Responses of Coenagrion puella (raw data)

a) with *Aedes aegypti* as prey

No	3	5	10	15	20	25	30	35
n	4	12	15	14	16	12	14	7
$\bar{x} \pm s_x$	1.50±0.50	2.08±0.48	2.47±0.64	2.93±0.55	2.06±0.56	1.75±0.65	1.43±0.55	2.14±0.62
s^2	1.00	2,74	6.12	4.21	5.00	5.02	4.24	2.69
Nep	0.82	1.27	2.19	2.86	3.38	3.78	4.10	4.37

Tt = 360 minutes; a = 0.0010 (2 l./minute); Th = 51.8885 minutes; $F_{1,6} = 0.069$; $\alpha > 0.25$;
mean variance = 3.88

Table 2.4. - Functional Responses of *Coenagrion puella* (raw data)

(continued)

b) with *Daphnia magna* as prey

No	5	10	20	40	60
n	6	9	6	7	6
$\bar{x} \pm s_{\bar{x}}$	2.50±0.89	2.44±0.71	5.17±0.91	9.43±1.31	10.33±2.88
s^2	4.70	4.53	4.97	12.01	49.77
Nep	1.77	3.19	5.26	7.69	9.03

Tt = 360 minutes; a = 0.0014 (2 l./minute); Th = 26.9682 minutes; $F_{1,8} = 6.4637$; $\alpha < 0.05$;
mean variance = 22.14

Table 2.4. - Functional Responses of *Coenagrion puella* (raw data)

(continued)

b) with *Daphnia magna* as prey (continued)

No	80	100	120	140	160
n	8	6	6	5	5
$\bar{x} \pm s_x$	8.25±1.99	9.50±2.29	5.83±2.34	10.80±2.15	12.20±2.25
s^2	31.64	31.46	32.97	23.11	26.22
Nep	9.86	10.43	10.84	11.15	11.39

Tt = 360 minutes; a = 0.0014 (2 l./minute); Th = 26.9682 minutes; $F_{1,8} = 6.4637$; $\alpha < 0.05$;
mean variance = 22.14

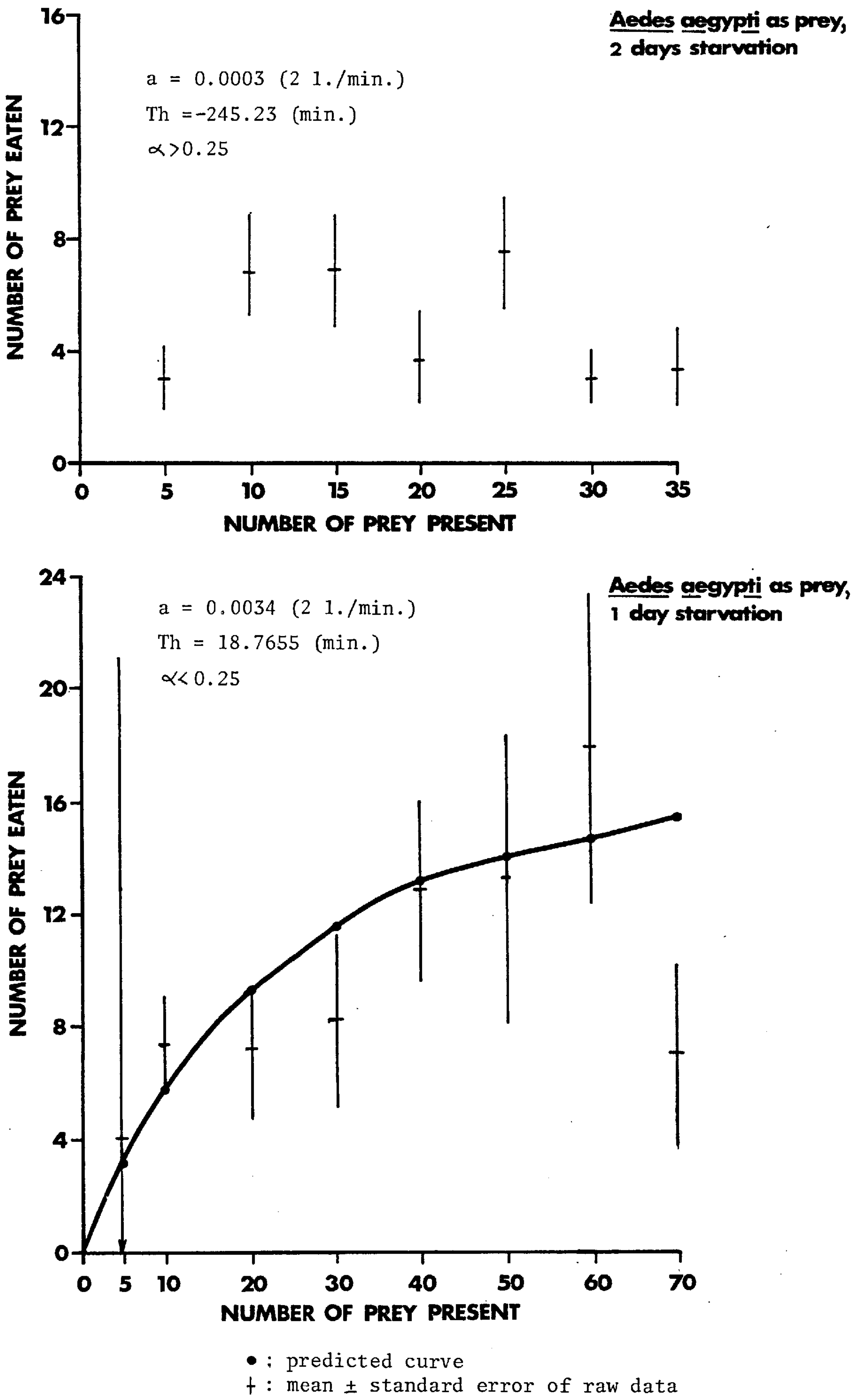


Figure 2.4. - Predicted and Observed (Raw Data) Functional Responses of Lestes sponsa

Figure 2.4. - (continued) Predicted and Observed (Raw Data) Functional Responses of *Lestes sponsa*

● : predicted curve

┼ : mean ± standard error of raw data

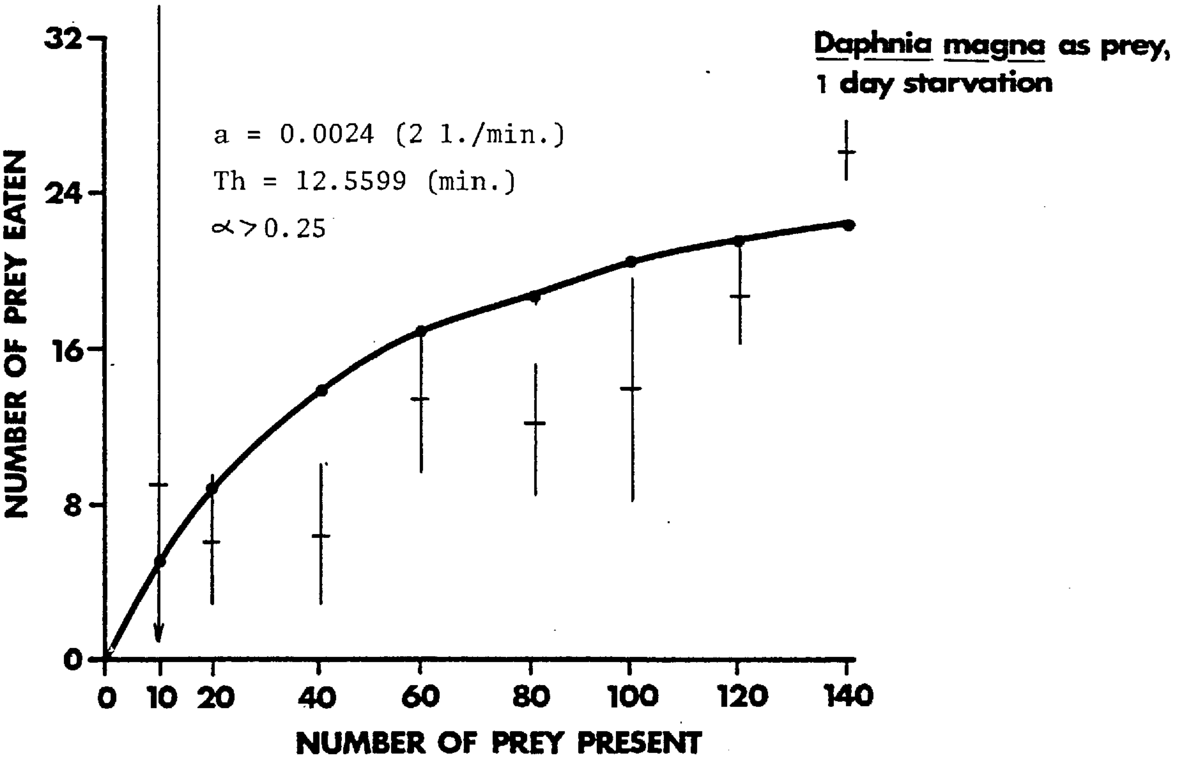


Table 2.5. - Functional Responses of *Lestes sponsa* (raw data)

a) with *Aedes aegypti* as prey, and 2 days starvation

No	3	5	10	15	20	25	30	35
n	0	4	5	6	8	7	8	8
$\bar{x} \pm s_x$		3.00±1.15	6180±1.66	6.83±2.02	3.75±1.59	7.57±2.05	3.00±1.07	3.38±1.57
s^2		5.29	13.78	24.48	20.21	29.29	9.14	19.70
Nep	No predicted numbers of prey eaten could be calculated, because the estimated handling time was negative.							

Tt = 360 minutes; a = 0.0003 (2 1./minute); Th = -245.23 minutes; $F_{1,5}$ = 0.8725; $\alpha > 0.25$;
mean variance = 17.41

Table 2.5. - Functional Responses of *Lestes sponsa* (raw data) (continued)

b) with *Aedes aegypti* as prey, and 1 day starvation

No	5	10	20	30	40	50	60	70
n	1	5	7	7	6	6	6	5
$\bar{x} \pm s_x$	4.00± ∞	7.40±1.86	7.14±2.42	8.14±3.12	12.67±3.23	13.17±5.22	17.67±5.58	6.80±3.18
s^2	∞	17.30	41.14	68.14	62.67	163.37	186.67	50.70
Nep	3.20	5.75	9.33	11.56	13.02	14.02	14.76	15.31

Tt = 360 minutes; a = 0.0034 (2 1/minute); Th = 18.7655 minutes; $F_{1,6}$ = 2.1508; $\alpha < 0.25$;
mean variance = 84.28

Table 2.5. - Functional Responses of *Lestes sponsa* (raw data)

(continued)

c) with *Daphnia magna* as prey, 1 day starvation

No	10	20	40	60	80	100	120	140
n	1	5	5	5	5	5	4	2
$\bar{x} \pm s_x$	9.00± ∞	6.00±3.35	6.40±3.80	13.40±3.83	12.20±3.69	14.00±5.86	18.75±3.30	26.50±1.50
s^2	∞	56.00	72.30	73.30	68.20	171.50	43.58	4.50
Nep	5.09	8.96	14.16	17.34	19.43	20.89	21.96	22.77

Tt = 360 minutes; a = 0.0024 (2 l./minute); Th = 12.5599 minutes; $F_{1,6} = 0.5190$; $\alpha > 0.25$;
mean variance = 69.91

2.2. Components of Variability in the Damselfly Predatory Response

2.2.1. Standardization of Predator and Prey Types

Two common indigenous damselfly species, Pyrrhosoma nymphula (Sulz.) and Coenagrion puella (L.) (Odonata; Zygoptera), were chosen as experimental predators. These two species are among the most widespread and abundant Zygopterans in England, and they occur together over much of their ranges. They are readily available in the field, and easily maintained in the laboratory. Their suitability for a comparative study on predation and prey preference was confirmed by the similarity of their life histories, and the simplicity of their predatory behaviour.

For the sake of brevity, these two predators will be designated in the following sections of the text of this thesis by their generic names alone. Any other Odonata species mentioned, will be referred to by their full species names. The life history and general ecology of both damselflies have been well documented (Gardner and MacNeill, 1950; Corbet, 1957; Macan, 1964 and 1974; Lawton, 1969, 1970a, 1971b, 1971c and 1972; Parr, 1970). However, the life histories of both populations studied in this project differed markedly from those reported in the literature.

Corbet(1954) categorized Odonata species as either 'spring species', with an early, well synchronized, emergence period, or 'summer species', with a later, more dispersed, emergence pattern. Although this classification has been shown to break down at lower latitudes (Paulson and Jenner, 1971; Beesley, 1972; Kime, 1974), most of the work done in England (Corbet, 1954, 1957 and 1962; Macan, 1964 and 1974; Lawton, 1969 and 1971c; Wells, 1974) supports the claim that Pyrrhosoma is a typical 'spring species', with a two year life cycle. A facultative diapause (Andrewartha, 1952; Danilevskii, 1965) during the autumn before emergence has been cited (Corbet, 1957; Tauber and Tauber, 1976) as the determinant for the synchronous emergence of the 'spring species'. After entering the final instar, larvae undergo diapause development, and morphogenesis is suspended until the temperature falls below a critical minimum temperature threshold, which breaks diapause. This ensures that ultimate instar larvae have accumulated in a pre-metamorphosis state by the early winter.

When warmer spring temperatures permit further morphogenesis, the larvae will be synchronized, so that as soon as metamorphosis is completed, emergence of the entire cohort will occur within a short period of time. In the case of Pyrrhosoma, ultimate instar larvae are reported to undergo diapause in their second winter, with the adults emerging synchronously in the early spring. Longfield (1937) stated that they first became abundant at the end of April and the beginning of May, while Corbet (1952) found that their main period of emergence was between May 20 and May 28, in a pond near Reading, Berks. Lawton (1971c) working farther north, in Durham, found that the main emergence period occurred at the end of May, and the beginning of June. However, about one half of the Pyrrhosoma larvae I collected in February 1975 (and due to emergence in the following spring), were in the penultimate instar, and had presumably spent only one year in larval development (Appendix 22).

Although Corbet includes Coenagrion puella in a list of the 'summer species' of Odonata occurring in Britain (Corbet, Longfield and Moore, 1960), life history studies on Coenagrion puella (Parr, 1970; Lawton, 1972) reveal that this species is difficult to classify categorically as a 'summer species'. Most of the population spends the winter before emergence in the penultimate instar, and Parr postulates the existence of a diapause at this stage. Such an autumn diapause is normally associated with 'spring species', although 'spring species' typically over-winter in the final instar. Furthermore, Coenagrion puella emerges early in the spring, at a time when most of the other emerging Odonata are classified as 'spring species' by Corbet (Corbet, Longfield and Moore, 1960). Longfield (1937) recorded Coenagrion puella as emerging during the second and third weeks in May, while Parr (1970) found that in Lancashire, most individuals emerged during the end of May, and the beginning of June. The population studied in this project did not conform to the typical 'summer species' pattern, either, and adult emergence took place within a relatively short period of time (Section 2.5.1.c)). Moreover, the population appeared to be exclusively univoltine (Appendix 22), unlike the populations studied by Parr and Lawton which had both univoltine and semivoltine fractions. These results are corroborated by the work of J. Cremona, on the Zygopteran populations in a pond in the New Forest. He found that only one third of the Pyrrhosoma population required two years for larval development, while the remaining fraction was univoltine. The similarity of the Pyrrhosoma and Coenagrion emergence patterns was also noted (J. Cremona, personal communication).

In addition, some experimental work was conducted on Lestes sponsa (Hansemann). This is a univoltine 'summer species' which completes larval development in a few months in the spring. The life history and predatory behaviour of this species and others in the genus have been well covered in the literature (Longfield, 1937; Corbet, Longfield and Moore, 1960; Corbet, 1956a and 1956b; Fischer, 1960, 1961, 1964, 1966, 1967). Raw data for this species are listed in Appendices 16-20.

The economical predatory strategy exhibited by these damselflies simplifies experimental observation and interpretation considerably. Damselflies are ambush predators. They do not pursue their prey, and capture is extremely rapid. These factors facilitate the calculation of the energetic costs associated with feeding, and simplify the detailed recording of predatory behaviour. Prey capture is stimulated by tactile cues to the antennae (Fischer, 1964; Richard, 1970), and hence feeding is largely independent of photoperiod (Johnson, Akre and Crowley, 1975). In addition, the reactive field is compact, which simplifies comparison of the two damselfly species.

In the context of these factors, the voracious appetite of Odonata larvae in general (Hinman, 1934; Sharaf and Tripathi, 1974; El Rayah, 1975; Benke, 1976) and their possible preference for large prey (Fischer, 1966 and 1967; Cloarec, 1977; Ross, 1967 and 1971), render the predatory behaviour and competetive interactions of the two species chosen both interesting and amenable to investigation.

Damselflies were collected from a small pond in Swinley Brick pits (ordnance survey grid reference SU 905 675) in 1975 and 1976, and from an adjacent pond which is slightly larger and deeper, in 1977.

These ponds are shown in Plate 2.1.. Numbers of each species collected on each visit are listed in Appendix 22. The larvae were brought into the laboratory, sorted, and placed near a window, in individual plastic containers holding approximately 200 ml. of a mixture of pond and tap water. They remained there, exposed to natural photoperiod and room temperature, for 48 hours, after which they were transferred to individual buckets filled with two litres of tap water and containing a twig providing a damselfly ambush site in a 15^{o} C. controlled temperature room. This experimental apparatus is shown in Plate 2.2.. Ultimate instar larvae were exposed to a photoperiod of 8 light: 16 dark hours, since this light regime has been found (Wells, 1974) to delay or prevent metamorphosis in Pyrrhosoma. (Similar effects have been documented for other Odonata species (Jenner, 1959; Lutz and Jenner, 1960 and 1964; Montgomery and Macklin, 1962; Lutz, 1964).). Penultimate and ante-penultimate instar larvae were exposed to a 16 light: 8 dark photoperiod, and were fed on either twenty mosquitos or fifty daphnia, three times a week (see Section 2.4.1.b)). When penultimate instar larvae moulted to the final instar, they were transferred to the 8 light: 16 dark photoperiod, and after a minimum of seven days of training (Section 2.1.2.), underwent experimental testing.

Experimental prey were standardized in the following way: ultimate instar Aedes aegypti (L.) larvae were raised in the laboratory at approximately 30^{o} C. They were fed on a mixture of ground dogfood and yeast, in bowls containing about one thousand larvae of the same age. Daphnia magna (Straus), bought from local pet shops, were maintained in the laboratory in buckets of distilled water with added chlorella culture, or in buckets of pond water from the Silwood Park Refectory fishpond. Experimental individuals were strained at least once through a sieve (with a mean between filament distance of 1.4 mm.), and then non-gravid individuals were selected as experimental prey. Any daphnia which had caught air under their carapace during straining, floated on the water surface in the sorting bowl, and these individuals were not included as experimental prey. In the following sections of this thesis, 'mosquitos' and 'daphnia' will refer to the standardized experimental prey types described above.

Both prey types seemed well suited to the experimental conditions. They fed and moved about freely in the experimental buckets, and no strong clumping effects were observed.

Both *Pyrrhosoma* and *Coenagrion* are known to take similar prey organisms on the field. Benke (1978) reported that dipteran larvae and small crustacea were important prey types for Odonata larvae. J. Cremona, studying the Zygopteran guild in a pond in Hampshire, found that ostracods and chironomids were the most important types of prey for late instar *Pyrrhosoma* and *Coenagrion* larvae. (J. Cremona, personal communication).

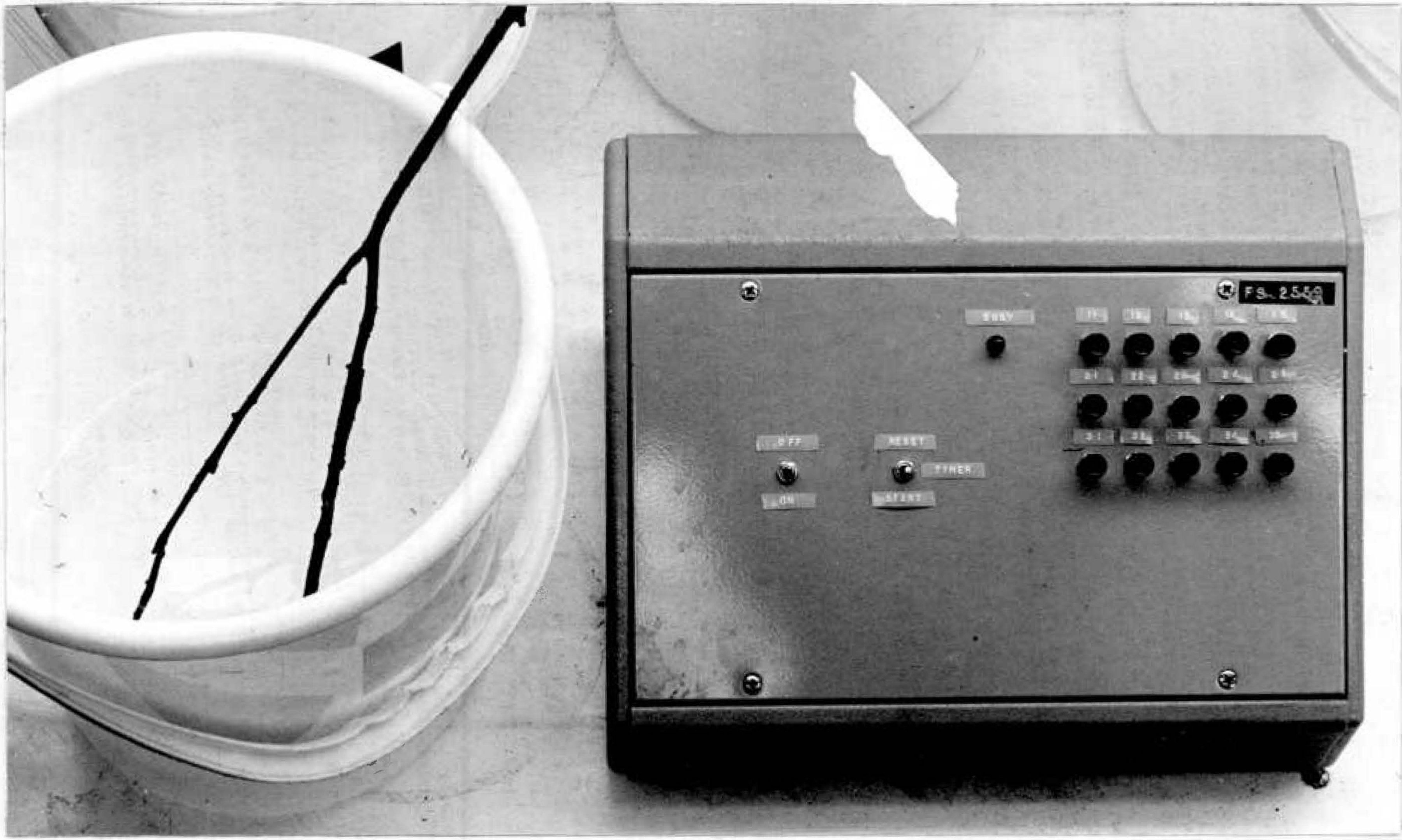
Since the particular species of chironomids and ostracods eaten in the field are difficult to culture in the laboratory, the mosquitos and daphnia described above, which are easily maintained in the laboratory, were used in the controlled predation experiments. For the purpose of comparison, these two prey types were considered as roughly analagous to the chironomids and ostracods taken by these damselflies in the field. Their size and dry weights are comparable. Ostracods inhabit the lower regions of a pond, close to the muddy bottom; daphnia were found to select similar microhabitat in the experiments reported in Section 2.2.4.. Chironomids and mosquito larvae inhabit similar weedy regions in a pond, and their speed and mode of movement are also very close. The most obvious difference between the mosquitos and chironomids, is their visibility; the mosquitos are much darker in colour. However, this should not greatly affect the damselflies' predatory success, since *Pyrrhosoma* and *Coenagrion* locate their prey primarily using tactile cues (Johnson, Akre and Crowley, 1975).

Plate 2.1. Swinley Brick Pits, showing the two ponds from which damselflies were collected.

(Above: pond visited in 1975 and 1976

Below: pond visited in 1977)

Plate 2.2. Experimental Apparatus, showing experimental bucket, containing twig and mosquitos, and Data Printer Keyboard (see Appendix for details of this instrument).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BUSY
OFF
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RESET
TIMER
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2.2.2. Effect of Age on Damselfly Feeding Rate

2.2.2.a) General Introduction

While the effect of predator instar, or developmental stage on predation rate has been examined in some detail (Murdoch, 1971 and 1972; Fox and Murdoch, 1974; Thompson, 1975), the investigation of changes in predator behaviour with age within each instar is not nearly so advanced. Evidence has been presented in the past showing that Odonata larvae cease feeding several days before emergence (Kormondy, 1959; Corbet, 1962). Lawton (1969, 1971b) also found this to be the case for Pyrrhosoma larvae in stage three metamorphosis. This cessation of feeding is due to the formation of the adult exoskeleton under the larval skin, and the accompanying histolysis of the labium, which hinders the use of the mouthparts (Whedon, 1927; Munscheid, 1933; Corbet, 1962). Indeed, some of the labial musculature may be totally destroyed during metamorphosis (Hinton and Mackerras, 1970). Lawton (1969, 1971b) also found that Pyrrhosoma's feeding rate declined throughout the week before the onset of stage three metamorphosis, when feeding ceased. Investigations were made to determine whether such age-effects operated on the feeding behaviour of the experimental predators.

2.2.2.b) Effect of Metamorphosis on Damselfly Feeding Rate

Graphs of the number of prey eaten vs. the number of days to emergence, and vs. the number of days from the previous moult (when known) were drawn for each predator type, for each prey type and density offered. These graphs indicated that feeding continued (albeit at a rather variable rate) until shortly before emergence of the adult, when predation ceased altogether. In all but three instances, Pyrrhosoma individuals ate at least one prey item, in trials conducted more than ten days before they were to emerge. In the case of Coenagrion, there was only one exception to this rule. L. sponsa was found to eat at least one prey item in all experimental trials conducted seven or more days prior to the individual's emergence.

On the basis of these results, all data for which the predator had been less than eleven (or seven in the case of L. sponsa) days from emergence were discarded. The number of replicates, and mean, standard error, and variance in the number of prey eaten for these pre-metamorphosis damselflies, as well as the predicted number of prey eaten, the estimated parameters $\underline{a}$ and $\underline{Th}$, and the $\underline{F}$ statistic, are presented in Figures 2.5. to 2.7. and Tables 2.6. to 2.8. Comparison of these results with those presented in Figures 2.2. to 2.4. and Tables 2.3. to 2.5. reveals a reduction in the variance, and an increase in the mean of the number of prey eaten at each prey density. However, the fit of the data to the Rogers (1972) model is still not significant. Assuming that there is an equal probability that the variance of the data for pre-metamorphosis predators, at a particular prey density is either greater than, or not greater than the corresponding variance when all data are included, then the binomial probabilities that the differences between the variances for the raw data and the pre-metamorphosis data are due to chance are presented in the following Table 2.9. This trend is further documented in Figure 2.1. and Table 2.2.

Table 2.9. - Binomial Test on Functional Response Variances

Binomial test for:

probability: s^2 (raw data) $\geqslant$ s^2 (pre-metamorphosis data) = ½
probability: s^2 (raw data) $<$ s^2 (pre-metamorphosis data) = ½

predator prey interaction	Pyrrho. eating mosq.	Pyrrho. eating daph.	Coenag. eating mosq.	Coenag. eating mosq.	Lestes eating mosq.	Lestes eating daph.	Lestes eating mosq.
					(1 day starvation)		
total no. of observations	71	68	94	65	42	32	46
binomial probability	.0078	.0440	.1093	.0440	.0078	.1563	.2500

Pyrrho. = Pyrrhosoma; Coenag. = Coenagrion; Lestes = Lestes sponsa
mosq. = mosquitos ; daph. = daphnia

This reduction in variance is significant at the 5% level for both interactions involving Pyrrhosoma, and for Coenagrion eating daphnia. For Coenagrion eating mosquitos, the binomial probability is just above 10%. This strongly suggests that, for Pyrrhosoma and Coenagrion at least, the exclusion of the pre-metamorphosis data provides an important control on the damselfly functional response. Hence, metamorphosis is certainly one of the factors responsible for the high variability in the raw functional response data, for these two damselflies. The lack of significance of this reduction in variance for Lestes sponsa may be related to this species' short life history (see Section 2.2.2.c) and 2.5.3.).

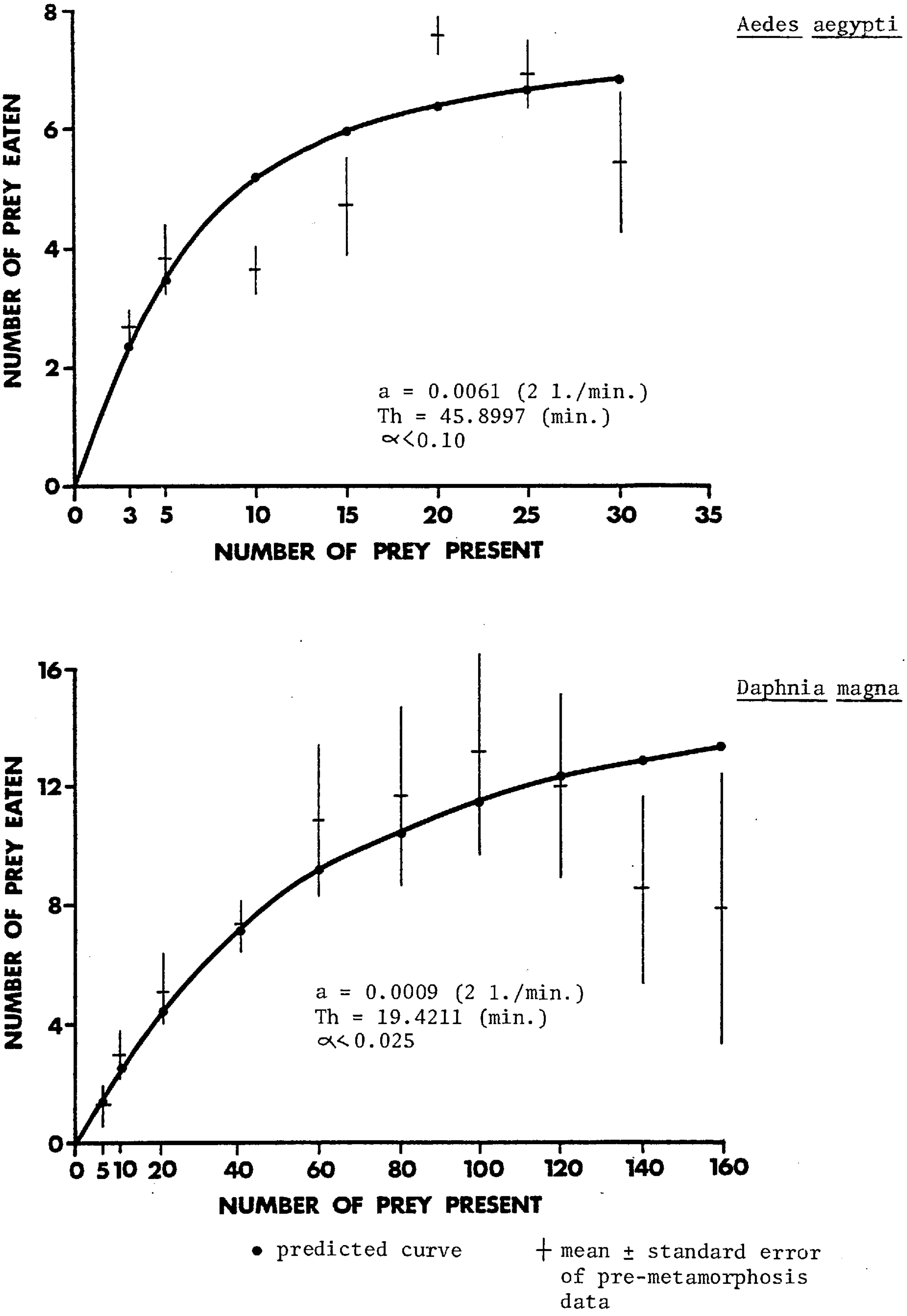


Figure 2.5. - Predicted and Pre-Metamorphosis Functional Responses of *Pyrrhosoma nymphula*

Table 2.6. - Functional Responses of *Pyrrhosoma nymphula* (pre-metamorphosis data)

a) with *Aedes aegypti* as prey

No	3	5	10	15	20	25	30	35
n	3	6	9	8	3	3	4	0
$\bar{x} \pm s_x$	2.67±0.33	3.83±0.60	3.67±0.41	4.75±0.90	7.67±0.33	7.00±0.58	5.50±1.19	-
s^2	0.34	2.16	1.50	6.41	0.34	1.00	5.66	
Nep	2.35	3.51	5.21	6.01	6.45	6.72	6.91	7.04

Tt = 360 minutes; a = 0.0061 (2 l./minute); Th = 45.8997 minutes; $F_{1,5} = 4.2353$; $\alpha < 0.10$;
mean variance = 2.49

Table 2.6. - Functional Responses of *Pyrrhosoma nymphula* (pre-metamorphosis data) (continued)

b) with *Daphnia magna* as prey

No	5	10	20	40	60
n	3	6	6	5	6
$\bar{x} \pm s_x$	1.33±0.67	3.00±0.86	5.17±1.25	7.40±0.93	11.00±2.60
s^2	1.33	4.44	9.38	4.32	40.56
Nep	1.30	2.45	4.38	7.19	9.11

Tt = 360 minutes; a = 0.0009 (2 1./minute); Th = 19.4211 minutes; $F_{1,8} = 7.9669$; $\alpha < 0.025$;
mean variance = 33.54

Continued....

Table 2.6. - Functional Responses of *Pyrrhosoma nymphula* (pre-metamorphosis data) (continued)

b) with *Daphnia magna* as prey (continued)

No	80	100	120	140	160
n	6	6	6	3	3
$\bar{x} \pm s_x$	11.83±3.00	13.33±3.40	12.17±3.18	8.67±3.18	8.00±4.51
s^2	54.00	69.36	60.67	30.34	61.02
Nep	10.49	11.53	12.33	12.97	13.50

Tt = 360 minutes; a = 0.0009 (21./minute); Th = 19.4211 minutes; $F_{1,8} = 7.9669$; $\alpha < 0.025$; mean variance = 33.54

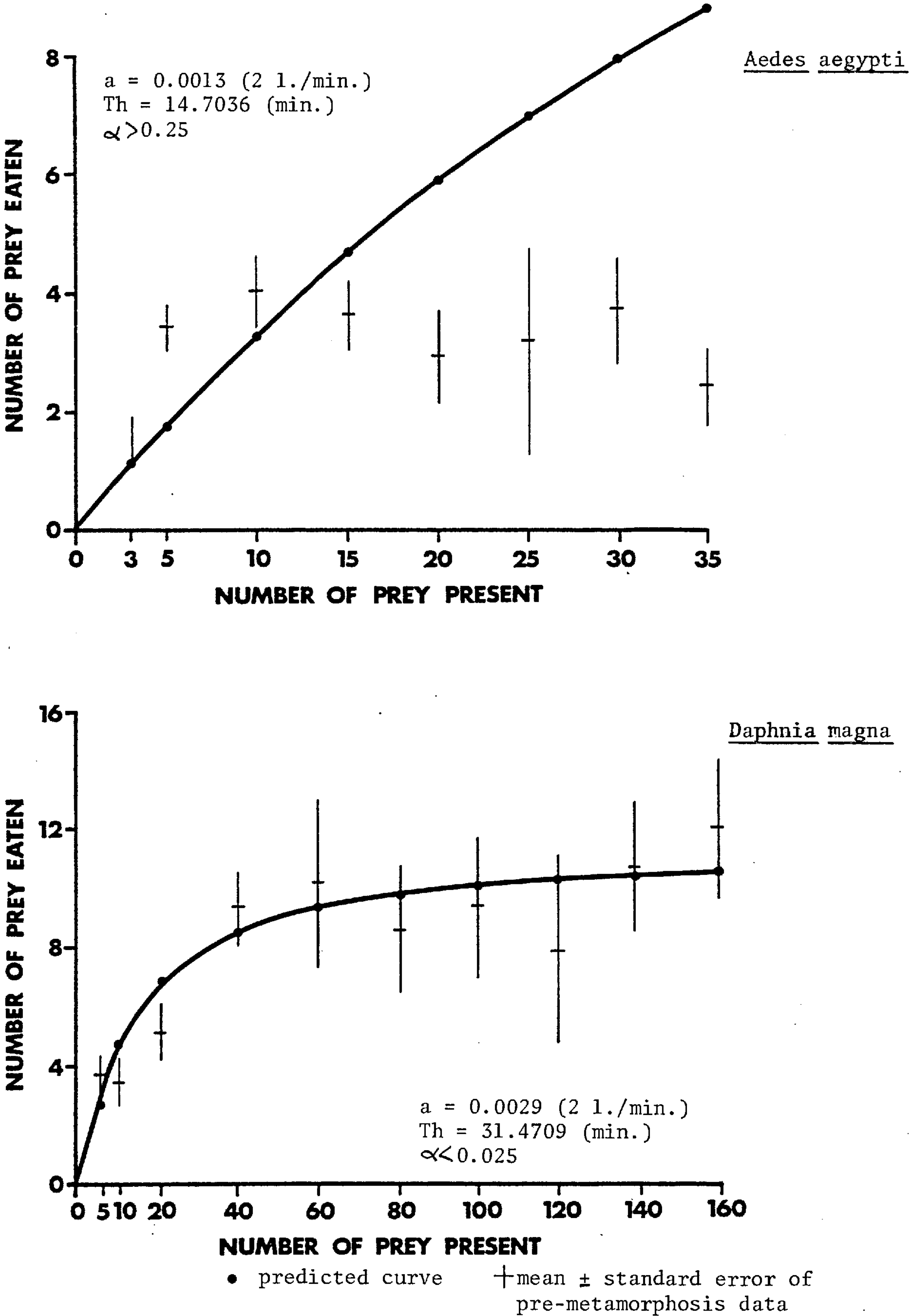


Figure 2.6. - Predicted and Pre-Metamorphosis Functional Responses of *Coenagrion puella*

Table 2.7. - Functional Responses of *Coenagrion puella* (pre-metamorphosis)

a) with *Aedes aegypti* as prey

No	3	5	10	15	20	25	30	35
n	4	6	9	10	9	4	5	6
$\bar{x} \pm s_x$	1.50±0.50	3.50±0.43	4.11±0.66	3170±0.62	3.00±0.83	3.25±1.60	3.80±0.86	2.50±0.67
s^2	1.00	1.10	3.86	3.80	6.25	10.25	3.70	2.69
Nep	1.08	1.76	3.33	4.72	5.96	7.08	8.08	8.98

Tt = 360 minutes; a = 0.0013 (2 1./minute); Th = 14.7036 minutes; $F_{1,6} = 0.0100$; $\alpha > 0.25$;
mean variance = 4.08

Table 2.7. - Functional Responses of *Coenagrion puella* (pre-metamorphosis data)

(continued)

b) with *Daphnia magna* as prey

No	5	10	20	40	60
n	4	6	6	7	6
$\bar{x} \pm s_x$	3.75±0.63	3.50±0.72	5.17±0.91	9.43±1.31	10.33±2.88
s^2	1.59	3.10	4.97	12.01	49.77
Nep	2.74	4.63	6.85	8.74	9.54

Tt = 360 minutes; a = 0.0029 (2 l./minute); Th = 31.4709 minutes; $F_{1,8} = 7.2876$; $\alpha < 0.05$;
mean variance = 22.30

Continued....

Table 2.7. - Functional Responses of *Coenagrion puella* (pre-metamorphosis data)

(continued)

b) with *Daphnia magna* as prey (continued)

No	80	100	120	140	140
n	7	6	4	5	5
$\bar{x} \pm s_x$	8.71±2.23	9.50±2.29	8.00±3.00	10.80±2.15	12.20±2.29
s^2	34.81	31.46	36.00	23.11	26.22
Nep	9.98	10.25	10.44	10.58	10.68

Tt = 360 minutes; a = 0.0029 (2 1./minute); Th = 31.4709 minutes; $F_{1,8}$ = 7.2876; $\alpha <$ 0.05 ;
mean variance = 22.30

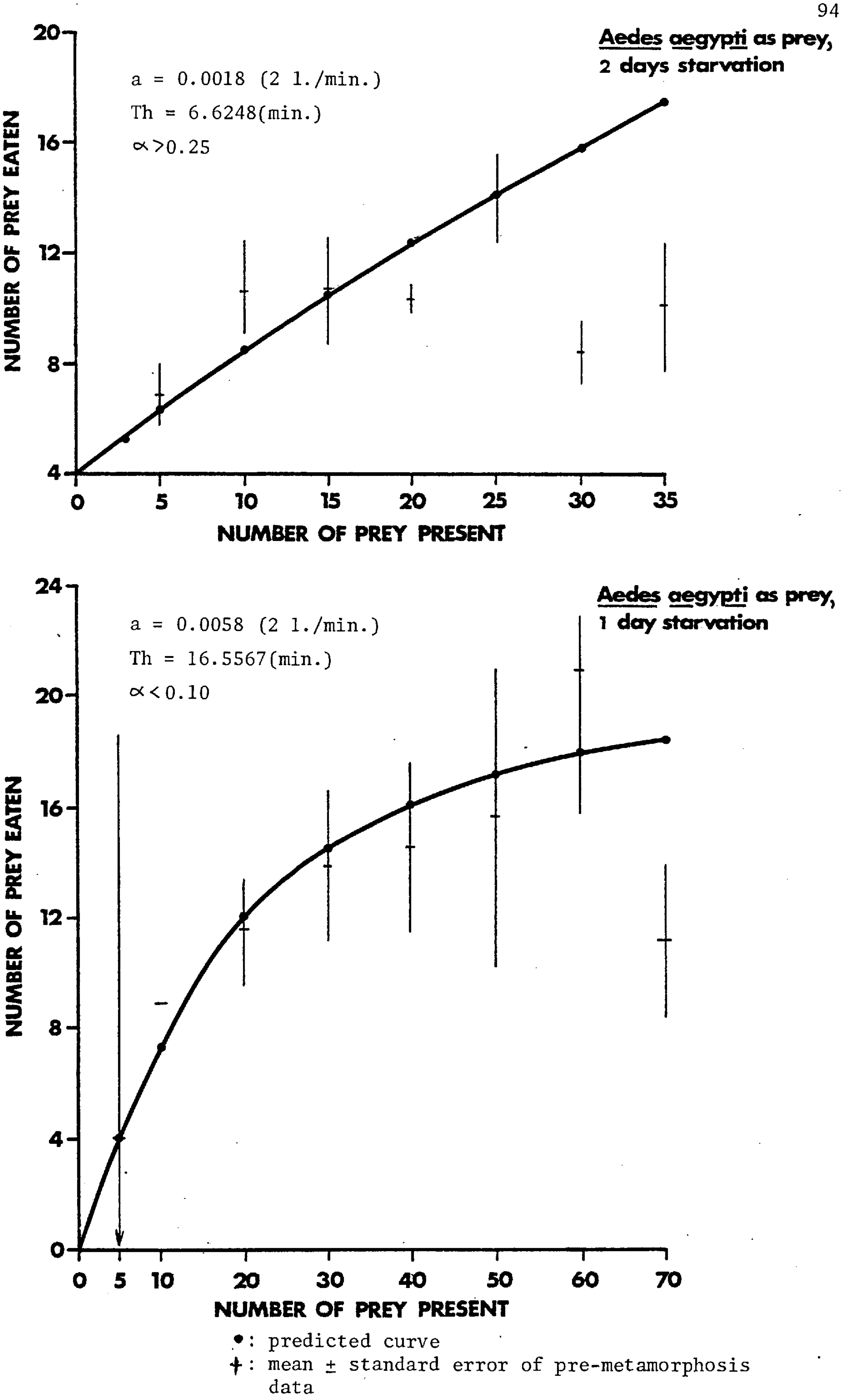


Figure 2.7. - Predicted and Pre-Metamorphosis Functional Responses of Lestes sponsa

Figure 2.7. - (continued) Predicted and Pre-Metamorphosis Functional Responses of *Lestes sponsa*

● : predicted curve
+ : mean ± standard error of pre-metamorphosis data

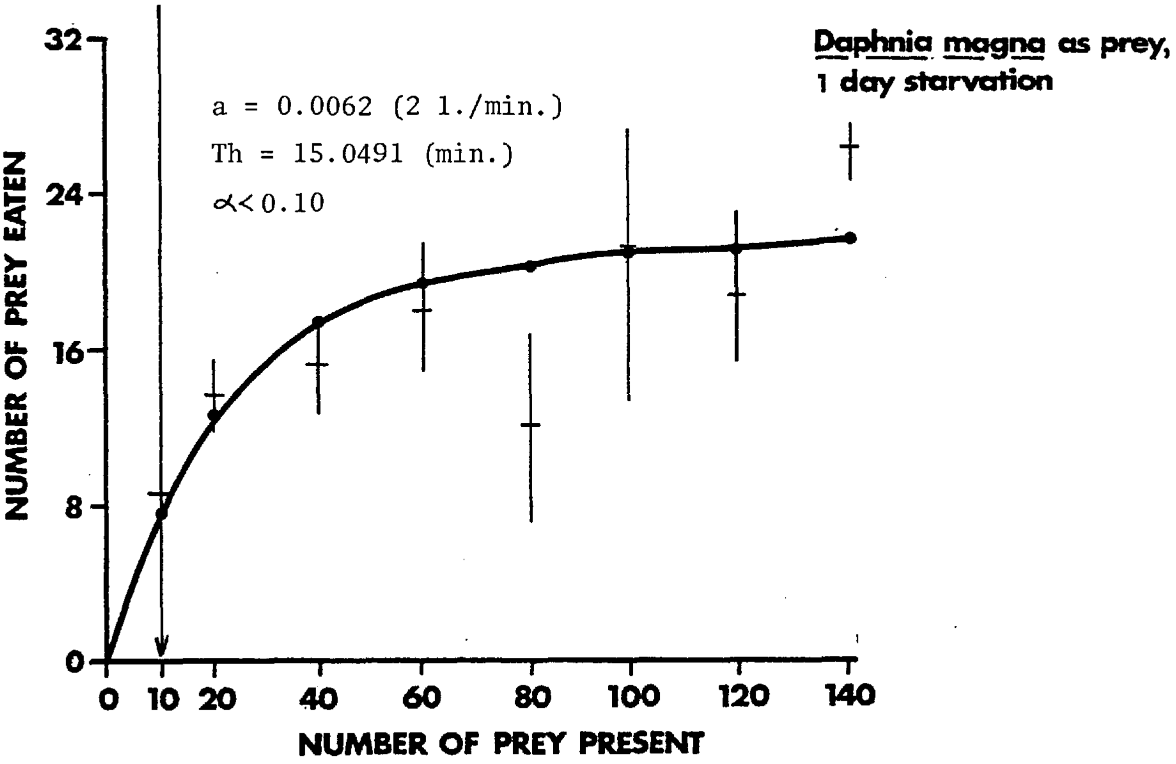


Table 2.8. - Functional Responses of *Lestes sponsa* (pre-metamorphosis data)

a) with *Aedes aegypti* as prey, and 2 days starvation

No	3	5	10	15	20	25	30	35
n	0	4	5	6	2	5	5	4
$\bar{x} \pm s_{\bar{x}}$	-	3.00±1.15	6.80±1.66	6183±2.02	6.50±0.50	10.20±1.62	4.60±1.21	6.25±2.39
s^2	-	5.29	13.78	24.48	0.50	13.20	7.30	22.92
Nep	1.40	2.31	4.48	6.52	8.43	10.23	11.91	13.50

Tt = 360 minutes; a = 0.0018 (2 l./minute); Th = 6.6248 minutes; $F_{1,5} = 0.0262$; $\alpha > 0.25$;
mean variance = 12.50

Table 2.8. - Functional Responses of *Lestes sponsa* (pre-metamorphosis data)

b) with *Aedes aegypti* as prey, and 1 day starvation

No	5	10	20	30	40	50	60	70
n	1	3	4	4	4	5	5	3
$\bar{x} \pm s_x$	4.00± ∞	9.00±0.00	11.75±1.97	14.00±2.71	14.75±3.12	15.80±5.52	21.20±5.89	11.33±2.85
s^2	∞	0.00	15.58	29.33	38.92	152.20	139.70	24.33
Nep	4.08	7.46	12.09	14.72	16.30	17.32	18.02	18.54

Tt = minutes; a = 0.0058 (2 l./minute); Th = 16.5567 minutes; $F_{1,6} = 4.6814$; $\alpha < 0.10$;
mean variance = 57.15

Table 2.8. - Functional Responses of Lestes sponsa (pre-metamorphosis data) (continued)

c) with Daphnia magna as prey, 1 day starvation

No	10	20	40	60	80	100	120	140
n	1	2	2	3	3	3	4	2
$\bar{x} \pm s_x$	9.00±∞	14.00±2.00	15.50±2.50	18.30±3.18	12.33±4.91	21.33±6.64	18.75±3.30	26.50±1.50
s^2	∞	8.00	12.50	30.33	72.33	132.33	43.58	4.50
Nep	7.78	12.87	17.67	19.67	20.71	21.35	21.78	22.08

Tt = 360 minutes; a = 0.0062 (2 l./minute); Th = 15.0491 minutes; $F_{1,6} = 5.0528$; $\alpha < 0.10$;
mean variance = 43.37

2.2.2.c) Effect of Pre-Metamorphosis Age on Damselfly Feeding Rate

Data on the variation in the number of prey eaten with predator age were examined in more detail. It was considered possible that some previously overlooked variation in predator feeding (prior to the ten days before emergence for which all data had already been discarded) due to ageing, or to the onset of metamorphosis, might have contributed to the high functional response variances. The possibility of such age-related predation was tested by lumping all the data for predators more than ten days from emergence, for all prey densities roughly on the flat part (or asymptote) of the functional response (<u>No</u> $\geqslant$ 15 for mosquitos; <u>No</u> $\geqslant$ 40 for daphnia). A Mann-Whitney test was performed, to determine whether young predator individuals (more than 20 days from emergence) ate significantly more prey items than older predator individuals (less than 21 days from emergence) (see Appendix 7 for details). (Note that predator age was measured in terms of days to emergence, rather than days from the previous moult). Young ultimate instar <u>Pyrrhosoma</u> and <u>Coenagrion</u> damselflies ate significantly more than older ones: $\alpha \leq .025$ for <u>Pyrrhosoma</u> eating mosquitos, $\alpha \leq .001$ for <u>Pyrrhosoma</u> eating daphnia, for <u>Coenagrion</u> eating mosquitos, and for <u>Coenagrion</u> eating daphnia. (Ultimate instar <u>L. sponsa</u> larvae behaved differently. Larvae starved for one day prior to experimentation ate significantly more mosquitos ($\alpha \leq .05$) when they were older (less than 13, but more than 6 days before emergence), but larvae starved for two days did not. Larvae starved for one day and fed daphnia ate significantly fewer ($\alpha \leqslant .05$) when they were older)

This indicated that there was a highly significant reduction in the feeding rate for both <u>Pyrrhosoma</u> and <u>Coenagrion</u>, as they aged. However, the non-parametric Mann-Whitney test can reveal nothing about the rate of decline in predation with age and the shape of the relationship between predator feeding and predator age. The simplest form for this relationship to take is a linear one. For every day of additional predator age, the average number of prey consumed could decline by a fixed amount. In order to test for this, the data used in the Mann-Whitney test were subsequently fitted to a straight line, using the linear regression technique. These data, and the lines fitted to them, are depicted in Figures 2.8. and 2.9. These regressions were significant at the 3% level for Pyrrhosoma, and at the 0.5% level for Coenagrion, while they were not significant at all for L. sponsa. Hence, a significant portion of the variation in damselfly predation was accounted for by the linear regression on damselfly age, for all predator-prey interactions involving Pyrrhosoma and Coenagrion. This strongly indicated that pre-metamorphosis predator age was another factor contributing to the damselfly functional response variability. If this age factor could be controlled for each predator-prey interaction, then any irregularities resulting from differing mean predator ages at each prey density would also be eliminated, revealing much more clearly the actual damselfly functional responses, for a particular predator age within the ultimate instar.

In order to control age in this way, the predator feeding data had to be standardized to a certain predator age. Some correction factor had to be devised which would permit transformation of the pre-metamorphosis data to corresponding data for predators of a standard age. Two different techniques to achieve such a correction were tested. First, the slopes of the linear relationships described above were used to standardize the pre-metamorphosis data. Then, because scanning of the age-related data (see Figures 2.8. and 2.9.) (note particularly the data for Pyrrhosoma eating daphnia) suggested that a logarithmic curve of the form:

$$\log_{10} \text{(number of prey eaten)} = a + b \times \text{(predator age)}$$

might provide a better fit to the data, a standardization technique based on this relationship was also tested.

There is considerable theoretical evidence that a logarithmic relationship is the most appropriate for use in modelling processes dependent on growth. In a treatise on insect growth, Hinton and Mackerras (1970) assert that "essentially, normal growth gives a straight line when plotted on a semi-log grid". Since the gradual inhibition of predation in damselflies approaching emergence is a direct of their completion of larval morphogenesis (Whedon, 1927; Munscheid, 1933; Corbet, 1962) the age-relations displayed in Figures 2.8. and 2.9. might be expected to assume a logarithmic form. Hence, these data were also modelled using a linear regression of $\log_{10}$ (Ne) versus predator age. The resulting relationships are detailed in Appendix 24.

Each type of age-relation then provided the basis for standardization of the functional response data with respect to damselfly age. It was considered highly likely that the rate of decline in damselfly predation with age would be the same at very low prey densities as at higher ones, despite the lower absolute numbers of prey eaten in the former situation. Therefore, the two models for age-related decline in damselfly predation, both derived from the data only on the asymptote of the functional response, were used to provide age-corrections for all the pre-metamorphosis data.

Correction of the functional response data for predator age proceeded as follows: A standard predator age of twenty days prior to emergence was chosen. This represented a half-way point through both the final larval instar and the period during which the damselflies were tested in the laboratory. Individuals of Pyrrhosoma and Coenagrion, entering the ultimate instar of the spring, spent an average of 39.00+4.00 days (n=7) and 41.09+7.33 days (n=22), respectively, in this instar.

For the linear model, the regressions (see Figures 2.8. and 2.9.) specified that for each predator-prey interaction:

$$\text{Ne (age X)} = \text{Ne (age 0)} + \text{slope} \times \text{(age X)}$$

$$\text{or: Ne (age X)} = \text{intercept} + \text{slope} \times \text{(age X)}$$

In the same way:

$$\text{Ne (age X + Y)} = \text{intercept} + \text{slope} \times \text{(age X + Y)}$$

Therefore:

$$\text{Ne (age X + Y)} = \text{Ne (age X)} + \text{slope} \times \text{(Y)} .$$

Consequently, to transform each Ne datum to the corresponding value for a predator of standard age, Nec, the difference between the predator's actual age and twenty was multiplied by the slope for the particular predator-prey interaction (Figures 2.8. and 2.9.). This value was then either subtracted from or added to, the original Ne, depending upon whether the actual predator age was greater than, or less than, twenty. For example, an original Ne of 4 mosquitos for a Pyrrhosoma individual aged 11 days before emergence, could be transformed to correspond to a Pyrrhosoma individual aged twenty in this way:

$$\underline{Nec} = 4 + 0.1852\ (20-11)$$
$$= 5.67$$

For the logarithmic model, the regressions (see Appendix 24) specified that for each predator-prey interaction:

$$\log\ (Ne\ (age\ X)) = intercept + slope \times (age\ X)$$

$$\text{or:}\quad Ne\ (age\ X) = antilog\ (intercept + slope \times (age\ X))$$
$$= {}_{10}\ (intercept + slope \times (age\ X))$$
$$= 10^{\ intercept} \times 10^{\ (slope \times (age\ X))}$$

In the same way:

$$Ne\ (age\ X + Y) = 10^{\ intercept} \times 10^{\ (slope \times (age\ X + Y))}$$
$$= 10^{\ intercept} \times 10^{\ slope\ (age\ X)} \times 10^{\ slope \times (Y)}$$

Therefore:

$$Ne\ (age\ X + Y) = Ne\ (age\ Y) \times 10^{\ slope \times (Y)}$$

Consequently, to transform each Ne datum to the corresponding value for a predator of standard age, Neclog, using the logarithmic model, the difference between the predator's actual age and 20 was multiplied by the slope for the particular predator-prey interaction (see Appendix 24). Ten was then taken to the power of this quantity. This value was then either divided into or multiplied by the original Ne, depending upon whether the actual predator age was greater than, or less than, twenty. For example, an original Ne of 4 mosquitos for a Pyrrhosoma individual aged 11 days before emergence, could be transformed to correspond to a Pyrrhosoma individual aged twenty in this way:

$$\underline{Neclog} = 4 \times 10^{\ (0.0161 \times (20\ -\ 11))}$$
$$= 5.58$$

Fresh mean, standard errors and variances in the number of prey eaten at each prey density were then calculated from the Neclog's, (see Appendices 25 and 26) and compared to Nec's calculated from the linear model.

The two types of age-corrections are clearly very similar. Both age-relations are highly significant, and both produce similar relative slope values, for each predator feeding on the two prey types. Application of both age-corrections reduces the mean variance in the number of prey eaten at each prey density. These similarities in the effects of the two different models do not negate the presence of a strong age-relation; they merely indicate that the number of prey eaten by young predators is rather variable, and can be simulated using either age-relation. In fact, when the logarithmic model is applied to the data for *Pyrrhosoma* and *Coenagrion*, the resulting curve is not far from linear, since the range of the values does not extend to many orders of magnitude.

While the linear and logarithmic models provided roughly similar fits to the age-relation data, (see Figures 2.8. and 2.9. and Appendix 24), the mean variance in the corrected number of prey eaten at each prey density was lower using the linear model, in all predator-prey interactions except that of *Coenagrion* eating daphnia (see Tables 2.10. and 2.11. and Appendices 25 and 26). For this reason, the linear model was chosen as a better basis for standardization of the pre-metamorphosis data.

The influence of this age-relation on the functional responses could now be quantified. Fresh means, standard errors, and variances in the number of prey eaten at each prey density, were calculated from the *Nec*'s. The pre-metamorphosis data, corrected for age using the above described linear technique, were then fitted to a Rogers functional response model using the traditional technique (see Section 1.2.). Negative parameters, which resulted in the case of *Coenagrion* eating daphnia, were avoided when data for prey densities 5 and 10 were omitted from the Rogers regression. The resulting *a*'s and *Th*'s, *Nep*'s and measures of significance are listed in Tables 2.10. and 2.11., and displayed in Figures 2.10. and 2.11.

Estimates of *a* and *Th* were also derived from the age-corrected data using the non-linear least squares method, documented in Cock (1977) (see Appendix 21). As these estimates for the functional response parameters did not differ greatly from the estimates derived using the Rogers regression, the latter estimates for *a* and *Th* were used throughout this study.

It is interesting to note that for both logarithmic and linear age-relation models, the slope describing the rate of decline, with age, of Pyrrhosoma predation on daphnia is relatively larger than that for mosquitos, while the reverse is true of Coenagrion. The differences between the slopes (using the linear model) describing the decline in predation by each damselfly on mosquitos, as opposed to daphnia, were tested statistically, as were the differences between the slopes describing the decline in predation on each prey type, by Pyrrhosoma, as opposed to Coenagrion (see Table 2.12.). In all cases, these differences are clearly significant. This fact, combined with the relative values of each damselfly's age-relation slopes for the two prey types, indicate that (while the feeding rates of both predator types on both prey types decline as the damselflies approach emergence), Pyrrhosoma's consumption of daphnia falls significantly more rapidly than its consumption of mosquitos, and Coenagrion's consumption of mosquitos falls significantly more rapidly than its consumption of daphnia. Furthermore, this difference between the two predators in their age-relations on each prey type is also significant. Hence, the initial preferences of Pyrrhosoma for daphnia, and of Coenagrion for mosquitos, are gradually eroded as they approach emergence.

While the elimination of metamorphosing larvae did seem to reduce the variability of the three L. sponsa functional responses, no consistent pre-metamorphosis age-related feeding was manifested by this species. L. sponsa larvae starved for one day appeared to eat more mosquitos but fewer daphnia as they aged. This behaviour reflects the extremely efficient use of the time available for predation necessitated by this species' very short larval life. Their rate of intake of large prey does not appear to be reduced prior to the onset of metamorphosis, and it may be that specialization on these larger, more profitable prey increases during the ultimate instar (Fischer, 1966).

Comparison of Tables 2.10. and 2.11. with Tables 2.6. and 2.7. reveals that, for most prey densities, the variances of the corrected Nec's are slightly lower than those of the original Ne's. Despite the high significance of the age-relations, (see Figures 2.8. and 2.9.) and the reduction in variability which results from correcting the data for age, the fit of the Rogers (1972) model to the data for the weak age relations (i.e. *Pyrrhosoma* eating mosquitos and *Coenagrion* eating daphnia) is not improved by these age-corrections (see Tables 2.6., 2.7., 2.10. and 2.11.). It is possible that predatory behaviour towards these non-preferred prey is more aberrant than behaviour concerning preferred prey. The apparent double hump in the age-corrected response of *Pyrrhosoma* to mosquitos, and the slightly sigmoid shape of *Coenagrion's* response to daphnia, may reflect real threshold - effects, whereby at some critical prey density, these alternate prey types suddenly become more visible, more accessible, less confusing, or in some way become more desirable prey for the particular predator. Alternatively, the age-relations may operate differently at very low prey densities, in these two cases. Application of the age-relations derived from data on the asymptotes of these functional responses could then result in apparently aberrant predation at low prey densities. The regressions determining the functional response parameters for those predator-prey interactions with strong age-relations, (i.e. *Pyrrhosoma* on daphnia and *Coenagrion* on mosquitos) yield greater *F*'s from the corrected than from the uncorrected data. In addition, the significance of these fits is raised by the application of the age-corrections to the raw data. These facts all indicate that, at least for the predator-prey interactions with strong age-relations, the functional responses based on the age-corrected data provide a better fit to the random predator equation (Rogers, 1972), and the *a*'s and *Th*'s thus derived are probably more accurate and reliable estimates, than those calculated from the uncorrected data.

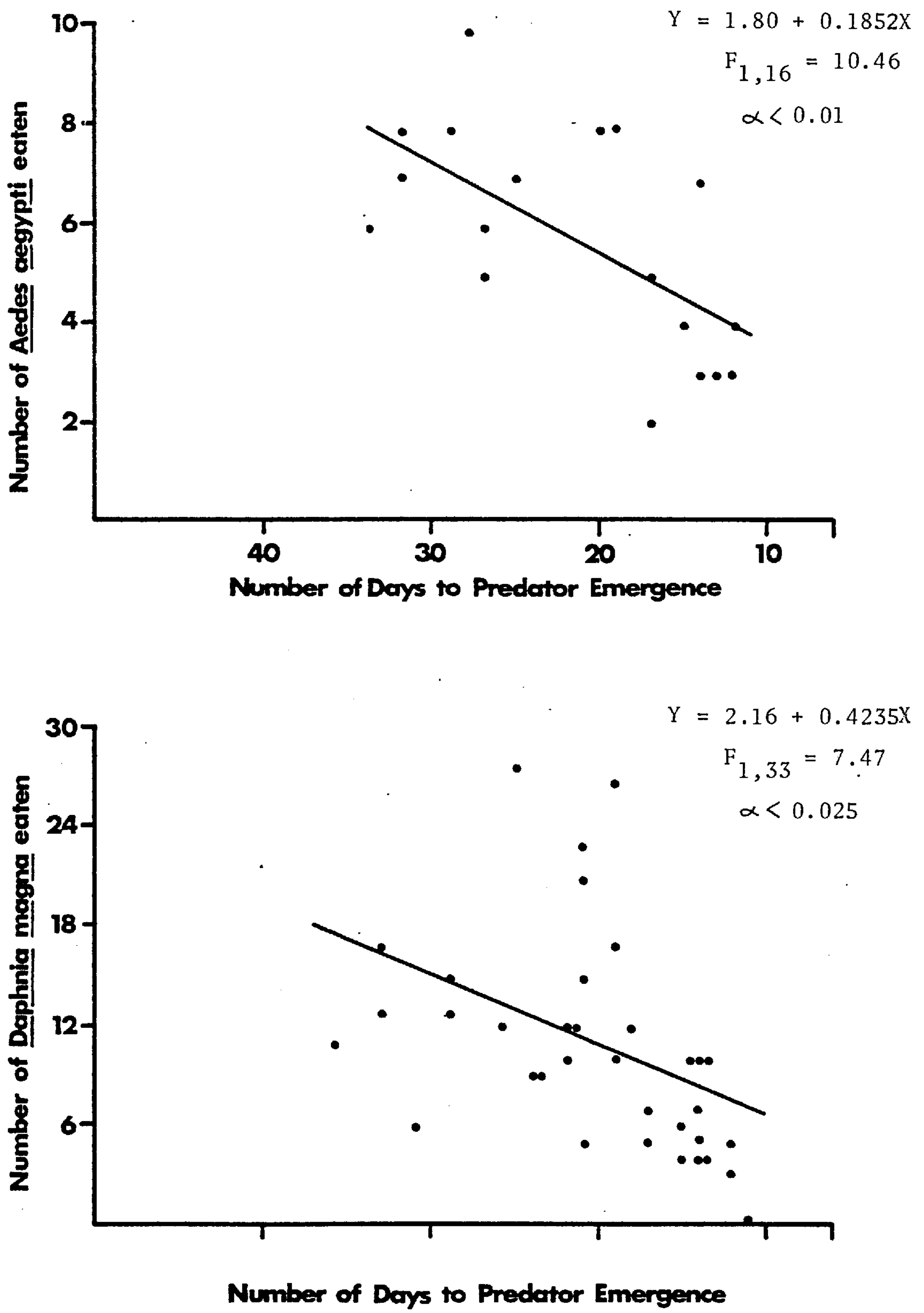
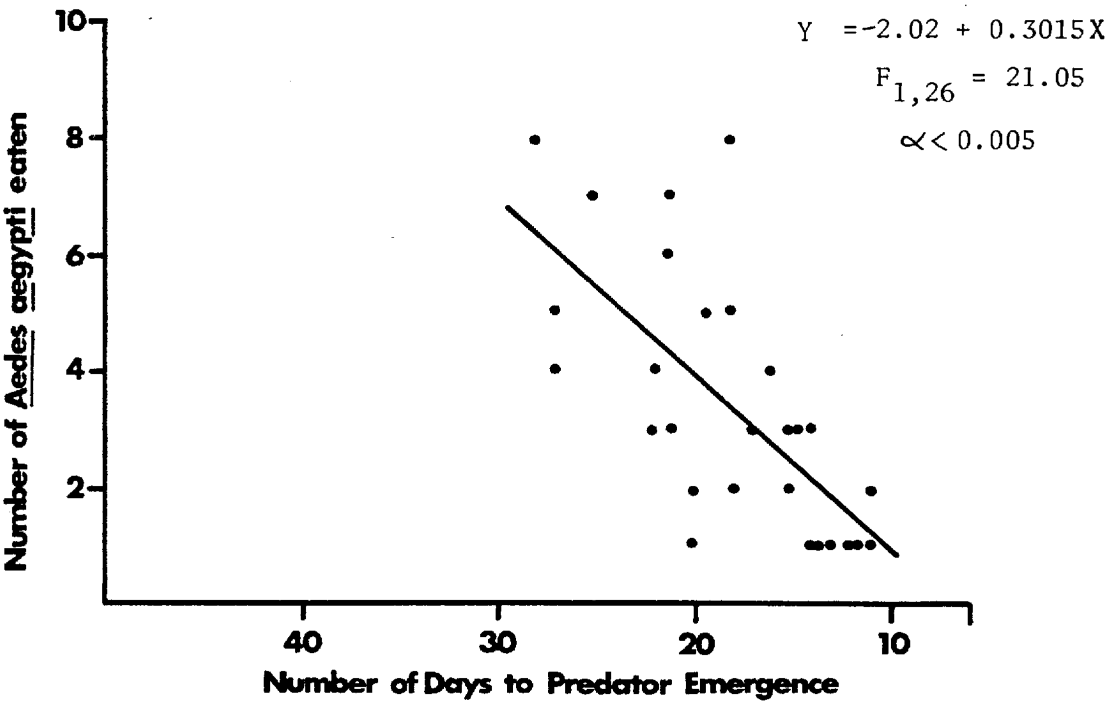


Figure 2.8. - Age-Related Predation: Pyrrhosoma nymphula

Number of Prey eaten vs. Number of Days to Predator Emergence, and the Regression line which best fits this relationship



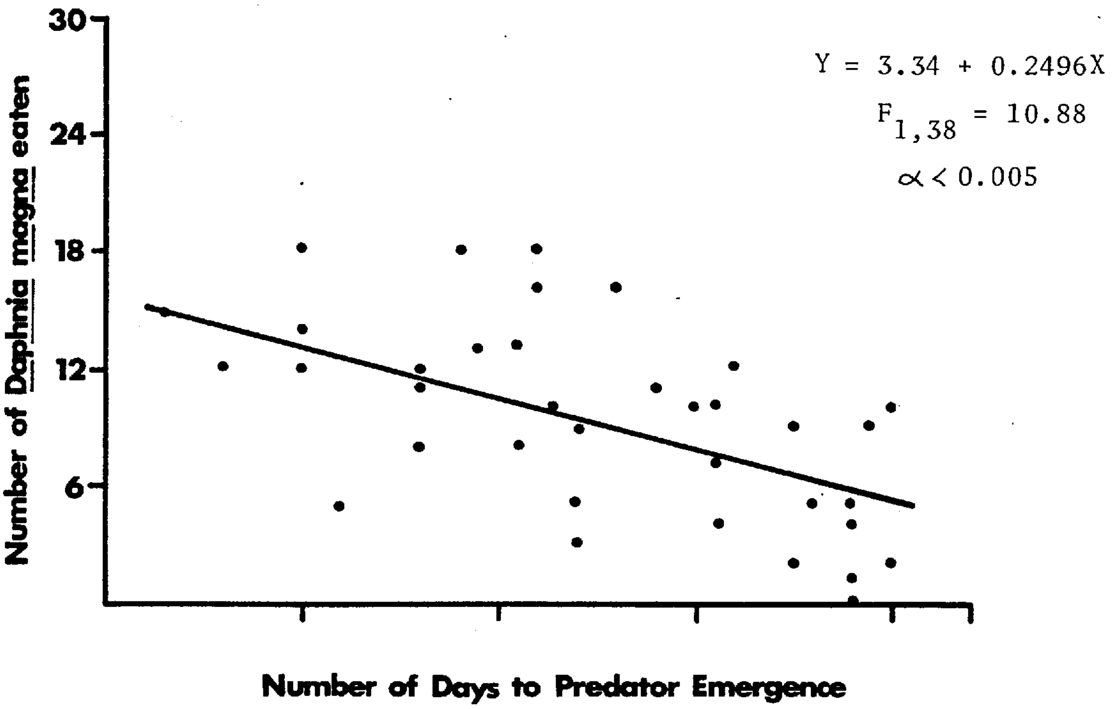
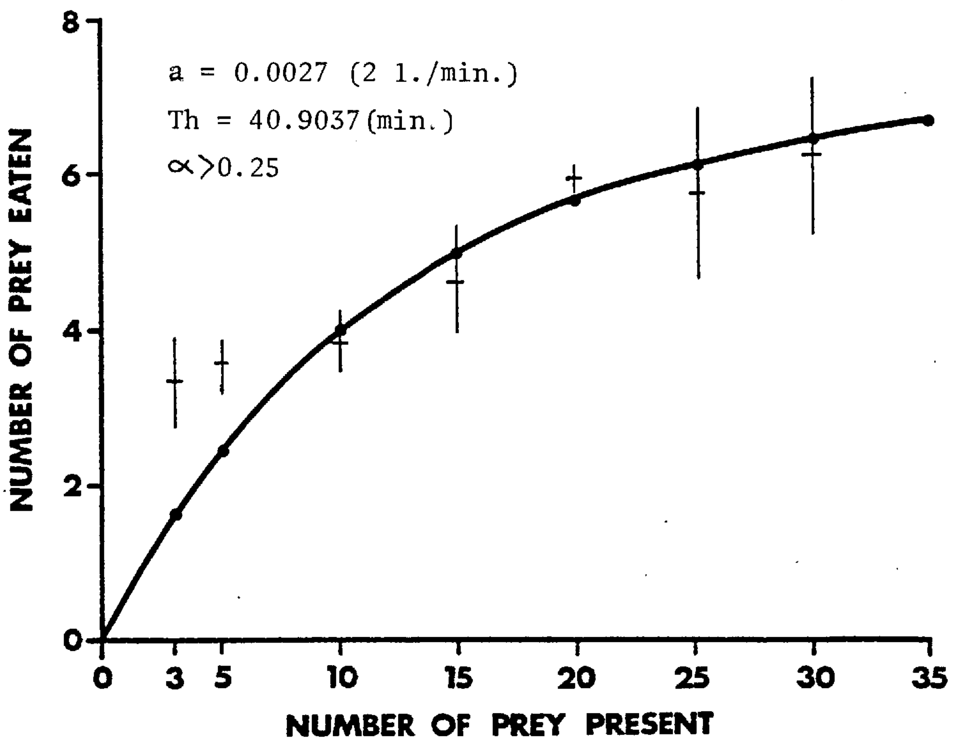


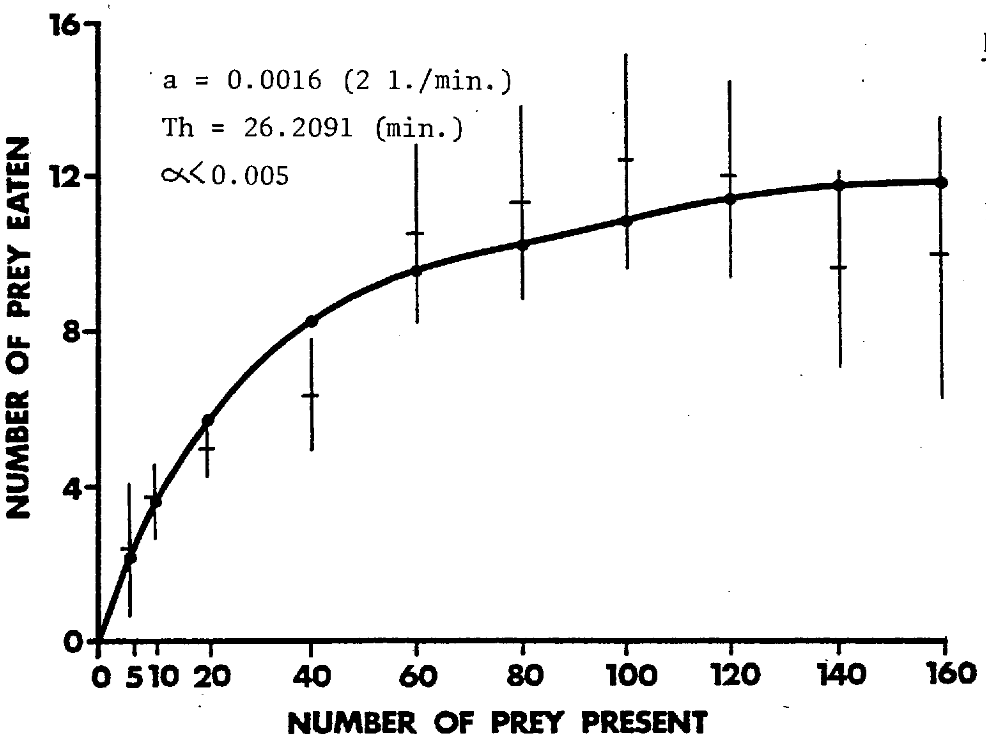
Figure 2.9. - Age-Related Predation: Coenagrion puella

Number of Prey Eaten vs. Number of Days to Predator Emergence, and the Regression line which best fits this relationship

Aedes aegypti



Daphnia magna



┼ : mean ± standard error of age-corrected data

● : predicted curve (from Rogers regression on Ne means

Figure 2.10. - Age-corrected Functional Responses (using linear asymptote corrections) for *Pyrrhosoma nymphula*

Table 2.10. - Functional Responses of *Pyrrhosoma nymphula* (corrected for age)

a) with *Aedes aegypti* as prey

No	3	5	10	15	20	25	30	35
n	3	6	9	8	3	3	4	0
$\bar{x} \pm s_{\bar{x}}$	3.41±0.61	3.65±0.31	3.89±0.37	4.70±0.65	6.06±0.16	5.89±1.15	6.38±0.97	-
s^2	1.12	0.58	1.22	3.39	0.08	3.96	3.78	-
Nep	1.64	2.51	4.07	5.07	5.74	6.21	6.56	6.83

Tt = 360 minutes; a = 0.0027 (2 l./minute); Th = 40.9037 minutes; $F_{1,5}$ = 0.6256; $\alpha > 0.25$;
mean variance = 2.02

Table 2.10. - Functional Responses of *Pyrrhosoma nymphula* (corrected for age) (continued)

b) with *Daphnia magna* as prey

No	5	10	20	40	60
n	3	6	6	5	6
$\bar{x} \pm s_x$	2.32±1.87	3.64±1.00	4.95±0.69	6.38±1.54	10.58± 2.35
s^2	10.45	6.01	2.82	11.79	33.13
Nep	1.95	3.49	5.71	8.24	9.59

Tt = 360 minutes; a = 0.0016 (2 1./minute); Th = 26.2091 minutes; $F_{1,8}$ = 21.5936; $\alpha < 0.005$; mean variance = 27.10

Continued....

Table 2.10. - Functional Responses of *Pyrrhosoma nymphula* (corrected for age) (continued)

b) with *Daphnia magna* as prey (continued)

No	80	100	120	140	160
n	6	6	6	3	3
$\bar{x} \pm s_x$	11.41±2.62	12.49±2.85	12.38±3.06	9.65±2.52	9.98±3.72
s^2	41.21	48.88	56.10	19.02	41.61
Nep	10.41	10.97	11.36	11.66	11.89

Tt = 360 minutes; a = 0.0016 (2 l./minute); Th = 26.2091 minutes; $F_{1,8} = 21.5936$; $\alpha < 0.005$; mean variance = 27.10

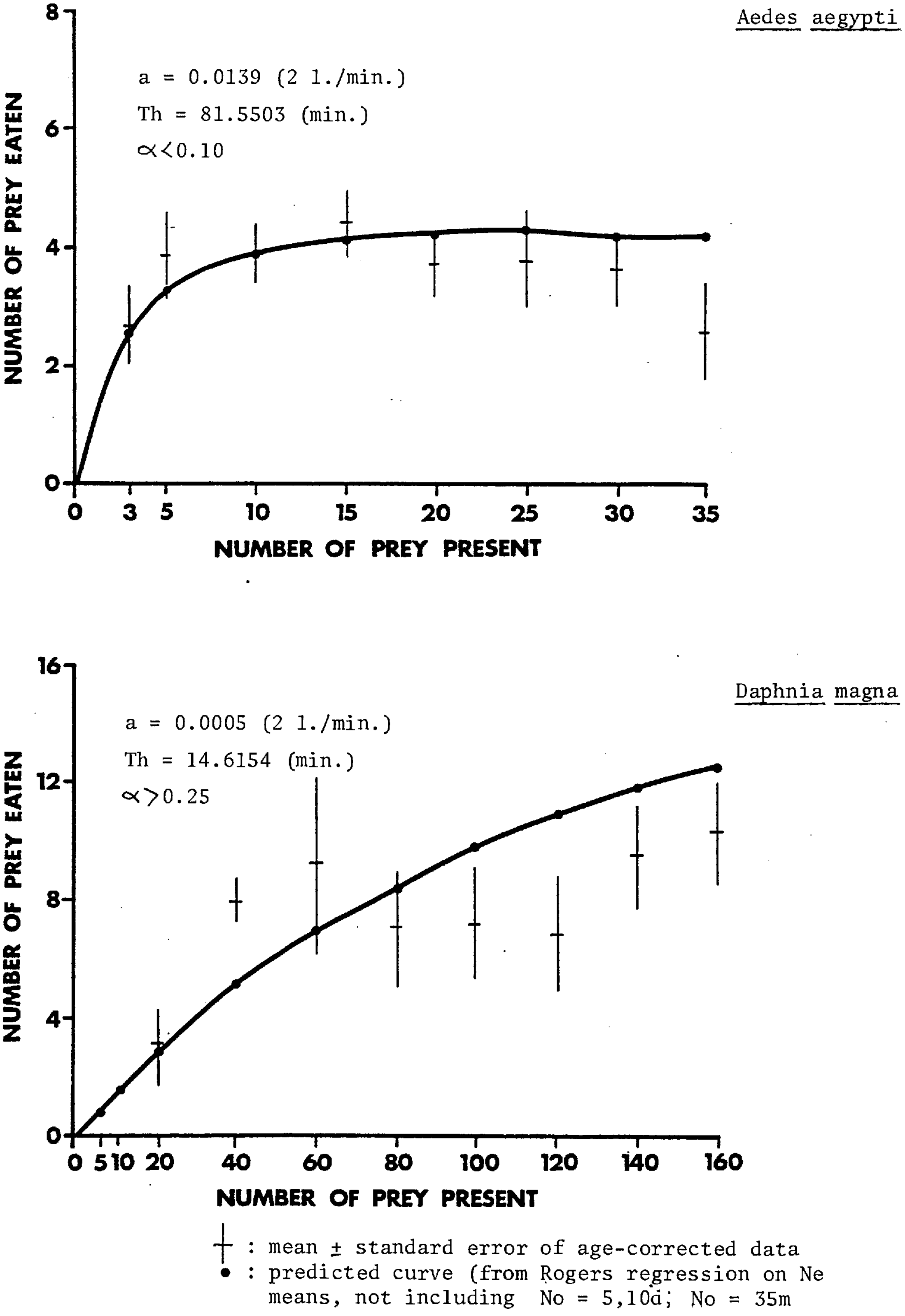


Figure 2.11. - Age-corrected Functional Responses (using linear asymptote correction, (not including No=35)) for *Coenagrion puella*

Table 2.11. - Functional Responses of *Coenagrion puella* (corrected for age)

a) with *Aedes aegypti* as prey

No	3	5	10	15	20	25	30	35
n	4	6	9	10	9	4	5	6
$\bar{x} \pm s_x$	2.71±0.62	3.90±0.77	3.94±0.54	4.45±0.60	3.77±0.55	3.85±0.80	3.68±0.66	2.65±0.81
s^2	1.55	3.55	2.58	3.56	2.73	2.58	2.17	3.91
Nep	2.61	3.41	3.97	4.13	4.21	4.25	4.27	4.30

$T_t = 360$ minutes; $a = 0.0139$ (2 l./minute); $T_h = 81.5503$ minutes; $F_{1,5} = 4.9124$; $\alpha < 0.10$;
mean variance = 2.83

Table 2.11. - Functional Responses of Coenagrion puella (corrected for age)

(continued)

b) with Daphnia magna as prey

No	5	10	20	40	60
n	4	6	6	7	6
$\bar{x} \pm s_x$	-0.49±1.36	-0.99±0.82	3.09±1.42	8.07±0.87	9.33±3.05
s^2	7.36	4.08	12.12	5.32	55.67
Nep	0.75	1.47	2.78	5.02	6.87

Tt = 360 minutes; a = 0.0005 (2 l./minute); Th = 14.6154 minutes; $F_{1,6}$ = 0.4001; $\alpha > 0.25$;
mean variance = 18.18

Continued....

Table 2.11. - Functional Responses of Coenagrion puella (corrected for age) (continued)

b) with Daphnia magna as prey (continued)

No	80	100	120	140	160
n	7	6	4	5	5
$\bar{x} \pm s_x$	7.07±1.92	7.25±1.88	6.88±2.10	9.65±1.81	10.40±1.81
s^2	25.77	21.15	17.63	16.42	16.30
Nep	8.40	9.71	10.82	11.78	12.62

Tt = 360 minutes; a = 0.0005 (2 l./minute); Th = 14.6154 minutes; $F_{1,6} = 0.4001$; $\alpha > 0.25$;
mean variance = 18.18

Table 2.12. - Tests for Differences Between the Slopes of the Age-Relations

To determine the significance of differences between the slopes of two linear regressions (of y_1 on x_1, and y_2 on x_2):

$$t_{(n_1+n_2-4)} = \sqrt{\frac{\Sigma y_1^2 - \dfrac{(\Sigma x_1y_1)^2}{\Sigma x_1^2} + \Sigma y_2^2 - \dfrac{(\Sigma x_2y_2)^2}{\Sigma x_2^2}}{n_1 + n_2 - 4}}$$

is compared to: $t_{(n_1+n_2-4,\alpha)}$ (Sokal and Rolph, 1969)

For the age-relations described in Figures 2.8. and 2.9.:

age relation / linear regression	*Pyrrhosoma nymphula* eating *Aedes aegypti*	*Pyrrhosoma nymphula* eating *Daphnia magna*	*Coenagrion puella* eating *Aedes aegypti*	*Coenagrion puella* eating *Daphnia magna*
n	18	35	28	40
Σy^2	688	5535	462	4913
Σxy	2422	8312	1932	11146
Σx^2	9325	16002	9798	30745
$(\Sigma xy)^2/\Sigma x^2$	629.0707	4317.5443	380.9577	4040.7649
t	5.1038	1.8256	5.4252	3.6917

and: $t_{(29, \alpha = 0.05)} = 1.65$; $t_{(29, \alpha = 0.005)} = 2.58$; therefore, the difference between the slopes of the two age-relations on mosquitos is significant at the 5% level, and the three other contrasts are significantly different at the 0.5% level.

2.2.3. Effect of Photoperiod and Artificial Light Source during Experimentation and Training Period

Damselfly larvae undergoing training or experimentation, were exposed to a photoperiod of 8 light: 16 dark hours, because this light regime had been found to delay or prevent metamorphosis in a number of Odonata species (see Section 2.2.1.). The light conditions in this experimental arrangement were unnatural in many ways: variation in light intensity and direction at dawn and dusk were ignored, and the intensity and wavelength of the light produced by the fluorescent tubes differed from that of the sun; nevertheless, such a photoperiod did roughly mimic winter light conditions in southern England. (At Ascot's approximate latitude, $51^{\circ}.20^{\circ}$N, the sun was up for 7 hours 56 minutes on December 21, 1977 (Delury, 1977).)

Functional response experiments reported in the recent past on Odonata and other invertebrates feeding on *Daphnia* species (i.e. Thompson, 1975) have been conducted entirely in the dark, in order to reduce the variance in numbers of prey eaten resulting from the clumping of the prey around light foci. While interpretable results have been obtained many times from illuminated feeding experiments on damselflies, using *Daphnia* as prey (Lawton, 1970a and 1971b; Lawton, Beddington and Bonser, 1974; Johnson, Akre and Crowley, 1975), this source of variation was considered as one possible cause for the masking of a type 2 functional response by excessive variability in the numbers of prey eaten.

Theoretical investigations, based upon the Pythagorean theorem, and simple physical principles, were undertaken. If the distance between the fluorescent tubes = D, and the distance between the tubes and the water surface = L, then, considering the effect of 6 fluorescent tubes on a point X beneath them, and assuming that these tubes can be treated as strip point sources, continuous along their length, the maximum variation in light intensity can be found by solving the expression:

$$\frac{1}{L^2 + \left(\frac{5D}{2} + X\right)^2} + \frac{1}{L^2 + \left(\frac{3D}{2} + X\right)^2} + \frac{1}{L^2 + \left(\frac{D}{2} + X\right)^2}$$

$$+ \frac{1}{L^2 + \left(\frac{D}{2} - X\right)^2} + \frac{1}{L^2 + \left(\frac{3D}{2} - X\right)^2} + \frac{1}{L^2 + \left(\frac{5D}{2} - X\right)^2}$$

for constant L and D, and for maximum X. (The variation in light intensity is an inverse function of the square of the distance travelled from the light source, in this case the hypotenuse of a right-angle triangle.) In this case, with D = 11.2 cm, and L = 72 cm, the difference between the solutions for X = 0, and X = 28 cm, is 5.4226 - 4.9094 = 0.5123, representing a variation of only 10% of the maximum light intensity (5.4226).

Measurements of variation in actual light intensity over the volume of water in the experimental arenas were made, with the aid of a photo-diode (R.S. component No. 305-462) mounted in a special waterproof casing, and connected to a sensitive current amplifier, giving a voltage output proportional to the light intensity of the photodiode. Two series of measurements were made; the first, with the photo-diode held vertically in the centre of the bucket at the 1 l. water level, 3 cm. above the bottom of the bucket (see Plate 2.3.), recorded the relative light intensity at eight equidistant angular positions around the 360° of the compass: the second, with the photo-diode held horizontally (see Plate 2.4.) recorded the light intensity at the water's surface, and in an upward, downward, and two sideways-facing positions, again at the 1 l. water level. Results are presented in Figure 2.12. Taking the maximum variation in relative light intensity around the points of the compass as a fraction of the light intensity at the water surface, we find that this figure is less than 5%. This reduction in the variation in light intensity from the theoretical figure of 10% can be attributed to 1) the theoretical assumption of strip point light sources, when the fluorescent tubes actually emit light from a broad band, and 2) the fact that a bucket would not normally be placed in a position where both minimum and maximum light intensity would be received.

Considering both the theoretical and actual calculations described above, it seems highly unlikely that such minor variations in light intensity could result in variation in prey behaviour sufficient to cause the poor fit of the data to the Rogers model.

Plate 2.3. Experimental Apparatus for light intensity measurements: with photo-diode held vertically in the centre of the bucket at the 1 l. water level, 3 cm. above the bottom of the bucket

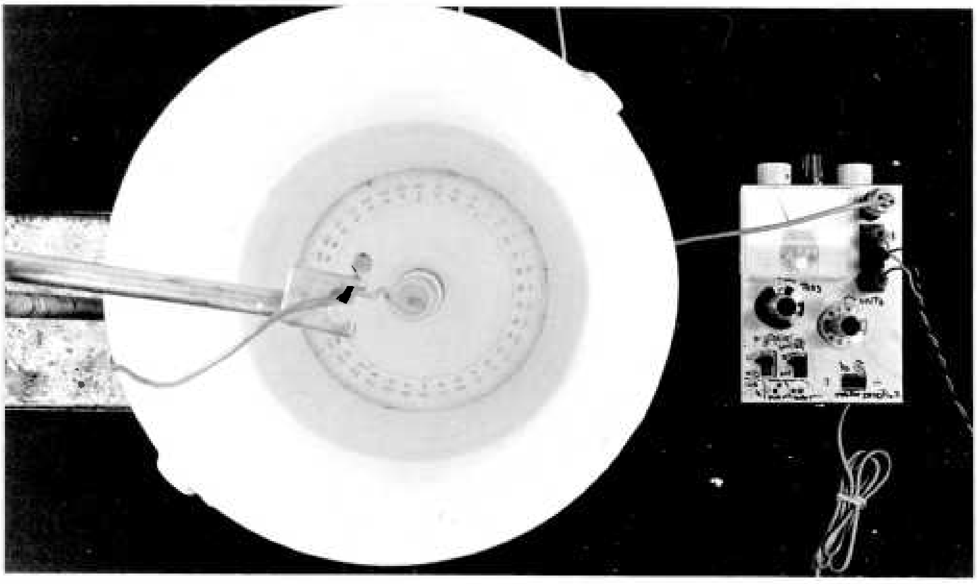


Plate 2.4. Experimental Apparatus for light intensity measurements: with photo-diode held horizontally in the centre of the bucket at the 1 l. water level, 3 cm. above the bottom of the bucket

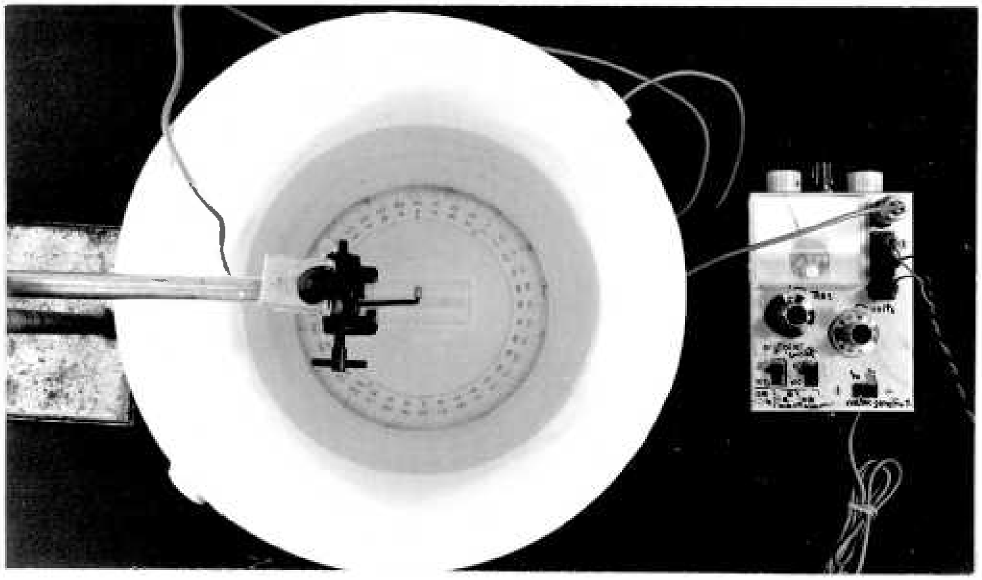
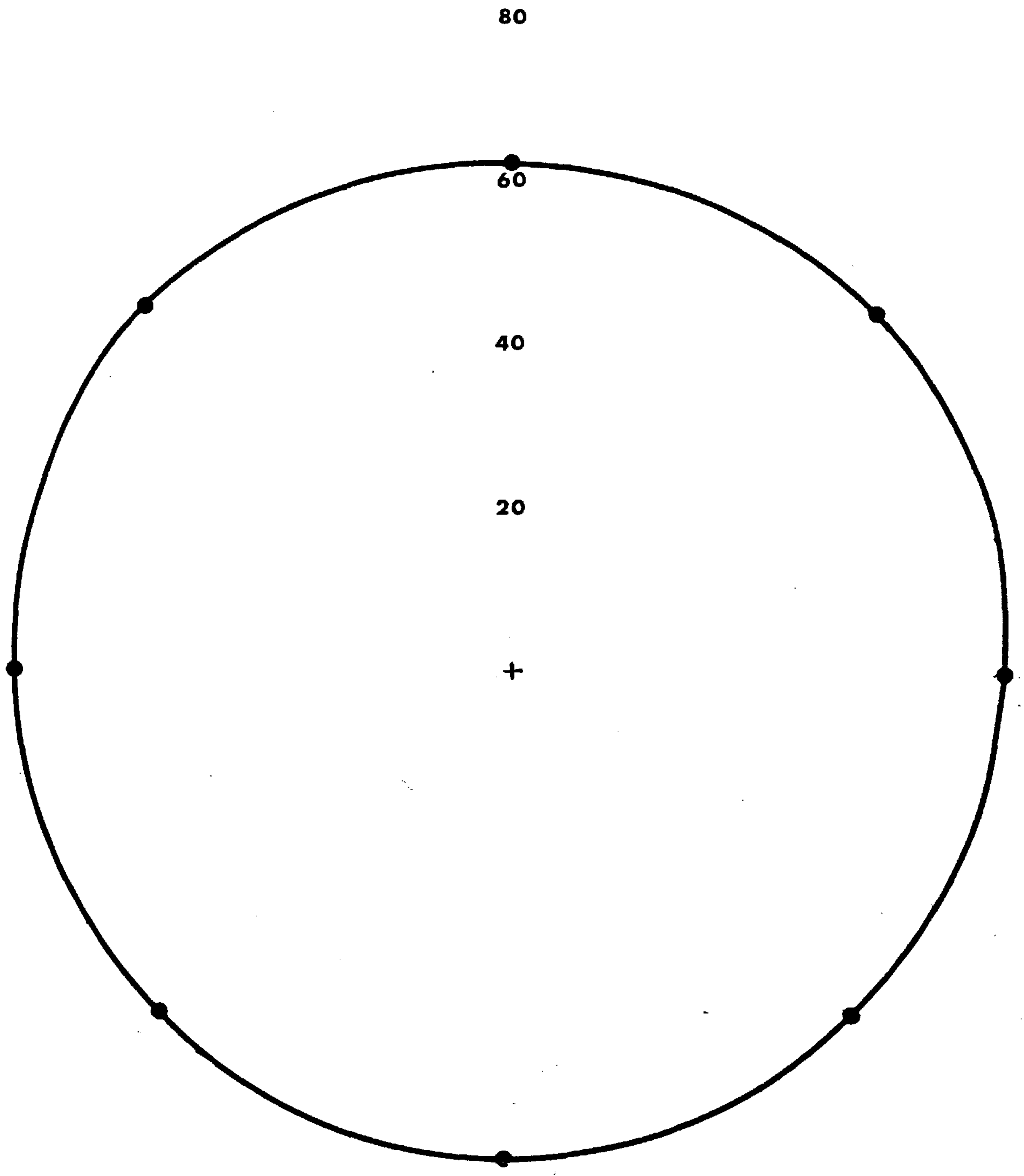


Figure 2.12. - Variation in Light Intensity 3 cm. above the Center of the experimental arena



Light intensity at water
surface = 92.5

At 3 cm. above the center
of the experimental arena:
light intensity facing up = 91.0
light intensity facing down = 53.4
average intensity tothe side = 56.6

2.2.4. Prey Distribution and its possible effect on Predator Feeding Behaviour

Behavioural experiments on Aedes aegypti and Daphnia magna indicate that both these species are negatively phototropic; they tend to aggregate in the area of their container which is farthest from the light source (Bates, 1949; Christophers, 1960; Clarke, 1930; Nayar and Sauerman, 1970; Rimet, 1967; Spooner, 1933). Clarke (1930) found that the vast majority of lab-reared D. magna tended to aggregate near the bottom of their tank, although dimming of the overhead light did induce them to clump temporarily near the water surface. He attributed this behaviour to a combination of negative phototropism and positive geotropism. Nayar and Sauerman (1970) found that under normal rearing conditions, A. aegypti larvae formed one or two tight aggregations in the corners of the rearing pan. They deduced that this behaviour was a photonegative response, since no such clumps were present under dark conditions. In a review of the literature on this subject, Christophers (1960) recorded similar observations, and also noted that the aggregations of A. aegypti can appear to be rather diffuse, since the larvae are forced to rise to the surface periodically, to breathe. In addition, Christophers (1960) remarked that photonegative behaviour may become more pronounced in the later larval instars of A. aegypti.

Since no detailed information on the exact distribution patterns of A. aegypti and D. magna could be found in the literature, a series of observations was made on each of these species. To render the results of these experiments relevant to the functional response experiments, the conditions described in Section 2.2.3. were reproduced as closely as possible, for these observations on prey distribution. The more distant overhead banks of fluorescent tubes in the environmental room were covered with opaque plastic, which resulted in a light source very similar to diffuse overhead light used in the functional response work.

Six glass chromatography tanks were filled with four litres each of dechlorinated water, and one of 10, 20, or 30 ultimate instar larvae of A. aegypti, or 20, 40, or 80 large individuals of D. magna was added to each tank (see Plate 2.5.). This resulted in prey densities comparable to 5, 10, and 15 mosquito larvae, and 10, 20, and 40 daphnia, per 2 litres of water: the arena size used in the functional response experiments. To provide a precise and accurate record of the distribution of each of these prey over time, a series of photographs was taken of the six tanks. After an initial period of acclimatization, a picture was taken of each tank, and then this cycle was repeated twelve times, so that the observations covered a period of more than an hour. The negatives were mounted as slides and projected against a trace of the tank, which was divided into nine cells, one each in the top, middle, and bottom rows, and the left, middle and right columns.

The counts of animals in each cell are listed in Appendix 27. Unfortunately, the total of the daphnia counts in all the cells is not always equal to the total daphnia density, since some individuals must have been too translucent to appear clearly in the photograph. If it can be assumed that this phenomenon was equally possible in each of the nine cells, then the distribution of the observed daphnia will accurately reflect the overall distribution of the total number of daphnia.

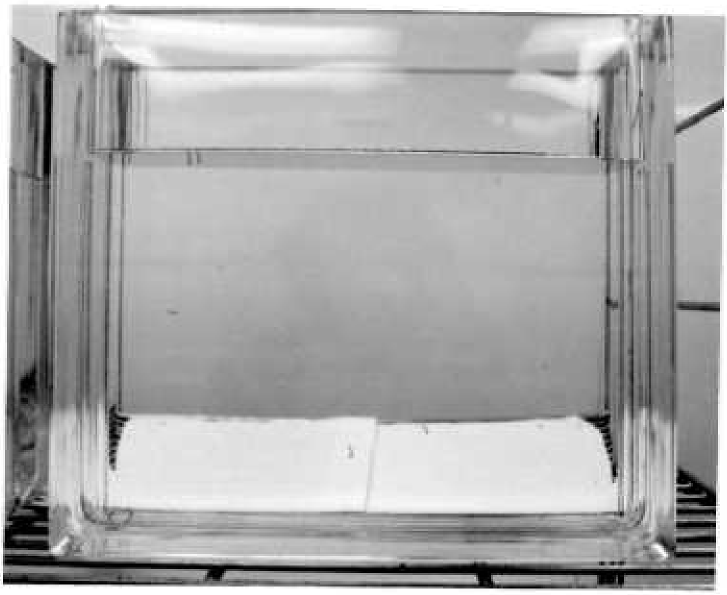
The null hypothesis that prey distribution was independent of locality in the tank, was tested using the heterogeneity G-test (Sokal and Rohlf, 1969), with the expected frequency of animals in each cell equal to the total number of daphnia divided by nine. To achieve expected frequencies close to 5, as required by this test, the data from four replicates were lumped for the tank with ten mosquitos, and in all other cases, the data from two replicates were lumped. The resulting statistics are listed in Appendix 27.

The highly significant G's, for all the tests, indicate that the observed prey distributions, though differing significantly from replicate to replicate, are clearly not independent of locality in the tank, and the null hypothesis must be rejected. For each prey density, the mean prey counts in each cell (see Appendix 27) illustrate the actual prey distribution. In all cases, the prey seem to aggregate in the bottom corners of the tank. *A. aegypti* larvae are present in other areas of the tank (particularily directly above their aggregation) far more than are *D. magna* individuals, presumably because they are in transit to or from the water surface, where they must breathe. These results conform to those observed in the field (J.K. Nayar, personal communication), whereby *A. aegypti* larvae tend to aggregate in the shade, occasionally clustering at the surface edges.

The effect of such prey aggregations on damselfly predatory behaviour may now be surmised. The clumped prey distribution may have 1) effectively reduced the proportion of prey available to the predator; 2) effectively increased the proportion of prey available to the predator; or 3) caused both of these effects, intermittently. The predominant damselfly perch site during the functional response experiments was on the lower part of the twig, near to the bottom edge of the bucket (personal observation). This location clearly coincides with the area of prey aggregation, excluding the possibility that prey availability was effectively reduced. The significant heterogeneity of the prey distribution in the replicates for each prey density, indicates that the prey clumps were not static, and moved from corner to corner in the bottom of the tanks. Similar behaviour in the functional response arenas would result in the prey clumps coinciding with the predator position for part of the time only. Hence prey availability would not be uniformly increased, either. The third alternative, that the effective proportion of prey available to the predator was sometimes higher than, and sometimes lower than, the expected average must be accepted. It is likely that this variability would average out over the six-hour duration of the functional response experiments, since the prey clumps moved about significantly in the hour that prey distribution was recorded. Therefore, prey aggregation probably did not contribute to the variability of the damselfly functional responses.

In conclusion, both prey types were found to aggregate at the bottom corners of the containers, but this is unlikely to have resulted in differential availability of the prey in different replicates of the functional response experiments. Furthermore, although the behaviour of A. aegypti appears to be less light-dependent than that of D. magna, the predator-prey interactions for which the Rogers model (Rogers, 1972) provided the poorest fit were not consistently those using daphnia as prey (Figures 2.10. and 2.11., Tables 2.10. and 2.11.). Since the possible clumping of D. magna during the feeding experiment did not prevent the resulting data for Pyrrhosoma nymphula from providing a significant fit to the Rogers model, it seems rather unlikely that this factor is the cause of the unusual functional responses on mosquitos.

Plate 2.5. Experimental Apparatus for measurements on Prey Distribution



2.2.5. Effect of Starvation Time Prior to Experimentation

Experiments were conducted on Lestes sponsa in 1974 and 1975, in order to determine the effects on this species of varying the starvation time prior to functional response experimentation. The experimental procedure was exactly as described in Section 2.1.2., except that in 1974, the damselflies were starved for only one day before experimentation, and the series of mosquito densities used was slightly different from that used subsequently. A total of 67 L. sponsa individuals were observed for 14952 and 5376 hours, with mosquitos and daphnia respectively as prey. (See Appendices 22 to 26). The results of these experiments are presented in Figures 2.4. and 2.7., and Tables 2.5. and 2.8.

Comparison of data for 24 hours starvation prior to experimentation with data for 48 hours starvation prior to experimentation reveals that longer starvation substantially reduces the variance, but may also somewhat reduce the mean of the number of prey eaten. An F test comparing the unweighted mean variance in numbers of mosquitos eaten with one vs. two days of pre-experimental starvation:

$$F_{(n1,\ n2)} = \frac{\text{mean } s1^2}{\text{mean } s2^2}, \qquad n1 = \sum_i (ni - 1), \ ni = n \text{ at prey density } i$$

yields $\alpha \leqslant 0.01$ for both the raw data, and the data for only those predators which were more than six days from emergence at the time of the experiment. This significantly increased variability in predator feeding behaviour after one day of starvation is probably a consequence of non-uniformity of gut fullness at this time, resulting in variable hunger in the predator individuals. Starved damselflies were observed to defecate almost invariably within 48 hours of prey deprivation. Such individuals will all have empty guts, and their hunger and hence their prey intake can be expected to be more uniform than for less starved predators. The possible reduction in prey intake resulting from increased predator starvation may be unique to short-lived damselfly species such as L. sponsa. The extreme growth efficiency necessitated by the brief larval life of this species results in voracious larval feeding in the field (Fischer, 1966 and 1967). Their extreme adaptation to frequent feeding and efficient energy conversion, probably mean that these damselflies have empty guts only very rarely, in their natural environment (Fischer, 1967). Such a condition may result in some confusion, weakening, and reduced predatory success, which may then lead to a reduced prey intake. Rather similar effects have been observed by E. Eveleigh (personal communication) in immatures of the mite *Phytoseiulus persimilis* (Athias-Henriot), when feeding on the spider mite *Tetranychus pacificus* (McGregor). In this species, individuals appear to become prey-shy after prolonged starvation, with the result that their prey intake is reduced.

The two day starvation period used in the four principle functional response experiments is shown above (for a similar-sized species of damselfly), to result in lower variances in the numbers of prey eaten than does a shorter starvation time. Thus, it is rather unlikely that inappropriate starvation time prior to experimentation resulted in such high predator variability that conventional predator feeding behaviour on mosquitos was masked.

2.2.6. Effect of Arena Size During Experimentation

The possible effects of arena size on predatory intake have not been examined in great detail in the past. Holling (1966) made a thorough study of the distance of reaction in the preying mantid Hierodula crassa (Giglio Tos). He also noted (Holling, 1961) that very high densities of prey could result in reduced predatory intake, as observed by Welty (1958) in goldfish feeding on Daphnia, and by Morris (personal communication to Holling) in a pentatomid bug Podisus maculiventris (Say) feeding on fall-webworm larvae Hyphantria cunea (Drury). Such confusion effects are far more likely, in smaller arenas in which high prey densities can easily be attained. Hokyo and Kawauchi (1975) working on the bug Podisus maculiventris (Say) feeding on Spodoptera litura larvae, also observed that the predator's attack rate appeared to be greater, and the handling time smaller, in experiments conducted in larger vessels, with comparable numbers of available prey. In other words, more prey were eaten at lower prey densities, in the larger vessels. Pruszynski (1973/4) found that the prey intake of the mite Phytoseiulus persimilis (Athias-Henriot) feeding on the spider mite Tetranchus urticae (Koch) was greatest, at a given prey density per square cm., on leaf discs with the greatest diameter.

These studies all imply that larger arena sizes could lead to a higher prey consumption. However, they do not relate arena size to the variance in numbers of prey eaten by the experimental predators. Practical work was undertaken, in an attempt to relate the experimental arena size to the variability in prey intake. During the spring of 1978, a series of functional response experiments was conducted. Replicates of experiments at five prey densities were tested in three different arenas (all of a similar cylindrical shape): a 150 ml. beaker containing 100 ml. water; a plastic jar containing 1 l. of water; and a plastic bucket containing 2 l. of water. A total of 263 successful experiments were completed (many of them concurrently). All the experimental arenas were roughtly cylindrical in shape, and during experimentation, all were supplied with a twig (or, in the case of the beaker, a cocktail stick) as a perch site.

Experiments proceeded in a manner very similar to that described in Section 2.1.2., except that the photoperiod used was 10 light: 14 dark hours. Since the experimental arenas were farther from the fluorescent tubes than those described in Section 2.2.3., precautions were taken to ensure that the light was non-directional and diffuse. (For discussion of this, see Section 2.2.4.). Opaque plastic sheets were attached to the glass under the bank of fluorescent tubes, producing a diffuse light source.

Ultimate instar larvae of Enallagma boreale (Selys), collected from the Albion Hills Conservation Area pond at 43^{o} 55' North, 79^{o} 50' West, were used as the experimental predators. E. boreale is a common, robust, northern species frequenting a wide variety of habitat types in Canada. It emerges early in the spring, in late May (in Southern Ontario), and is abundant as an adult until mid-June. Larval life probably lasts one or two years, depending on prey abundance, and the duration of the warm season. When present, this species is often the most common Zygopteran inhabitant of the particular area, (Walker, 1953). Large Daphnia magna cultured from laboratory stock, and sorted in the way described in Section 2.2.1., were used as the experimental prey.

As in the previous experiments, a Kolmogorov-Smirnov test was applied to the mean number of prey eaten by each sex, at each prey density in each arena. The results of these tests are listed in Appendix 15. In no case was the sex of the damselfly found to have a significant effect on the number of prey eaten. Hence data for both sexes were pooled. Zero data were then examined, to determine whether any of the individual damselflies ate consistently few prey, or any of the experimental replicates were affected by the imminent emergence of the predator. As a result of this examination of the data, all the experimental replicates involving one individual which consistently ate few prey, and three of the replicates involving an individual which subsequently died, were omitted from the analysis. The only zero data remaining were from experiments in the 2 l. arena, and involved individuals which were neither close to emergence, or moult, nor abnormal in their predation in other replicates. Consequently these data were retained.

The above investigation revealed no strong pre-metamorphosis effects on feeding. In addition, any age-correction would have to be applied independently to the experimental replicates for each arena, and the direct comparison of the results for each arena size would not be possible. For these reasons, the statistical analysis and the estimation of the functional response parameters were based on the raw experimental data. The functional response parameters for the Rogers (1972) model were estimated using the linear regression technique described in Section 1.2.

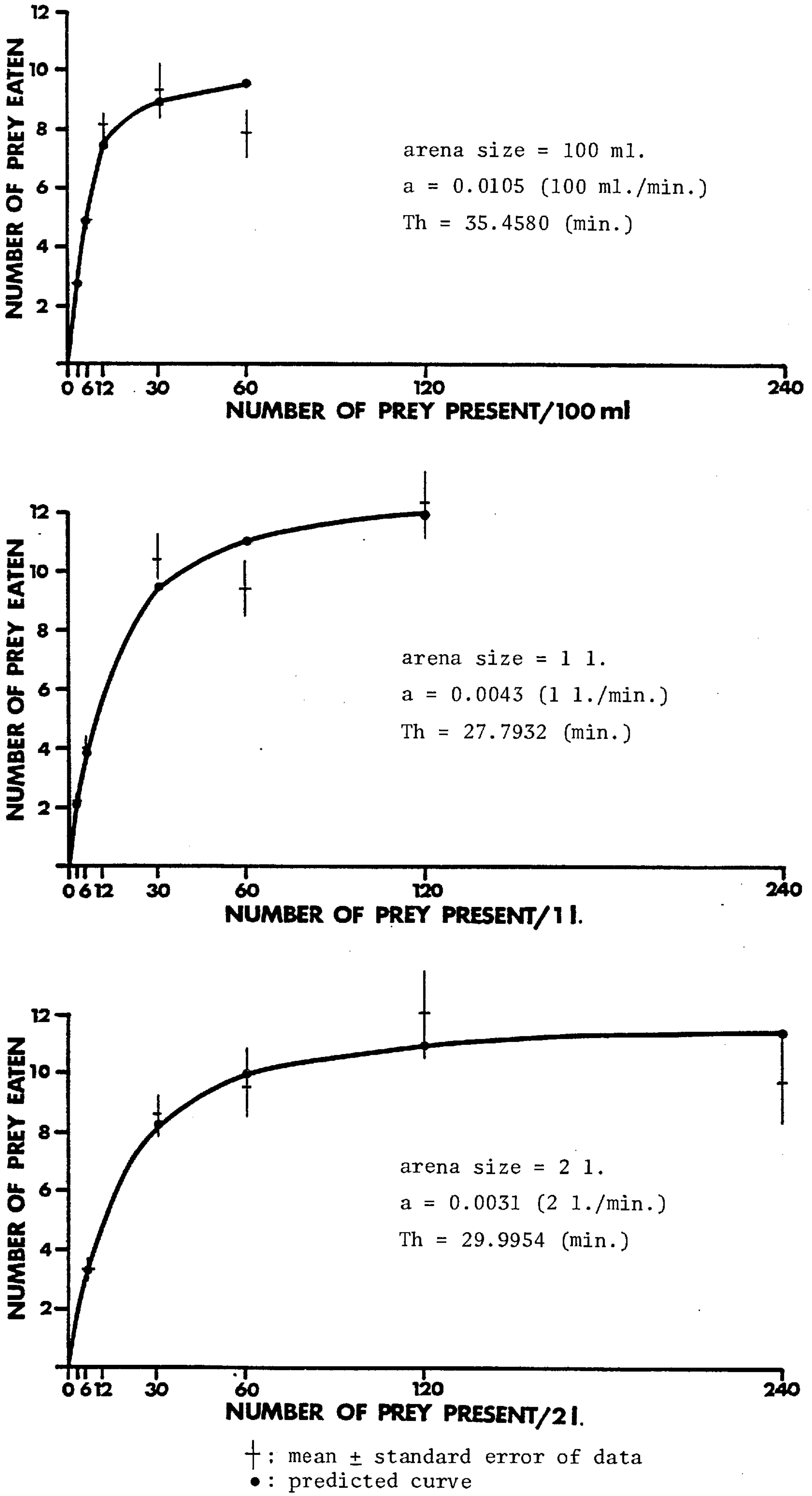
Information on the individual damselflies used, and the data from the experimental replicates are tested in Appendices 28-31. Table 2.13. summarizes the results of these experiments, and Figures 2.13. and 2.14. present these results graphically, in the first case using abscissas of prey numbers and in the second case using abscissas of prey density/2 l. water. Table 2.14. presents a comparison of the means and variances of the number of prey eaten in each arena size; basing this comparison first on prey numbers, and then on prey density/2 l. water.

Figures 2.13. and 2.14., and Tables 2.13. and 2.14. all indicate that arena size strongly affects both the mean and the variance of the number of prey eaten. When the data for each arena size are compared in terms of the absolute prey density per 2 l. water, it is obvious that more prey are consumed in the larger containers than in the 100 ml. container. This trend is expressed in the parameters of the functional response model, estimated from the data for each arena size. Although the handling time does not very greatly between the three series of experiments, the attack rate (when compared in equivalent units) clearly increases with increasing arena size. Nevertheless, the slightly lower handling time for the 1 l. arena size does result in highest prey consumption in this container, when high prey densities/2 l. water are compared.

The variance of the data increases, too, with increasing arena size, for comparable absolute prey densities/ 2 l. water. This increase in variance was found to be significant at the 1% level, when the mean variance for 1 l. and 100 ml. (for absolute prey densities of 60, 120, and 240 prey/2 l. water) were compared using the F test $(20.81/2.73 \gg F_{0.01,\ 13,\ 17})$.

Comparison of the variances in the age-corrected number of prey eaten by Pyrrhosoma and Coenagrion with those for the Enallagma boreale at Daphnia magna densities of 60 and 120 in a 2 l. arena, reveals roughly similar figures (see Tables 2.10., 2.11., and 2.13.), while the variances in number of prey eaten in the 100 ml. arena are much closer to Thompson's (1975) results, in which a 75 ml. arena was used. Such small experimental arenas render clumped prey distributions like those described in Section 2.2.4. much less likely, and this is probably the main reason for the relatively uniform functional response data produced by these experiments.

This dependence of the variance of the functional response data on arena size, is probably responsible, at least in part, for the high functional response variances found in the experiments with Pyrrhosoma and Coenagrion where arena size was 2 l. While this variability renders statistical analysis of the functional response data more difficult, there is little doubt that it is a realistic reflection of field feeding behaviour. The natural feeding habitats of these predators are obviously not limited to the 2 l. or even smaller arenas used in predation experiments.



arena size = 100 ml.
a = 0.0105 (100 ml./min.)
Th = 35.4580 (min.)

arena size = 1 l.
a = 0.0043 (1 l./min.)
Th = 27.7932 (min.)

arena size = 2 l.
a = 0.0031 (2 l./min.)
Th = 29.9954 (min.)

┼ : mean ± standard error of data
● : predicted curve

Figure 2.13. - Functional Responses of *Enallagma boreale* to *Daphnia magna* in Arenas of Different Sizes

Table 2.13. - Functional Responses of *Enallagma boreale* to *Daphnia magna*

a) in a 100 ml. arena

No	3	6	12	30	60
n	18	22	20	20	19
$\bar{x} \pm s_x$	2.83±0.09	5.00±0.29	8.35±0.56	9.50±0.96	7.95±0.94
s^2	0.15	1.81	6.24	18.47	16.94
Nep	2.81	5.09	7.52	9.17	9.68

Tt = 360 minutes ; a = 0.0105 (100 ml./minute); Th = 35.4580 minutes; $F_{1,3}$ = 15.80; $\alpha < 0.05$; mean variance = 8.72

Table 2.13. - Functional Responses of *Enallagma boreale* to *Daphnia magna* (continued)

b) in a 1 l. arena

No	3	6	30	60	120
n	18	15	16	14	14
$\bar{x} \pm s_x$	2.22±0.19	3.93±0.45	10.50±1.11	9.50±1.12	12.57±1.34
s^2	0.65	3.07	19.60	17.65	25.19
Nep	2.18	3.96	9.70	11.23	12.07

Tt = 360 minutes; a = 0.0043 (1 l./minute); Th = 27.7932 minutes; $F_{1,3} = 40.04$; $\alpha < 0.01$; mean variance = 13.23

Table 2.13. - Functional Responses of *Enallagma boreale* to *Daphnia magna* (continued)

c) in a 2 1. arena

No	6	30	60	120	240
n	20	16	18	15	18
$\bar{x} \pm s_x$	3.40±0.36	8.69±0.88	9.67±1.23	12.20±1.58	9.78±1.57
s^2	2.57	12.36	27.29	37.31	44.18
Nep	3.31	8.42	10.02	10.96	11.47

Tt = 360 minutes; a = 0.0031 (2 1./minute); Th = 29.9954 minutes; $F_{1,3}$ = 22.97; $\alpha <$ 0.025; mean variance = 24.74

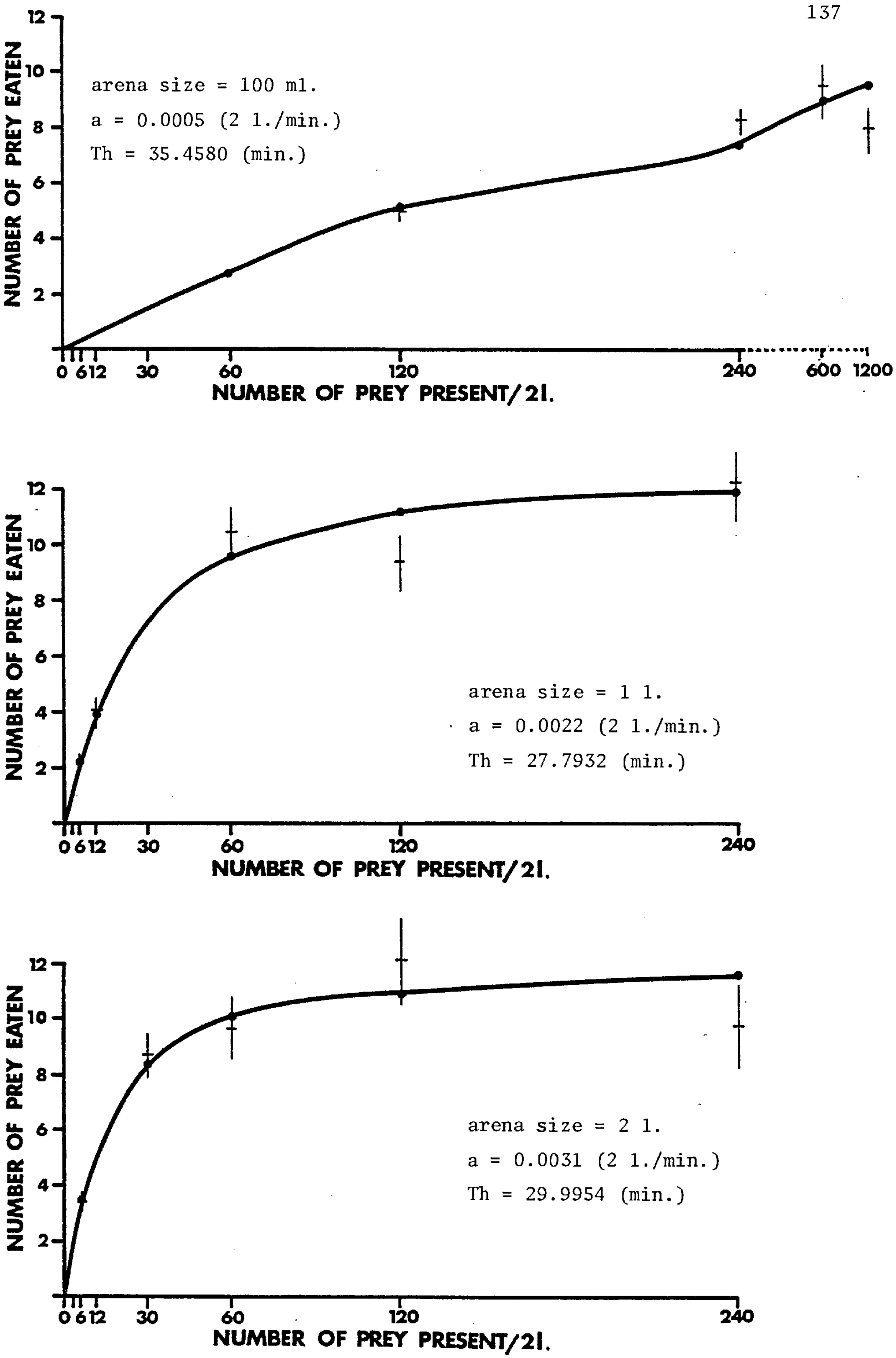


Figure 2.14. - Functional Responses of Enallagma boreale to Daphnia magna: Different Arena Sizes Compared Using the Same Units

Table 2.14. - The Effects of Arena Size on the Mean and Variance of the Number of *Daphnia magna* eaten by *Enallagma boreale*

statistic / arena size / comparison	mean			variance		
	100 ml.	1 l.	2 l.	100 ml.	1 l.	2 l.
a) prey numbers:						
3	2.83	2.22		0.15	0.65	
6	5.00	3.93	3.40	1.81	3.07	2.57
12	8.35			6.24		
30	9.50	10.50	8.69	18.47	19.60	12.36
60	7.95	9.50	9.67	16.94	17.65	27.29
120		12.57	12.20		25.19	37.31
240			9.78			44.18
mean of values for 6, 30 and 60	7.48	7.98	7.25	12.41	13.44	14.07
b) prey density/ 2 l.						
6		2.22	3.40		0.65	2.57
12		3.93			3.07	
30			8.69			12.36
60	2.83	10.50	9.67	0.15	19.60	72.29
120	5.00	9.50	12.20	1.81	17.65	37.31
240	8.35	12.57	9.78	6.24	25.19	44.18
600	9.50			18.47		
1200	7.95			16.94		
mean of values for 60, 120 and 240	5.39	10.86	10.55	2.73	20.81	36.26

2.2.7. Individual Characteristics and Pre-experimental Conditioning

While great effort was made to control both the predator and the prey individuals used in the feeding experiments, and the training regime and experimental conditions, it was considered possible that residual variability in the number of prey eaten could still have masked actual type 2 functional responses in the experiments on *Pyrrhosoma* and *Coenagrion* eating mosquitos. The relatively low number of experimental replicates might have led to an unrealistically high estimate of the actual variability in prey intake. Alternatively, individual differences in the predatory appetites caused by differing field experiences or possibly genetic makeup might have added to the predatory variability. Such effects have been noted by Wellington (1957) and Partridge (1976).

The variances in the age-corrected numbers of mosquitos and daphnia eaten by each predator from densities of 5, 10 and 20 prey (see Tables 2.10. and 2.11.), were compared, to determine whether the damselflies were more variable when mosquitos were offered as prey. In all cases, the variance in numbers of mosquitos eaten is considerably lower than the comparable variance in numbers of daphnia eaten at the same prey density. Assuming that there is an equal probability ($=\frac{1}{2}$) that: the variance in numbers of mosquitos either does, or does not exceed that for daphnia at the same prey density and, lumping the data for *Pyrrhosoma* and *Coenagrion*, the application of a binomial test yields a probability of: $\binom{6}{5}\frac{1}{2}^{6} = 0.093$. Despite the influence of the higher mean numbers of daphnia eaten at these prey densities, it is still highly unlikely that spurious variability in numbers of mosquitos eaten actually exceeds that for numbers of daphnia eaten. Consequently, the relatively low variances in numbers of mosquitos eaten are not likely to mask conventional predator behaviour, when the higher variances in numbers of daphnia eaten (by *Pyrrhosoma*, at least)still do not prevent a good fit to the Rogers (1972) model.

Similarly, the number of replicates for the functional response experiments on mosquitos (particularly at the directly comparable prey densities of 5 and 10, where the responses of both Pyrrhosoma and Coenagrion are rather irregular) is usually as large, or larger than the comparable number of replicates for the experiments on daphnia. The average number of (pre-metamorphosis) replicates per prey density on mosquitos and daphnia are 5.14 and 5.00 for Pyrrhosoma, and 6.63 and 5.60 for Coenagrion. In view of the fact that the age-corrected functional responses of Pyrrhosoma to daphnia are successfully fitted by the Rogers model, while the comparable, but on average better replicated mosquito curves are not, it seems unlikely that dearth of replicates is responsible for the poor fit of the Rogers model to the mosquito data.

Another factor possibly influencing functional response variability was examined. The pre-metamorphosis data, corrected for age, (Figures 2.10. and 2.11.) may have incorporated some spurious variability resulting from differing long-term appetites in the damselfly predators. It is possible that during early larval life spent in the field, each predator might have become accustomed to a certain rate of prey intake, and this conditioned appetite level might possibly have been retained in the laboratory. This would result in consistently high or low numbers of prey eaten for particular predator individuals. All the experimental data for individual predators which ate extremely high numbers of prey were examined in detail, to determine whether large prey intake was a consistent characteristic of these damselflies. In all cases involving Pyrrhosoma and Coenagrion (see Appendices 11-14), the intake of these predators was low, or average, in the other experimental trials in which they were used (although a similar examination resulted in discarding the data for two Enallagma boreale individuals).

A final test of predator standardization was undertaken. For each predator-prey interaction, the data on the adult dry weights of each predator were related to the age-corrected number of prey eaten, (Appendices 5 to 8, and 11 to 14) using the correlation coefficient *r*. (See Appendix 32). In very few cases was *r* significant at the 5% level, and hence variation in predator weight could not be considered to influence prey intake.

2.2.8. Summary, and Assessment of Damselfly Predatory Variability

The previous Sections 2.2.1. to 2.2.7. have been devoted to examining the effects of a series of factors on damselfly predatory behaviour. Many of the experimental conditions and damselfly characteristics were found to have pronounced effects on the shape and the variability of the functional responses.

The age of the damselfly, within the ultimate instar, clearly has a strong influence on the number of prey that are eaten. Elimination of all data for Pyrrhosoma and Coenagrion individuals within ten days of emergence increased the mean number of prey eaten and significantly reduced the variability of the functional response data (except in the case of Coenagrion eating mosquitos, where the reduction in variance was almost significant). The remaining pre-metamorphosis data was still strongly dependent on predator age; for each predator-prey interaction, the data were significantly fitted by a linear regression relating the decline in the number of prey eaten to damselfly age. Application of age-corrections based on these relationships further reduced the variability in the functional response data. Summing the effects of metamorphosis, and pre-metamorphosis age on damselfly predation, it can be seen that recently-moulted ultimate instar larvae experince a steady gradual decline in their feeding on each prey type, until, a week or two before they emerge, the onset of metamorphosis physically hinders predation, at which point their feeding drops to a minimal level or may even cease altogether.

Practical and theoretical investigations into the light intensity and distribution in the experimental arenas were conducted, but these factors seemed to be sufficiently uniform to have little effect on predator or prey behaviour. The distributions of both prey types was also examined. They were found to be strongly clumped, in the same areas of the arena that were usually occupied by the experimental predators, but the continual movement of the prey clumps was deemed sufficient to prevent differential prey availability in the different functional response replicates.

The duration of damselfly starvation prior to the functional response experiments was found to strongly influence predation by L. sponsa. A two day starvation period resulted in lower functional response variability than a one day starvation period did, presumably because more uniform gut clearance was ensured by the longer period. Arena size also was an important influence on functional response variability. Large arenas resulted in more variable damselfly functional responses, and also, generally, in higher prey intake. No consistent general differences in appetite between non-specific damselfly individuals could be found.

The above summary makes very clear the importance of rigorous controls on the experimental conditions and predators. Functional response data is obviously very sensitive to changes in the predator's age, hunger, and the experimental arena size. But these independent effects are complicated by the interactions of several factors, to produce even stronger influences on damselfly behaviour. These predators not only eat fewer prey as they age; their intake of different prey types declines at different rates. In this way, age affects the proportions of different prey which will be eaten, as well as the numbers. Light distribution and prey distribution are also interdependent. The review of the literature in Section 2.2.4. made it clear that concentrated directional light sources produce more pronounced prey clumps than do diffuse, non-directional light sources. A more subtle interaction exists between prey distribution and arena size. Small arenas render prey clumps less likely, and result in more uniform predator consumption.

These subtle, complex interactions further complicate analysis of functional response data. Firm control on all these factors must be maintained, in order to produce more uniform, regular functional responses. Yet every additional control removes the experimental situation further from the natural one. In all cases, the conditions producing more variable predator behaviour are those which are more likely in the field: non-synchronous age distribution within the ultimate instar; frequent feeding, large feeding habitats, directional, non-diffuse light, all these things are usual in the ponds inhabited by damselfly larvae. It is unfortunate that the increasing rigour and sophistication of laboratory experiments seems to give them less and less relevance to the natural behaviour of the experimental subjects.

The series of controls imposed on the experimental predators, the experimental conditions, and, finally, the analysis of the experimental data still did not succeed in producing the uniform, regular type 2 functional responses expected. Elimination of the data for metamorphosing predators, and correction of the remaining data for pre-metamorphosis predator age, did reduce the variability in the functional response data, and, for the two predator-prey interactions with pronounced age-relations, the fit of the Rogers (1972) model to the data was considerably improved. However, this was not the case for the functional responses for _Pyrrhosoma_ eating mosquitos and _Coenagrion_ eating daphnia. These curves remained irregular, though no more variable (in fact the reverse) than the other two, successfully modelled, functional responses. The possibility that the variation in the Rogers equation parameters themselves could be responsible for these rather aberrant functional responses is investigated in the following Section 2.3.

2.3. The Effect of Prey Density on Parameters of the Damselfly Functional Response

2.3.1. Observations and Discussion

A preliminary hypothesis that variability in attack rate or handling time could have been responsible for the rather unusual damselfly functional responses, prompted the following observations, during the spring of 1976. The actual attack rates, handling times, and activity levels of both predator species were measured over the first two hours of each six hour experimental trial, for three mosquito densities.

The experimental routine was exactly the same as that described in Section 2.1.2., except that more data were tabulated for the first two hours of each experiment. Three predators were observed at a time, feeding on five, ten, and fifteen mosquitos respectively. The time in seconds of each successful capture, unsuccessful capture, unattempted capture, completion of feeding movements, and perch change was recorded, for each predator. An automatic UNIDEC printing counter, produced by English Numbering Machines, and with ancillary electronics designed and constructed by A.C. Easty, was used to tabulate observations (see Appendix 33). The keyboard for this device is displayed in Plate 2.2.

All functional response parameters were measured for each individual prey capture, rather than being averaged over the whole experimental period, as is usual when these parameters are estimated mathematically. Handling time, Th, was estimated as the period between the time of a successful capture, and the completion of feeding movements following that capture. The search time preceding each capture, Ts, was estimated as the period between completion of the previous feeding movements (or the start of the experiment, in the case of the first capture), and the next successful capture. An empirical attack rate for each prey capture, a, was estimated using the formula:

$$a = \frac{1}{(\mathrm{No}-\mathrm{Ne}) \qquad \mathrm{Ts}} \quad .$$

This was derived from the disc equation formula (Section 1.2.);

$$Ne = No\ a\ \text{total}\ Ts$$

where total Ts refers to the total amount of time spent searching throughout the experiment.

By re-arranging:

$$a = \frac{Ne}{No\ \ \text{total}\ Ts}$$

dividing the numerator and the denominator by Ne:

$$a = \frac{1}{No\ \ \ Ts}$$

where Ts now refers to the search time prior to one prey capture only, and adjusting to incorporate exploitation effects:

$$a = \frac{1}{(No-Ne)\ \ \ Ts}$$

While this estimate of a will tend to be slightly biased when prey exploitation is high and (No-Ne) is low (C. Kent, personal communication), most of the measurements reported here were made at relatively low levels of prey exploitation, and hence this formula was considered to be an adequate estimate for a. Estimated attack rates, a, and mean handling times, Th, are displayed in Figure 2.15.

The raw data and summaries of two-way analysis of variance carried out on the data are listed in Appendix 34. Mann-Whitney tests were carried out, to compare the attack rates and handling times of different prey densities. Details of the results are listed in Appendix 15. Coenagrion's attack rate was found to be significantly lower at No = 10 than at either No = 5 or No = 15. Pyrrhosoma's handling time was found to be lower at No = 5 than at No = 15, at a significance level of $\alpha = 0.095$. Furthermore, an analysis of variance on the importance of prey density and number of prey eaten as factors affecting the damselflies' attack rates and handling times revealed that Pyrrhosoma's attack rate is significantly affected by prey density.

Data on predator activity were analyzed in terms of the mean number of perch changes between one successful capture (or the start of the experiment) and the next successful capture, and the mean interval between these perch changes, when they occurred. These data are presented in Figures 2.16. and 2.17., and the raw activity data, and multiple regressions of these two measures on No and Ne are listed in Appendix 35. For both predator species, activity tends to increase with increasing prey density. This trend is significant for *Pyrrhosoma*, but not quite $(0.10 > \alpha > 0.05)$ for *Coenagrion*. In addition, *Pyrrhosoma* becomes significantly more active, as more prey are eaten. This increased activity may be partially responsible for the significant decline in *Pyrrhosoma*'s handling time at high prey densities. More frequent perch changes could curtail the time spent in handling each prey item. Greater reactive distance, and hence attack rate, may be another consequence of *Pyrrhosoma*'s increased activity at high prey densities, but this is clearly not the case for *Coenagrion*. For this damselfly, the more frequent perch changes at high prey densities are accompanied by a reduction in the attack rate, suggesting that confusion may account for the increased activity, and declining success of this predator at high prey densities.

Data on unattempted captures, ua, and unsuccessful captures, us, were incorporated into general measures of strike success, ss, and capture success, cs. Strike success was defined as the fraction of successful strikes, Ne', over attempted strikes, $Ne' + us$, during the two hour observation period:

$$ss = \frac{Ne'}{Ne' + us} \quad .$$

Capture success was defined as the fraction of successful captures, Ne', over possible captures, Ne' and $us + ua$, during the two hour observation period:

$$cs = \frac{Ne'}{Ne' + us + ua} \quad .$$

Mean strike success and capture success at each prey density are presented in Figure 2.18. The raw data, and linear regressions relating these measures to prey density, for each predator species, are listed in Appendix 36. Both *Pyrrhosoma* and *Coenagrion* appear to be slightly more successful at low prey densities, although this relationship is not significant in either case.

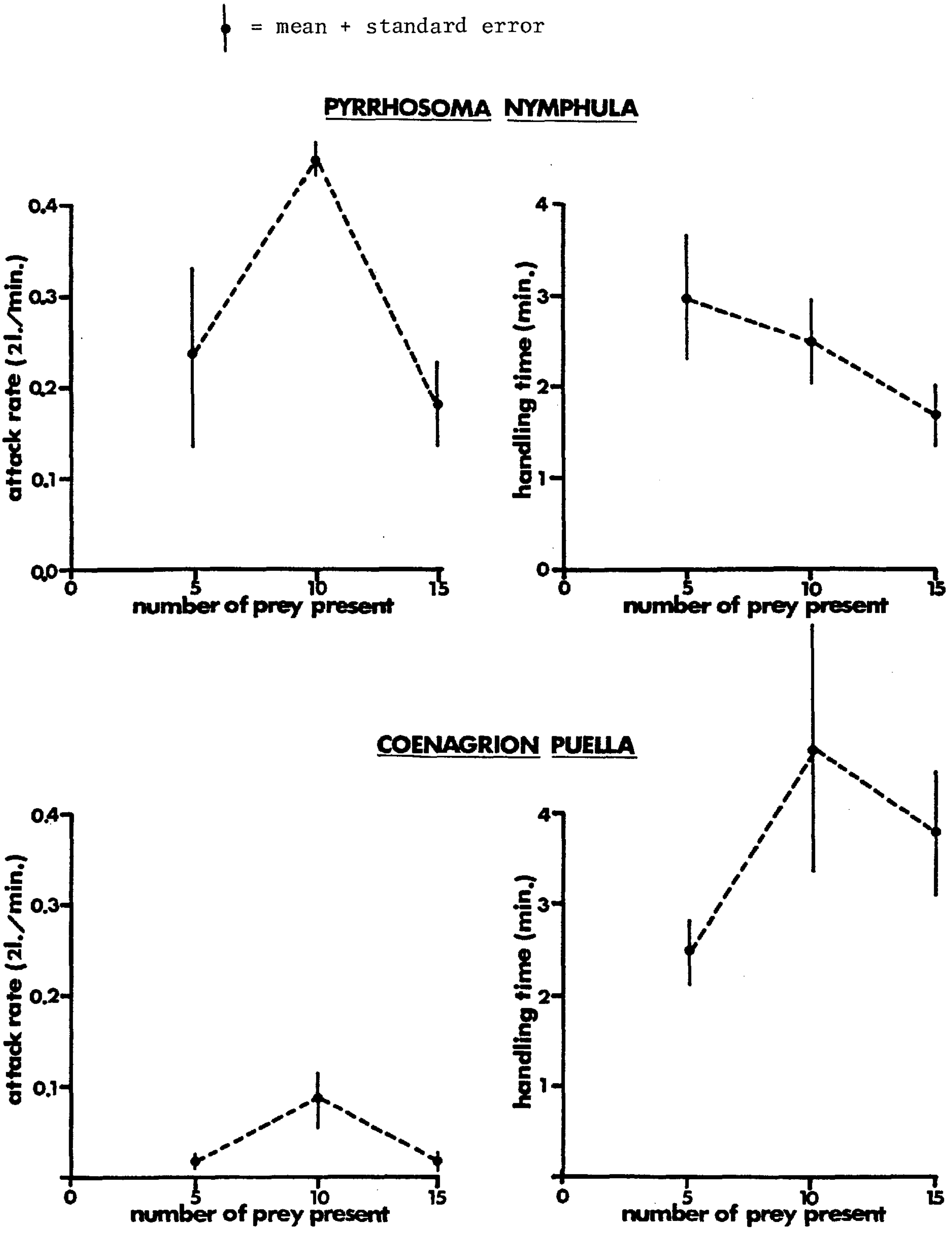
The behaviour of the predators observed in this study is obviously affected by changes in satiation and prey density. Although the number of replicates used in the sit and watch experiments was low, there is clear evidence, for both predators, that $\underline{a}$ and $\underline{Th}$ are altered by changes in $\underline{No}$, and, to a much lesser extent, by changes in $\underline{Ne}$. It is recognized that the relationships between the variables measured above are not necessarily linear. Nevertheless, the linear regression provides a quick and easy measure of the direction and strength of these interactions. The two predator species react in markedly different ways to these changes. In brief, Pyrrhosoma becomes a more successful predator on mosquitos as their density increases, whereas Coenagrion becomes less successful. Paul Giller, observing Notonecta glauca (L.) and Notonecta maculata predatory behaviour in relatively large arenas (over 1 l.) also found that their handling times and intercatch times (a variable inversely related to attack rate) varied with prey density, and with the number of prey that had already been eaten (P. Giller, personal communication).

When examined in the light of the simulations discussed in Section 2.3.2., the results of the sit and watch experiments do correspond to the patterns of the actual functional responses depicted in Figures 2.10. and 2.11. At high prey densities, handling time appears to set a limit on the number of prey which can be consumed, in a given period of time, and the effect of a decrease in handling time at high prey densities is to increase the number of prey eaten. (See Figures 2.20. and 2.23.). Hence, the gradual but significant decline in Pyrrhosoma's handling time with prey density could easily result in the double hump apparent in Figure 2.10. In the case of Coenagrion, the simultaneous rises in both attack rate and handling time between prey densities 5 and 10, and declines in both parameters between prey densities 10 and 15 would tend to cancel each other out (see Figures 2.22. and 2.23.). However, the decline in attack rate may continue at prey densities higher than 15 causing the visible reduction in the number of prey eaten at these high prey densities (Figure 2.11.).

In an attempt to determine which of the sub-components of a and Th was responsible for the age-related changes in predation discussed in Section 2.2.2.c), checks were run on the sit and watch data for each predator feeding on mosquitos. Appendix 37 lists the results of fitting linear regressions to the relations between attack rate, handling time, capture success, strike success, and activity and predator age. None of: attack rate, handling time, capture success nor strike success is significantly related to age, for either damselfly.

Although the overall numbers of prey eaten during the sit and watch experiments could be corrected for the effect of predator age, the behavioural variables under observation could not be. The interactions between predator age and capture success, strike success, activity, and the observed attack rate and handling time were neither pronounced enough nor consistent enough to merit correction of the data presented earlier in this section. In all cases, experiments were randomized with respect to the individual predators used, and hence predator age is unlikely to have biased the results of the sit and watch experiments.

Figure 2.15. - Observed Functional Response Parameters (averaged over the first two captures)



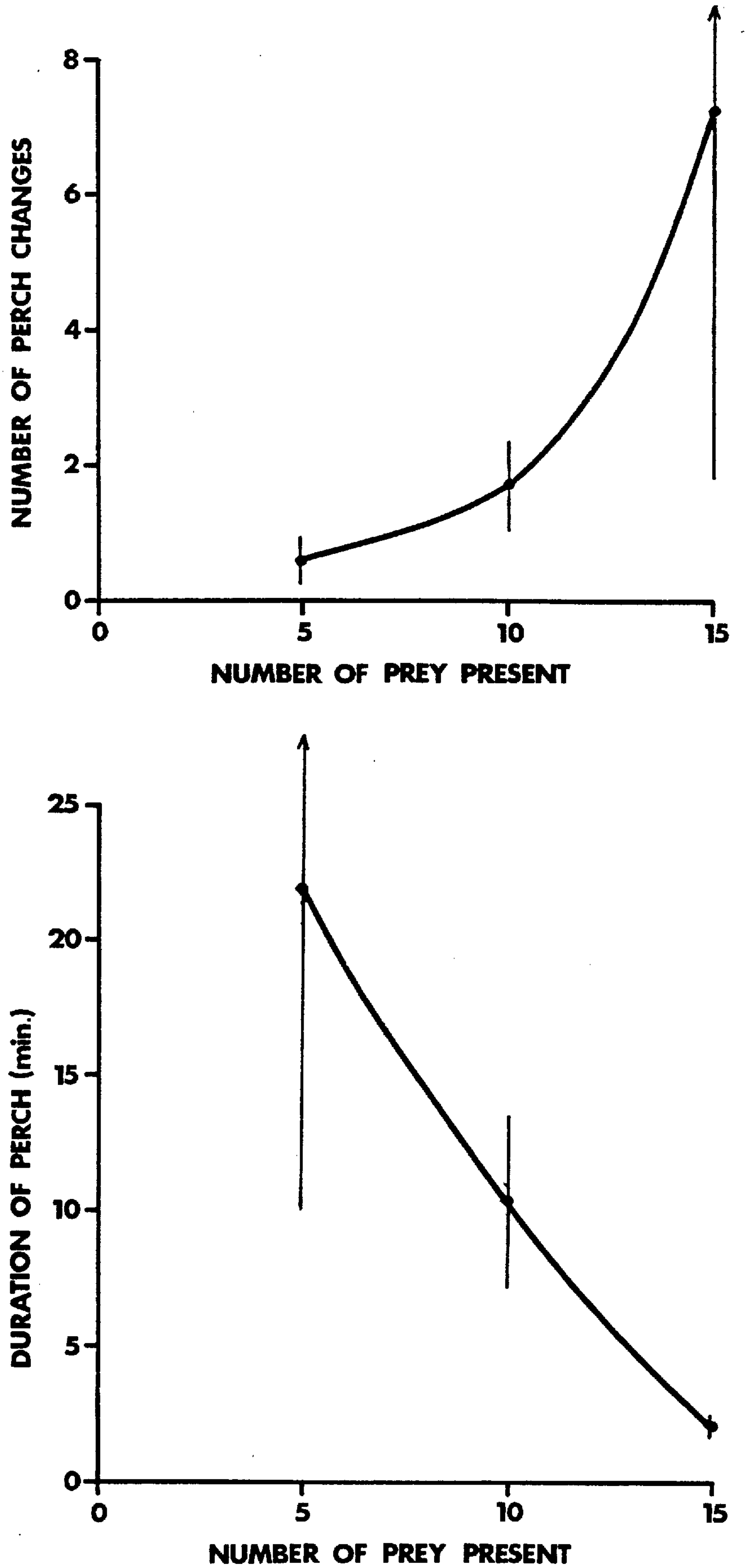
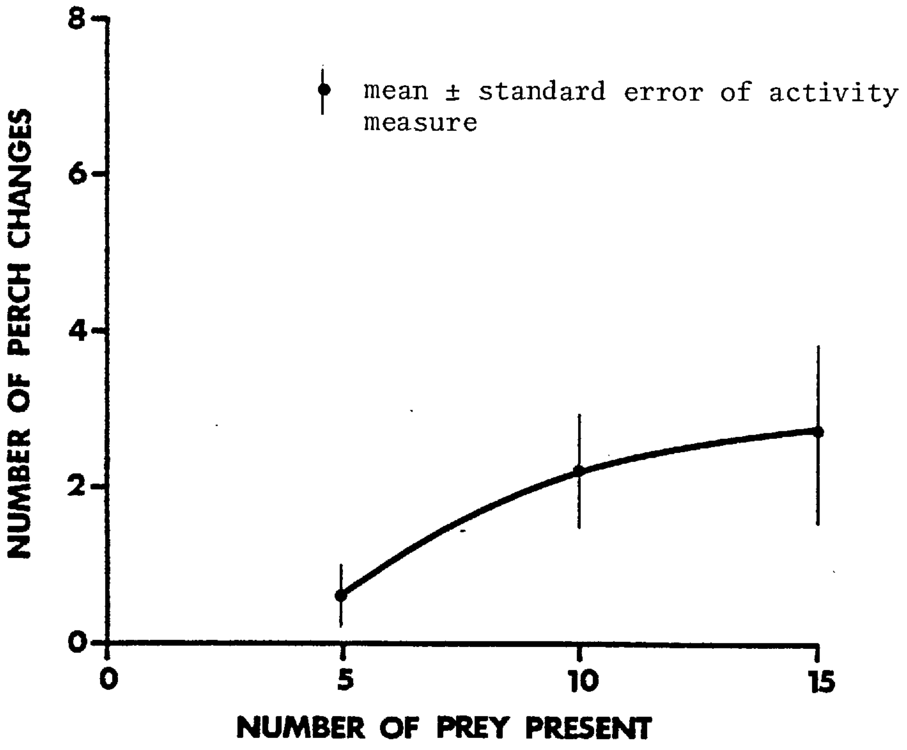


Figure 2.16. - Activity Data for *Pyrrhosoma nymphula* eating *Aedes aegypti*

ł mean ± standard error of activity measure



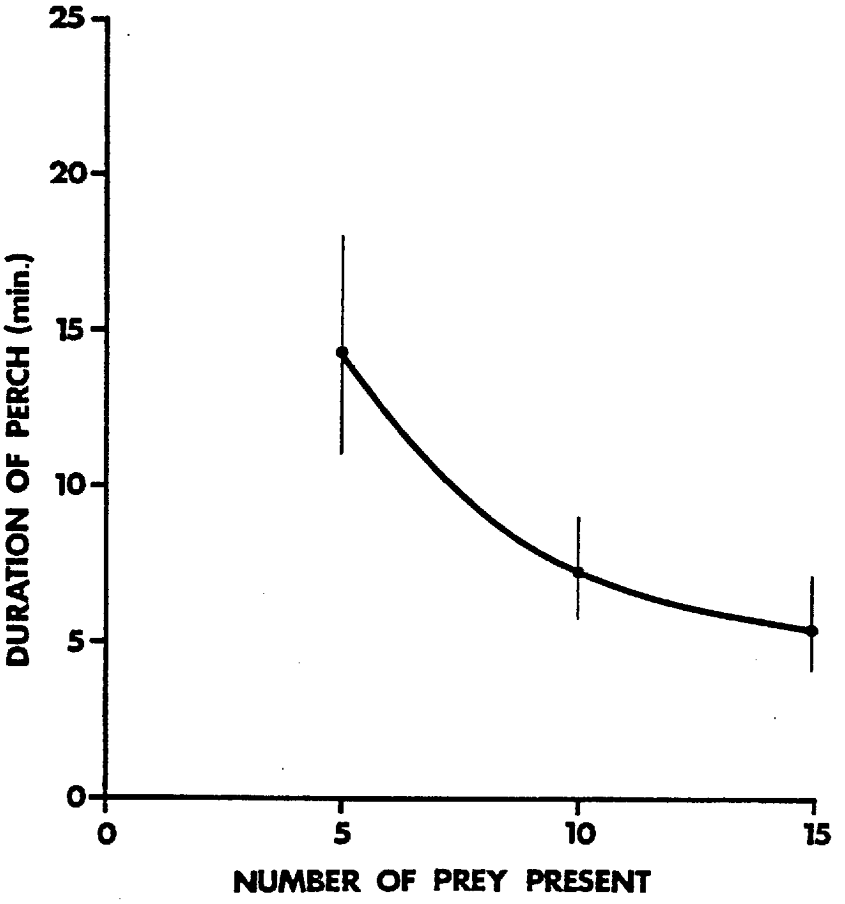
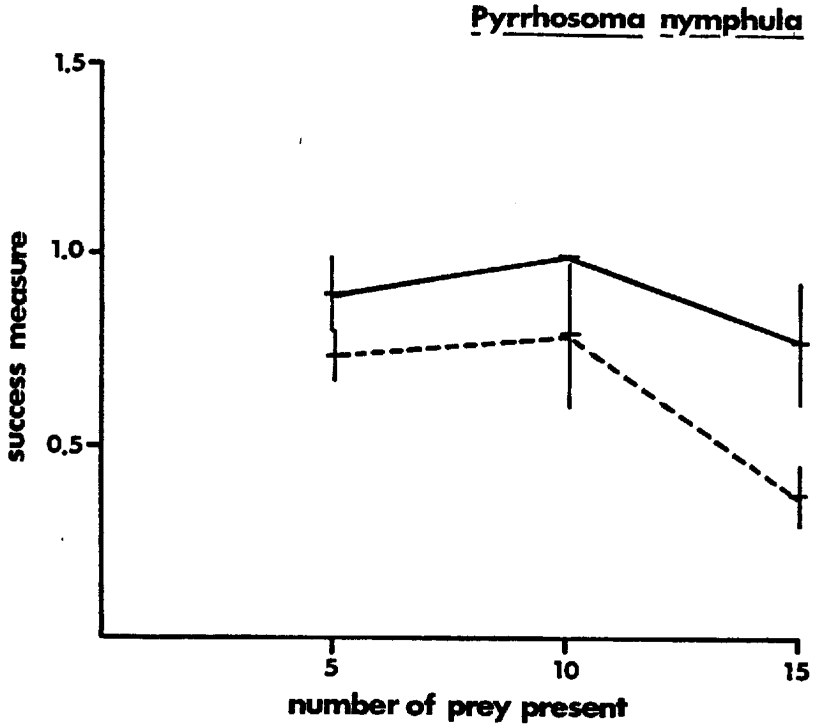
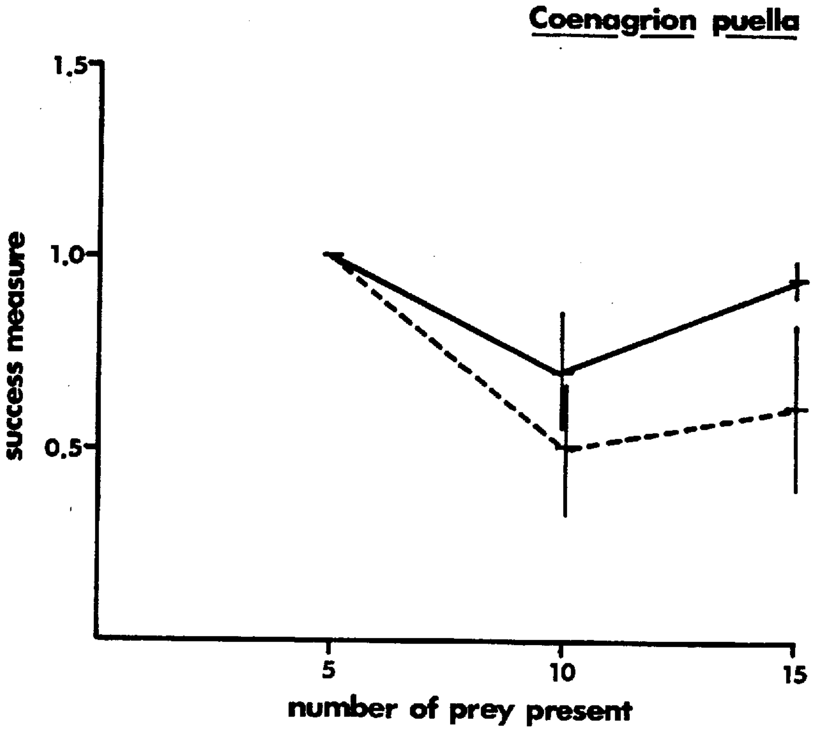


Figure 2.17. - Activity Data for *Coenagrion puella* eating *Aedes aegypti*

Figure 2.18. - Strike Success and Capture Success Data

+ : mean ± standard error of measure
– : strike success --- capture success





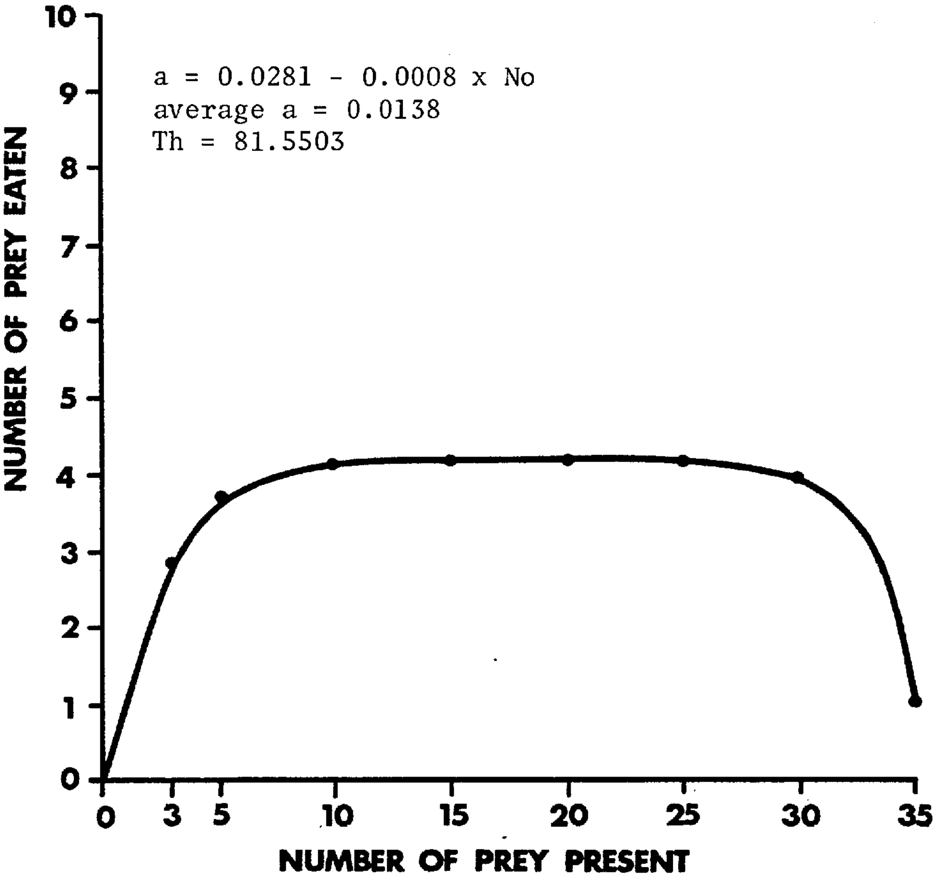
2.3.2. Simulations

A series of simulations was conducted, in order to test the effects on the functional response curve, of changes in the functional response parameters with prey density. Since only general indications of the dependence of the functional response curve shape on the attack rate and handling time were sought, simple linear relations were used to model changes in a and Th. These linear functions were incorporated in a general computer program, which calculated the predicted number of prey eaten, using the Rogers (1972) formula, at a series of prey densities. In order to facilitate comparison, linear functions were chosen for a and Th, which resulted in mean functional response parameters equivalent to those estimated for either *Pyrrhosoma* or *Coenagrion*, feeding on mosquitos (see Tables 2.10. and 2.11.). The results of these simulations are displayed in Figures 2.19. to 2.23.

The effects of these changes in attack rate only with prey density are shown in Figure 2.19. A decrease in a in relation to prey density results in a domed functional response; an increase in a with prey density results in a sigmoid curve which is close to a straight line, until No = 25, and starts to level off only at very high prey densities. The results of simulations using similar changes in handling time are displayed in Figure 2.20. It can be seen that these results are roughly opposite: a decrease in Th causing a functional response curve which is nearly a straight line, and an increase in Th causing a slightly domed curve. When these analagous effects of changes in a and Th are combined, the results are, predictably, even more extreme (see Figure 2.21.). A decrease in a combined with an increase in Th results in a rapidly rising curve, with a slope approaching infinity. An increase in a combined with a decrease in Th, results in a markedly domed functional response. The more interesting cases, when a and Th both increase, or both decrease, are displayed in Figure 2.22. The results reported in Section 2.3.1. indicate that, for *Pyrrhosoma* and *Coenagrion* at least, the functional response parameters may be more likely to vary together, like this, than in opposite directions. Although the basic assumptions of constant attack rate and handling time are not met in either case, (Figure 2.22.a and b) the corresponding variation in a and Th seems to have a masking effect, resulting in normal-looking functional responses. Hence, it is clearly possible to obtain a type-2 functional response, when the assumptions of the Rogers model are not satisfied. This phenomenon may be fairly common, and measured functional responses which conform to the type-2 Rogers model may, in many cases, mask variable predatory behaviour.

In order to clarify the implications of the above simulations for the actual functional responses, displayed in Figures 2.10. and 2.11., the pattern of changes in a and Th observed in the sit and watch experiments, was incorporated into the computer program used above. The sit and watch results displayed in Figure 2.15. were multiplied by an appropriate factor, to bring them closer to the estimated parameters of Tables 2.10. and 2.11. (See Section 2.3.3.). For both predators, the mean observed handling times at each prey density (for the first two prey captures) were multiplied by 20, and for Pyrrhosoma the mean observed attack rates (also for the first two prey captures) were divided by 100; for Coenagrion they were divided by 3. For each functional response parameter, and each damselfly, the values at prey density 5 were also used at prey density 3, and the values at prey density 15 were used for all higher prey densities. Then these data, reflecting the pattern of the sit and watch results for each damselfly, were plugged in to the computer program to calculate the predicted number of prey eaten, using the Rogers model. The results are displayed in Figure 2.23. They are remarkably like the functional response curves for Pyrrhosoma and Coenagrion feeding on mosquitos, which are displayed in Figures 2.10. and 2.11. Despite various differences, possibly consequences of the slightly different mean a and Th values used, the overall shape of the curves is similar. The simulated curve for Pyrrhosoma shows a clear double hump, although the initial rise to the first plateau is not so rapid as in Figure 2.10. The simulated curve for Coenagrion shows the plateau at prey densities between 5 and 10, and the subsequent rise. The plateau in the simulated curve after prey density 15 lends support to the hypothesis that a further decline in Coenagrion's attack rate at prey densities above 15 may be responsible for the depressed tail on the curve in Figure 2.11.

Figure 2.19. - Simulated Functional Responses with a as a linear function of prey density



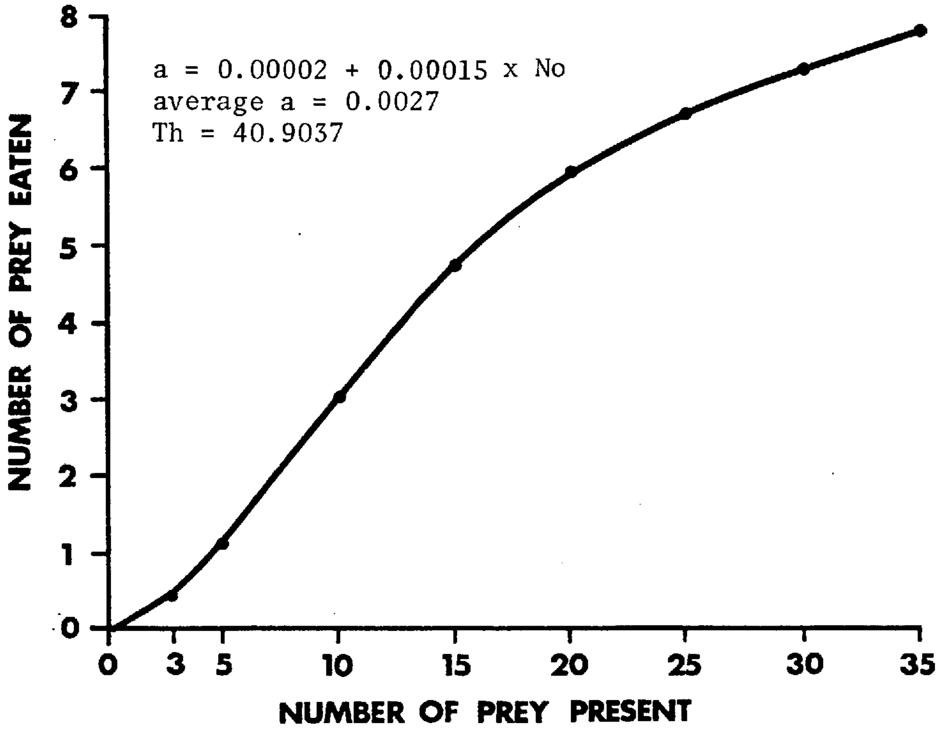
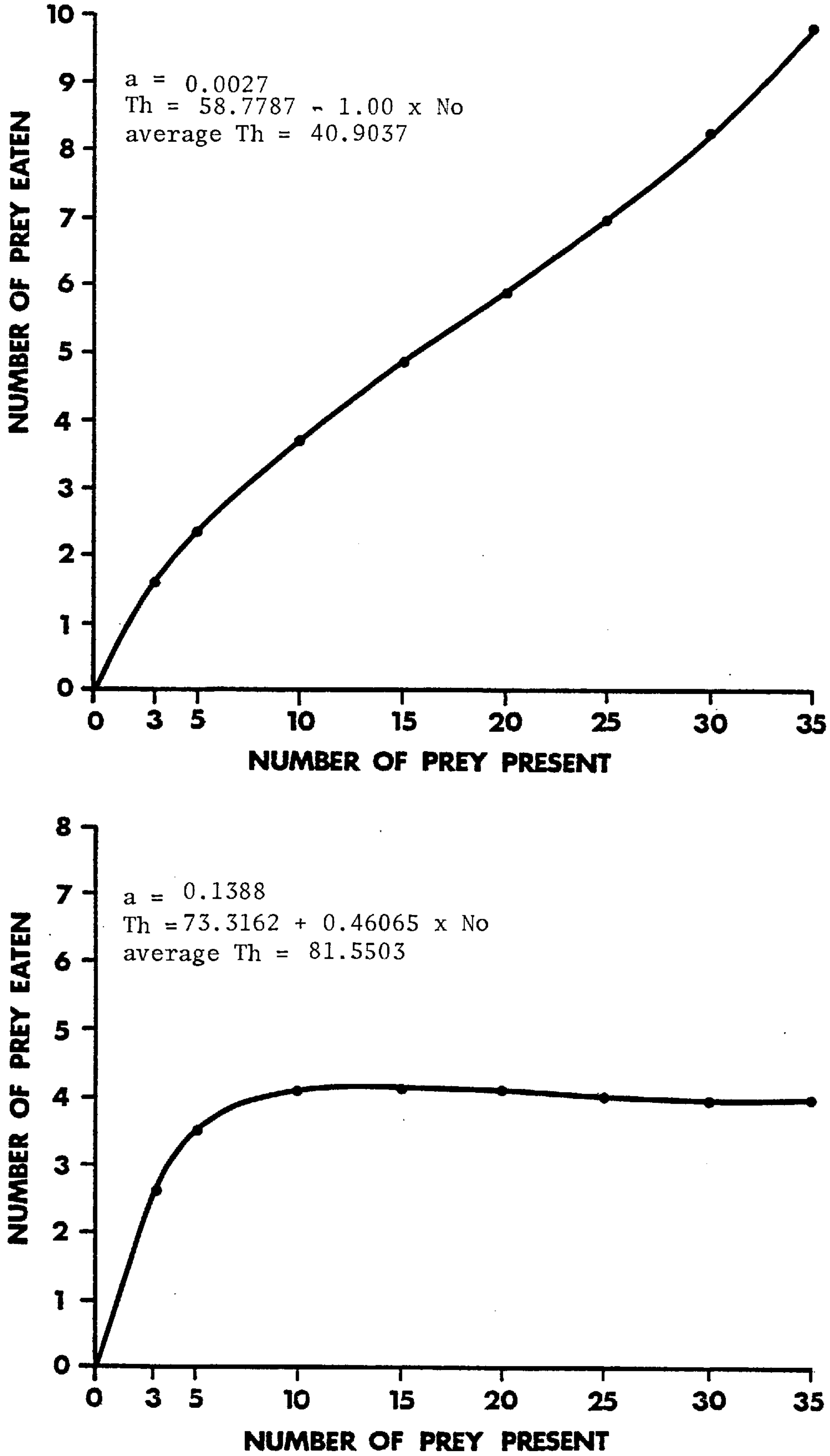


Figure 2.20. - Simulated Functional Responses with Th as a linear function of prey density



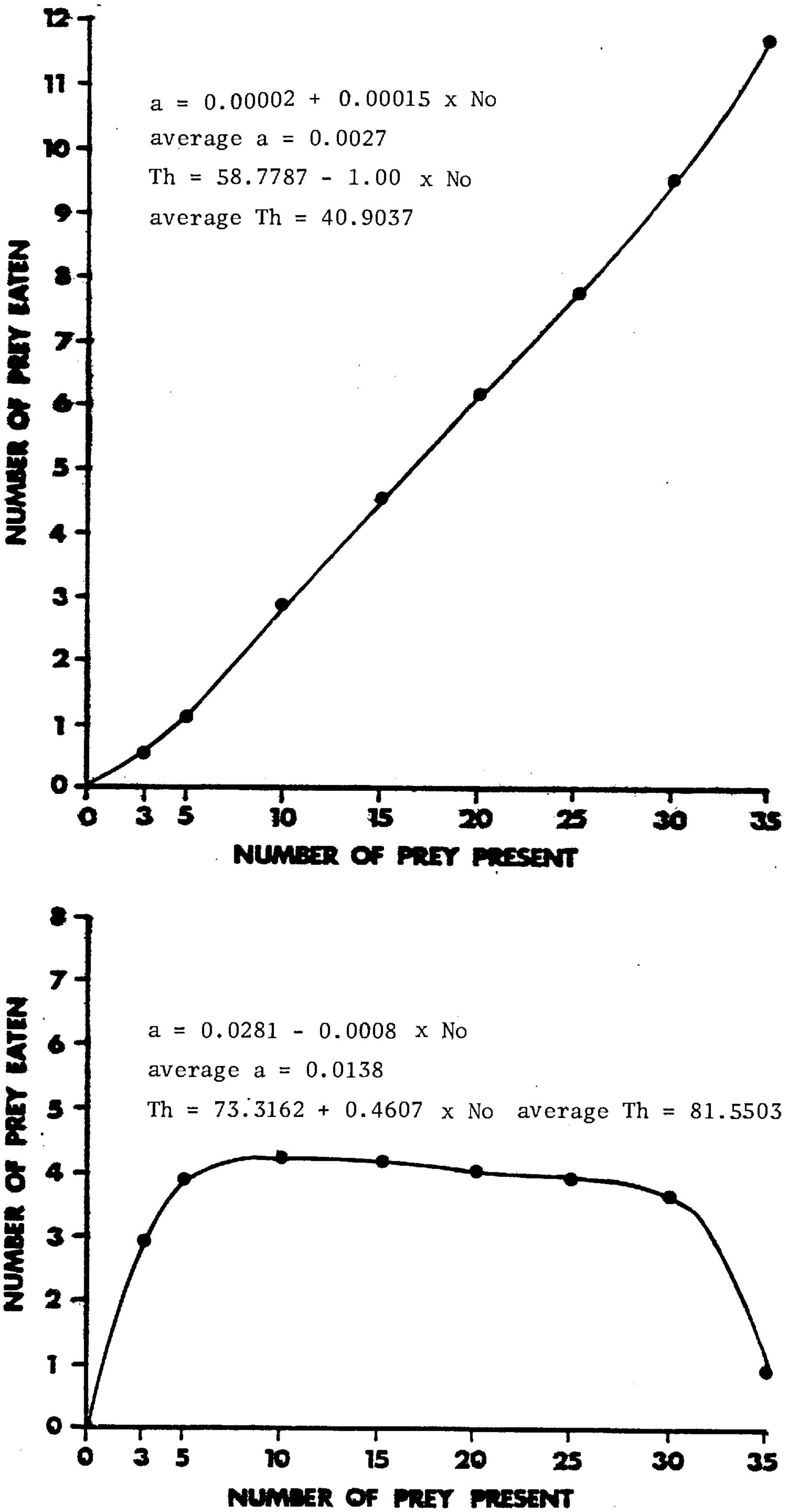
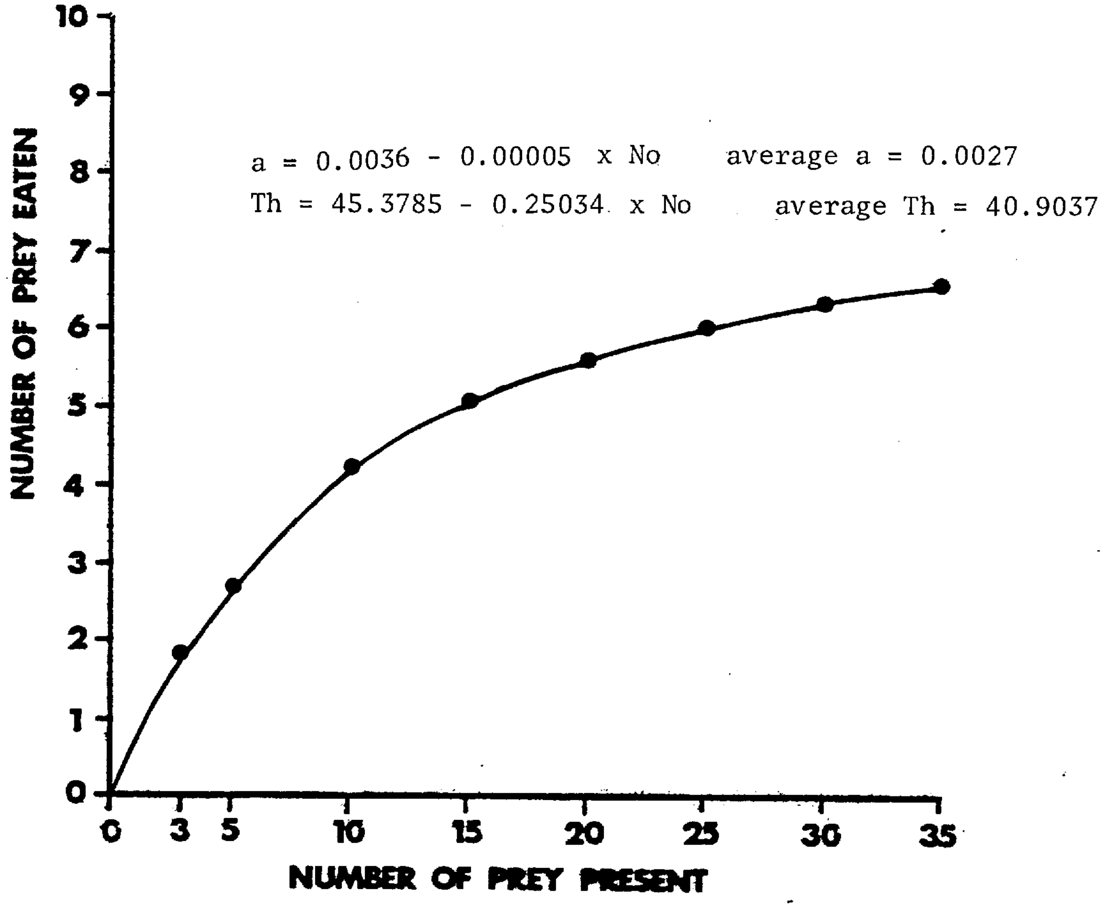


Figure 2.21. - Simulated Functional Responses with a and Th as linear functions of prey density

Figure 2.22. - Simulated Functional Responses with a and Th as linear functions of prey density



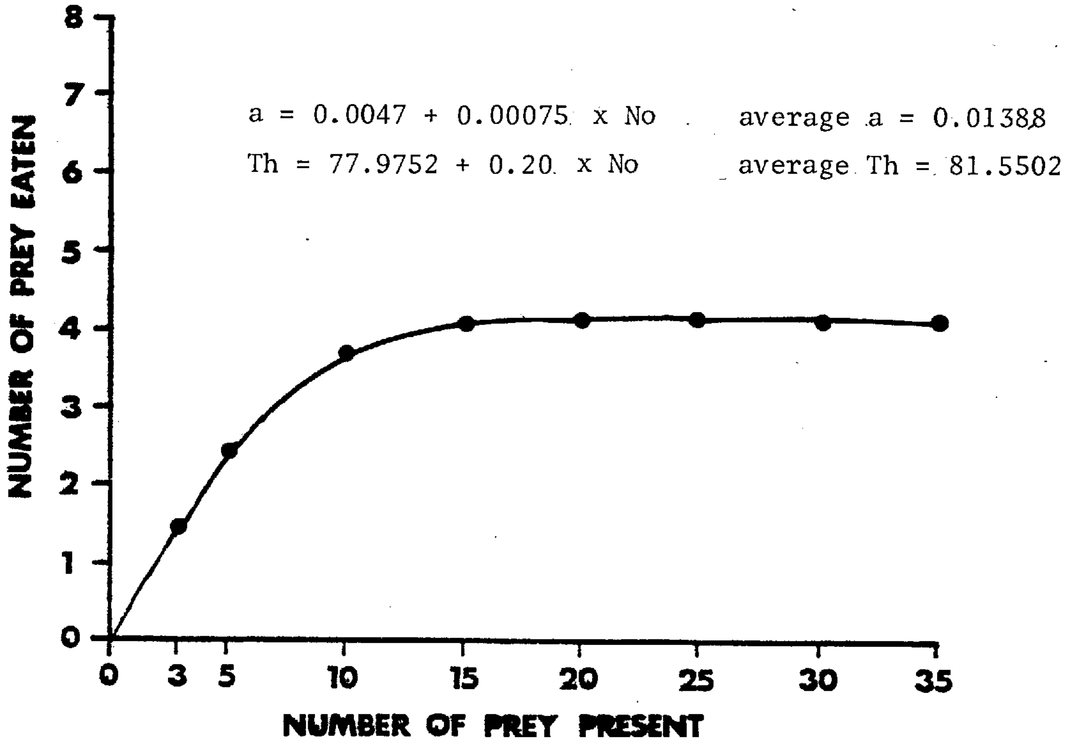
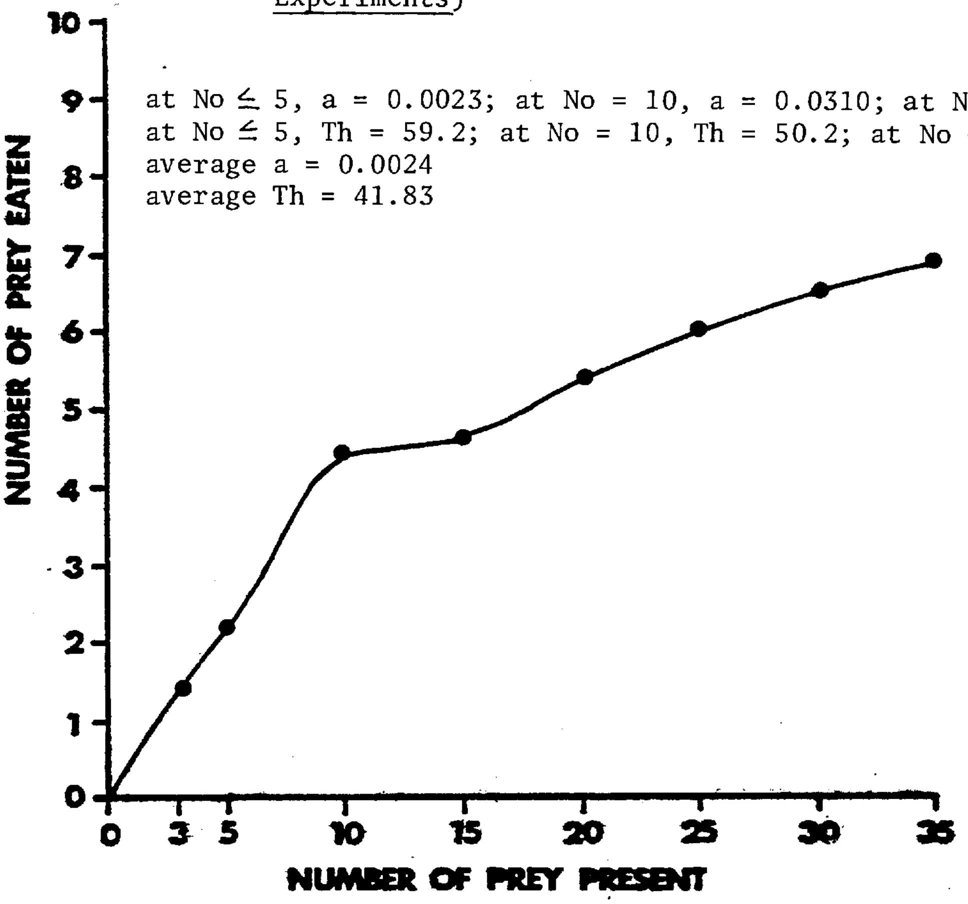
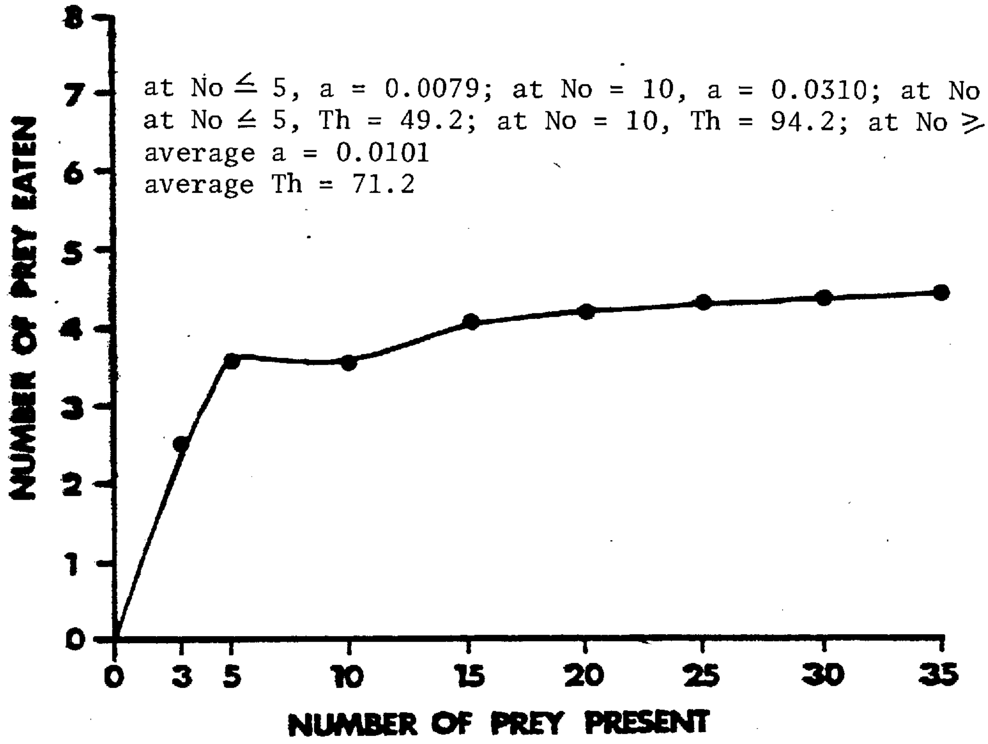


Figure 2.23. - Simulated Functional Responses of Pyrrhosoma nymphula and Coenagrion puella with a and Th as non-linear functions of Prey Density (based on sit and watch Experiments)



at No ≤ 5, a = 0.0023; at No = 10, a = 0.0310; at No ≥ 15, a =0.0018
at No ≤ 5, Th = 59.2; at No = 10, Th = 50.2; at No ≥ 15, Th = 33.2
average a = 0.0024
average Th = 41.83



at No ≤ 5, a = 0.0079; at No = 10, a = 0.0310; at No ≥ 15, a = 0.0069
at No ≤ 5, Th = 49.2; at No = 10, Th = 94.2; at No ≥ 15, Th = 75.4
average a = 0.0101
average Th = 71.2

2.3.3. Comparison of Observed and Derived Functional Response Parameters

Holling (1959b) and Thompson (1975) discussed possible causes of bias in the estimates for a and Th. Holling (1959b) found that direct measurement could lead to underestimation of Th, since empirical observation could determine the duration of prey capture, but could not often recognize the termination of the digestive pause. Thompson (1975) pointed out two ways in which derivation of the functional response parameters from experimental data could result in overestimation of a and underestimation of Th. However, the discrepancies in the estimates of a and Th observed in this study are in the opposite direction to those discussed by Thompson (1975).

Table 2.15. - Values for Observed and Derived Functional Response Parameters (observed parameters are averaged over all No, Ne)

parameter	Pyrrhosoma empirical	derived	Coenagrion empirical	derived
a (2 l./min.)	0.1528	0.0027	0.3956	0.0139
Th (min.)	2.3548	40.9037	3.9239	81.5503

In Table 2.15. the functional response parameters a and Th which were derived from the experimental numbers of prey eaten (corrected for age to 20) (Tables 2.10. and 2.11.) are compared to the parameters which were measured empirically in the sit and watch experiments (Figure 2.15.), and then averaged over prey density and the number of prey eaten, for each damselfly. For both predator species, the derived a's are smaller than those measured empirically by a factor of over twenty, and the derived Th's are greater than those measured empirically by a factor of about twenty. Calculation of the random predator equation (Rogers, 1972) using the empirical estimates for a and Th results in very high predicted numbers of mosquitos eaten, with predicted Ne values rounding off to the corresponding No in all cases (see Appendix 38).

It seems clear from Table 2.15. that the derived a values substantially underestimate the attack rates of both predators. This is not surprising, since the derived functional response parameters were calculated from the numbers of prey consumed by each predator over a six hour experimental period, while the sit and watch experiments lasted only two hours. It seems reasonable to suppose that after a period of starvation, a predator's feeding rate will initially be high, and will then decline after successive captures. This supposition is not borne out by the sit and watch data (see Appendix 34) because the empirical estimates for a were calculated from the formula:

$$a = \frac{1}{Ts\ (No - Ne)}$$

which is based on the mean time spent in searching prior to each capture, and ignores any time after the last capture. The estimates for a derived from the random predator equation (Rogers, 1972) do incorporate this period of time after the last capture, and the averaging of this time with the time spent in search prior to captures lowers the consequent derived estimates of a.

This indicates that the attack rates measured in the sit and watch experiments represented some sort of maximum value for a, whereby all the time considered to be spent in searching, actually did lead up to a capture. On the other hand, the measure of search time incorporated in the derives estimate of a:

$$Ts = Tt - Th\ Ne$$

assumes that all the time not spent in handling prey is devoted to searching for prey. As pointed out by Holling (1963), this need not be the case, and some portion of the experimental period Tt may be spent in activity unrelated to feeding. Damselflies are searchers, in Schoener's (1969a, 1969b) terminology (Section 1.3.2.), and probably put aside time for prey searching which can not be devoted simultaneously to any other activity. It seems unlikely that all of the time during the experiments was spent exclusively in searching for, and eating, prey.

In an attempt to quantify the proportion of the six hour experimental period which was actually devoted to predation by each predator, a series of calculations of the random predator equation (Rogers, 1972) was conducted, assuming a and Th values equal to those estimated empirically, and using a series of fractions of six hours, as values for Tt (see Appendix 38). The values of Tt which resulted in predicted Ne's most closely resembling the actual numbers of mosquitos eaten (corrected for age to 20) as listed in Tables 2.10. and 2.11. was:

Tt = 15 minutes

for both *Pyrrhosoma* and *Coenagrion*. In other words, *Pyrrhosoma* and *Coenagrion*, feeding in the way observed in the sit and watch experiments, devoted only about 1/24 of the six hour experimental period to predation. The remaining time was presumably spent in activity which was exclusive to predatory behaviour.

The handling times measured empirically are substantially lower than those derived from the random predator equation (Rogers, 1972), but the Th values estimated from the sit and watch experiments are probably not underestimates in this case. Holling's (1959b) observation that empirically measured handling times may exclude the time necessary for digestive pause rests on the assumptions that 1) a digestive pause after consumption of a prey item is essential before another prey item can be consumed and 2) there is no external indication of the completion of this digestive pause. In the sit and watch experiments, Th was measured as the period between a successful prey capture and the subsequent completion of feeding movements. The last feeding movements were invariably cleaning motions, in which the labium was groomed, and any remaining bits of prey were removed. It was possible for another capture to be initiated before the completion of these motions, and in some cases, a second capture was made before the completion of feeding movements associated with the first capture had been recorded. It seems likely that the time needed for this grooming exceeded that necessary for the digestive pause after each prey capture. (Of course, if digestive pause is considered to be a cumulative effect, unlike in Holling's definition, then the time spent after the last capture is included in the total handling time. In this case, observed handling times would be underestimates.) These observations suggest that if Holling's definition is accepted, then the empirical handling time measured in the sit and watch experiments was realistic. The derived Th was probably an overestimate, resulting from the same overall decline in feeding during the last four hours of the functional response experiments which caused the underestimation of the derived values for a.

In summary, the average functional response parameter values measured directly in the sit and watch experiments revealed that the parameter values derived from the random predator equation (Rogers, 1972) substantially underestimated a and overestimated Th. This discrepancy was probably due to the inclusion in the derived parameter estimates of time spent by both predators in activities unrelated to feeding. It is suggested that the actual proportion of the six hour experimental period devoted to predatory activities was very low. However, this does not invalidate conclusions based on comparing the derived parameters, since their relative values are similar. The observed and derived estimates of the functional response parameters indicate that Coenagrion's attack rate and handling time both exceed Pyrrhosoma's.

2.4. Experiments with Two Prey Types

2.4.1. Energetics

2.4.1.a) Introduction

Measurements of predator and prey energetics were undertaken, in order to determine 1) the relative calorific values of mosquitos and daphnia, to aid in devising single and mixed prey training diets offering a standard quantity of calories, and 2) the relative metabolic running costs of *Pyrrhosoma* and *Coenagrion*, any differences providing a rough estimate of the relative costs of predation for the two predator types.

2.4.1.b) Calorimetry

The average calorific values of experimental mosquitos and daphnia were determined using a Newham Electronics Microbomb Calorimeter with a Venture Servoscribe potentiometric recorder. The mean calorific value of one individual of each prey type was determined during the spring of 1975, from replicates of one hundred mosquitos and two hundred daphnia. The resulting values were: 4.31±0.46 joules (1.03±0.11 calories) and 1.67±0.04 joules (0.40±0.01 calories) for mosquitos and daphnia respectively. Fresh determinations (for four replicates of one hundred mosquitos and two replicates of two hundred daphnia) in the spring of 1976 yielded mean values per individual of 4.48±0.92 joules (1.07±0.22 calories) for mosquitos, and 1.59±0.04 joules (0.38±0.01 calories) for daphnia.

The average calorific value of daphnia tissue, 4355.25±244.90 gm. cal./gm. dry weight, was very similar to the 4419 gm. cal./gm. dry weight figure reported by Golley (1961) for daphnia.

Based on the above measurements, the approximate calorific equivalent of two mosquitos to five daphnia was used in determining predator training diets (Sections 2.1.2. and 2.4.2.). It is recognized that, due to their lighter cuticle, mosquitos may be more easily digested than daphnia. This could result in a net gain to a predator of more energy from two mosquitos than from five daphnia. However, any attempt to accurately determine the final quantity of energy gained by a given predator consuming a prey item, would necessarily involve a detailed study of the various energetic costs and gains incurred at each stage of the predation process. While such a study would certainly prove interesting, the time available for this thesis did not permit a detailed investigation of the energetics of predation.

2.4.1.c) Respirometry

Measurements of the mean oxygen consumption by each experimental predator type were made during April and May of 1976, using a Rank Oxygen Electrode, with a Venture Servoscribe potentiometric recorder. Each damselfly larva was left in a 6 ml. Quickfit bulb containing distilled water and approximately one square cm. of plastic screening, for a period of twenty minutes at 15° C., before water was extracted and its oxygen content measured. The average respiratory rates for Pyrrhosoma and Coenagrion respectively (exlcuding data for individuals less than eleven days prior to emergence), were 4.10±3.29 $\mu 1.0_2$ / animal / hour (n = 6), (0.0014±0.0011 joules/ animal / second) and 3.55±1.94 $\mu l.0_2$ / animal / hour (n = 12) (0.0012±0.0007 joules/ animal/ second). Differences between the respiratory rates of the two damselfly species were tested, using a Mann-Whitney U test, and were not found to be significant at the 5% level (see Appendix 39). Hence, the two predator types were considered to have roughly equivalent respiratory rates.

The rather high variability in these respiratory data is perhaps due in part to age-related changes in metabolic rate (Lawton, 1969 and 1971c). For Coenagrion at least, inclusion of data for individuals within ten days of emergence substantially increased the mean respiratory rate, and similar effects have been reported for Pyrrhosoma (Lawton, 1969 and 1971c). In general, these results reveal a considerably lower respiratory rate for Pyrrhosoma than that measured by Lawton (1969 and 1971c) at 16° C. during these months of the spring. Transformation of the results reported here, to 16° C., using the method described by Lawton (1971c):

$$
\begin{aligned}
\begin{array}{l}\text{respiratory}\\ \text{rate at } 16^{\circ}\text{C.}\end{aligned}\quad &= \text{antilog}_{10}\ (\log_{10}\ \begin{array}{c}\text{respiratory}\\ (\text{rate at } 15^{\circ}\text{C.})\end{array} + 0.0494\,\mu l.0_2/\text{hr.} \\
&= \text{antilog}_{10}\ (\log_{10}\ (4.10) + 0.0494)\,\mu l.0_2/\text{hr.} \\
&= 4.56\,\mu l.0_2/\text{hr.} \\
&= 0.0015 \text{ joules/animal/second}
\end{aligned}
$$

does result in a higher estimate, but one which is still lower than Lawton's (1971c) for April and May. It is closer to his measurement of Pyrrhosoma's respiratory rate in February. This descrepancy may be due to the later average onset of metamorphosis for the experimental Pyrrhosoma, than for the field individuals tested by Lawton (1969 and 1971c). Many of the Pyrrhosoma tested for respiratory rate in the laboratory had recently moulted from the penultimate instar, and hence were probably not undergoing metamorphosis, whereas Lawton's field population was reported to be in premetamorphosis by April, and in stage 2 metamorphosis by May.

2.4.2. Experimental Techniques and Results

The experimental routine was exactly the same as that described in Section 2.1.2., except that the predators were trained and tested on combinations of both prey types. Two densities of each prey type were chosen for the mixed prey trials: ten and twenty for mosquitos, and forty and eighty for daphnia. In each case, the lower density corresponds to a point on both predators functional response curves at which the slope is still steep, and the higher density corresponds to a point at which the slope is approaching zero. The two predator species were tested on all four combinations of mosquito and daphnia densities, $\underline{Nom}$:$\underline{Nod}$; 10:40, 10:80, 20:40, and 20:80.

The training diets were designed to offer the predators a standardized quantity of energy, equivalent to the fifty daphnia or twenty mosquitos used for the single prey experiments, with the same proportions of mosquitos and daphnia as in the next experiment. To achieve this, a system of simultaneous equations was solved for $\underline{m}$, the training density of mosquitos, and $\underline{d}$, the training density of daphnia. One equation constrained the training diet to the standardized quantity of calories:

$$2.5\ m + d = 50$$

and the other equation constrained the training diet to the appropriate proportions of mosquitos and daphnia:

$$m\ Nod - d\ Nom = 0$$

The solutions (to the nearest unit) for all the mixed prey combinations, $\underline{Nom}$:$\underline{Nod}$, were:

m = 8 and d = 31 for Nom:Nod = 10:40

and Nom:Nod = 20:80

m = 5 and d = 38 for Nom:Nod = 10:80

m = 11 and d = 22 for Nom:Nod = 20:40

The mixed prey experiments were conducted during the spring of 1976 and 1977. A Wilcoxon test on the differences between the 1976 and 1977 age-corrected mean number of mosquitos eaten, Nem, and daphnia eaten, Ned, yielded non-significant results (at the 5% level) for both predator species (see Appendix 15). Hence, data from both years were lumped.

Experimental results (corrected for age to twenty days prior to emergence) are presented in Figures 2.24. to 2.28. and Tables 2.16. and 2.17. (see Appendices 39 and 40 for raw data). Predicted results refer to the Nem and Ned values calculated recursively (using Newton's approximation) from the two prey extensions of the random predator equation (Rogers, 1972; Lawton, Beddington and Bonser, 1974), using the functional response parameters derived from the age-corrected functional responses (Tables 2.10. and 2.11.).

The competition coefficients, estimating the effect of *Coenagrion* on *Pyrrhosoma*, α PnCp, and the effect of *Pyrrhosoma* on *Coenagrion*, αCpPn, were calculated from the equation proposed by Schoener (1974). Based on the frequency of each prey type in the diet of each predator, dPnm, dPnd, dCpm, and dCpd, for example:

$$dPnm = \frac{Nem\ (Pn)}{Nem\ (Pn) + Ned\ (Pn)} ,$$

the frequency of each prey type in the environment, fm, and fd, for example:

$$fm = \frac{Nom}{Nom + Nod} ,$$

the calorific value of each prey type, bm, and bd, in this case:

$bm = 2.5$, and

$bd = 1.0$,

and the total number of prey eaten by each predator, *TPn*, and *TCp*, for example:

$$TPn = Nem\ (Pn) + Ned\ (Pn),$$

then the effect of *Coenagrion* on *Pyrrhosoma*, for instance:

$$\alpha\, PnCp = \frac{(TCp)}{(TPn)} \quad \frac{(dPnm/fm)\ (dCpm/fm)\ bm +}{(dPnm/fm)^2\ bm +}$$

$$\text{(continued)} \quad + \quad + \frac{(dPnd/fd)\ \ (dCpd/fd)\ bd}{+\ (dPnd/fd)^2\ bd} .$$

This index measures the effect of one individual of *Coenagrion* on one individual of *Pyrrhosoma* in comparison to the effect of one individual of *Pyrrhosoma* on another.

The measures of diet breadth refer to the inverse of the denominator of the competition coefficient equation, as suggested by Levins (1968). For example, *Pyrrhosoma*'s diet breadth would be equal to:

$$\frac{1}{(dPnm/fm)^2\ bm + (dPnd/fd)^2\ bd} .$$

the index *c* in Table 2.17. refers to Murdoch's (1969) measure of prey preference, in this case:

$$c = \frac{Nem\ /\ Ned}{Nom\ /\ Nod} .$$

The indices *Em* and *Ed* refer to Ivlev's more sensitive index of preference, *E*, (Ivlev, 1961), which varies from minus one to zero, for decreasing negative preference, and varies from zero to positive one for increasing positive preference. In this case:

$$Em = \frac{(Nem\ /\ (Nem + Ned)) - (Nom\ /\ (Nom + Nod))}{(Nem\ /\ (Nem + Ned)) - (Nom\ /\ (Nom + Nod))} .$$

For a discussion of other preference indices see Cock (1977).

Estimation of the mixed prey functional response parameters was attempted, using the multiple regression technique described in Lawton, Beddington and Bonser (1974). The two prey random predator model was not an appropriate simulation of the Pyrrhosoma or Coenagrion data, since the resulting a and Th parameters were negative in many cases (see Appendix 42).

It is clear from Tables 2.16. and 2.17. that more mosquitos, and in many cases, fewer daphnia, are eaten by both predators than was predicted by the two prey extensions of the random predator equation (Rogers, 1972; Lawton, Beddington and Bonser, 1974).

The observed (age-corrected) and predicted numbers of prey eaten were compared statistically for each predator-prey interaction, using the one-tailed Walsh test. For all predator-prey interactions $\alpha \leqslant 0{,}062$ (see Appendix 15). Hence, Pyrrhosoma and Coenagrion both ate significantly more mosquitos, Coenagrion also ate significantly more daphnia, and Pyrrhosoma ate significantly fewer daphnia, than would have been expected on the basis of the two prey extensions to the random predator equation (Rogers, 1972; Lawton, Beddington and Bonser, 1974), using the parameters measured in the single predator-single prey functional responses (corrected for age). As a result of these observed departures from the expected results, the preference indices calculated from the observed results also differed significantly from those calculated from the expected results. Walsh tests revealed that for both Pyrrhosoma and Coenagrion, the observed c's, Em's and Ed's were significantly different from those that were expected.

Furthermore, the strong preference of Pyrrhosoma for mosquitos is clarified by application of the chi-squared test to the observed (age-corrected) data to determine whether predation on one prey type is affected by the density of the alternate prey type. For Pyrrhosoma, daphnia density did not affect predation on mosquitos. However, the number of mosquitos present significantly ($\alpha \leqslant 0.02$) affected the number of daphnia eaten by Pyrrhosoma, indicating a pronounced preference for the mosquito prey type. This information is strengthened by the application of Walsh tests to the differences between the observed and expected diet breadths. Pyrrhosoma's actual diet is significantly narrower than what was expected, revealing a dramatic and unanticipated preference for mosquitos.

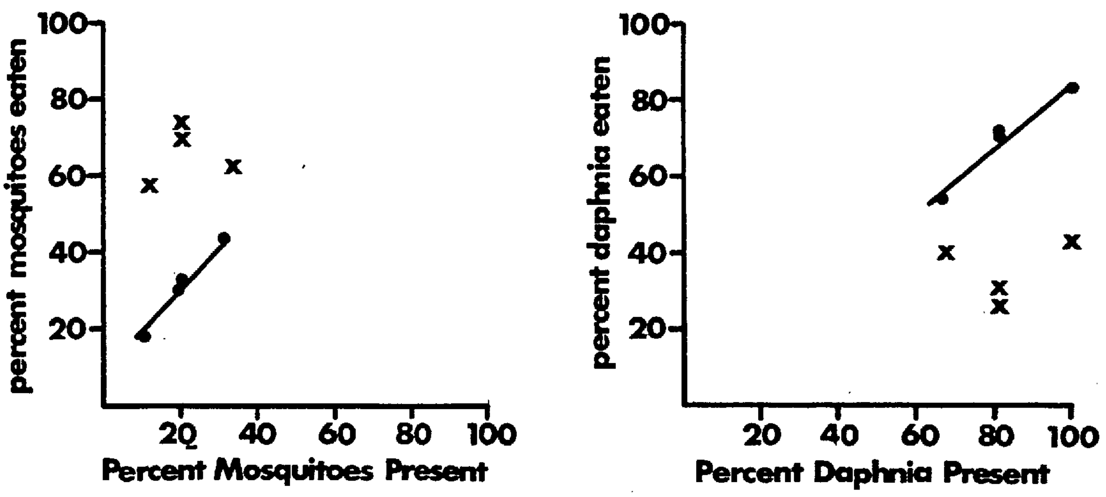
For Coenagrion, the density of each prey type did not affect feeding on the other type, and Coenagrion 's actual diet was not significantly narrower than expected. Preference for mosquitos by both predators appears to increase, when mosquitos are in a smaller minority, resulting in narrower predator diet breadths for these mixed prey combinations. At all prey density combinations, Coenagrion has a narrower diet than Pyrrhosoma. Consequently, Coenagrion has a greater competitive effect on Pyrrhosoma than vice versa.

Figure 2.24. - Mixed Prey Results

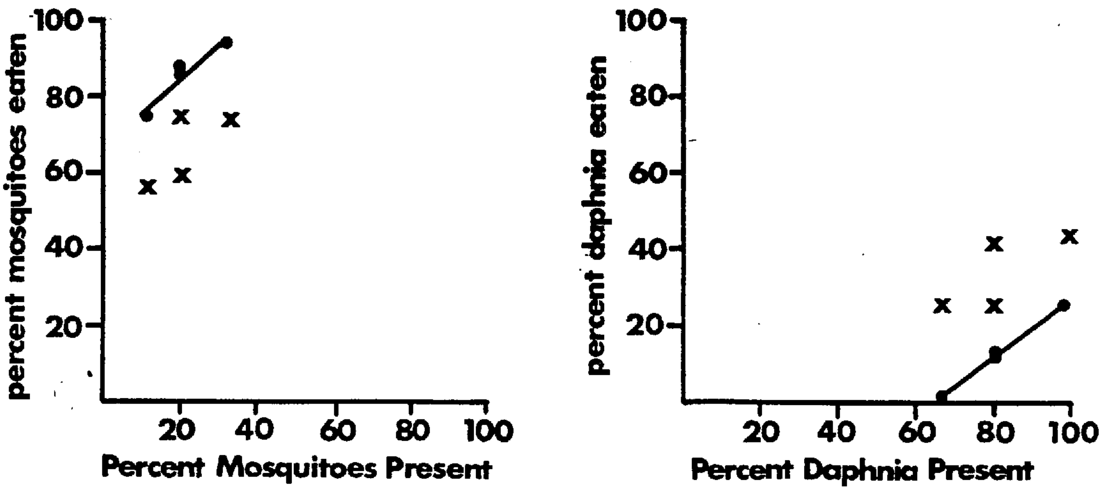
● expected results

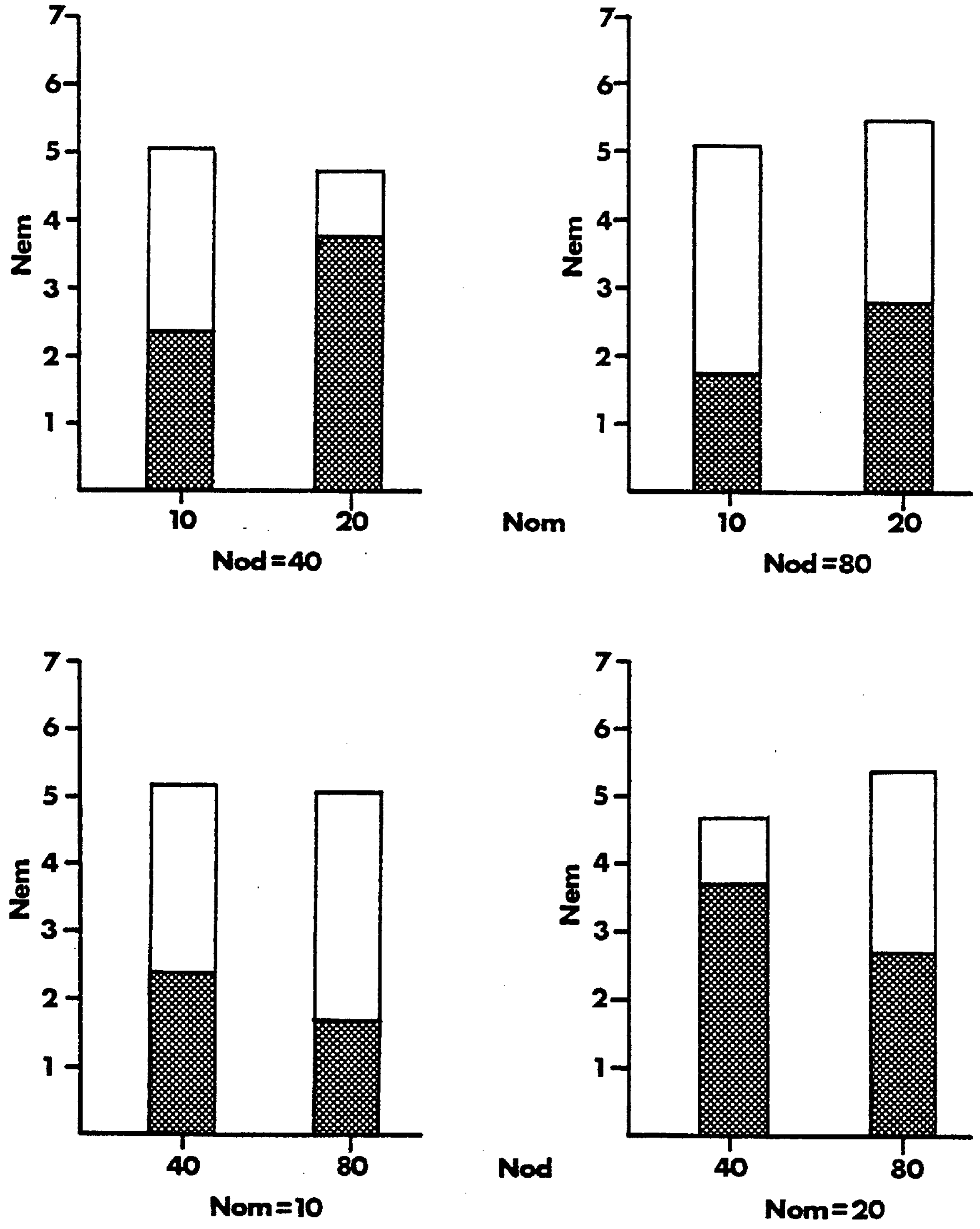
x observed results

PYRRHOSOMA NYMPHULA



COENAGRION PUELLA

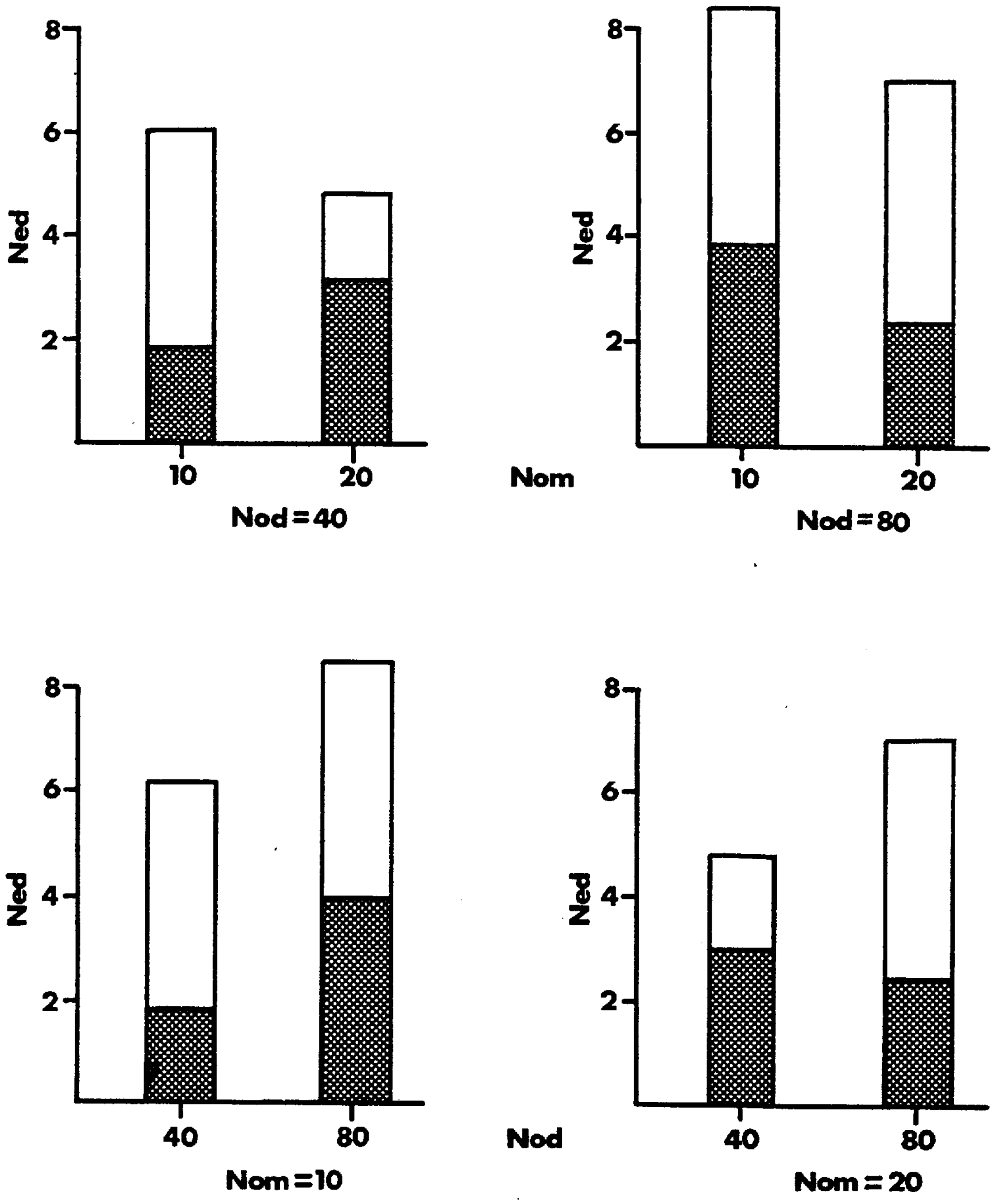




clear:observed results; hatched:expected results

Nom = number of mosquitos present
Nod = number of daphnia present
Ned = number of daphnia eaten

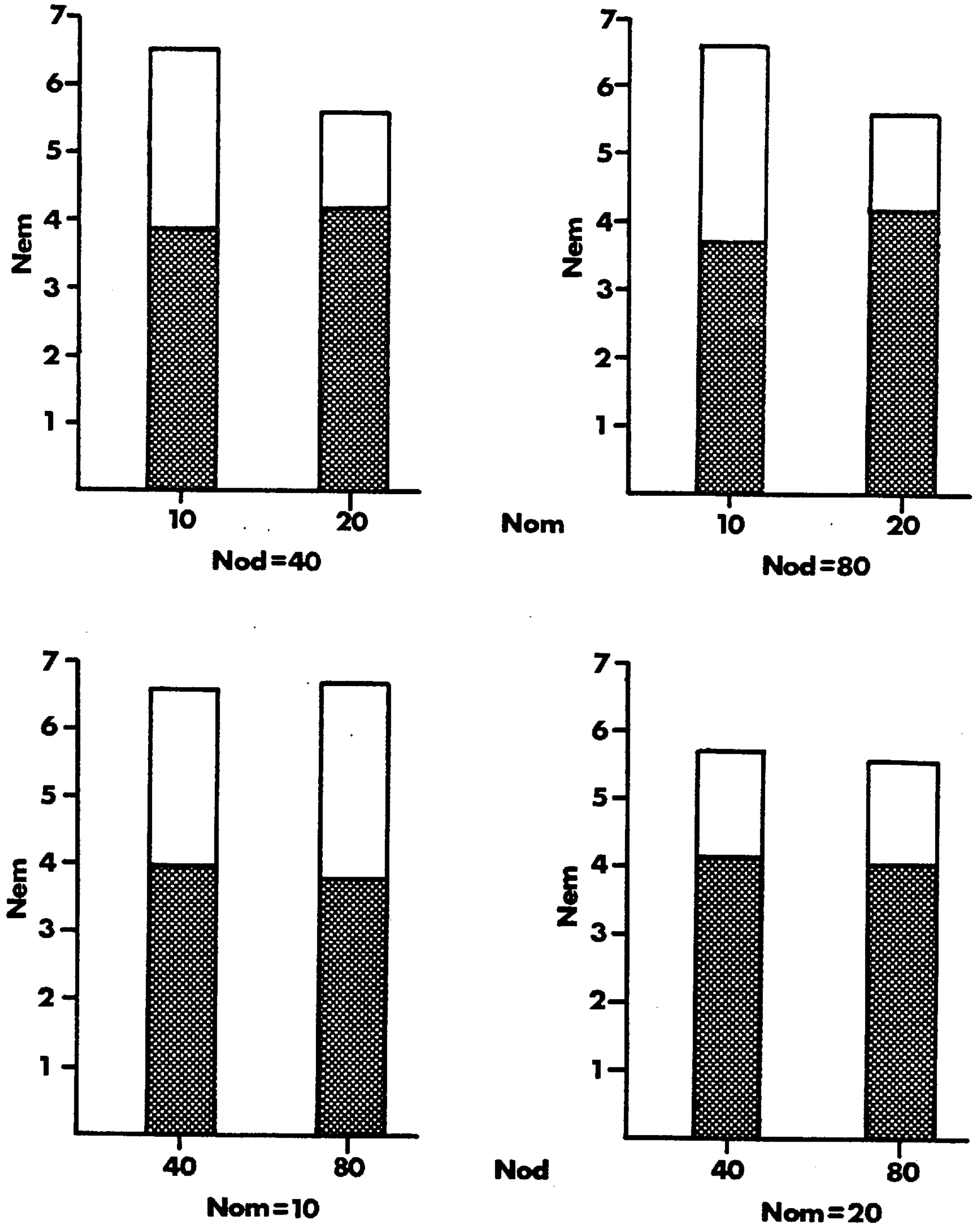
Figure 2.25. - Mixed Prey Results for *Pyrrhosoma nymphula* eating *Aedes aegypti*



hatched:observed results; clear:expected results

Nom = number of mosquitos present
Nod = number of daphnia present
Ned = number of daphnia eaten

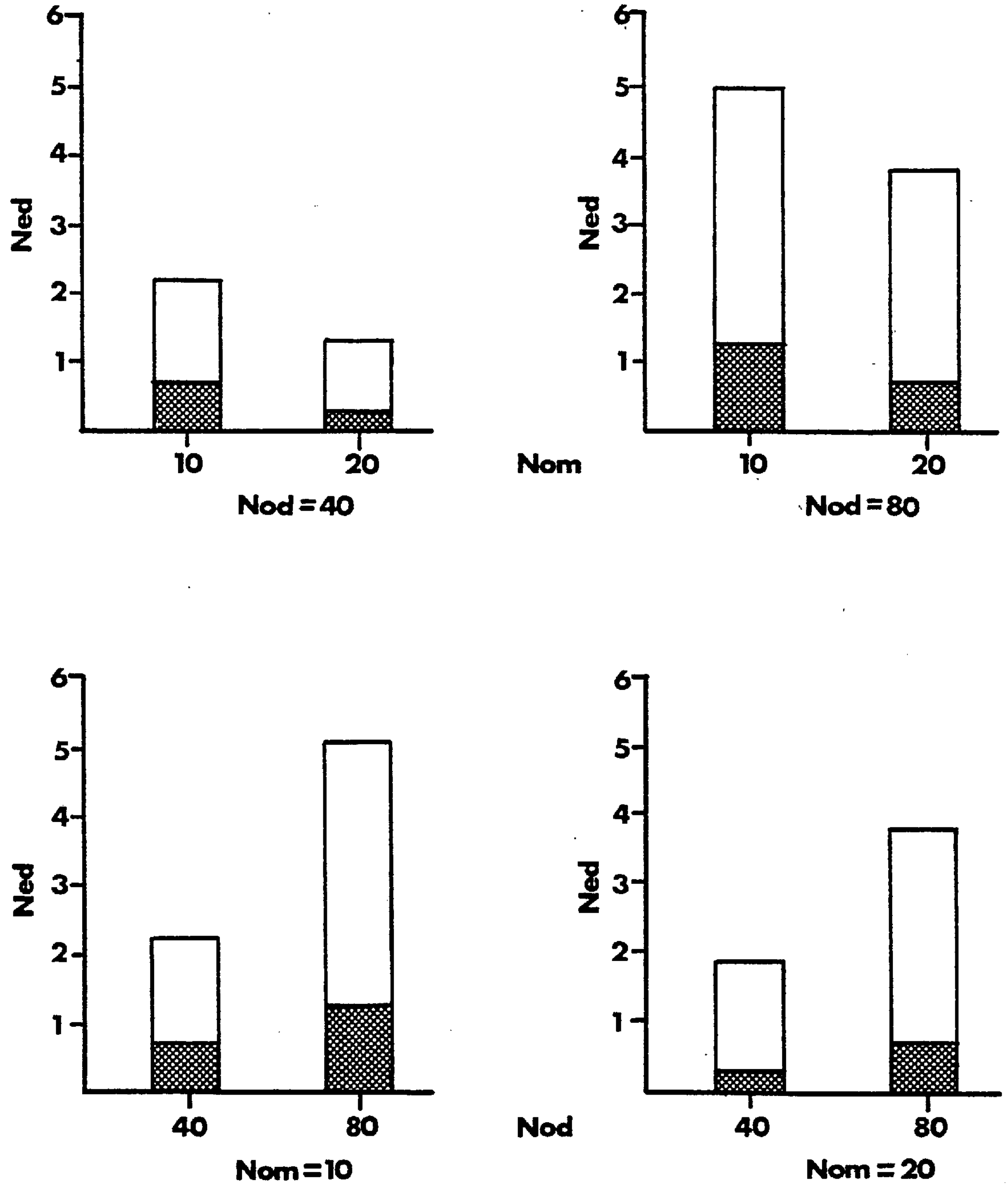
Figure 2.26. - Mixed Prey Results for *Pyrrhosoma nymphula* eating *Daphnia magna*



clear:observed results; hatched:expected results

Nom = number of mosquitos present
Nod = number of daphnia present
Ned = number of daphnia eaten

Figure 2.27. - Mixed Prey Results for *Coenagrion puella* eating *Aedes aegypti*



clear:observed results; hatched:expected results

Nom = number of mosquitos present
Nod = number of daphnia present
Ned = number of daphnia eaten

Figure 2.28. - Mixed Prey Results for *Coenagrion puella* eating *Daphnia magna*

Table 2.16. - Observed (Age-Corrected) and Predicted Mixed Prey Results

prey	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*
No	10	40	10	80	20	40	20	80
Pyrrhosoma nymphula								
n	7	7	7	7	8	8	8	8
observed Ne $(\bar{x} \pm s_x)$	5.27±0.86	1.85±0.74	5.24±0.73	3.99±1.15	4.83±0.66	3.09±1.61	5.53±0.71	2.38±0.62
predicted Ne	2.42	6.05	1.71	8.42	3.84	4.74	2.88	7.04
Coenagrion puella								
n	7	7	6	6	7	7	6	6
observed Ne $(\bar{x} \pm s_x)$	6.52±0.47	2.25±0.54	6.57±0.71	5.08±1.07	5.62±0.42	1.89±0.49	5.60±0.14	3.83±1.04
predicted Ne	3.87	0.65	3.77	1.27	4.15	0.31	4.10	0.62

2.4.3. Hypothesis Testing

2.4.3.a) Introduction

The comparison of the results of these mixed prey experiments with the predictions generated by a random predator model (Rogers, 1972; Lawton, Beddington and Bonser, 1974), of the results of the functional response experiments, facilitated the testing of a number of the hypotheses discussed in the Introduction. In this way, null hypotheses of (1) ' no exercise of innate prey preference', (2) 'no exercise of behavioural prey preference' and (3) 'no switching' could be tested against the alternative hypotheses of (1) 'innate prey preference exists', (2) 'behavioural prey preference exists' and (3) 'switching exists' by comparing the mixed prey results with those predicted by the mixed prey extensions of the random predator equation (Lawton, Beddington and Bonser, 1974), using the functional response parameters derived from the single prey experiments. Similarly, the null hypothesis of (4) 'no change in diet breadth with a reduction in prey abundance' could be tested against (4a) 'diet expansion accompanies a reduction in prey abundance' (the Foraging Theory Hypothesis), or (4b) 'diet contraction accompanies a reduction in prey abundance' (the Niche Theory Hypothesis) by comparing the results for a prey mixture with equivalent prey proportions, but a higher absolute prey density, to results for a prey mixture with equivalent prey proportions, but a lower absolute prey density. An outline of this regime of hypothesis testing is presented in Table 2.18. These four hypotheses will be tested in turn. Acceptance or rejection of the null hypothesis will be determined first on the basis of results for predators standardized to age twenty.

One section will be devoted to each null hypothesis:
prey preference ((1) + (2)) will be discussed in Section 2.4.3.b); switching (3) in Section 2.4.3.c); changes in diet breadth (4) in Section 2.4.3.d). Speculation on the original hypothesis, regarding changes in predator diet breadth due to competitive exploitation of prey, will only be considered tentatively in Section 2.5., since time did not permit experimentation on predator coexistence.

Table 2.17. -Measures of Diet Breadth, Competition, and Prey Preference for Mixed Prey Results

	Nom=10; Nod=40	Nom=10; Nod=80	Nom=20; Nod=40	Nom=20; Nod=80
Pyrrhosoma nymphula				
Observed Diet Breadth	0.0291	0.0149	0.1125	0.0325
Predicted Diet Breadth	0.1694	0.1489	0.1995	0.1653
Observed α PnCp	1.2384	1.2501	1.1424	1.0144
Predicted α PnCp	1.3974	1.9458	0.9665	1.2488
Observed c	11.39	10.51	3.13	9.29
Predicted c	0.29	0.17	0.43	0.29
Observed Em	0.57	0.68	0.30	0.56
Predicted Em	0.18	0.21	0.13	0.18
Observed Ed	-0.51	-0.35	-0.26	-0.45
Predicted Ed	-0.06	-0.03	-0.08	-0.06

Table 2.17. -Measures of Diet Breadth, Competition, and Prey Preference for Mixed Prey Results (continued)

	Nom=10; Nod=40	Nom=10; Nod=80	Nom=20; Nod=40	Nom=20; Nod=80
Coenagrion puella				
Observed Diet Breadth	0.0288	0.0151	0.0768	0.0448
Predicted Diet Breadth	0.0218	0.0864	0.0503	0.0212
Observed α PnCp	0.8075	0.7999	0.8678	0.9843
Predicted α PnCp	0.6322	0.4564	0.9014	0.7081
Observed c	11.59	10.35	5.95	5.83
Predicted c	23.82	23.75	26.77	26.45
Observed Em	0.57	0.67	0.39	0.49
Predicted Em	0.62	0.74	0.48	0.63
Observed Ed	-0.51	-0.34	-0.46	-0.32
Predicted Ed	-0.70	-0.39	-0.81	-0.72

Table 2.18. - Null and Alternative Hypotheses, and Criteria for Rejecting the Null Hypotheses

Ho	H1	Criterion for Rejecting Ho and Accepting H1	H2	Criterion for Rejecting Ho and Accepting H2
(1) no exercise of innate prey preference by the predator	The predator prefers *Aedes aegypti*	Em > Ed (for the observed age-corrected data)	The predator prefers *Daphnia magna*	Ed > Em (for the observed age-corrected data)
(2) no exercise of behavioural prey preference by the predator, over and above any innate preference.	The predator prefers *Aedes aegypti*	At all mixed prey combinations, the predator's observed Em is greater than that predicted by the mixed prey extensions to the random predator equation, using *a* and *Th* derived from the functional response experiments	The predator prefers *Daphnia magna*	At all mixed prey combinations, the predator's observed Ed is greater than that predicted by the mixed prey extensions to the random predator equation, using *a* and *Th* derived from the functional response experiments
(3) no switching by the predator	The predator switches	In the mixed prey experiments, the predator eats proportionately more of each prey type when it is abundant, relative to the other prey type	--	--

Table 2.18. - Null and Alternative Hypotheses, and Criteria for Rejecting the Null Hypotheses (continued)

Ho	H1	Criterion for Rejecting Ho and Accepting H1	H2	Criterion for Rejecting Ho and Accepting H2
(4) no change in diet breadth with changes in prey abundance	Diet expansion accompanies a decrease in prey abundance (The Foraging Theory Hypothesis)	In the mixed prey experiments, at lower absolute but equivalent relative prey densities, the predator takes prey in more similar proportions to those available, than at higher absolute, but equivalent relative prey densities	Diet contraction accompanies a decrease in prey abundance (The Niche Theory Hypothesis)	In the mixed prey experiments, at lower absolute but equivalent relative prey densities, the predator takes prey in less similar proportions to those available, than at higher absolute, but equivalent relative prey densities

2.4.3.b) Prey Preferences

Examination of Table 2.17., and Figures 2.24 to 2.28. reveals that both predators (at age twenty), have an innate preference for mosquitos over daphnia. *Pyrrhosoma* and *Coenagrion* consistently manifest a positive preference for mosquitos, and a negative preference for daphnia, as reflected in the *Em* and *Ed* preference indices for the observed age-corrected data. However, such a preference is predicted by the mixed prey extensions to the random predator equation, since the data which they generate also results in positive *Em* and negative *Ed* indices.

In order to determine whether a behavioural preference for mosquitos exists, over and above the innate preference, the observed (age-corrected) data and the data predicted from the mixed prey extensions to the random predator equation must be compared. Table 2.16. shows clearly that both predators eat more mosquitos than predicted by the mixed prey extensions to the random predator equations. Ivlev's preference index, *Em*, calculated from the observed (age-corrected) data averages + 0.53 for both predators, and *Ed* averages -0.39 and -0.41 for *Pyrrhosoma* and *Coenagrion* respectively. The same indices, calculated from the predicted mixed prey results, average + 0.18 and + 0.62 for mosquitos, and -0.06 and -0.66 for daphnia, for the respective predators.

Statistical comparisons of the observed and predicted preference indices *Em*, and *Ed*, using the two-tailed randomization test (see Appendix 15) indicate that for *Pyrrhosoma*, the observed *Em* is significantly larger, ($\alpha \leqslant 0.06$) and the observed *Ed* is significantly smaller ($\alpha \leqslant 0.06$), than would have been expected on the basis of the two prey extensions to the random predator equation. Preference for mosquitos is significantly greater for *Pyrrhosoma* than had been expected. Hence, *Pyrrhosoma* manifests a significant behavioural preference for mosquitos.

Pyrrhosoma clearly preferred mosquitos much more than was expected, from the predicted mixed prey results. At all prey density combinations, this damselfly ate significantly more mosquitos and fewer daphnia than predicted. Hence, the rather weak preference for mosquitos reflected in the predicted *E* indices is much magnified in the corresponding indices calculated from the actual results. The mean actual *Em* is roughly 3.0 times that predicted, and the mean actual *Ed* is approximately 6 1/2 times that predicted. *Pyrrhosoma*'s predatory behaviour in an arena of mixed prey is obviously quite different from its behaviour when only one prey type is available. This suggests that *Pyrrhosoma* has considerable behavioural plasticity. While is is able to feed successfully on a variety of potential prey types, it can select from a prey mixture, the prey which will yield the greatest net benefit.

In the case of *Coenagrion*, the contrast between actual and expected results is not so extreme. The observed *Em* is significantly smaller ($\alpha \leqslant 0.06$) and the observed *Ed* significantly larger ($\alpha \leqslant 0.06$) than would have been expected on the basis of the two prey extensions to the random predator model, indicating significantly less preference for mosquitos than had been expected. While more mosquitos were eaten than predicted by the mixed prey extensions of the random predator equation, more daphnia than expected were eaten as well, resulting in no behavioural preference for mosquitos. Consequently, although *Coenagrion* does exhibit slightly less preference for mosquitos than expected, the actual and predicted *E* indices do not differ greatly. The mean actual *Em* and *Ed* indices are, respectively, 0.85 and 0.62 times those predicted.

To summarize, the numbers of mixed prey eaten by each predator were roughly similar. Both damselflies exhibited an innate preference for mosquitos over daphnia.

Pyrrhosoma displayed a further behavioural preference for mosquitos, taking more of them, and fewer daphnia, than had been expected. *Coenagrion*'s prey choice was closer to that predicted, and although more of both prey types were eaten than had been expected, *Coenagrion* exhibited no behavioural preference for mosquitos.

2.4.3.c) Switching

the null case of 'no switching' results from the exercise of a constant level of prey preference by the predator. The index c, equal to the ratio of the two prey types eaten divided by the ratio of the two prey types available, will be constant under these circumstances. Alternatively, if switching is operating, the index c will increase as the ratio of the two prey types available increases. Although it is considered advisable to keep total prey density constant while testing for switching, in theory this constraint is not required (Murdoch and Oaten, 1975). Therefore the mixed prey data presented in Tables 2.16. and 2.17. have been analyzed to determine whether switching operates in these two cases.

The c indices based on the actual mixed prey data are clearly not constant for either damselfly. If this is a reflection of switching, then c for the mixed prey combination of 20 mosquitos: 40 daphnia should be greater than c for 20 mosquitos : 80 daphnia, or c for 10 mosquitos : 40 daphnia, which should be greater than c for 10 mosquitos : 80 daphnia.

Averaging the c values for mixed prey combinations of 10 mosquitos : 40 daphnia and 20 mosquitos : 80 daphnia yields mean c indices of 10.34 for Pyrrhosoma and 8.71 for Coenagrion. For both predators, these c values are less than those for 10 mosquitos : 80 daphnia, and greater than those for 20 mosquitos : 40 daphnia. Therefore, the direction of the change in c is opposite to that predicted for switching. Both predators take proportionately more mosquitos when they are a smaller minority of the available prey.

The predicted mixed prey consumption of each predator leads to the expectation that both predators will switch to a very limited extent. However, in both cases the predicted c values are very nearly constant (Table 2.17.), indicating that had the predators behaved as they were expected to, on the basis of the mixed prey extensions to the random predator equation, they would both have exercised a fairly constant preference for mosquitos, at all relative mosquito densities.

2.4.3.d) Predator Diet Breadth, Prey Abundance, and Predator Competition

The effect of a reduction in prey abundance on predator diet breadth can be tested in two ways, using the mixed prey results in Tables 2.16. and 2.17. The calculated diet breadths for mixed prey combinations of 20 mosquitos : 80 daphnia can be compared to those for 10 mosquitos : 40 daphnia. In addition, the estimated competition coefficients can be related directly to predator diet breadth. Diet breadth for the mixed prey combination when competitive effects are greatest, can be compared to that for the mixed prey combinations when competitive effects are least important.

For both predators, diet breadth is predicted to increase slightly when mixed prey abundance drops from 20 mosquitos : 80 daphnia to 10 mosquitos : 40 daphnia. This is an inevitable consequence of the random predator model, whereby proportionately more prey of both prey types are taken at lower prey densities. The actual mixed prey results do not conform to these predictions. When 10 mosquitos : 40 daphnia are available, Pyrrhosoma's diet breadth is slightly lower, and Coenagrion's diet breadth is much lower, than when 20 mosquitos : 80 daphnia are available. This is accounted for by the tendency of both damselflies to consume more mosquitos, and fewer daphnia, when overall prey abundance is reduced. Presumably, mosquitos are relatively more available (conspicuous) in a mixture of 10 mosquitos : 40 daphnia than in a mixture of 20 mosquitos : 80 daphnia. They may be eaten prior to daphnia at the lower mixed prey combination, with the result that daphnia are taken only when predator hunger is minimal. At the higher mixed prey combination, the abundance of available daphnia may precipitate earlier consumption of daphnia by the predator, leaving less room in the gut for mosquitos.

Observation of the sequence in which mixed prey are consumed would be extremely interesting. While foraging theory suggests that a predator is likely to become increasingly selective, as its hunger is satisfied, many of the foraging theory models incorporate sequential consumption of prey types, ordered by the predator's preference for each. Niche theory does not make a direct comment on this question, but the implication is that a predator will feed as selectively as it is able, within the limitations set by prey availability. This suggests that a predator, exposed to two prey types, would consume preferred prey first, non-preferred prey constituting a diet supplement at times of very low preferred prey availability. The mixed prey data discussed above is consistent with this conjecture that prey types are taken in sequence, particularly at lower prey densities. Observations on Notonecta maculata (Fab.) (F.D. Williams, personal communication), revealed a similarly ordered pattern of predation on houseflies, mosquitos, and gammarus prey types. It would be instructive to perform continuous observations on mixed prey predation, similar to those reported in Section 2.3.1. on single prey predation.

In absolute terms, the diets of both predators are narrower than was expected from the predicted mixed prey results. This effect is statistically significant for Pyrrhosoma, since the predicted and actual results differ more for Pyrrhosoma than for Coenagrion (Section 2.4.2.).

Linear regressions relating predicted diet breadths to predicted competition coefficients reveal that although both predators can be expected to narrow their diets when the intensity of interspecific competition is increased, only Pyrrhosoma actually behaves in this way (see Appendix 43). The direction of these trends relating niche breadth to competition must be inverse for the two predator species, since their diet breadths are affected in similar ways by the different mixed prey combinations, while their competition coefficients are inversely related.

It is notable that the damselfly most strongly affected by competition, Pyrrhosoma, is the one which responds to an increase in competition by narrowing its diet, in accordance with the Niche Theory Hypothesis. Coenagrion, which, on average, is affected less by Pyrrhosoma than by another conspecific individual, reacts to an increase in interspecific competition in the way predicted by the Foraging Theory Hypothesis. Presumably, the effects of competition by *Pyrrhosoma* on *Coenagrion* are not critical, and diet expansion does not exacerbate these effects unduly. On the other hand, the effects of competition by *Coenagrion* on *Pyrrhosoma* are much more severe. *Coenagrion*'s average diet breadth (0.0414) is narrower than *Pyrrhosoma*'s (0.0473). In accordance with the predictions made by Pulliam (1974) (Section 1.3.2.), competition by a generalist predator (*Pyrrhosoma*) has resulted in expansion of the original predator's (*Coenagrion*'s) diet, while competition by a specialist (*Coenagrion*) has resulted in contraction of the original predator's (*Pyrrhosoma*'s) diet.

To summarize, the mixed prey results broadly support the Niche Theory Hypothesis. While an increase in prey abundance was expected to produce a slight decrease in diet breadth, it actually had the reverse effect on both damselfly species. This corresponds to the outcome predicted by niche theory for the fourth hypothesis (Table 2.18.). An increase in competition is associated with diet contraction, for *Pyrrhosoma*, but these two factors are inversely related for *Coenagrion*. Hence this test supports niche theory, in the case of *Pyrrhosoma*, but indicates that *Coenagrion* behaves more in accordance with the predictions of foraging theory.

While both damselflies are capable of some short-term flexibility, their predatory behaviour appears to be under more severe evolutionary control than had been anticipated. Contrary to the results of most of the short-term studies reported in Section 1.5., these predators behave largely in accordance with the predictions of niche theory. This conclusion is supported by the work of Ross (1967, 1971) who found that *Anax junius* (Drury) larvae narrowed their diet, when prey were scarce, or when predator competition was intense. Prolonged coexistence of several damselfly species in the field, may have resulted in innate predatory behaviour which operates to reduce the competitive effects of prey exploitation.

2.5. Relevance to the Field

2.5.1. Population Predation Model

2.5.1.a) Hypothesis and Assumptions

The inverse age-related changes in the prey preference of *Pyrrhosoma* and *Coenagrion* proposed in Section 2.2.2. may operate to reduce competition between these two predators in the field. Ultimate instar damselfly larvae naturally require more food than younger larvae (Thompson, 1975; Beesley, 1972). Despite the lower temperatures prevalent during the early spring, ultimate instar *Pyrrhosoma* individuals have been estimated (Lawton, 1971b) to have a field feeding rate in February and March as high as that during the previous July and August. Odonata mortality is known to be high during emergence (Corbet, 1962; Benke and Benke, 1975; Kime, 1974) and it is probable that density dependent regulation of damselfly population size occurs primarily at this time. Consequently, the ultimate instar cohorts of *Pyrrhosoma* and *Coenagrion* are likely to be large, relative to the food available, in the early spring. Macan (1966) documented a population of *Pyrrhosoma nymphula* in a moorland fishpond where, he claimed, intraspecific competition for food was so severe that the unsuccessful portion of the population suffered delayed development. Under these circumstances, competition for prey will be intense, and any subtle mechanism reducing this competition will be advantageous to both predator species. The tentative hypothesis proposed here is that inverse age-related changes in the prey preference of the two damselfly species may constitute such a mechanism.

The mathematical model formalizing this hypothesis rests on one crucial assumption. The age-related predation suggested by data collected in the laboratory must be applicable to field populations of *Pyrrhosoma* and *Coenagrion*. This assumption is supported by the field history of the experimental predators. All had spent the majority of their life in the same small pond. Furthermore, the vast majority of the experimental predators emerged successfully (see Appendices 5 - 10), which implies that their physiological processes were not fundamentally altered by laboratory conditions. (see Sections 2.2.1. and 2.5.1.d) for further details). In addition, field work conducted by J. Cremona (personal communication) on *Pyrrhosoma* and *Coenagrion* in the New Forest, supports the premise that their post-diapause prey preferences are for smaller and larger prey respectively. In the field, final instar *Pyrrhosoma*'s predominant prey type is ostracods, whereas final instar *Coenagrion*'s is chironomid larvae.

2.5.1.b) Extension of Age-related Predation to a Series of Damselfly Age Classes

In order to simulate damselfly predation throughout the ultimate larval instar, the predicted numbers of mosquitos and daphnia eaten for a series of predator ages had to be calculated. To achieve this, for each predator-prey interaction, a number of functional responses were derived for different predator ages, using the procedure described in Section 2.2.2. to standardize predator age. The ultimate larval instar was divided into four age classes, each lasting ten days (for mean duration of ultimate instars see Section 2.2.2.). Predicted numbers of prey eaten at predator age twenty, Nep predict (Tables 2.10. and 2.11.), were transformed to correspond to the midpoints of each predator age class: thirty-five, twenty-five, fifteen, and five days before emergence. The appropriate mean slope for the particular predator-prey interaction (Figures 2.8. and 2.9.) was multiplied by the difference between the projected predator age and age twenty, and this value was then either added to or subtracted from the relevant predicted Nep, depending upon whether the projected age was greater or less than twenty days prior to emergence. (For example, the predicted Nep value for *Coenagrion* eating daphnia, at a prey density of 40, is 5.02. The corresponding Nep value for *Coenagrion* aged fifteen days before emergence will be:

$$5.02 - ((20 - 15) \times 0.2496) = 3.77)$$

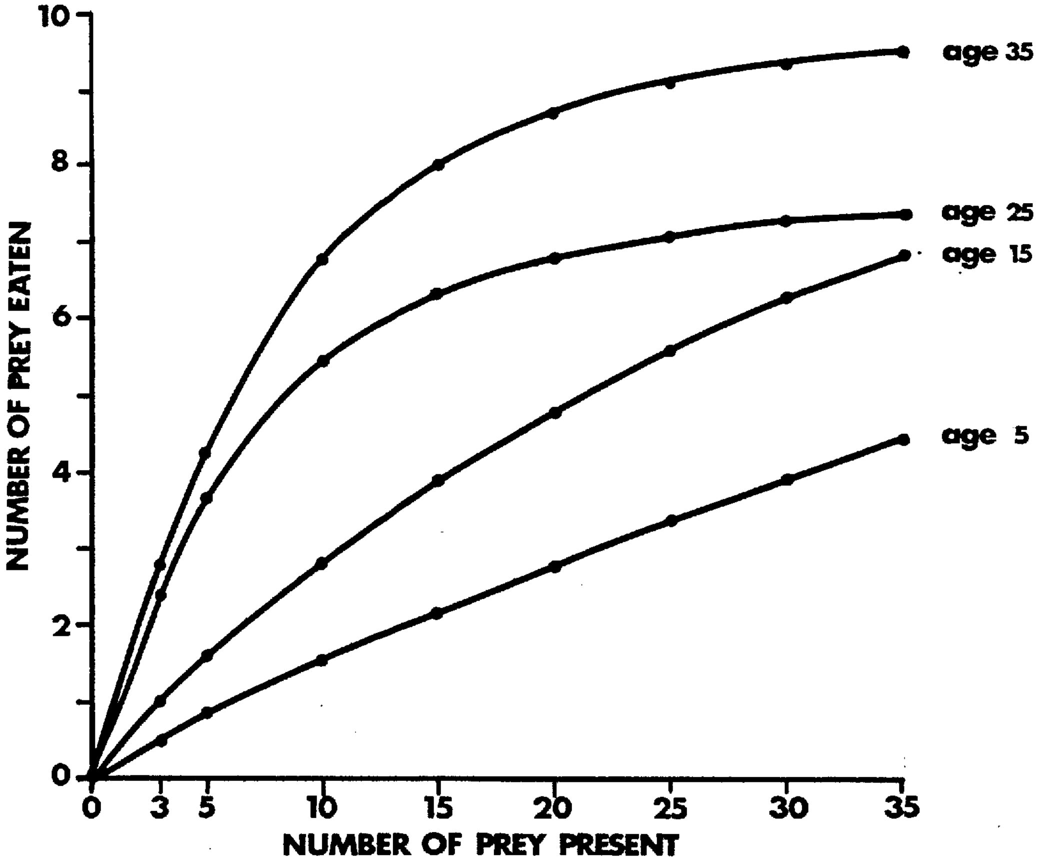
Estimations of a and Th were derived from these new Nec's in the usual way (Section 2.1.3.), and these regressions, as well as the new Nec data for each predator age on which they are based, are listed in Tables 2.19. to 2.22. Graphs of each functional response, projected for predator ages thirty-five, twenty-five, fifteen, and five days before emergence, are presented in Figures 2.29. and 2.30. The projected Nep's for age five *Pyrrhosoma* and *Coenagrion* are probably slight overestimates of the actual number of prey which would be consumed by damselflies of this age. By five days before emergence, both species would almost certainly have entered stage three metamorphosis, and feeding would probably have ceased completely.

It can be seen from Tables 2.19. to 2.22. that for the predator-prey interactions which are strongly affected by predator age, a declines and Th tends to increase as the damselfly approaches emergence. This holds for Pyrrhosoma feeding on daphnia, and for Coenagrion feeding on mosquitos (although in the former case, Th does not increase monotonically). For the other two predator-prey interactions, which are more weakly affected by predator age, both a and Th decrease as the damselfly approaches emergence (although in the case of Pyrrhosoma eating mosquitos, Th does not decline monotonically). An obvious consequence of these effects is the gradual erosion of Pyrrhosoma's initial preference for daphnia, and Coenagrion's initial preference for mosquitos. As the two damselfly species age, the changes in their prey preferences are inverse.

Predicted numbers of prey eaten from a mixture of prey, by each age class of each predator species, were derived in the same way as the predicted Nem and predicted Ned values in Table 2.16. The attack rate and handling time for each age class of each predator species (Tables 2.19., 2.20., 2.21., and 2.22.) were substituted into the mixed prey extensions of the random predator equation (Rogers, 1972; Lawton, Beddington and Bonser, 1974; Cock, 1977), to calculate predicted numbers of both prey types eaten, Nem and Ned, from each particular mixed prey combination. These results are listed in Table 2.23. (As mentioned in Section 2.4.3.b), these results are more likely to be realistic for Coenagrion than for Pyrrhosoma.) These data obviously reflect the inverse age-related changes in prey preference manifest by the two predator species. Post-diapause (age thirty-five) Pyrrhosoma has a pronounced preference for daphnia which gradually wanes as it approaches emergence, while Coenagrion's initial preference for mosquitos is similarly eroded.

Figure 2.29. - Functional Responses for Four Age Classes of *Pyrrhosoma nymphula*

a) with *Aedes aegypti* as prey



b) with *Daphnia magna* as prey

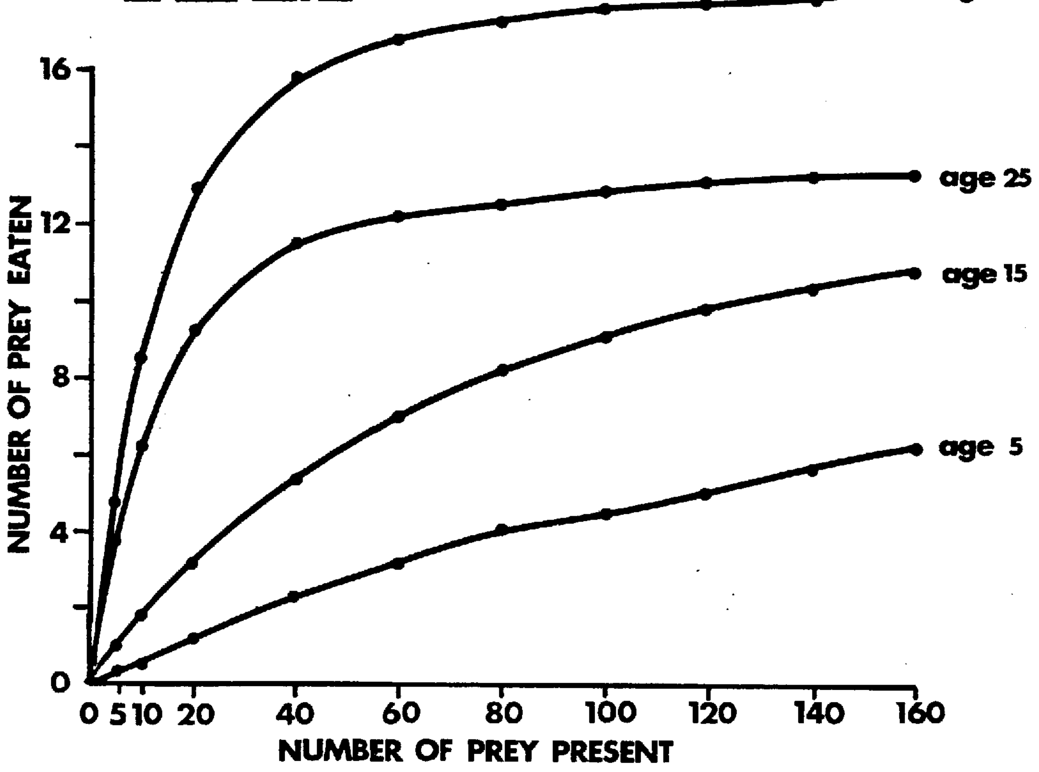


Table 2.19. - Age-Related Functional Responses of *Pyrrhosoma nymphula* to *Aedes aegypti*

predator age	No variable	3	5	10	15	20	25	30	35
35	derived Ne	4.42	5.28	6.85	7.85	8.52	8.99	9.34	9.61
	predicted Ne	2.71	4.23	6.75	7.98	8.64	9.03	9.29	9.48
25	derived Ne	2.57	3.43	5.00	5.99	6.67	7.14	7.49	7.76
	predicted Ne	2.42	3.64	5.44	6.29	6.75	7.04	7.23	7.37
15	derived Ne	0.71	1.58	3.14	4.14	4.81	5.29	5.64	5.91
	predicted Ne	0.95	1.50	2.77	3.84	4.77	5.56	6.25	6.85
5	derived Ne	-	-	1.29	2.29	2.96	3.43	3.79	4.06
	predicted Ne	0.45	0.74	1.43	2.10	2.73	3.33	3.90	4.45

Regressions and Functional Response Parameters

predator age	n	intercept	slope	F	significance	a(2 l./min.)	Th(min.)
35	6	-3.13	0.30	162.02	**	0.0087	34.1463
25	8	-2.34	0.29	54.14	**	0.0065	43.9416
15	8	-0.38	0.02	4.56	n.s.	0.0011	23.6237
5	6	-0.16	0.0063	0.785	n.s.	0.0004	13.8546

in all cases, Tt = 360 min.

** = significance at the 1% level
* = significance at the 5% level
n.s. = not significant

Table 2.20 - Age-Related Functional Responses of *Pyrrhosoma nymphula* to *Daphnia magna*

predator age	No variable	5	10	20	40	60	80	100	120	140	160
35	derived Ne	8.30	9.84	12.07	14.59	15.94	16.76	17.32	17.72	18.01	18.25
	predicted Ne	4.61	8.42	12.89	15.80	16.76	17.23	17.51	17.69	17.82	17.91
25	derived Ne	4.07	5.61	7.83	10.35	11.70	12.53	13.08	13.48	13.78	14.01
	predicted Ne	3.64	6.22	9.11	11.29	12.12	12.55	12.82	13.00	13.12	13.22
15	derived Ne	-	1.37	3.60	6.12	7.47	8.29	8.85	9.25	9.54	9.78
	predicted Ne	0.90	1.72	3.13	5.30	6.87	8.06	8.99	9.73	10.34	10.84
5	derived Ne	-	-	-	1.88	3.23	4.06	4.61	5.01	5.31	5.54
	predicted Ne	0.30	0.58	1.12	2.10	2.96	3.72	4.40	5.01	5.55	6.05

Table 2.20. - Age-Related Functional Responses of *Pyrrhosoma nymphula* to *Daphnia magna* (continued)

Regressions and Functional Response Parameters

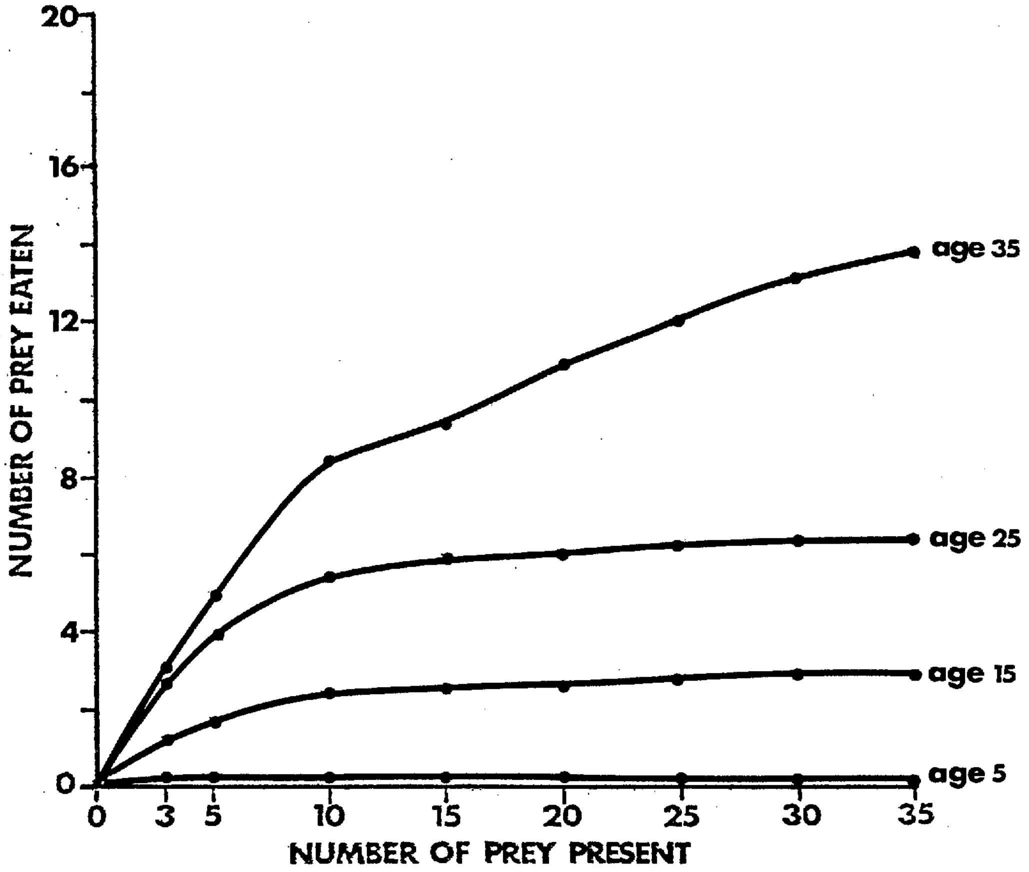
predator age	n	inter-cept	slope	F	signi-ficance	a(2 l./min.)	Th(min.)
35	10	-3.38	0.18	2.99	n.s.	0.0094	19.3947
25	10	-1.77	0.13	41.35	**	0.0049	25.8997
15	9	-0.21	0.01	14.50	**	0.0006	22.1843
5	7	-0.06	0.004	5.04	n.s.	0.0002	22.7907

in all cases, Tt = 360 min.

** = significant at the 1% level
* = significant at the 5% level
n.s. = not significant

Figure 2.30. - Functional Responses for Four Age Classes of *Coenagrion puella*

a) with *Aedes aegypti* as prey



b) with *Daphnia magna* as prey

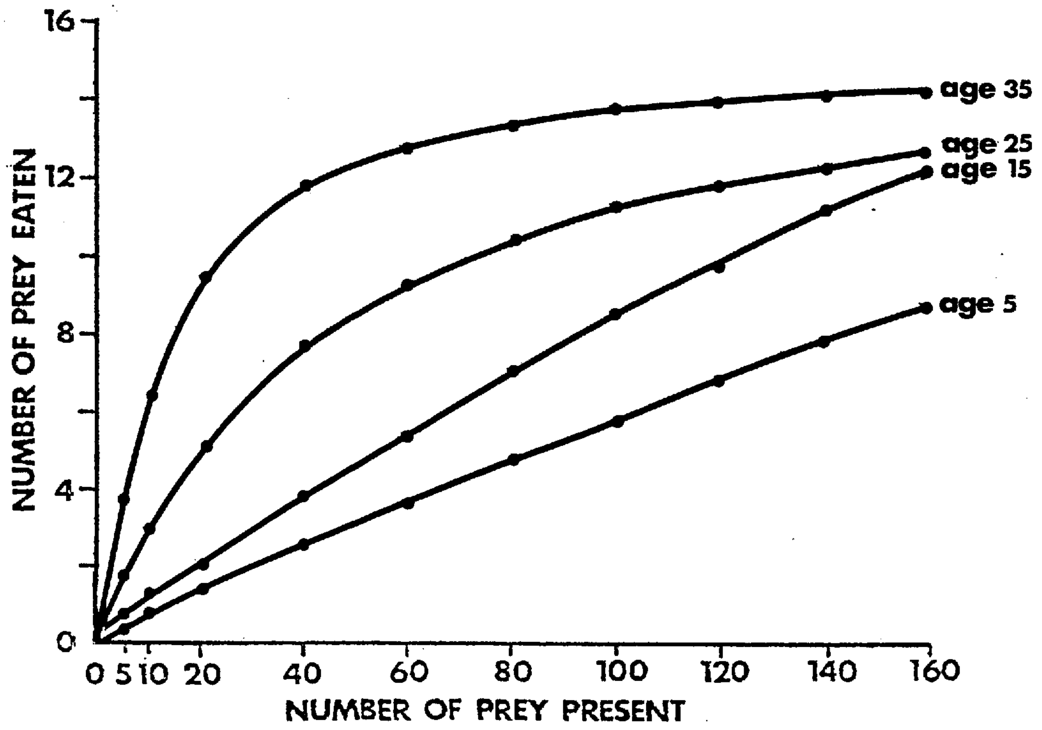


Table 2.21. - Age-Related Functional Responses of *Coenagrion puella* to *Aedes aegypti*

predator age	No variable	3	5	10	15	20	25	30	35
35	derived Ne	-	-	8.49	8.65	8.73	8.77	8.80	8.82
	predicted Ne	3.00	5.00	8.47	9.48	11.08	12.29	13.22	13.96
25	derived Ne	-	4.91	5.48	5.64	5.71	5.76	5.79	5.81
	predicted Ne	2.72	4.00	5.41	5.90	6.13	6.26	6.34	6.40
15	derived Ne	1.10	1.90	2.46	2.62	2.70	2.74	2.77	2.79
	predicted Ne	1.20	1.65	2.26	2.56	2.73	2.84	2.92	2.97
5	derived Ne	-	-	-	-	-	-	-	-
	predicted Ne	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Regressions and Functional Response Parameters

predator age	n	intercept	slope	F	significance	a(2 1./min.)	Th(min.)
35	6	-42.60	4.81	143.28	**	0.1183	40.6160
25	8	-3.95	0.59	0.44	n.s.	0.0110	53.3409
15	8	-0.81	0.24	25.64	**	0.0022	107.5070
5	-	-	-	-	-	-	-

in all cases, Tt = 360 min.

** = significance at the 1% level

* = significance at the 5% level

n.s. = not significant

Table 2. 22. - Age-Related Functional Responses of *Coenagrion puella* to *Daphnia magna*

predator age	No / variable	5	10	20	40	60	80	100	120	140	160
35	derived Ne	4.50	5.21	6.52	8.77	10.61	12.15	13.45	14.56	15.53	16.36
	predicted Ne	3.55	6.15	9.23	11.74	12.74	13.27	13.60	13.82	13.97	14.09
25	derived Ne	2.00	2.71	4.03	6.27	8.11	9.65	10.95	12.07	13.03	13.87
	predicted Ne	1.50	2.78	4.80	7.46	9.11	10.22	11.01	11.60	12.05	12.42
15	derived Ne	-	0.22	1.53	3.77	5.62	7.16	8.46	9.57	10.53	11.37
	predicted Ne	0.46	0.91	1.80	3.51	5.14	6.71	8.20	9.63	11.00	12.32
5	derived Ne	-	-	-	1.28	3.12	4.66	5.96	7.08	8.04	8.88
	predicted Ne	0.30	0.59	1.17	2.31	3.42	4.50	5.56	6.59	7.59	8.57

Table 2.22. - Age-Related Functional Responses of *Coenagrion puella* to *Daphnia magna* (continued)

Regressions and Functional Response Parameters

predator age	n	intercept	slope	F	significance	a(2 l./min.)	Th(min.)
35	10	-1.62	0.11	7.58	*	0.0045	24.0909
25	10	-0.41	0.03	21.59	**	0.0011	23.0744
15	8	-0.109	0.001	1.75	n.s.	0.0003	4.9627
5	5	-0.06	0.000	72.99	n.s.	0.0002	4.2353

in all cases, Tt = 360 min.

** = significant at the 1% level
* = significant at the 5% level
n.s. = not significant

Table 2.23. - Predicted numbers of Mixed Prey eaten by one individual of each predator age class

Pyrrhosoma nymphula

prey mixture	10 *Aedes aegypti* & 40 *Daphnia magna*		10 *Aedes aegypti* & 80 *Daphnia magna*		20 *Aedes aegypti* & 40 *Daphnia magna*		20 *Aedes aegypti* & 80 *Daphnia magna*	
predator age	number of *Aedes aegypti* eaten	number of *Daphnia magna* eaten	number of *Aedes aegypti* eaten	number of *Daphnia magna* eaten	number of *Aedes aegypti* eaten	number of *Daphnia magna* eaten	number of *Aedes aegypti* eaten	number of *Daphnia magna* eaten
35	2.76	11.79	1.69	14.49	4.38	9.38	2.91	12.51
25	2.53	7.88	1.63	10.07	3.89	6.02	2.73	8.39
15	2.06	4.61	1.63	7.22	3.65	4.08	2.96	6.53
5	1.26	2.00	1.13	3.56	2.42	1.91	2.17	3.42

Coenagrion puella

prey mixture	10 *Aedes aegypti* & 40 *Daphnia magna*		10 *Aedes aegypti* & 80 *Daphnia magna*		20 *Aedes aegypti* & 40 *Daphnia magna*		20 *Aedes aegypti* & 80 *Daphnia magna*	
predator age	number of *Aedes aegypti* eaten	number of *Daphnia magna* eaten	number of *Aedes aegypti* eaten	number of *Daphnia magna* eaten	number of *Aedes aegypti* eaten	number of *Daphnia magna* eaten	number of *Aedes aegypti* eaten	number of *Daphnia magna* eaten
35	7.40	2.00	6.68	3.29	8.28	0.80	7.87	1.51
25	4.64	2.42	4.08	4.09	5.62	1.30	5.21	2.38
15	2.23	1.21	2.19	2.38	2.70	0.70	2.68	1.39
5	0.00	2.31	0.00	4.50	0.00	2.31	0.00	4.50

2.5.1.c) Ultimate Instar Damselfly Age Structure

Simulation of the field population predation by Pyrrhosoma and Coenagrion required estimation of the age structure of the ultimate instar larval cohorts. (See Section 2.2.1.) Emergence data collected in this laboratory study for 1975 (see Appendices 5 - 10) gives mean emergence dates for Pyrrhosoma and Coenagrion as April 10±28 days (n = 36) and May 20±24 days (n = 35) respectively. Coenagrion emerged later than Pyrrhosoma, but was apparently equally well synchronized. Based on these facts, and the ambiguous status of Coenagrion as a 'summer species', both Pyrrhosoma and Coenagrion emergence curves were modelled in a similar way.

The mean emergence times of the laboratory populations were approximately the same as the field emergence periods given in Longfield (1937). Although the experimental damselflies had been exposed to an artificially short day photoperiod, this had evidently not delayed the onset of metamorphosis. This indicates that diapause had been broken by the time the damselflies were collected and brought into the laboratory. It seems clear that at this stage, post-diapause morphogenesis progressed relentlessly. Metamorphosis could not be prevented by the imposition of conditions capable of preventing it in damselflies still undergoing diapause development (Wells, 1974). Therefore, mean and median emergence dates for the experimental damselflies were used to simulate field population emergence.

2.5.1.d) Simulation of Population Predation

Damselfly emergence data was simulated using the lognormal distribution. This distribution has been used to simulate the emergence of red bollworm adults (Diparopsis castanea) (Murdie and Campion, 1972; Murdie, personal communication), and similar, positively skewed distributions have been used to simulate insect population development times, which also manifest a pronounced positive tail (Stinner, Rabb and Bradley, 1974; Sharpe et al., 1977). Data presented in Lawton (1969) confirms that such a skewed emergence curve is also characteristic of Pyrrhosoma populations in the field. Despite insufficient data to verify the goodness of fit of these particular emergence curves to the theoretical lognormal probability distribution, this positively skewed distribution appeared to most closely resemble the laboratory damselfly emergence data. Furthermore, the lognormal distribution is characterized by the mean exceeding the median, which exceeds the mode, and this is the case for both damselfly emergence curves. Figure 2.31. displays the actual and simulated cumulative emergence curves.

January 1, 1975 was chosen as day 1 for the lognormal simulation of both damselfly emergence curves. By this date, all of the Pyrrhosoma larvae due to emerge in the spring, and the semivoltine fraction of the Coenagrion population due to emerge in the spring, were in the final instar, and had completed diapause development (Corbet, 1957b; Lawton, 1971b; Parr, 1970). Although it is vanishingly probable that any individuals of either predator species would have completed metamorphosis by this date, it is convenient to use January 1 as the theoretical first day of emergence, since this facilitates the calculation of the age structure of the damselfly populations throughout the spring, when competition is likely to be intense. Hence each particular day, x, during the emergence period of each damselfly species, was defined in terms of the number of days elapsed since January 1.

Normal distribution parameters μ and σ were derived from the laboratory emergence data for each species, using the formulae for the lognormal distribution (Colquhoun, 1971):

$$\mu = \log\ (\text{median})$$

$$\sigma^2 = \frac{\log\ (\text{mean}) - \log\ (\text{median})}{1.1513}$$

Each date, x, during the emergence period for each predator species, was then transformed to its standard normal counterpart, z , using the formula:

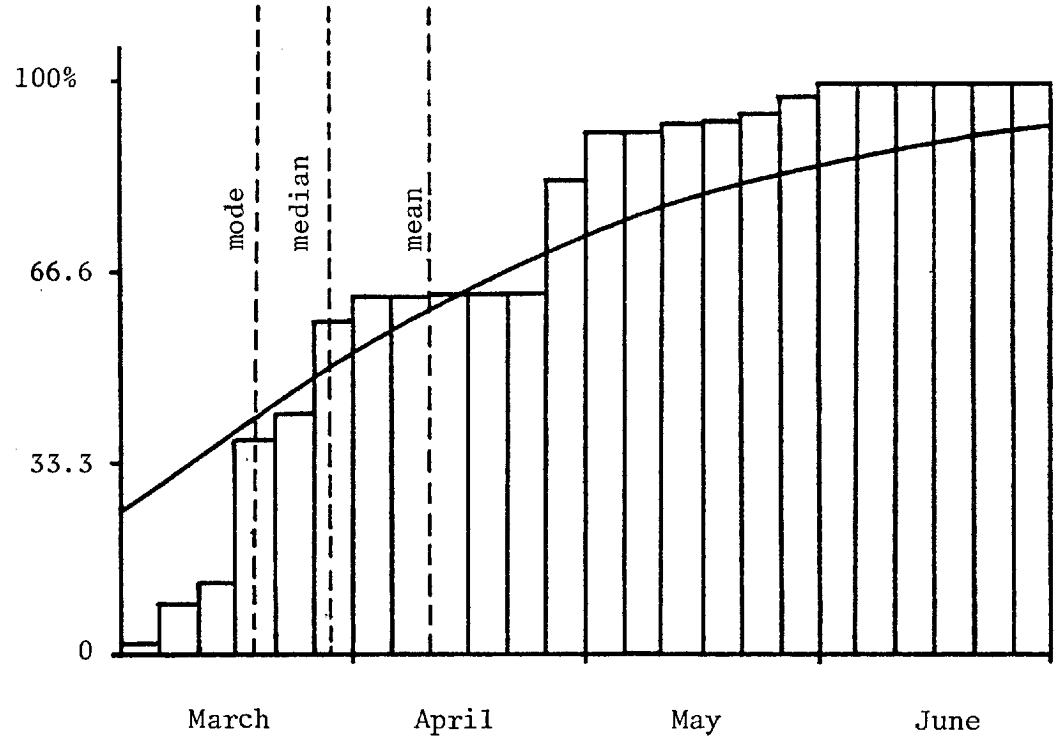
$$z = \frac{\log\ (x) - \mu}{\sigma} .$$

The normal probability integral for each z then represents the proportion of the damselfly population which has emerged by date x. From these proportions, the fraction of the damselfly population in each of the four age classes defined in Section 2.5.1.b) was calculated retroactively. For example, the same proportion of the damselfly population emerging between date x and date x+10, was obviously between 1 and 10 days prior to emergence between dates x-10 and date x. (For results of above calculations, see Appendix 44).

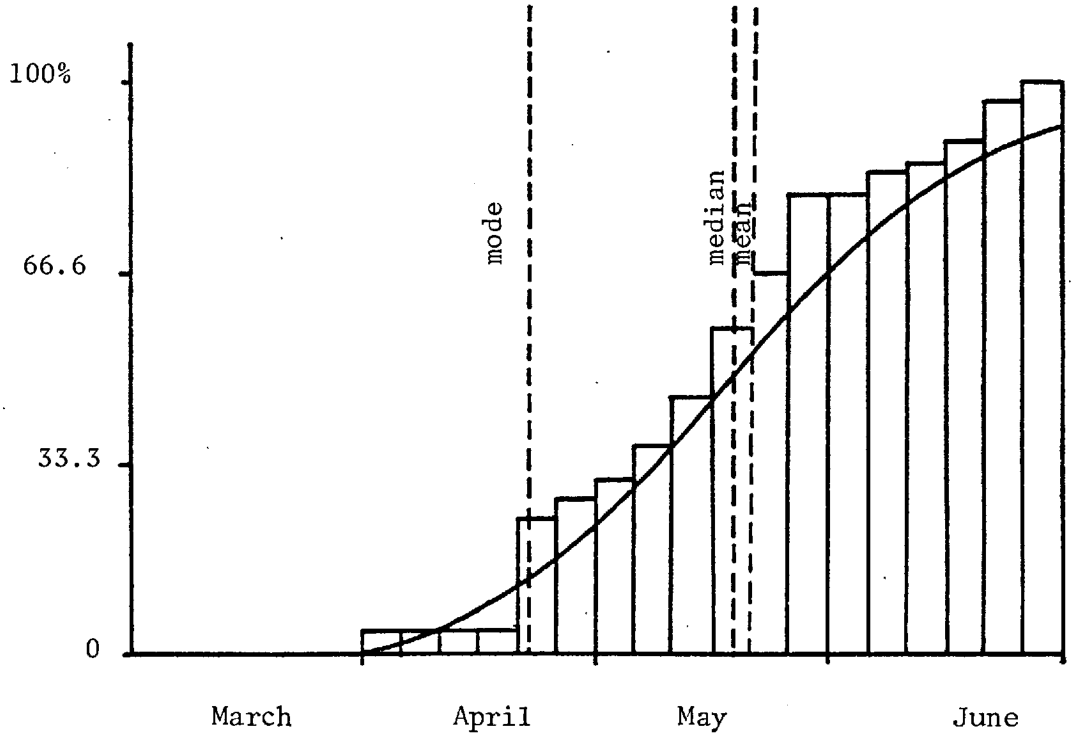
Summing the products of the proportion of each damselfly population in each age class and the appropriate Ne factor for each prey type, provides a very hypothetical estimate of the average number of each prey type eaten by an average individual of that predator population, on that particular day during the spring.

Figure 2.31.- Cumulative Percentage of Damselflies Emerged

Pyrrhosoma nymphula



Coenagrion puella



The histograms represent data collected in this study in 1975, and the curves represent the lognormal simulation of the population emergence pattern.

2.5.1.e) Model Results

The model discussed in the previous section simulated the hypothetical average number of each prey type eaten by an average individual of each predator population, NePn and NeCp, for five day intervals from December 1, 1974 to August 18, 1975. The results, computed for the combinations of mixed prey studied experimentally (Section 2.4.), are presented in Appendix 45. Estimates of the total number of each prey type eaten by an average individual of each predator species, over the period from 1/12/1974 to 18/8/1975, NEPN and NECP, were also calculated, as were estimates of the total quantity of energy consumed by each predator throughout the spring, the absolute overlap in prey eaten by the two predators, AO, the overlap in joules in prey eaten by the two predators, JO, and the relative overlap in prey eaten by the two predators, RO. Formulae used to calculate these overlap estimates were based on the area under the curve formed by the number of prey eaten at each date by the less voracious predator:

$$AO = \sum_{1/12/74}^{18/8/75} (\text{minimum of } (NePn,\ NeCp))$$

$$JO = AO \times 2.5 \times 4.184 \text{ for mosquitos}$$

$$JO = AO \times 4.184 \text{ for daphnia}$$

$$RO = \frac{AO}{NEPN + NECP} \ .$$

Results of these calculations are presented in Table 2.24. (For an example of the computer program, and its output, see Appendix 46).

Examination of Table 2.24. and Appendix 45 reveals a clear division of resources between Pyrrhosoma and Coenagrion. One Pyrrhosoma individual eats many more daphnia than a Coenagrion individual throughout the spring, while one Coenagrion individual eats many more mosquitos than a *Pyrrhosoma* individual during the same period. The proportion of each predators intake which is less than the intake of the competing predator, throughout the spring (i.e. $\frac{AO}{NEPN}$ and $\frac{AO}{NECP}$); emphasizes these differences. *Pyrrhosoma*'s intake of mosquitos is virtually eclipsed by *Coenagrion*'s, and the reverse is true for daphnia. Furthermore, only a small fraction of *Pyrrhosoma*'s intake of daphnia is overlapped by *Coenagrion*'s daphnia intake. This is especially true when daphnia are rare, relative to mosquitos, in the environment. Under these circumstances, *Coenagrion*'s preference for mosquitos is most pronounced (Table 2.17.). Similarly, *Coenagrion*'s intake of mosquitos is only barely overlapped by *Pyrrhosoma*'s. Again, this overlap is smallest when mosquitos are rarest relative to daphnia, and *Pyrrhosoma* is exercising its greatest preference for daphnia.

These differences are clearly reflections of the prey preferences of the young, post-diapause (age 35) larvae (Table 2.23.). The damselflies are most voracious at this stage, and consequently, their prey choice has a pronounced effect on the feeding of the population as a whole. This is especially true in the late winter, when young final instar larvae are predominant in both damselfly populations, and when prey are least abundant. In fact, this model may slightly underestimate the differences in prey consumption between these two damselfly species, since the old (age five) larvae are assumed in the model (Section 2.5.1.b)) to continue feeding at a very low rate, right up until emergence. In reality, both predator types probably cease feeding before they reach this age, and their prey preferences just before they stop feeding are likely to differ more than they do in the projected age five data. (However, this effect is somewhat countered by the fact that *Pyrrhosoma* may take fewer daphnia than predicted (see Section 2.4.3.b).)

The differences in the total number of joules consumed by each damselfly reflect the higher energy content of mosquitos, when compared to daphnia. *Coenagrion*'s strong predicted selection of mosquitos therefore results in a high intake of calories, whereas *Pyrrhosoma's* higher predicted consumption of daphnia provides it with fewer calories per prey captured, and a lower total energy intake. Any differences in the digestibility of these two prey species would tend to accentuate the differences in the total energy consumed by each predator species, because mosquitos have a lower proportion of carapace to body volume, and are likely to be more efficiently digested than daphnia.

As temperatures rise in the spring, and prey become more abundant, damselfly exploitation probably has a decreasing effect on prey density. Consequently, each predator species is less likely to affect the prey resources available to the other, as spring wears on. It is notable that the inverse damselfly prey preferences gradually become less pronounced at this time. This suggests that the resource division discussed above may be critical. Overlap in resource use would certainly be greater, and competition would be more intense, without the inverse age-related preferences of these two predators. It is conceivable that the continued coexistence of these two large damselfly populations would not otherwise be possible.

Table 2.24. - Model Results

prey	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*
prey density	10	40	10	80	20	40	20	80
Total number of prey eaten by one individual of *Pyrrhosoma nymphula* (NEPN)	67.17	266.56	42.69	333.50	107.90	213.00	74.09	288.58
Total number of joules consumed by one individual of *Pyrrhosoma nymphula*	1817.89		1841.90		3356.61		1982.40	
Total number of prey eaten by one individual of *Coenagrion puella* (NECP)	225.31	68.96	203.52	115.82	253.37	31.40	240.78	59.53
Total number of joules consumed by one individual of *Coenagrion puella*	2645.27		2613.41		2781.63		2767.63	

Continued....

Table 2.24. - Model Results (continued)

prey	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*
prey density	10	40	10	80	20	40	20	80
Absolute Overlap (AO)	66.59	68.96	42.42	115.82	106.56	3140	73.37	59.53
Overlap in Joules (JO)	696.53	288.53	443.71	484.59	1114.62	131.38	767.45	249.07
Relative Overlap (RO)	0.23	0.21	0.17	0.26	0.29	0.13	0.23	0.17
AO/NEPN	0.99	0.26	0.99	0.35	0.99	0.15	0.99	0.21
AO/NECP	0.30	1.00	0.21	1.00	0.42	1.00	0.30	1.00

2.5.2. Discussion of Changes in Damselfly Predatory Behaviour with Age

The incorporation of age-structure into the ultimate instar cohorts of Pyrrhosoma and Coenagrion (see Section 2.5.1.b)) permits further analysis of the damselflies' predatory behaviour throughout this instar. The predicted numbers of mixed prey eaten by an individual in each age class of each species can be monitored. This will give some indication of the changes in predator preference, diet breadth and competition which are predicted to occur, as each of the damselfly species approaches emergence.

Obviously, the realism of these predicted results will be limited by 1) the accuracy with which the predicted mixed prey results mimic the actual mixed prey results, for predators aged 20 (see Tables 2.16. and 2.17.), and 2) the accuracy with which the age-relations mimic actual damselfly behaviour (see Figures 2.8. and 2.9.). Section 2.4.3.b) discusses the actual and predicted mixed prey results for both predators at age 20. It is noted that the actual results are similar to those predicted for Coenagrion, but Pyrrhosoma exercises considerably more preference for mosquitos than was predicted. This has obvious consequences for the mixed prey results projected for each predator age class. The Nem's and Ned's predicted for Coenagrion at each age are more likely to be realistic than those predicted for Pyrrhosoma (Table 2.23.).

The accuracy of the age-relation is discussed at length in Section 2.2.2.c). As noted there, it is likely that the stronger age-relations (i.e. Pyrrhosoma eating daphnia, and Coenagrion eating mosquitos), are more accurately simulated than the weaker ones. This will hold for the mixed prey results projected for each predator age class. The behaviour predicted for Pyrrhosoma eating daphnia, and Coenagrion eating mosquitos, is probably more realistic than the behaviour predicted for Pyrrhosoma eating mosquitos, and Coenagrion eating daphnia.

The average preference indices, Em, Ed and c, calculated from the mixed prey results predicted for each age class of each predator species are listed in Table 2.25. These indices reflect the same changes in predator preference as were discussed in Section 2.2.2. Post-diapause (age 35) Pyrrhosoma has a very slight preference for daphnia, which is gradually eroded as the damselfly ages. At twenty-five days before emergence, there is a slight preference for mosquitos, and by age fifteen the preference for mosquitos has been firmly established, and is increasing. Just before emergence, Pyrrhosoma very definitely prefers mosquitos to daphnia. However, the above data must be regarded with a certain amount of scepticism. The observed Pyrrhosoma behaviour at age twenty reveals a much stronger preference for mosquitos than the mixed prey extensions to the random predator equation predicted. Therefore, although the direction of the projected changes in Pyrrhosoma's preference is probably correct, the degree of preference for mosquitos has probably been underestimated.

The projected change in Coenagrion's prey preference is practically the reverse of Pyrrhosoma's. A rather strong post-diapause (age 35) preference for mosquitos is manifested, after which preference for daphnia gradually increases, and finally exceeds preference for mosquitos just before the damselfly emerges.

It must be borne in mind that while these changes in the relative numbers of prey eaten are taking place, the absolute numbers of prey eaten are declining, as both damselflies age. Hence, a strong preference for mosquitos shortly before emergence could result in lower consumption of mosquitos than a weaker preference would, earlier in the instar.

The c values predicted for each predator age reflect the trends documented in Section 2.4.3.c). Although the c values change with predator age, there is little difference between these values at the different mixed prey combinations for each age. Switching on to mosquitos is predicted only for Coenagrion at age 35, which displays a most pronounced preference for mosquitos.

Table 2.26. lists predator diet breadths and competition coefficients, for all predator age class combinations, for the mixed prey combination of 10 mosquitos : 40 daphnia. Since the relationships between the relative availability of mosquitos, predator diet breadths, and predator competition coefficients are generally preserved, despite changes in predator age (see Appendices 46 - 8), data are included in the text for this mixed prey combination alone. (One consistent exception is that an increase in the relative abundance of mosquitos does not increase diet breadth either for Pyrrhosoma age thirty-five, or for Coenagrion aged five).

Predator diet breadth changes in accordance with the age-related changes in prey preference discussed in Section 2.4.3. As Pyrrhosoma ages, it specializes increasingly on mosquitos, and its diet becomes narrower, while the reverse is true of Coenagrion. The competition coefficients undergo corresponding changes. As Pyrrhosoma ages, and becomes more of a specialist, it is more strongly affected by Coenagrion's similar preference for mosquitos.

On the other hand, as Coenagrion ages, and expands its diet to include more daphnia, it affects Pyrrhosoma less. The above process is reversed, when applied to Pyrrhosoma's effect on Coenagrion.

It is notable that only when Pyrrhosoma is younger than Coenagrion does Pyrrhosoma's effect on Coenagrion exceed Coenagrion's on Pyrrhosoma. These circumstances are very improbable, given Pyrrhosoma's earlier emergence in the spring, and in most natural situations Coenagrion will have a greater effect on Pyrrhosoma than vice versa. In fact, Coenagrion's effect on Pyrrhosoma is most adverse under the most likely circumstances, when Coenagrion is young and Pyrrhosoma is old.

Table 2.25. - Preference and Switching Indices for Age-Related Mixed Prey Results

predator age	35	25	15	5
Pyrrhosoma nymphula				
average Em	-0.03	0.10	0.22	0.32
average Ed	0.01	-0.03	-0.08	-0.14
c for Nom: Nod = 20:40	0.93	1.29	1.79	2.53
average c for Nom: Nod = 10:40, 20:80	0.94	1.29	1.80	2.53
c for Nom: Nod = 10:80	0.93	1.29	1.81	2.54
Coenagrion puella				
average Em	0.60	0.54	0.53	-0.00
average Ed	-0.62	-0.42	-0.39	0.12
c for Nom: Nod = 20:40	0.47	8.65	7.71	0
average c for Nom: Nod = 10:40, 20:80	0.61	8.22	7.54	0
c for Nom: Nod = 10:80	0.72	7.98	7.36	0

Table 2.26. - Age-Related Changes in Diet Breadths and Competition Coefficients, for Mixed Prey Densities of 10 *Aedes aegypti* and 40 *Daphnia magna*

Pyrrhosoma nymphula age	*Coenagrion puella* age	*Pyrrhosoma nymphula* diet breadth	*Coenagrion puella* diet breadth	α PnCp	αCpPn
35	35	0.3052	0.0257	1.8969	0.3830
35	25	↓	0.0367	1.2215	0.6239
35	15	↓	0.0378	0.5874	1.3022
35	5	↓	0.6400	0.0612	5.0893
25	35	0.2163	0.0257	2.3952	0.3494
25	25	↓	0.0367	1.5318	0.5652
25	15	↓	0.0378	0.7362	1.1790
25	5	↓	0.6400	0.0570	3.4249
15	35	0.1500	0.0257	3.2530	0.2809
15	25	↓	0.0367	2.0692	0.4520
15	15	↓	0.0378	0.9940	0.9426
15	5	↓	0.6400	0.0558	1.9866
5	35	0.1011	0.0257	5.6002	0.1714
5	25	↓	0.0367	3.5476	0.2746
5	15	↓	0.0378	1.7037	0.5724
5	5	↓	0.6400	0.0681	0.8580

3. General Discussion

3.1. Damselfly Guild Ecology

In the preceding sections of this chapter, various aspects of the behaviour and natural history of two damselfly species have been discussed. The sit and watch experiments, the age-related predation, and the mixed prey experiments have been examined in turn, and interpreted independently. The four original hypotheses have been tested. It is only when all these results are related to the field ecology of these two damselfly species, that their meaning becomes clear. The separate and often tentative conclusions suggest a definite pattern in the relationships between these two predator species and the environment.

Pyrrhosoma is usually found in rather acidic ponds, where productivity is low. In these areas, high densities of large prey are uncommon. Young final instar larvae, whose feeding rate is maximal, eat daphnia in preference to mosquitos in the laboratory (Section 2.5.2.), and ostracods have been found to form the bulk of the diet of these particular larvae in the field (J. Cremona, personal communication). Most of the prey available in acidic ponds are small, and in this context, the preference for small prey exhibited by these Pyrrhosoma larvae is not surprising.

Nevertheless, considerable behavioural plasticity permits this damselfly to feed successfully on a variety of prey types. When exposed to a mixture of prey, Pyrrhosoma is able to selectively eat the prey type which is most efficiently metabolized (Section 2.4.2.). These are important attributes for a predator with a long and variable life history.

Pyrrhosoma can take between one and three years to complete larval development (Macan, 1974), and intraspecific competition for food has been cited as the probable determinant for this polymorphism (Macan, 1966). Arguments based on the theory of inclusive fitness support this conjecture. The small, and largely inbreeding populations of Pyrrhosoma found in ponds like Swinley Brick Pits, are probably composed of quite closely related individuals, and in such circumstances, intraspecific competition for the richest ambush sites is unlikely to lead to competitive interference and aggression. The less successful competitors are probably willing to accept inferior microhabitats, with the consequent delay in larval development which accompanies a reduced feeding rate (Hassan, 1976). Hence, some Pyrrhosoma individuals are relegated to very poor microhabitats, where overall prey abundance is extremely low.

Flexible feeding behaviour is a great advantage in such situations, when efficient use of all the food and space available is essential (Southwood, 1977). Using Schoener's (1971) terminology (Section 1.3.1.), Pyrrhosoma adopts the strategy of a time minimizer, consuming the energy necessary to complete development as rapidly as possible, in order to minimize the number of years spent in the larval stage.

Coenagrion is best adapted to rather different habitats, and is usually found in rich, eutrophic ponds. In such environments, the aquatic community is relatively complex, and large prey are probably far more abundant than in acidic ponds. Both in the laboratory, where mosquitos are taken in preference to daphnia (Section 2.4.2.), and in the field, where chironomid larvae have been observed to be the dominant prey (J. Cremona, personal communication), young ultimate instar Coenagrion larvae appear to adopt a highly selective predatory strategy. The narrow diet and the strong and rather rigid specialization on large prey exhibited by these Coenagrion larvae are clearly advantageous only when large prey are abundant.

Coenagrion almost always completes larval development within one year, and attains an adult weight similar to Pyrrhosoma's (see Appendices 5 - 10) in approximately half the time. Time is clearly the limiting factor for Coenagrion (Southwood, 1977). It is therefore very important for this species to feed in such a way that its growth efficiency is maximal. Coenagrion adopts a predatory strategy similar to Schoener's (1971) energy maximizer. (Jacobs (1955) found that dragonfly male fertility is correlated with the ability to hold a territory and the exercise of intra-specific aggression. It would be of interest to determine whether larval feeding affects this ability in Coenagrion , as predicted by Schoener's (1971) theory of the energy maximizing strategy.) Since larval development time is more or less fixed, larvae will benefit from consuming as much energy as possible during this period. Coenagrion probably has a higher rate of energy intake than Pyrrhosoma (Table 2.24.), and may have a lower energetic cost of maintenance (Section 2.4.1.). The exercise of preference for prey yielding a large energy return is another way of ensuring high growth efficiency, and the disadvantages of such a strategy are minimal in eutrophic environments. Reduced predatory success on high densities of small prey (as exhibited by Coenagrion's Necp when compared to Pyrrhosoma's Necp at daphnia densities of sixty to 120 per two litres of water (Tables 2.10. and 2.11.), is unlikely to seriously hinder larval development in a productive pond where large prey are readily available.

These two damselflies, together with a third species, Lestes sponsa (Hansemann), form the Zygopteran guild at Swinley Brick Pits, where the experimental predators were collected. Lestes sponsa is a univoltine species which completes larval development in a few months in the spring. In many ways, this species adopts a more extreme form of the specialist strategy employed by Coenagrion. Strong preferences for very large ephemeropteran prey have been documented (Fischer, 1966 and 1967), and all larval development is restricted to a period in the late spring, when prey abundance is high. Lestes sponsa appears to be adapted to frequent feeding. Experiments carried out in 1974 and 1975 on this species, indicate that starvation confuses these larvae, and reduces the mean numbers of prey eaten (see Section 2.2.5.). For this species, efficiency in the use of the time available for predation is crucial. Larval moulting is rapid, and metamorphosis reduces feeding for only a very brief period before emergence (Fischer, 1966 and 1967) (see Section 2.2.2.b)).

The three species comprising the damselfly guild at Swinley Brick Pits represent a series, in terms of their diet breadth, and the duration of their larval life. Each species has a corresponding position with regard to the ecological succession of these ponds. Pyrrhosoma has a broad diet and a long life, and is adapted to relatively unproductive, acidic, and deep aquatic environments. This species was probably the first Zygopteran to colonize the area, and was able to survive when prey were scarce, by eating all potential prey encountered, and by lengthening its life cycle to accommodate reduced growth efficiency. Coenagrion has a narrower diet, and a shorter larval life than Pyrrhosoma , and probably invaded the pond after Pyrrhosoma , when productivity was higher and large prey had become more abundant. By this time Pyrrhosoma was well established, whereas Coenagrion's density probably rose gradually, as eutrophication advanced, large prey became more plentiful, and Pyrrhosoma was gradually displaced by Coenagrion's superior competitive ability (Section 2.4.2.). Lestes sponsa, with an even narrower diet, and shorter larval life than Coenagrion, was probably the most recent damselfly colonist of this pond. Only when there was a reliably high density of large prey, could Lestes sponsa be successful.

These conjectures lend some support to the hypothesis that size-selective predation by a dominant predator can favour the existence of another predator, adapted to feed on the dominant predator's non-preferred prey (Dodson, 1970). In the system studied here, Coenagrion may reduce chironomid density to the point at which a surplus of the resources normally used by chironomids, are absorbed by ostracod and cladoceran populations. The increased density of these prey types may then provide a secure food resource for Pyrrhosoma populations in eutrophic ponds.

In the period between 1974 and 1977, when this study was conducted, the ponds at Swinley Brick Pits became increasingly eutrophic (Plate 2.1.). Aided by the drought in the summer of 1976, which concentrated the aquatic organisms in a smaller volume of water, the productivity of these ponds rose, while their size decreased. In 1975 and 1976, *Pyrrhosoma* was far more abundant than *Coenagrion* at Swinley Brick Pits, but in 1977, after the drought, these proportions were reversed (Appendix 22). Two distinct ecological factors are probably responsible for these changes in the damselfly species abundances.

Short lived organisms have an enhanced ability to track environmental changes. In the summer of 1976, the *Pyrrhosoma* larvae were trapped in the dessicating pond, and the adult fraction of the population probably oviposited in this same pond, at a time when it still contained some water. *Coenagrion*, emerging later, was prevented by the low water level from ovipositing in the pond from which it had emerged, and was forced to oviposit in the adjacent deeper pond, thus avoiding dessication of the young larvae later in the summer.

Coenagrion's superior competitive ability (Section 2.4.2.) is the other probable cause for the change in the proportions of *Pyrrhosoma* and *Coenagrion* at Swinley Brick Pits. As the ponds became more eutrophic, *Coenagrion*'s predatory strategy was probably favoured more than *Pyrrhosoma*'s less selective predation. *Coenagrion* may have gradually outcompeted *Pyrrhosoma*, to become the dominant Zygopteran at this pond, as it is in the productive New Forest pond studied by J. Cremona (personal communication). Eventually, as Swinley Brick Pits become still more productive and more vulnerable to dessication, the dominant position may be adopted by *Lestes sponsa*. By this time, *Pyrrhosoma* may be absent altogether, and *Coenagrion* may be much less abundant, as the prolonged and frequent periods during which the pond is dry prove increasingly disruptive to *Coenagrion*'s life cycle.

The different strategies adopted by Pyrrhosoma and Coenagrion are roughly analagous to the *K* and *r* strategies described by Southwood (1977). Pyrrhosoma resembles Southwood's *K* species, for which synchronous emergence, long generation time and short reproductive life are offset by efficiency in the use of food and space. Coenagrion is closer to Southwood's *r* species, with a short life cycle, and highly efficient use of time. It would be interesting to determine whether the other attributes of these two species conform to the pattern described by Southwood. Are fecundity, dispersal level, and variability of population density over time, greater for Coenagrion than for Pyrrhosoma, as Southwood's theory predicts? Future research on these matters would doubtless prove rewarding.

One ecological factor for which the results of this study differ from the pattern described by Southwood (1977), is intraspecific competition. Whereas *K* species are predicted to invest heavily in mechanisms for intraspecific competition, Pyrrhosoma probably does not. As the theory of inclusive fitness would predict for a small, inbreeding population, Pyrrhosoma probably accepts poorer ambush sites, rather than engaging in aggressive intraspecific encounters. Alternatively, Coenagrion is almost certainly more competitive than Pyrrhosoma, having a more inflexible life history, and being less able to absorb any developmental delays due to the reduced feeding rate which accompanies competitive failure.

3.2. Damselfly Predatory Variability

The series of experiments described in Section 2. were designed to test hypotheses regarding alternative predatory strategies. I attempted to examine these rather sophisticated theories of field ecology using the traditional experimental method. A simple laboratory experiment was established which eliminated the influence of almost all variables except those under investigation - the number and type of prey available to the predator. While conducting these experiments, and answering some of the original questions posed, unanticipated complexities in the predatory process became apparent, and further questions posed themselves. Why are the functional responses of these damselflies variable, and also rather irregular?

These uncertainties prompted further investigations into damselfly predation. How do the various controls in the experimental situation affect damselfly feeding behaviour? The experiments in Section 2.2. revealed that damselfly predation is sensitive to a complex assemblage of interacting factors. The type of artificial lighting affects the prey distribution, which is in turn granted more or less scope for clumping by the size of the experimental arena. The position of the predator in the arena, and the location and degree of movement of any prey clumps also can limit or accentuate predatory variability. The hunger of the predator affects both the variance and the mean number of prey eaten. Finally, the age of the damselfly within the ultimate instar was shown to be crucial in determining the number and proportion of prey eaten by the damselflies. The more rigorous control of all these factors reduced the variability of the functional response data considerably, but did not result in consistent type 2 functional response curves.

These irregularities were further investigated by sit and watch experiments, in which the parameters of the random predator equation (Rogers, 1972) were measured empirically (see Section 2.3.).

The resulting observations were combined with theoretical simulations of the effects of varying parameters on the shape of the functional response curve. This confirmed that attack rate and handling time probably do vary with prey density in many cases, and that these variations can be masked, so that the resulting functional response curves in no way betray the violation of the assumptions on which the functional response model rests.

The mixed prey experiments revealed further sensitivity and flexibility in damselfly predatory behaviour. (see Section 2.4.). Neither predator behaved in quite the way predicted. While the expected innate preference for mosquitos was confirmed, for both damselflies, Pyrrhosoma displayed more, and Coenagrion less, preference than had been expected. This behavioural preference for Pyrrhosoma for mosquitos reveals considerable behavioural flexibility; the presence of alternative prey is clearly yet another factor influencing damselfly predation.

The cumulative effects of all these factors are incorporated into a model of damselfly field predation in Section 2.5. This does illustrate general predatory strategies which would minimize competition between the two damselfly species. Nevertheless, the general conclusion of this thesis must be that the complexity of the predatory process is enormous; variation in most external circumstances is likely to alter the way damselflies eat. Until this process is better understood, direct application of predation theory to the field situation is unlikely to yield precise, accurate predictions.

4. Conclusions

A series of experiments investigating predation by *Pyrrhosoma nymphula* and *Coenagrion puella* on *Aedes aegypti* and *Daphnia magna* revealed the influence of a number of factors on damselfly predatory behaviour.

1) Damselfly age within the ultimate instar was found to significantly affect the numbers and proportions of prey eaten. A linear regression was used to model the decline in damselfly feeding as age increased. The declines in the two damselflies' feeding rates on each prey type were significantly different.
2) Experiments on *Lestes sponsa* revealed that the period of starvation prior to experimentation also affected the variance and mean number of prey eaten. Experiments conducted after two days of starvation produced more uniform data than those conducted after only one day of starvation.
3) Distribution of the two prey types was found to be clumped, but the proximity of the clumps to the experimental predators, the continual movement of the clumps, and the uniform light conditions within each experimental arena almost certainly prevented this factor from differentially affecting different experimental replicates.
4) Arena size was found to have an important influence on damselfly predatory variability. Functional response variances were much higher in experiments conducted in larger arenas.
5) Expirical measurements of the functional response parameters during predation experiments revealed that changes in prey density probably do alter these parameters, in some cases. Computer simulations illustrated possible effects of changing functional response parameters, and revealed that in some cases, changes in attack rate and handling time may cancel each other out, to produce seemingly normal type 2 functional response curves.

6) Experiments with both prey types available to the predators in one arena, revealed that both predators have innate preferences for mosquitos over daphnia. Pyrrhosoma has a further behavioural preference for mosquitos, over and above the preference predicted by the mixed prey extensions to the random predator equation.

7) Neither predator switched. Both species ate a higher proportion of mosquitos when they were relatively rarer.

8) Pyrrhosoma had a broader diet than Coenagrion and was strongly affected by competition from Coenagrion, whereas on the whole, intraspecific competition affected Coenagrion more than interspecific competition did. Both predators' diet breadths increased with an increase in prey abundance. This was correlated with an increase in Pyrrhosoma's competitive effect on Coenagrion, while Coenagrion affected Pyrrhosoma most when Pyrrhosoma's diet was most specialized.

9) A mathematical model, based on the age-related predation, was developed. This model simulated the number of prey of each type eaten by each age class of each damselfly species throughout the spring. The inverse changes in the prey preferences of the two predators are suggested as one possible mechanism for reducing the intensity of competition between these two species in the field.

10) Implications of these results for the field ecology of the local damselfly guild are discussed, and the feeding behaviour of each predator is related to its life cycle and natural history.

11) The sensitivity of damselfly predatory behaviour to all these factors is discussed, and the unfortunate increase in predatory variability, with more natural, realistic experimental conditions is noted.

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APPENDIX

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APPENDIX 1 - Damselfly Feeding Rate Data (1974)

No.	10	20	30	40	50	60
Ne/hour (mosquitos) during:						
1st	5	5	9	13	13	14
2nd	1	0	1	1	1	0
3rd and 4th	1	0.5	0.5	0.5	1.5	0
5th and 6th	0.5	0.5	0.5	0.5	0.5	0
7th to 24th hours	-	0.4	0.5	0.8	0.9	0.7

APPENDIX 2 - Control *Daphnia magna* Mortality Data (untreated results from 1974)

No = 10		No = 20		No = 40		No = 60		No = 80		No = 100		No = 120		No = 140	
number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead
0	0	0	0	3	.075	1	.017	3	.04	5	.05	7	.06	6	.04
0	0	0	0	0	0	3	.05	2	.025	6	.06	4	.03	4	.029
1	.1	1	.05	2	.05	3	.05	4	.05	4	.04	2	.017	12	.086
1	.1	0	0	0	0	1	.017	1	.013	1	.01	3	.025	7	.05

For these data: $\bar{x}$ = 0.0354 ± 0.0292 (n = 32)

APPENDIX 3 - Experimental Daphnia magna Mortality Data (untreated results from 1975) for:

Pyrrhosoma nymphula

No = 5		No = 10		No = 20		No = 40		No = 60	
number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead
1	.2	0	0	1	.05	1	.025	2	.033
1	.2	3	.3	1	.05	2	.05	2	.033
0	0	0	0	2	.1	0	0	4	.067
1	.2	3	.3	1	.05	8	.2	2	.033
0	0	2	.2	3	.15	6	.15	5	.083
		1	.1	1	.05			3	.05
		1	.1	4	.2			5	.083
								10	.167
								3	.05

for these data: $\bar{x} = 0.0989 \pm 0.0721$ (n = 62)
and the Kruskal-Wallis $H = 9.87$, for which $0.5 > \alpha > 0.3$
at 9 degrees of freedom. (Pyrrhosoma nymphula)

Coenagrion puella

No = 5		No = 10		No = 20		No = 40		No = 60	
number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead
1	.2	0	0	3	.15	2	.05	9	.15
0	0	1	.1	0	0	2	.05	1	.017
						0	0		

APPENDIX 3 - Continued

Pyrrhosoma nymphula

No = 80		No = 100		No = 120		No = 140		No = 160	
number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead
7	.09	2	.02	11	.092	35	.11	20	.125
3	.04	4	.04	10	.083	11	.08		
3	.04	10	.1	7	.06	19	.13		
1	.01	10	.1	13	.11	16	.11		
10	.125	10	.1	7	.06	17	.12		
6	.075	12	.12	8	.067	19	.13		
				10	.083	20	.14		
				29	.24	17	.12		

Coenagrion puella

No = 80		No = 100		No = 120		No = 140		No = 140	
number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead	number dead	fraction dead
14	.18	6	.06	9	.075	22	.16	10	.06
7	.09	2	.02			4	.029	14	.09

Continued....

APPENDIX 3 - Continued

for these data : $\bar{x} = 0.0741 \pm 0.0644$ ($n = 20$) and the Kruskal-Wallis $H = 4.24$, for which $.9 > \alpha > .8$ at 9 degrees of freedom. (*Coenagrion puella*)

APPENDIX 4 - List of Symbols Used in Text

General Symbols used throughout Thesis:

n = number of replicates

$\overline{x}$ = mean

s = standard deviation

r^2 = the square of the correlation coefficient

(r was also used in Section 1.3.2. to mean a particular size class of prey at a certain distance from the predator, and in Section 3. to mean the 'r strategy' as opposed to the 'k strategy')

F = the variance ratio statistic, equal to s_1^2/s_2^2

α = level of significance (as a decimal or percentage)

Functional Response Parameters:

a = predator attack rate (arena units searched/second)

Th = predator handling time (seconds)

Tt = duration of the experiment (seconds)

Ts = predator searching time (seconds)

No = number of prey offered

Ne = number of prey eaten

Nec = number of prey eaten (corrected for predator age)

Neclog = number of prey eaten (corrected for predator age using the logarithmic model)

Nep = predicted number of prey eaten

Necp = predicted number of prey eaten (corrected for predator age)

Parameters for the Two Prey Random Predator Model:

a_1 = predator attack rate for prey type 1 (arena units searched/sec.)

a_2 = predator attack rate for prey type 2 (arena units searched/sec.)

Th_1 = predator handling time for prey type 1 (sec.)

Th_2 = predator handling time for prey type 2 (sec.)

No_1 = number of prey type 1 offered

No_2 = number of prey type 2 offered

Nom = number of mosquitos offered

Nod = number of daphnia offered

Ne_1 = number of prey type 1 eaten

Ne_2 = number of prey type 2 eaten

Nem = number of mosquitos eaten

Nemc = number of mosquitos eaten (corrected for predator age)

Ned = number of daphnia eaten

Nedc = number of daphnia eaten (corrected for predator age)

Symbols used in Section 1.3.2.:

di = density of prey type i

ci = calorie content of prey type i

ti = pursuit and handling time for prey type i

Symbols used in Section 1.4.:

N1 = fundamental niche of species 1

N2 = fundamental niche of species 2

$N1 \cdot N2$ = area of niche overlap for species 1 and 2

Symbols used in Section 2.3.1.:

Ne'= number of prey eaten during the two hour sit and watch experiment

ua = number of unattempted captures

us = number of unsuccessful captures

cs = capture success

ss = strike success

Symbols used in Section 2.4.2.:

m = number of mosquitos in training diet (or m = mosquitos)

d = number of daphnia in training diet (or d = daphnia)

dij = frequency of prey j in diet of predator i

fj = frequency of prey j in the environment

bj = calorific value of prey j

Ti = total number of prey eaten by predator i

Symbols used in Section 2.5.1.:

x = day in the Spring of 1975

AO = absolute overlap

JO = overlap in joules

RO = relative overlap

Nei = simulated average number of prey eaten by predator i for a five day interval during the Spring of 1975

NEI = simulated total number of prey eaten by predator I throughout the Spring of 1975

Normal Distribution Parameters:

μ = mean

σ^2 = variance

σ = standard deviation

z = standard normal deviate

Other Symbols used in Text:

BPC = between phenotype component of niche breadth

WPC = within phenotype component of niche breadth

c = Murdoch's index of preference

E = Ivlev's index of preference

Em = index of preference for mosquitos

Ed = index of preference for daphnia

α ij = competition coefficient representing the effect of species j on species i

APPENDIX 5 - 1975 Data on *Pyrrhosoma nymphula* Individuals

Identification number	Sex	Date of moult into ultimate instar	Date of adult emergence	Dry weight of exuvium (mg.)	Dry weight of adult (mg.)
1	F	-	17/3/75	6.7	10.1
2	-	-	19/3/75	-	-
3	M	-	12/3/75	9.1	8.4
4	-	-	19/3/75	-	-
5	-	-	19/3/75	-	-
6	F	-	22/3/75	5.1	8.1
7	F	-	19/3/75	2.7	9.4
8	M	-	10/3/75	1.3	9.1
10	-	-	19/3/75	-	-
11	F	-	10/3/75	6.0	10.1
12	F	-	15/3/75	1.6	9.7
13	M	-	20/3/75	6.5	9.6
14	M	-	19/3/75	10.3	10.8
24	-	-	29/3/75	1.6	-
25	M	-	29/3/75	2.9	6.9
26	-	-	10/3/75	3.5	-
27	F	-	24/3/75	2.4	8.9
28	M	-	3/4/75	5.1	7.4
29	M	-	28/3/75	4.2	9.5
30	-	-	31/3/75	-	9.3
32	F	-	28/3/75	4.9	8.8
33	F	-	31/3/75	3.3	7.1
35	F	16/3/75	28/4/75	8.8	9.1
36	F	16/3/75	29/4/75	9.5	-
40	M	24/3/75	1/5/75	4.5	8.1
41	F	24/3/75	29/4/75	3.3	8.6
42	F	24/3/75	3/5/75	-	-
49	F	26/3/75	31/5/75	7.1	9.5
50	M	-	29/4/75	1.5	8.3
51	M	-	29/4/75	1.3	8.4
52	M	-	5/5/75	1.5	9.1
62	M	-	27/5/75	1.2	-
63	F	28/5/75	3/7/75	7.0	9.8
64	F	-	13/5/75	-	7.7
65	-	-	22/5/75	1.5	-

APPENDIX 6 - 1975 Data on *Coenagrion puella* Individuals

Identification number	Sex	Date of moult into ultimate instar	Date of adult emergence	Dry weight of exuvium (mg.)	Dry weight of adult (mg.)
15	-	3/3/75	21/4/75	1.0	-
16	-	27/2/75	21/4/75	0.9	-
17	M	17/3/75	28/4/75	-	5.9
18	-	3/3/75	21/4/75	-	-
19	-	23/2/75	21/4/75	-	-
20	-	13/3/75	25/4/75	-	-
22	-	27/2/75	21/4/75	0.7	-
23	-	3/3/75	21/4/75	0.9	-
31	F	-	1/4/75	-	6.9
37	M	3/4/75	13/5/75	0.5	4.0
38	-	-	9/5/75	0.9	-
39	-	-	18/5/75	1.1	-
44	-	25/3/75	5/5/75	-	-
45	-	21/4/75	27/5/75	0.7	-
46	-	14/4/75	22/5/75	-	-
47	F	16/4/75	24/5/75	0.9	6.8
48	F	30/3/75	8/5/75	0.8	5.1
53	-	22/4/75	22/5/75	-	-
54	-	-	18/5/75	0.9	-
55	-	-	12/5/75	0.8	-
56	F	22/5/75	26/6/75	1.0	5.7
57	-	26/4/75	dead26/4/75	-	-
58	-	18/5/75	24/6/75	0.9	-
59	F	13/5/75	13/6/75	1.1	7.0
60	-	18/5/75	24/6/75	0.8	-
61	-	-	30/5/75	0.7	-
66	M	-	26/5/75	0.6	5.4
67	-	-	26/5/75	0.8	-
68	-	-	22/5/75	0.8	-
69	M	-	6/6/75	-	-
70	F	-	13/5/75	0.9	5.3
71	M	-	18/5/75	0.7	5.6
72	-	12/5/75	19/6/75	0.7	-
73	M	29/5/75	3/7/75	0.8	5.0
74	M	16/5/75	19/6/75	0.6	6.5

APPENDIX 7 - 1976 Data on *Pyrrhosoma nymphula* Individuals

Identification number	Sex	Date of moult into ultimate instar	Date of adult emergence	Dry weight of exuvium (mg.)	Dry weight of adult (mg.)
1	F	-	15/3/75	1.50	8.99
5	M	-	8/3/76	0.79	8.83
6	M	-	11/3/76	1.40	9.67
7	M	-	9/3/76	1.21	8.38
8	M	8/3/76	8/4/76	1.92	7.88
11	F	-	27/3/76	1.03	8.71
12	F	-	25/3/76	1.76	8.83
13	M	-	18/3/76	1.20	8.02
14	F	-	23/3/76	1.43	10.92
15	F	-	21/3/76	1.33	-
16	M	-	18/3/76	0.99	-
17	F	-	21/3/76	1.18	-
18	M	-	25/3/76	1.02	7.51
19	-	8/3/76	15/4/76	-	8.85
21	M	-	8/4/76	1.39	9.12
22	-	-	10/4/76	1.28	-
23	-	-	7/4/76	1.23	-
24	-	-	12/4/76	-	-
25	M	-	5/4/76	1.10	7.83
26	M	-	6/4/76	1.12	7.52
30	F	26/3/76	29/4/76	1.33	9.44
31	M	29/3/76	4/5/76	1.11	7.62
35	-	-	10/4/76	1.25	-
36	-	-	13/4/76	-	-
37	-	-	13/4/76	-	-
38	M	-	13/4/76	1.17	8.74
39	F	-	20/4/76	1.15	8.03
41	F	28/3/76	1/5/76	1.17	8.74
42	F	-	11/5/76	1.70	9.32
47	M	-	1/5/76	1.01	8.69
48	-	-	25/4/76	1.12	-
49	-	-	25/4/76	1.12	-
50	-	-	25/4/76	1.32	-
51	-	-	25/4/76	1.11	-
54	F	10/5/76	10/6/76	2.65	9.06

APPENDIX 8 - 1976 Data on *Coenagrion puella* Individuals

Identification number	Sex	Date of moult into ultimate instar	Date of adult emergence	Dry weight of exuvium (mg.)	Dry weight of adult (mg.)
2	F	-	6/3/76	1.12	8.16
3	M	20/2/76	21/3/76	0.85	6.43
4	M	-	16/3/76	0.98	7.94
10	M	25/3/76	22/4/76	0.86	5.15
27	M	-	12/4/76	0.80	5.70
28	F	27/3/76	24/4/76	0.90	8.14
29	F	23/4/76	27/5/76	1.12	7.48
33	F	19/4/76	16/5/76	1.02	8.02
34	F	17/4/76	14/5/76	0.96	6.21
40	M	30/3/76	29/4/76	1.02	6.69
45	F	1/5/76	1/6/76	0.65	4.58
46	F	30/4/76	30/5/76	0.85	5.66
52	-	10/5/76	6/6/76	-	-
53	F	-	14/6/76	0.81	6.31
55	F	27/4/76	23/5/76	1.17	6.73
56	M	27/4/76	25/5/76	0.77	5.10
57	-	24/4/76	22/5/76	-	-

APPENDIX 9 - 1977 Data on *Pyrrhosoma nymphula* Individuals

Identification number	Sex	Date of moult into ultimate instar	Date of adult emergence
1	-	-	1/3/77
2	-	17/2/77	20/3/77
12	F	-	28/2/77
13	M	-	24/2/77
14	-	-	26/2/77
15	-	-	1/3/77

APPENDIX 10 - 1977 Data on *Coenagrion puella* Individuals

Identification number	Sex	Date of moult into ultimate instar	Date of adult emergence
3	-	11/2/77	6/3/77
4	-	10/2/77	10/3/77
5	-	10/2/77	9/3/77
6	-	17/2/77	12/3/77
7	-	12/2/77	6/3/77
8	-	15/2/77	12/3/77
9	F	10/2/77	6/3/77
10	-	10/2/77	6/3/77
11	M	16/2/77	16/3/77
16	M	16/2/77	15/3/77
17	M	15/2/77	15/3/77
18	F	15/2/77	12/3/77
19	F	12/2/77	8/3/77
20	-	12/2/77	6/3/77
21	F	12/2/77	10/3/77
22	-	12/2/77	6/3/77
23	-	9/2/77	10/3/77
24	F	10/2/77	7/3/77
25	-	9/2/77	10/3/77
26	M	9/2/77	12/3/77
27	-	11/2/77	6/3/77
28	F	11/2/77	8/3/77
29	F	14/2/77	8/3/77
30	M	7/2/77	10/3/77
31	-	12/2/77	6/3/77
32	-	7/2/77	10/3/77
33	F	12/2/77	8/3/77
34	F	9/2/77	12/3/77
35	-	7/2/77	9/3/77
37	F	11/2/77	7/3/77
38	-	8/2/77	9/3/77
39	F	14/2/77	8/3/77
40	-	10/2/77	7/3/77
41	F	10/2/77	6/3/77
42	M	7/2/77	10/3/77
43	-	9/2/77	12/3/77
44	-	11/2/77	6/3/77
45	M	10/2/77	6/3/77

APPENDIX 11 - Raw Data for Functional Response of *Pyrrhosoma nymphula* to *Aedes aegypti*

No = 3			No = 5			No = 10			No = 15			No = 20			No = 25			No = 30		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
3	40	10/4/75	5	35	27/3/75	0	30	27/3/75	6	36	27/3/75	0	33	27/3/75	0	33	3/4/75	8	36	10/4/75
2	42	17/4/75	5	35	3/4/75	5	42	3/4/75	5	41	3/4/75	8	40	3/4/75	8	35	10/4/75	4	40	17/4/75
3	49	15/5/75	2	36	17/4/75	4	41	10/4/75	3	41	17/4/75	7	42	10/4/75	1	35	24/4/75	0	40	24/4/75
			0	40	1/5/75	4	35	17/4/75	1	41	24/4/75	0	30	24/4/75	7	49	1/5/75	0	42	1/5/75
			0	65	15/5/75	1	42	24/4/75	1	49	29/5/75	0	52	1/5/75				3	62	15/5/75
			0	62	22/5/75	3	49	22/5/75	10	63	5/6/75	8	49	8/5/75				7	63	19/6/75
			5	62	12/6/75	0	6	4/3/75	0	7	4/3/75	0	63	26/6/75						
			0	5	4/3/76	4	11	11/3/76	3	12	11/3/76									
			2	15	11/3/76	1	14	15/3/76	0	13	15/3/76									
			2	18	15/3/76	2	11	18/3/76	0	12	18/3/76									
			0	17	18/3/76															
			0	18	22/3/76	0	14	22/3/76	5	8	22/3/76									
			4	21	29/3/76	2	23	29/3/76	4	22	29/3/76									
			0	24	2/4/76	0	26	23/4/76	0	25	2/4/76									
			0	22	5/4/76	4	30	5/4/76	0	23	5/4/76									
			4	41	12/4/76	3	31	12/4/76	2	30	12/4/76									
			2	41	19/4/76	5	42	19/4/76	2	30	19/4/76									
			0	49	22/4/76				1	50	22/4/76									

APPENDIX 12 - Raw Data for Functional Response of *Pyrrhosoma nymphula* to *Daphnia magna*

No = 5			No = 10			No = 20			No = 40			No = 60		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
2	14	6/3/75	5	1	27/2/75	6	2	27/2/75	7	3	27/2/75	21	4	27/2/75
2	28	6/3/75	1	7	27/2/75	0	8	27/2/75	5	10	27/2/75	5	11	27/2/75
			6	14	27/2/75	8	24	27/2/75	6	25	27/2/75	11	28	27/2/75
1	1	13/3/75	1	26	27/2/75	7	27	27/2/75	9	25	6/3/75	15	32	27/2/75
0	6	13/3/75	2	1	6/3/75	7	6	6/3/75	10	29	6/3/75	4	2	6/3/75
0	7	13/3/75	3	30	6/3/75	3	13	6/3/75				10	5	6/3/75
0	28	27/3/75	0	2	13/3/75	0	10	13/3/75				0	12	13/3/75
0	29	27/3/75	0	2	13/3/75									
			0	32	27/3/75									

APPENDIX 12 (continued) - Raw Data for Functional Response of *Pyrrhosoma nymphula* to *Daphnia magna*

No = 80			No = 100			No = 120			No = 140			No = 160		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
23	5	27/2/75	28	6	27/2/75	5	3	6/3/75	8	11	6/3/75	3	27	13/3/75
12	12	27/2/75	12	13	27/2/75	5	8	6/3/75	5	26	6/3/75	4	32	13/3/75
13	29	27/2/75	17	30	27/2/75	10	27	6/3/75	0	5	13/3/75	17	33	13/3/75
13	33	27/2/75	10	7	6/3/75	12	32	6/3/75	0	13	13/3/75			
10	4	6/3/75	4	10	6/3/75	12	33	6/3/75	0	14	13/3/75			
0	12	6/3/75	9	24	6/3/75	4	4	13/3/75	5	25	13/3/75			
						7	24	13/3/75	15	28	13/3/75			
						27	30	13/3/75	6	29	13/3/75			
						0	25	13/3/75	0	24	27/3/75			

APPENDIX 13 - Raw Data for Functional Response of *Coenagrion puella* to *Aedes aegypti*

No = 3			No = 5			No = 10			No = 15		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
1	37	1/5/75	4	44	3/4/75	5	44	10/4/75	2	44	17/4/75
3	45	1/5/75	3	54	1/5/75	0	44	1/5/75	3	39	1/5/75
1	47	15/5/75	2	67	15/5/75	0	38	8/5/75	5	47	8/5/75
1	45	15/5/75	0	53	15/5/75	3	46	8/5/75	3	53	8/5/75
			4	10	8/4/76	0	39	15/5/75	0	67	22/5/75
			1	28	15/4/76	0	46	15/5/75	0	45	22/5/75
			5	46	6/5/76	6	72	22/5/75	3	72	29/5/75
			1	34	10/5/76	5	59	22/5/75	3	74	29/5/75
			2	55	13/5/76	7	40	8/4/76	4	28	8/4/76
			0	57	17/5/76	2	40	15/4/76	2	10	15/4/76
			0	29	20/5/76	5	55	6/5/76	8	34	26/4/76
			3	52	24/5/76	0	33	10/5/76	5	56	6/5/76
						1	45	13/5/76	1	56	13/5/76
						3	52	17/5/76			
						0	55	20/5/76	2	46	20/5/76

APPENDIX 13 (continued) - Raw Data for Functional Response of *Coenagrion puella* to *Aedes aegypti*

No = 20			No = 25			No = 30			No = 35		
Ne	Ind No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
1	44	24/4/75	0	38	1/5/75	0	48	1/5/75	2	56	29/5/75
7	46	1/5/75	2	55	1/5/75	6	53	1/5/75	1	60	5/6/75
7	47	1/5/75	2	45	8/5/75	0	37	8/5/75	5	56	5/6/75
3	54	8/5/75	0	54	15/5/75	0	39	8/5/75	2	58	12/6/75
0	55	8/5/75	4	61	15/5/75	1	66	15/5/75	1	56	12/6/75
1	68	15/5/75	2	47	22/5/75	0	71	15/5/75	4	73	12/6/75
4	69	15/5/75	2	69	29/5/75	0	66	22/5/75	0	74	19/6/75
2	69	22/5/75	8	73	5/6/75	5	58	29/5/75			
1	61	22/5/75	0	69	5/6/75	4	60	29/5/75			
3	59	29/5/75	0	59	12/6/75	0	61	29/5/75			
1	72	5/6/75	1	60	12/6/75	0	59	5/6/75			
1	58	5/6/75	0	56	19/6/75	3	74	5/6/75			
1	74	12/6/75									
0	58	19/6/75				0	72	12/6/75			
0	60	19/6/75									
1	73	19/6/75				1	73	26/6/75			

APPENDIX 14 - Raw Data for Functional Response of _Coenagrion puella_ to _Daphnia magna_

No = 5			No = 10			No = 20			No = 40			No = 60		
Ne	Ind No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
5	16	13/3/75	6	19	6/3/75	5	16	6/3/75	15	22	6/3/75	5	23	13/3/75
4	37	27/3/75	1	18	27/3/75	3	19	27/3/75	9	15	27/3/75	22	23	27/3/75
4	38	3/4/75	4	38	27/3/75	3	22	3/4/75	4	16	3/4/75	2	19	3/4/75
2	39	3/4/75	4	39	27/3/75	5	20	3/4/75	7	18	3/4/75	14	17	3/4/75
0	22	17/4/75	2	15	3/4/75	9	48	17/4/75	9	17	17/4/75	9	37	24/4/75
0	15	17/4/75	4	37	3/4/75	6	46	17/4/75	11	38	17/4/75	10	48	24/4/75
4	31	6/3/75	0	23	17/4/75				11	31	27/2/75			
			1	19	17/4/75									
			0	31	27/3/75									

APPENDIX 14 (continued) - Raw Data for Functional Response of *Coenagrion puella* to *Daphnia magna*

No = 80			No = 100			No = 120			No = 140			No = 160		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
12	19	13/3/75	18	18	13/3/75	5	22	27/3/75	14	15	13/3/75	12	22	13/3/75
3	16	27/3/75	11	17	27/3/75	1	16	10/4/75	8	20	27/3/75	5	18	10/4/75
10	23	3/4/75	2	20	10/4/75	13	38	10/4/75	4	15	10/4/75	16	48	10/4/75
0	22	10/4/75	5	39	10/4/75	1	16	17/4/75	12	17	10/4/75	18	47	24/4/75
8	37	10/4/75	9	38	24/4/75	13	39	17/4/75	16	39	24/4/75	10	31	13/3/75
10	37	17/4/75	12	45	24/4/75	2	20	24/4/75						
5	17	24/4/75												
18	46	24/4/75												

APPENDIX 15 - Statistical Tests conducted on Data

1. A Mann-Whitney U test on differences in respiratory rate between *Pyrrhosoma nymphula* and *Coenagrion puella* (all data for larvae more than ten days from emergence) yielded a U value of 39. For $n_1 = 6$, $n_2 = 12$, the critical U at the 5% level of significance is 14. Therefore, the differences in respiratory rate between these two species are not significant.

2. Kolmogorov-Smirnov tests of differences in mean *Ne* for each *No*, between males and females (1975 data) yielded:

	Pyrrhosoma nymphula				*Coenagrion puella*			
	Uncorrected Data		Corrected Data		Uncorrected Data		Corrected Data	
	Aedes aegypti	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*
n	3	8	3	6	4	2	4	2
K_D	1.9	3.3	1.6	1.1	2.4	0.8	1.6	1
critical K_D at 5% level significance	n.s.	n.s.	n.s.	n.s.	n.s.	trivial	n.s.	trivial

n.s. = not significant

trivial = test is trivial when $n \leq 3$

3. Mann-Whitney U tests on differences in *Nec's*, between different years, yielded:

	1975 v.s. 1977				1975 v.s. 1976					
	Coenagrion puella eating *Aedes aegypti*		*Coenagrion puella* eating *Daphnia magna*		*Pyrrhosoma nymphula* eating *Aedes aegypti*			*Coenagrion puella* eating *Aedes aegypti*		
No	10	20	40	80	5	10	15	5	10	15
n_1	4	4	4	4	2	4	4	3	4	4
n_2	4	8	7	7	4	5	4	3	5	6
U	4	10	11	6	4	10	8	9	10	6
Probability of getting a value $< U$	0.17	0.39	0.32	0.08	0.60	0.55	0.56	0.56	0.56	0.13

In all cases, the probability of getting such U values is greater than 5%. Therefore any differences in *Nec* between years are not significant

4. Wilcoxon tests on the differences in mean *Nem*'s and *Ned*'s, between 1976 and 1977 mixed prey results, yielded T values of 5 and 3 for *Pyrrhosoma nymphula* and *Coenagrion puella* respectively. For n = 8, T must be less than 4 to be significant at the 5% level, and for n = 6 (in the case of *Coenagrion puella* for which there was only one observation for Nom:Nod = 10:80 in 1976), T must be equal to 0, to be significant at the 5% level. Therefore the differences between the 1976 and 1977 mixed prey results are not significant for either predator.

APPENDIX 15 (continued) - Mann-Whitney tests on a and Th (data for first two captures only)

Test		n_1	n_2	U	α
Pyrrhosoma nymphula:	is a(No=15) $<$ a(No=10)?	7	9	17	n.s.
	is a(No=5) $<$ a(No=10)?	5	9	13	n.s.
	is Th(No=5) $<$ Th(No=15)?	4	5	4	0.095
Coenagrion puella:	is a(No=15) $>$ a(No=10)?	7	6	7	0.026
	is a(No=5) $>$ a(No=10)?	6	4	3	0.033
	is Th(No=5) $<$ Th(No=10)?	6	4	10	0.381
	is Th(No=15) $<$ Th(No=10)?	6	6	19	0.461

n.s. = not significant

APPENDIX 15 (continued) - Tests on Differences between Predicted and Observed Mixed Prey Results

Differences between Predicted and Observed Results

mixed prey combination \ predator and prey	Pyrrhosoma nymphula Aedes aegypti	Pyrrhosoma nymphula Daphnia magna	Coenagrion puella Aedes aegypti	Coenagrion puella Daphnia magna
10 Aedes aegypti : 40 Daphnia magna	2.85	-4.20	2.65	1.60
10 Aedes aegypti : 80 Daphnia magna	3.53	-4.43	2.80	3.81
20 Aedes aegypti : 40 Daphnia magna	0.99	-1.65	1.47	1.58
20 Aedes aegypti : 80 Daphnia magna	2.65	-4.66	1.50	3.21

For Pyrrhosoma nymphula eating daphnia, the largest difference is less than zero, and for the other three predator-prey interactions, the smallest difference is greater than zero. Using the randemization test, all these differences are significant at the 5% level.

APPENDIX 15(continued) - Chi Square tests to determine Predator Preferences

Data for Number of Each Prey Type Eaten (corrected for age)

	10m	40d	10m	80d	20m	40d	20m	80d
Pyrrhosoma nymphula	7.74	4.69	2.81	5.58	4.26	1.31	3.74	3.69
	5.11	3.96	3.11	8.96	6.19	2.42	4.81	0.00
	6.89	0.00	5.26	0.00	2.96	0.00	4.26	1.31
	3.89	0.00	8.37	0.85	5.67	13.81	5.56	4.27
	7.26	1.31	4.81	3.58	8.48	3.39	9.93	4.12
	4.74	2.69	6.11	3.54	4.44	0.00	6.89	0.00
	1.26	0.31	6.19	5.42	3.19	0.42	4.56	2.27
					*3.48	*3.39	*4.48	*3.39
Column Total	36.89	12.96	36.66	27.93	35.19	21.35	39.04	15.66
Coenagrion puella	4.70	2.75	3.70	4.75	4.00	1.00	5.70	1.75
	7.10	2.25	6.00	8.00	5.10	0.25	5.70	2.75
	6.70	0.00	7.10	1.25	6.90	2.75	5.90	2.75
	*5.70	*0.75	6.00	5.00	4.90	3.75	5.71	4.25
	8.60	2.50	8.60	3.50	*5.90	*0.75	5.70	8.75
	7.00	4.00	8.00	8.00	7.11	1.75	4.90	2.75
	5.81	3.50			5.41	3.00		
Column Total	39.91	15.00	39.40	30.50	33.42	12.50	33.61	23.00

m = mosquitos

d = daphnia

*: These data (chosen by random selection) were omitted from the calculations to keep the number of replicates constant, for each experimental treatment.

APPENDIX 15(continued) - Chi Square tests to determine Predator Preferences (continued)

Pyrrhosoma nymphula:

1. does the number of daphnia present affect predation on mosquitos?
2. does the number of mosquitos present affect predation on daphnia?

Nem	10m	20m
40d	36.89	35.19
80d	36.66	39.04

Total = 147.75

Ned	40d	80d
10m	12.96	27.93
20m	12.35	15.66

Total = 77.90

1 $\chi^2 = 0.1127$, $\alpha = 0.80$ 2 $\chi^2 = 5.13$, $\alpha = 0.05$

Coenagrion puella:

1. does the number of daphnia present affect predation on mosquitos?
2. does the number of mosquitos present affect predation on daphnia?

Nem	10m	20m
40d	39.91	33.42
80d	39.40	33.61

Total = 146.34

Ned	40d	80d
10m	15.00	30.50
20m	12.50	23.00

Total = 81.00

1 $\chi^2 = 0.0038$, $\alpha = 0.99$ 2 $\chi^2 = 0.05$, $\alpha = 0.90$

m = mosquitos
d = daphnia

APPENDIX 15 (continued) - Kolmogorov-Smirnov tests for sex differences in predation by *Enallagma boreale*

Small Arena Size (100 ml.)

No	♂			♀			D.
	n	Ne ± s_x	cumulative frequency	n	Ne ± s_x	cumulative frequency	
3	10	3 + 0.00	0.0879	4	3.00 ± 0.00	0.0909	-0.0030
6	9	4.78 ± 1.30	0.2279	6	5.33 ± 0.82	0.2524	-0.0245
12	12	7.83 ± 2.92	0.4572	4	8.00 ± 1.41	0.4948	-0.0376
30	10	11.40 ± 4.99	0.7912	2	7.00 ± 1.41	0.7070	-0.0842 n.s.
60	8	7.13 ± 4.85	1.00	6	9.67 ± 3.88	1.00	0.00
	Total:34.14			Total:33.00			

Medium Arena Size (1 l.)

No	♂			♀			D
	n	Ne + s_x	cumulative frequency	n	Ne + s_x	cumulative frequency	
3	9	2.67 ± 0.50	0.0707	6	2.00 ± 0.89	0.0577	0.0130
6	7	4.14 ± 1.95	0.1803	3	4.00 ± 1.00	0.1731	0.0072
30	8	10.63 ± 4.44	0.4619	3	7.67 ± 5.03	0.3943	0.0676
60	9	9.89 ± 3.69	0.7238	3	8.00 ± 5.57	0.6250	0.0988 n.s.
120	7	10.43 ± 5.62	1.00	1	13.00 ± ∞	1.00	0.0
	Total:37.76			Total:34.67			

n.s. = not significant

Continued....

APPENDIX 15 (continued) - Kolmogorov-Smirnov tests for sex differences in predation by *Enallagma boreale*

Large Arena Size (2 l.)

No	♂			♀			D.
	n	Ne ± s_x	cumulative frequency	n	Ne ± s_x	cumulative frequency	
6	11	3.82 ± 1.40	0.0932	3	3.67 ± 0.58	0.0685	0.0247
30	7	7.29 ± 1.70	0.2710	4	11.75 ± 3.86	0.2877	-0.0167
60	11	8.82 ± 2.82	0.4861	3	7.67 ± 0.58	0.4309	0.0552 n.s.
120	9	9.78 ± 5.95	0.7246	2	15.50 ± 2.12	0.7201	0.0045
240	7	11.29 ± 8.34	1.00	3	15.00 ± 3.00	1.00	0.0
	Total:41.00			Total:53.59			

n.s. = not significant

APPENDIX 16 - 1974 Data on *Lestes sponsa* Individuals

Identification number	Sex	Date of moult into ultimate instar	Date of adult emergence
39	-	14/6/74	2/7/74
40	M	12/6/74	30/6/74
41	M	12/6/74	30/6/74
43	F	11/6/74	30/6/74
44	M	11/6/74	30/6/74
45	F	11/6/74	27/6/74
46	F	16/6/74	4/7/74
47	F	7/6/74	25/6/74
48	M	12/6/74	2/7/74
49	F	11/6/74	30/6/74
50	M	17/6/74	8/7/74
51	M	11/6/74	30/6/74
52	F	14/6/74	2/7/74
53	M	17/6/74	8/7/74
54	F	30/6/74	29/7/74
55	F	26/6/74	17/7/74
56	M	24/6/74	17/7/74
57	M	24/6/74	22/7/74
58	F	24/6/74	22/7/74
59	F	19/6/74	15/7/74
60	M	14/6/74	2/7/74
61	F	21/6/74	18/7/74
62	F	14/6/74	3/7/74
63	F	30/6/74	17/7/74
64	F	8/7/74	2/8/74
65	F	30/6/74	7/8/74
66	M	30/6/74	17/7/74
67	M	17/6/74	17/7/74
68	F	21/6/74	18/7/74
69	M	8/7/74	7/8/74

APPENDIX 17 - 1975 Data on *Lestes sponsa* Individuals

Identification number	Sex	Date of moult into ultimate instar	Date of adult emergence
178	F	-	18/7/75
179	F	-	18/7/75
180	M	-	7/8/75
181	F	27/6/75	31/7/75
182	M	27/6/75	30/7/75
185	M	18/7/75	25/7/75
187	F	7/7/75	29/7/75
192	M	-	10/7/75
193	F	-	29/7/75
194	M	-	10/7/75
195	M	-	18/7/75
196	F	-	10/7/75
197	F	-	11/7/75
198	M	-	8/7/75
199	M	-	10/7/75
200	F	-	11/7/75
201	M	-	10/7/75
202	M	-	10/7/75
203	M	-	29/7/75
204	M	-	18/7/75
205	M	-	28/7/75
206	M	-	22/7/75
207	F	14/7/75	2/8/75
208	-	9/7/75	dead 2/8/75
209	M	-	18/7/75
211	F	-	1/8/75
212	F	-	5/8/75
213	M	-	21/7/75

APPENDIX 18 - Raw Data for Functional Response of *Lestes sponsa* to *Aedes aegypti* (2 days starvation)

No = 5			No = 10			No = 15			No = 20			No = 25			No = 30			No = 35		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
1	179	3/7/75	6	180	3/7/75	5	181	3/7/75	7	182	3/7/75	6	178	3/7/75	1	202	10/7/75	2	194	10/7/75
1	178	10/7/75	10	193	10/7/75	2	195	10/7/75	0	197	10/7/75	2	200	10/7/75	5	203	10/7/75	0	179	10/7/75
5	181	10/7/75	10	182	10/7/75	8	209	10/7/75	6	180	10/7/75	8	204	10/7/75	6	206	10/7/75	2	178	17/7/75
5	187	17/7/75	1	193	17/7/75	2	180	17/7/75	0	179	17/7/75	9	205	10/7/75	5	205	17/7/75	10	182	17/7/75
			7	208	17/7/75	9	203	17/7/75	0	204	17/7/75	0	195	17/7/75	0	206	17/7/75	0	209	17/7/75
						15	207	24/7/75	5	187	24/7/75	14	181	17/7/75	0	180	24/7/75	0	193	24/7/75
									12	203	24/7/75	14	208	24/7/75	7	181	24/7/75	5	211	24/7/75
									0	205	24/7/75				0	182	24/7/75	10	212	24/7/75

APPENDIX 19 - Raw Data for Functional Response of *Lestes sponsa* to *Aedes aegypti* (one day starvation)

No = 5			No = 10			No = 20			No = 30		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
4	46	20/6/74	9	43	13/6/74	7	44	13/6/74	12	45	13/6/74
			9	51	18/6/74	15	49	18/6/74	10	47	18/6/74
			9	39	20/6/74	15	40	20/6/74	22	41	20/6/74
			0	44	25/6/74	10	50	25/6/74	12	53	25/6/74
			10	62	28/6/74	0	45	25/6/74	0	47	25/6/74
						1	60	28/6/74	1	52	28/6/74
						2	39	28/6/74	0	43	28/6/74

APPENDIX 19 (continued) - Raw Data for Functional Response of *Lestes sponsa* to *Aedes aegypti* (one day starvation)

No = 40			No = 50			No = 60			No = 70		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
16	47	13/6/74	18	49	13/6/74	14	51	13/6/74	0	49	25/6/74
11	45	18/6/74	10	44	18/6/74	23	43	20/6/74	0	51	25/6/74
23	48	20/6/74	36	52	20/6/74	41	60	20/6/74	17	62	20/6/74
9	67	25/6/74	4	59	25/6/74	16	68	25/6/74	8	61	25/6/74
0	48	28/6/74	0	41	28/6/74	0	40	28/6/74	9	56	28/6/74
17	46	28/6/74	11	57	28/6/74	12	58	28/6/74			

APPENDIX 20 - Raw Data for Functional Response of *Lestes sponsa* to *Daphnia magna* (1 day starvation)

No = 10			No = 20			No = 40			No = 60		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
9	65	19/7/74	0	50	4/7/74	0	53	4/7/74	12	67	4/7/74
			12	57	4/7/74	13	58	4/7/74	22	54	4/7/74
			2	56	12/7/74	1	61	12/7/74	1	68	12/7/74
			16	64	12/7/74	18	69	12/7/74	11	66	12/7/74
			0	58	19/7/74	0	57	19/7/74	21	69	19/7/74

APPENDIX 20 (continued) - Raw Data for Functional Response of *Lestes sponsa* to *Daphnia magna* (1 day starvation)

No = 80			No = 100			No = 120			No = 140		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
9	59	4/7/74	21	68	4/7/74	26	61	4/7/74	28	56	4/7/74
22	55	4/7/74	10	63	4/7/74	19	66	4/7/74	25	58	12/7/74
4	67	12/7/74	6	59	12/7/74	10	57	12/7/74			
20	63	12/7/74	0	55	12/7/74	20	54	12/7/74			
6	54	19/7/74	33	64	19/7/74						

APPENDIX 21 - Estimates of Functional Response Parameters Using the Non-Linear Least Squares Technique

Predator-Prey Interaction	Attack Rate (2 l./min.)	Handling Time (min.)
Pyrrhosoma nymphula eating *Aedes aegypti*		
raw data	0.0023	72.7366
pre-metamorphosis data	0.0051	48.0629
age-corrected data	0.0070	55.5822
Pyrrhosoma nymphula eating *Daphnia magna*		
raw data	0.0017	33.4824
pre-metamorphosis data	0.0018	28.5631
age-corrected data	0.0016	26.9118
Coenagrion puella eating *Aedes aegypti*		
raw data	0.0137	166.3790
pre-metamorphosis data	0.0131	101.6939
age-corrected data	1.1725	95.9609
Coenagrion puella eating *Daphnia magna*		
raw data	0.0019	31.9385
pre-metamorphosis data	0.0023	31.4489
age-corrected data	0.0009	30.4250
	0.0008	29.2302
Lestes sponsa eating *Aedes aegypti*		
raw data (2 days starvation)	0.0272	68.7272
raw data (1 day starvation)	0.0045	25.5377
pre-metamorphosis data (2 days starvation)	0.0121	47.7900
pre-metamorphosis data (1 day starvation)	0.0095	20.6575
Lestes sponsa eating *Daphnia magna*		
raw data (1 day starvation)	0.0006	2.1236
pre-metamorphosis data (1 day starvation)	0.0060	16.3310

APPENDIX 21 - Estimates of Functional Response Parameters Using the Non-Linear Least Squares Technique

(continued)

Predator-Prey Interaction	Attack Rate (2 l./min.)	Handling Time (min.)
Enallagma boreale eating *Daphnia magna*		
arena = 100 ml.	0.0239	39.6709
arena = 1 l.	0.0048	28.7651
arena = 2 l.	0.0038	31.5202

Estimates of the Predicted Number of Prey Eaten, Using the Non-Linear Least Squares Technique

Predator and Treatment Number of *Aedes aegypti* present	3	5	10	15	20	25	30	35
Pyrrhosoma nymphula								
raw data	1.34	1.94	2.88	3.39	3.70	3.91	4.06	
pre-metamorphosis data	2.19	3.25	4.82	5.60	6.03	6.31	6.50	
age-corrected data	2.39	3.46	4.80	5.35	5.63	5.80	5.92	
Coenagrion puella								
raw data	1.77	1.95	2.06	2.10	2.11	2.12	2.13	2.14
pre-metamorphosis data	2.37	2.89	3.25	3.35	3.40	3.43	3.45	3.46
age-corrected data	3.00	3.74	3.75	3.75	3.75	3.75	3.75	3.75
Lestes sponsa (2 days starvation)								
raw data		4.23	4.88	5.02	5.08	5.12	5.14	5.15
pre-metamorphosis data		4.25	5.96	6.54	6.81	6.97	7.07	7.14

APPENDIX 21 - Estimates of the Predicted Number of Prey Eaten, Using the Non-Linear Least Squares Technique (continued)

Predator and Treatment / Number of *Daphnia magna* present	5	10	20	40	60
Pyrrhosoma nymphula					
raw data	1.95	3.39	5.29	7.21	8.15
pre-metamorphosis data	2.12	3.74	5.93	8.23	9.38
age-corrected data	1.95	3.48	5.66	8.12	9.42
Coenagrion puella					
raw data	2.12	3.67	5.69	7.71	8.67
pre-metamorphosis data	2.40	4.11	6.25	8.24	9.15
age-corrected data	1.11	2.05	3.56	5.59	6.88
Lestes sponsa					
(2 days starvation)					
raw data		1.89	3.74	7.33	10.78
pre-metamorphosis data		7.57	12.30	16.58	18.32

Predator and Treatment / Number of *Daphnia magna* present	80	100	120	140	160
Pyrrhosoma nymphula					
raw data	8.70	9.06	9.31	9.50	9.65
pre-metamorphosis data	10.06	10.50	10.81	11.05	11.22
age-corrected data	10.21	10.74	11.12	11.41	11.63

APPENDIX 21 - Estimates of the Predicted Number of Prey Eaten, Using the Non-Linear Least Squares Technique (continued)

Predator and Treatment Number of *Daphnia magna* present	80	100	120	140	160
Coenagrion puella					
raw data	9.23	9.59	9.85	10.03	10.18
pre-metamorphosis data	9.66	9.99	10.21	10.38	10.50
age-corrected data	7.76	8.40	8.88	9.26	9.56
Lestes sponsa					
(2 days starvation) raw data	14.10	17.30	20.38	23.34	
pre-metamorphosis data	19.23	19.79	20.16	20.43	

Predator and Treatment Number of *Aedes aegypti* present	5	10	20	30	40	50	60	70
Lestes sponsa								
(1 day starvation) raw data	3.52	6.04	8.94	10.40	11.23	11.76	12.13	12.40
pre-metamorphosis data	4.60	8.33	12.46	14.17	15.03	15.53	15.86	16.10

Predator and Treatment Number of *Daphnia magna* present	3	6	12	30	60	120	240
Enallagma boreale 100 ml. arena	2.99	5.74	7.93	8.71	8.91		
1 l. arena	2.26	4.10		9.67	11.03	11.76	
2 l. arena		3.66		8.62	9.93		11.03

APPENDIX 22 - Damselfly Collection Data (number of larvae in each instar, collected on each date)

	Pyrrhosoma nymphula			*Coenagrion puella*		
Date	penultimate instar	ultimate instar	total	ante-penultimate and penultimate instars	ultimate instar	total
4/2/75	14	18	32	9	0	9
5/2/75	6	7	13	4	0	4
15/3/75	5	7	12	15	4	19
21/4/75	1	3	4	5	3	8
5/5/75	1	3	4	3	7	10
1975 total			65			50
29/1/76	0	2	2	0	0	0
9/2/76	1	3	4	2	0	2
29/2/76	0	10	10	0	0	0
18/3/76	2	4	6	7	1	8
23/3/76	3	5	8	4	0	4
13/4/76	1	5	6	5	0	5
1976 total			36			19

Date	*Pyrrhosoma nymphula*			*Coenagrion puella*		
	penultimate instar	ultimate instar	total	ante-penultimate and penultimate instars	ultimate instar	total
24/1/77	1	5	6	39	0	39

APPENDIX 23 - Statistics on Age-Relation Linear Regressions (using data only from the asymptotes of the functional responses: $15 \leq No \leq 30$ for *Aedes aegypti*, and $40 \leq No \leq 160$ for *Daphnia magna*)

predator	*Pyrrhosoma nymphula*	*Pyrrhosoma nymphula*	*Coenagrion puella*	*Coenagrion puella*
prey	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*
n	18	35	28	40
inter-cept	1.80	2.16	-2.02	3.34
slope	0.1852	0.4235	0.3015	0.2496
F	10.46	7.47	21.05	10.88
α	$\alpha < 0.01$	$\alpha < 0.025$	$\alpha < 0.005$	$\alpha < 0.005$

APPENDIX 24 - Linear Regressions Relating $\log_{10}Ne$ to Predator Age (for $No \geqslant 15$ for *Aedes aegypti*, and $No \geqslant 40$ for *Daphnia magna*)

predator	*Pyrrhosoma nymphula*		*Coenagrion puella*	
prey	*Aedes aegypti*	*Daphnia magna*	*Aedes aegypti*	*Daphnia magna*
n	18	35	28	40
inter-cept	0.38	0.47	-0.34	0.48
slope	0.0161	0.0237	0.0432	0.0165
F	10.81	12.96	23.10	12.34
α	$\alpha < 0.005$	$\alpha < 0.005$	$\alpha < 0.005$	$\alpha < 0.005$

APPENDIX 25 - Functional Responses of *Pyrrhosoma nymphula* (data corrected for age using the logarithmic relation)

a) with *Aedes aegypti* as prey

No	3	5	10	15	20	25	30	35
n	3	6	9	8	3	3	4	0
$\bar{x} \pm s_x$	3.14 ± 0.55	3.52 ± 0.37	3.77 ± 0.41	4.46 ± 0.57	5.56 ± 0.22	5.81 ± 1.25	6.40 ± 1.16	
s^2	0.89	0.81	1.51	2.56	0.14	4.68	5.39	
Nep	1.54	2.37	3.92	4.95	5.67	6.19	6.58	6.89

Tt = 360 minutes ; a = 0.0024 (2 l./minute) ; Th = 39.0208 minutes ; $F_{1,5}$ = 0.3963; $\alpha > 0.25$;
mean variance = 2.28

APPENDIX 25 - Functional Responses of *Pyrrhosoma nymphula* (data corrected for age using the logarithmic relation)

(continued)

b) with *Daphnia magna* as prey

No	5	10	20	40	60
n	3	6	6	5	6
$\bar{x} \pm s_x$	1.36 ± 0.81	3.12 ± 0.80	4.48 ± 1.05	6.79 ± 1.22	10.14 ± 2.36
s^2	1.93	3.87	6.64	7.48	33.49
Nep	1.50	2.78	4.79	7.46	9.10

Tt = 360 minutes; a = 0.0011 (2 1./minute); Th = 23.1190 minutes; $F_{1,8} = 28.9760$; $\alpha < 0.005$;
mean variance $\doteq$ 27.48

APPENDIX 25 - Functional Responses of *Pyrrhosoma nymphula* (data corrected for age using the logarithmic relation)

(continued)

b) with *Daphnia magna* as prey

No	80	100	120	140	160
n	6	6	7	3	3
$\bar{x} \pm s_x$	10.56 ± 3.06	11.18 ± 2/35	11.69 ± 2.85	9.33 ± 2.51	9.28 ± 4.3
s^2	56.09	33.06	56.93	18.84	56.47
Nep	10.21	10.99	11.58	12.04	12.40

Tt = 360 minutes; a = 0.0011 (2 1./minute); Th = 23.1190 minutes; $F_{1,8}$ = 28.9760; $\alpha < 0.005$;
mean variance = 27.48

APPENDIX 26 - Functional Responses of *Coenagrion puella* (data corrected for age using the logarithmic relation)

a) with *Aedes aegypti* as prey

No	3	5	10	15	20	25	30	35
n	4	6	9	10	9	4	5	6
$\bar{x} \pm s_x$	1.99 ± 0.19	4.39 ± 0.86	3.78 ± 0.59	4.67 ± 0.75	3.24 ± 0.57	3.13 ± 0.70	3.41 ± 0.73	2.65 ± 0.65
s^2	0.15	4.44	3.18	5.67	2.90	1.96	2.67	2.56
Nep	1.72	2.57	3.97	4.77	5.26	5.60	5.84	6.02

Tt = 360 minutes; a = 0.0031 (2 l./minute); Th = 49.6721 minutes; $F_{1,6}$ = 0.2725; $\alpha > 0.25$;
mean variance = 2.94

APPENDIX 26 - Functional Responses of *Coenagrion puella* (data corrected for age using the logarithmic relation)

(continued)

b) with *Daphnia magna* as prey

No	5	10	20	40	60
n	4	6	6	7	6
$\bar{x} \pm s_x$	2.09 ± 0.48	1.61 ± 0.22	4.00 ± 1.01	7.61 ± 1.10	9.18 ± 2.48
s^2	0.92	0.28	6.16	8.47	36.79
Nep	1.36	2.45	4.08	6.07	7.21

Tt = 360 minutes ; a = 0.0010 (2 l./minute) ; Th = 32.2004 minutes; $F_{1,8}$ = 7.1851; $\alpha < 0.05$;
mean variance = 12.50

Continued ....

APPENDIX 26 - Functional Responses of Coenagrion puella (data corrected for age using the logarithmic relation)

(continued)

b) with Daphnia magna as prey (continued)

No	80	100	120	140	160
n	7	6	4	5	5
$\bar{x} \pm s_x$	6.29 ± 1.73	6.38 ± 1.36	5.78 ± 1.88	8.87 ± 1.84	8.96 ± 1.36
s^2	20.89	11.16	14.16	16.96	9.27
Nep	7.94	8.44	8.81	9.09	9.32

Tt = 360 minutes; a = 0.0010 (2 1./minute); Th = 32.2004 minutes; $F_{1,8}$ = 7.1851; $\alpha < 0.05$;
mean variance = 12.50

APPENDIX 27 - Prey Distribution Data and Analysis (data represents numbers of animals found in each cell)

cell / prey density	top left	top middle	top right	middle left	middle middle	middle right	bottom left	bottom middle	bottom right	G statistic	degrees of freedom	significance
10 *Aedes aegypti* per 4 l. water	3	1	1	0	0	1	3	1	0			
	1	0	2	0	0	2	3	2	0			
	3	1	1	0	0	1	2	1	1			
	0	0	0	0	0	0	6	1	3	33.94	1	α≤0.001
	2	0	1	1	1	0	3	1	1			
	2	0	2	2	0	0	3	1	0			
	1	0	0	1	1	2	3	1	1			
	2	0	0	1	0	0	4	0	3	25.52	1	α≤0.001
	1	1	0	2	0	1	2	3	0			
	3	0	0	0	1	1	3	1	1			
	0	0	0	1	1	1	5	1	1			
	1	1	1	0	0	1	6	0	0	27.58	1	α≤0.001
								Total G	=	87.04	3	α≤0.001
pooled data	19	4	8	8	4	10	43	13	11	67.90	1	α≤0.001
								heterogeneity G	=	19.14	2	α≤0.001
mean data	1.58	0.33	0.67	0.67	0.33	0.83	3.58	1.08	0.92			

Continued....

APPENDIX 27 - Prey Distribution Data and Analysis (data represents numbers of animals found in each cell) (continued)

cell / prey density	top left	top middle	top right	middle left	middle middle	middle right	bottom left	bottom middle	bottom right	G statistic	degrees of freedom	significance
20 *Aedes aegypti*	1	0	1	1	1	3	5	4	4			
per 4 l.water	5	0	0	1	0	2	3	3	6	27.60	1	$\alpha \leq 0.001$
	3	1	4	3	0	1	4	2	2			
	2	0	3	1	0	0	6	4	4	24.15	1	$\alpha \leq 0.001$
	5	1	1	2	1	0	3	4	3			
	1	0	3	0	0	0	7	4	5	28.63	1	$\alpha \leq 0.001$
	3	0	1	0	2	1	7	2	4			
	1	0	2	1	0	2	5	7	2	28.40	1	$\alpha \leq 0.001$
	0	1	0	1	1	2	7	5	3			
	1	0	0	1	2	3	4	4	5	31.70	1	$\alpha \leq 0.001$
	0	0	1	2	1	1	6	3	6			
	0	1	1	4	4	0	3	5	2	27.13	1	$\alpha \leq 0.001$
									Total G =	167.61	6	$\alpha \leq 0.001$
pooled data	22	4	17	17	12	15	60	47	46	110.07	1	$\alpha \leq 0.001$
									heterogeneity G =	57.54	5	$\alpha \leq 0.001$
mean data	1.83	0.33	1.42	1.42	1.00	1.25	5.00	3.92	3.83			

Continued....

APPENDIX 27 - Prey Distribution Data and Analysis (data represents numbers of animals found in each cell) (continued)

prey density \ cell	top left	top middle	top right	middle left	middle middle	middle right	bottom left	bottom middle	bottom right	G statistic	degrees of freedom	significance
30 *Aedes aegypti* per 4 l. water	1	2	0	3	0	2	14	4	4			
	1	2	0	0	0	0	17	8	2	89.62	1	α≤0.001
	8	4	0	2	1	0	10	2	3			
	2	0	0	1	1	1	17	6	2	66.19	1	α≤0.001
	1	2	1	3	1	1	11	8	2			
	7	1	4	3	0	3	7	3	2	28.79	1	α≤0.001
	2	1	1	2	0	0	8	4	2			
	5	0	0	3	0	1	14	6	1	90.13	1	α≤0.001
	4	0	0	3	0	1	18	0	4			
	3	0	0	1	0	0	20	4	2	119.73	1	α≤0.001
	5	2	0	1	0	0	16	2	4			
	9	3	1	2	0	1	8	6	0	65.83	1	α≤0.001
										Total G= 460.30	6	α≤0.001
pooled data	48	17	7	24	3	10	170	53	28	398.03	1	α≤0.001
										heterogeneity G = 62.27	5	α≤0.001
mean data	4.00	1.42	0.58	2.00	0.25	0.83	14.17	4.42	2.33			

Continued....

APPENDIX 27 - Prey Distribution Data and Analysis (data represents numbers of animals found in each cell)

(continued)

cell / prey density	top left	top middle	top right	middle left	middle middle	middle right	bottom left	bottom middle	bottom left	G statistic	degrees of freedom	significance
20 *Daphnia magna* per 4 l. water	1	1	1	0	0	0	9	3	5	49.34	1	$\alpha \leq 0.001$
	2	1	2	0	0	0	4	8	3			
	2	1	0	0	0	0	6	7	4	63.02	1	$\alpha \leq 0.001$
	0	0	1	0	0	0	6	7	6			
	0	0	0	0	1	0	8	7	4	69.07	1	$\alpha \leq 0.001$
	1	0	1	0	0	0	6	8	4			
	0	1	1	0	0	0	7	5	6	56.03	1	$\alpha \leq 0.001$
	1	1	2	0	0	0	7	5	4			
	0	0	0	1	0	0	6	6	7	62.84	1	$\alpha \leq 0.001$
	0	1	2	0	0	0	8	5	4			
	0	1	0	0	0	0	6	6	7	81.35	1	$\alpha \leq 0.001$
	0	0	0	0	0	0	9	5	6			
								Total G =		381.66	6	$\alpha \leq 0.001$
pooled data	7	7	10	1	1	0	82	72	60	354.36	1	$\alpha \leq 0.001$
							heterogeneity G =			27.30	5	$\alpha \leq 0.001$
mean data	0.58	0.58	0.83	0.08	0.08	0.00	6.83	6.00	5.00			

Continued....

APPENDIX 27 - Prey Distribution Data and Analysis (data represents numbers of animals found in each cell)
(continued)

cell / prey density	top left	top middle	top right	middle left	middle middle	middle right	bottom left	bottom middle	bottom right	G statistic	degrees of freedom	significance
40 *Daphnia magna* per 4 l. water	0	0	0	0	0	0	2	6	30			
	0	0	0	0	0	0	5	14	17	197.17	1	$\alpha \leq 0.001$
	1	0	0	0	0	1	4	8	26			
	1	0	0	0	0	1	13	5	20	171.23	1	$\alpha \leq 0.001$
	1	1	1	0	0	0	7	6	20			
	2	0	0	0	3	1	11	9	14	113.98	1	$\alpha \leq 0.001$
	0	0	0	0	0	0	4	10	24			
	0	0	1	0	0	1	7	9	22	180.00	1	$\alpha \leq 0.001$
	0	0	1	0	0	0	9	6	21			
	0	0	1	0	0	0	16	3	20	177.21	1	$\alpha \leq 0.001$
	1	0	1	0	0	0	9	7	22			
	1	1	3	0	0	0	7	6	22	152.71	1	$\alpha \leq 0.001$
									Total G =	992.30	6	$\alpha \leq 0.001$
pooled data	7	2	8	0	3	4	94	89	258	930.74	1	$\alpha \leq 0.001$
									heterogeneity G =	61.56	5	$\alpha \leq 0.001$
mean data	0.58	0.17	0.67	0.00	0.25	0.33	7.83	7.42	21.50			

Continued....

APPENDIX 27 -Prey Distribution Data and Analysis (data represents numbers of animals found in each cell)

(continued)

cell / prey density	top left	top middle	top right	middle left	middle middle	middle right	bottom left	bottom middle	bottom right	G statistic	degrees of freedom	significance
80 *Daphnia magna* per 4 l. water	8	7	4	1	2	3	28	5	8	144.17	1	$\alpha \leq 0.001$
	3	7	0	2	2	2	32	10	5			
	4	8	2	1	0	1	25	12	21	169.08	1	$\alpha \leq 0.001$
	4	7	1	3	0	0	33	8	10			
	7	7	1	2	0	1	32	9	14	140.61	1	$\alpha \leq 0.001$
	3	3	0	0	3	0	29	10	14			
	3	2	1	2	1	0	29	10	12	133.85	1	$\alpha \leq 0.001$
	4	3	6	0	2	1	26	6	15			
	6	4	4	2	1	0	27	7	16	147.51	1	$\alpha \leq 0.001$
	3	2	3	0	0	0	32	7	13			
	4	2	2	1	1	2	25	6	18	176.11	1	$\alpha \leq 0.001$
	7	12	2	2	2	0	31	9	15			
								Total G	=	911.33	6	$\alpha \leq 0.001$
pooled data	58	66	26	18	11	11	349	96	167	873.86	1	$\alpha \leq 0.001$
								heterogeneity	G =	37.47	5	$\alpha \leq 0.001$
mean data	4.83	5.50	2.17	1.50	0.92	0.92	29.08	8.00	13.92			

APPENDIX 28 - 1978 Data on Enallagma boreale Individuals

Identification number	Sex	date of moult into ultimate instar	date of adult emergence
1	M	15/5/78	20/7/78
2	-	15/6/78	-
4	F	11/5/78	10/7/78
5	-	15/5/78	28/7/78
6	-	13/5/78	31/7/78
7	F	15/5/78	12/7/78
8	M	13/5/78	14/7/78
9	F	10/5/78	15/7/78
10	-	14/6/78	-
11	F	11/5/78	14/7/78
12	-	15/5/78	-
13	F	10/5/78	7/7/78
14	M	5/6/78	21/8/78
15	-	18/5/78	23/7/78
16	F	13/5/78	18/7/78
17	M	15/5/78	25/7/78
18	F	17/5/78	19/7/78
19	-	16/5/78	-
20	M	15/5/78	17/7/78
22	M	17/5/78	25/7/78
24	M	18/5/78	2/7/78
25	M	15/5/78	20/7/78
26	M	16/5/78	7/7/78
27	M	11/5/78	7/7/78
28	-	1/6/78	-
29	M	23/5/78	31/7/78
30	M	17/5/78	12/7/78
31	M	16/5/78	20/7/78
32	F	10/5/78	9/7/78
33	F	15/5/78	15/7/78
34	-	16/5/78	-
35	M	15/5/78	21/7/78
36	M	11/5/78	13/7/78
37	-	15/5/78	9/7/78

APPENDIX 28 - 1978 Data on *Enallagma boreale* Individuals (continued)

Identification number	Sex	date of moult into ultimate instar	date of adult emergence
38		13/5/78	9/7/78
39		9/5/78	5/7/78
40		11/5/78	9/7/78
41		9/5/78	dead by 27/6/87
42	M	17/5/78	20/7/78
43	M	11/5/78	4/7/78
44		12/6/78	
45	M	13/5/78	9/7/78
46	M	15/5/78	17/7/78
47		9/6/78	
48	M	13/5/78	6/7/78
49		1/6/78	21/8/78
50	M	15/5/78	12/7/78
51	M	13/5/78	11/7/78
53	M	13/5/78	4/7/78

APPENDIX 29 - Raw Data for Functional Response of *Enallagma boreale* to *Daphnia magna* in a 100 ml. arena

No = 3			No = 6			No = 12			No = 30			No = 60		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
3	18	18/5	4	9	18/5	5	1	18/5	6	4	18/5	5	11	18/5
3	35	18/5	5	33	25/5	11	40	18/5	8	13	18/5	6	16	18/5
3	8	25/5	6	12	1/6	3	42	18/5	3	22	18/5	2	30	18/5
3	4	1/6	6	40	1/6	4	46	18/5	.5	51	18/5	4	34	18/5
3	16	1/6	6	50	1/6	7	9	25/5	6	5	1/6	4	53	18/5
3	25	1/6	6	18	8/6	7	13	25/5	9	6	1/6	5	19	25/5
3	32	1/6	1	28	8/6	10	18	25/5	14	17	8/6	7	27	25/5
3	42	1/6	6	38	8/6	9	30	1/6	6	19	8/6	6	34	25/5
3	43	1/6	5	9	8/6	10	37	1/6	15	26	8/6	13	18	1/6
3	1	8/6	4	46	8/6	11	45	1/6	10	42	8/6	2	27	1/6
3	24	8/6	6	48	8/6	8	46	1/6	12	43	8/6	13	22	8/6
3	39	8/6	4	50	8/6	10	15	8/6	19	45	8/6	11	34	8/6
2	36	8/6	5	42	15/6	12	20	8/6	12	53	8/6	12	51	15/6
2	49	8/6	5	43	15/6	6	29	8/6	4	47	15/6	4	53	15/6
3	51	8/6	6	13	15/6	11	31	8/6	7	49	15/6	15	18	15/6
3	18	22/6	6	17	15/6	8	32	8/6	9	10	15/6	13	29	15/6
3	29	22/6	6	9	22/6	10	45	15/6	13	12	15/6	9	4	22/6
2	47	22/6	5	12	22/6	8	46	15/6	8	22	22/6	10	13	22/6
			6	15	22/6	7	1	22/6	16	30	22/6	10	49	22/6
			5	20	22/6	10	10	22/6	8	34	22/6			
			5	28	22/6									
			2	48	22/6									

APPENDIX 30 - Raw Data for Functional Response of *Enallagma boreale* to *Daphnia magna* in a 1 l. arena

No = 3			No = 6			No = 30			No = 30			No = 120		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
1	13	11/5	6	25	18/5	3	9	11/5	3	32	11/5	21	15	15/6
1	19	18/5	2	36	18/5	7	7	18/5	4	20	18/5	16	25	15/6
3	31	18/5	1	48	18/5	5	37	18/5	5	27	18/5	12	34	15/6
3	45	18/5	4	12	18/5	12	41	18/5	7	32	18/5	14	35	15/6
2	32	25/5	4	4	25/5	16	30	25/5	13	22	25/5	13	37	15/6
3	26	25/5	5	16	25/5	16	38	25/5	9	51	25/5	16	39	15/6
3	45	25/5	4	42	25/5	14	40	25/5	11	53	25/5	17	40	15/6
2	48	25/5	5	43	25/5	13	41	25/5	15	15	1/6	13	7	22/6
3	1	1/6	3	33	1/6	4	46	25/5	11	22	1/6	1	27	22/6
3	13	1/6	5	34	1/6	10	8	1/6	10	35	1/6	8	35	22/6
2	24	1/6	6	39	1/6	13	9	1/6	16	51	1/6	11	38	22/6
2	41	1/6	6	48	1/6	9	20	1/6	10	53	1/6	8	42	22/6
1	16	15/6	1	6	15/6	18	26	1/6	14	4	15/6	17	46	22/6
3	22	15/6	2	19	15/6	10	26	15/6	5	19	22/6	9	50	22/6
2	1	15/6	5	31	22/6	10	25	22/6						
3	9	15/6				8	36	22/6						
1	11	22/6												
2	16	22/6												

APPENDIX 31 - Raw Data for Functional Response of *Enallagma boreale* to *Daphnia magna* in a 2 l. arena

No = 6			No = 30			No = 60			No = 120			No = 240		
Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date	Ne	Ind. No.	date
0	5	18/5	7	8	18/5	3	41	11/5	10	38	18/5	7	5	15/6
0	6	18/5	7	43	18/5	7	17	18/5	7	39	18/5	15	11	15/6
-	-	-	5	50	18/5	5	26	18/5	18	12	25/5	17	20	15/6
-	-	-	7	1	25/5	7	33	18/5	6	20	25/5	3	28	15/6
3	5	25/5	7	6	25/5	8	11	25/5	9	35	25/5	12	32	15/6
3	7	25/5	4	15	25/5	7	25	25/5	12	39	25/5	18	33	15/6
1	24	25/5	6	17	25/5	6	29	25/5	17	36	1/6	21	36	15/6
4	36	25/5	8	7	1/6	9	31	25/5	17	11	8/6	13	38	15/6
3	50	25/5	10	17	1/6	10	37	25/5	22	12	8/6	9	44	15/6
3	19	1/6	10	4	8/6	8	11	1/6	14	16	8/6	15	48	15/6
2	29	1/6	14	5	8/6	27	38	1/6	13	30	8/6	8	50	15/6
5	31	1/6	11	6	8/6	6	14	8/6	20	40	8/6	11	2	22/6
5	8	8/6	17	7	8/6	11	25	8/6	13	8	15/6	17	14	22/6
4	13	8/6	12	7	15/6	11	27	8/6	5	51	22/6	6	37	22/6
4	33	8/6	9	14	15/6	14	37	8/6	0	53	22/6	1	39	22/6
5	35	8/6	5	44	22/6	10	8	22/6				2	40	22/6
5	30	15/6				14	17	22/6				0	43	22/6
5	31	15/6				11	24	22/6				1	45	22/6
3	24	15/6												
4	27	15/6												
5	5	22/6												
4	6	22/6												

APPENDIX 32 - Correlations of Number of Prey Eaten (corrected for age) with Predator weight (dry weight of adult)

1. *Pyrrhosoma nymphula* eating *Aedes aegypti*

number of prey offered	3	5	10	15	20	25	30
n	2	5	7	6	2	2	2
r	-	0.55	0.55	0.27	-	-	-
significance	-	n.s.	n.s.	n.s.	-	-	-

2. *Pyrrhosoma nymphula* eating *Daphnia magna*

number of prey offered	5	10	20	40	60	80	100	120	140	160
n	3	5	4	4	3	4	4	5	3	3
r	0.74	0.89	-0.71	0.70	0.61	0.14	-0.99	0.57	-0.13	-1.00
significance	n.s.	**	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	**

3. *Coenagrion puella* eating *Aedes aegypti*

number of prey offered	3	5	10	15	20	25	30	35
n	2	2	5	6	3	1	2	4
r	-	-	0.80	0.11	0.90	-	-	-0.30
significance	-	-	*	n.s.	*	-	-	n.s.

* = significant at the 5% level
** = significant at the 1% level
n.s.= not significant

APPENDIX 32 - Correlations of Number of Prey Eaten (corrected for age) with Predator weight (dry weight of adult)
(continued) (continued)

4. *Coenagrion puella* eating *Daphnia magna*

number of prey offered	5	10	20	40	60	80	100	120	140	160
n	1	1	1	2	3	2	1	0	1	3
r	-	-	-	-	1.00	-	-	-	-	-0.37
significance	-	-	-	-	**	-	-	-	-	n.s.

* = significant at the 5% level

** = significant at the 1% level

n.s.= not significant

APPENDIX 33 - Description of Printing Counter and Keyboard

Preliminary sit and watch experiments, conducted in 1974, revealed the need for instrumentation to aid in recording damselfly behaviour. Events were so brief, and they proceeded in such rapid sequence, that recording these data by hand inevitably resulted in the observer missing some events. Rustrak type recorders were considered unsuitable for this purpose, because they are imprecise regarding time and inadequate for recording fifteen distinct events, and because they require tedious interpretation of their paper output. While it was recognised that the conception and construction of new equipment requires time that might otherwise be used for experimentation, in this case the prospect of complete and accurate experimental results provided sufficient justification for the production of a suitable recording instrument.

An English Numbering Machine 4850 Data Printer was adapted for recording observations during the sit and watch experiments by Mr. A.C. Easty. A fifteen button keyboard was constructed, the three rows of buttons corresponding to the three predators under observation, and the five columns of buttons corresponding to the five events being investigated. (Theoretically, 99 distinct events could be recorded, since two data wheels provided a maximum event number of 99.) A clock, incorporated in the apparatus, kept track of the time in seconds which had elapsed since the timer switch on the keyboard was reset at the beginning of the experiment. Four timing wheels provided a maximum count of 9999 seconds. Whenever any event occurred, the appropriate keyboard button was depressed, and the number of the event and the time in seconds of its occurrence were printed. Because the unit has a resolution of one second, the maximum error in the time recorded was one second. At the end of each experiment, a printed list recorded all the events which had occurred during the experiment, and the times at which each had been observed. In this way, the experimental results were immediately available in compact and easily interpreted form.

The only difficulties arising in the use of this device were connected with jamming of the paper spool, and continual spinning of the printing wheels. The first problem was solved by attaching a weight to the end of the paper output, which ensured that the paper spool moved freely. The second problem was avoided by depressing one of the event keys before starting the experiment. This procedure loaded the keyboard memory and gave the printer a homing command, preventing the data wheels from revolving until they were given a fresh command.

A more detailed account of the circuitry involved in the construction of the keyboard and the keyboard-data printer interface, is contained in a users manual kept by Dr. S. McNeill at Silwood Park.

APPENDIX 34 - Functional Response Parameters (observed) for damselflies eating Aedes aegypti

damselfly	No	Ne	n	a(2 l./min.) $(\bar{x} \pm s_x)$	n	Th(min.) $(\bar{x} \pm s_x)$
Pyrrhosoma nymphula	5	1	2	0.3909 ± 0.21	2	1.7584 ± 0.24
		2	2	0.0675 ± 0.02	2	4.1500 ± 0.95
		3	1	0.4762 ± ∞	0	
		4	1	0.3371 ± ∞	1	1.7000 ± ∞
	10	1	4	0.0493 ± 0.04	4	2.6959 ± 0.72
		2	2	0.0371 ± 0.02	1	1.7667 ± ∞
		3	2	0.1680 ± 0.16	1	1.5500 ± ∞
	15	1	4	0.1414 ± 0.09	2	1.3167 ± 0.15
		2	3	0.2273 ± 0.09	3	1.8833 ± 0.57
		3	3	0.0712 ± 0.05	3	2.3267 ± 0.08
		4	2	0.0875 ± 0.08	2	3.2833 ± 0.80
Coenagrion puella	5	1	3	0.0340 ± 0.03	3	2.10 ± 0.36
		2	2	0.0080 ± 0.0018	1	3.55 ± ∞
		3	2	0.0080 ± 0.0017	2	3.28 ± 2.68
	10	1	5	0.0575 ± 0.05	2	1.98 ± 0.20
		2	5	0.1366 ± 0.04	3	5.37 ± 2.53
		3	3	2.5319 ± 2.48	3	4.03 ± 1.56
		4	2	0.0175 ± 0.01	2	3.78 ± 1.87
		5	2	2.5192 ± 2.48	2	4.98 ± 1.43
	15	1	4	0.0282 ± 0.0168	3	3.53 ± 1.17
		2	3	0.0106 ± 0.0071	3	4.02 ± 0.97
		3	3	0.0108 ± 0.0069	3	4.93 ± 0.61
		4	1	0.0205 ± ∞	1	2.82 ± ∞
		5	1	0.0058 ± ∞	1	3.23 ± ∞

Analysis of variance on a and Th data, considering Ne and No as Main Effects

damselfly	Pyrrhosoma nymphula		Coenagrion puella	
parameter	a	Th	a	Th
No d.f.	2	2	2	2
F	3.864	0.524	1.225	0.518
α	0.044	0.999	0.313	0.999

Continued....

APPENDIX 34(continued) - Functional Response Parameters (observed)for damselflies eating *Aedes aegypti* (continued)

Analysis of variance on *a* and *Th* data, considering *Ne* and *No* as Main Effects(continued)

damselfly		*Pyrrhosoma nymphula*		*Coenagrion puella*	
parameter		a	Th	a	Th
Ne	d.f.	3	3	4	4
	F	0.250	0.558	1.108	0.787
	α	0.999	0.999	0.378	0.999

APPENDIX 35 - Activity data for damselflies eating *Aedes aegypti*

incl. = including

damselfly	No	Ne	n	mean no. of perch changes	n	mean duration of perch (min.) not incl. zero data
				$(\bar{x} \pm s_x)$		$(\bar{x} \pm s_x)$
Pyrrhosoma nymphula	5	0	2	0.00 ± 0.00	0	-
		1	2	0.50 ± 0.50	1	4.48 ± ∞
		2	2	1.50 ± 1.50	1	31.70 ± ∞
		3	1	0.00 ± ∞	0	-
		4	1	1.00 ± ∞	1	9.92 ± ∞
	10	0	4	2.25 ± 1.60	3	12.91 ± 11.12
		1	4	0.75 ± 0.48	2	6.40 ± 3.30
		2	2	0.50 ± 0.50	1	9.40 ± ∞
		3	2	4.00 ± 2.00	2	27.57 ± 23.18
	15	0	4	0.75 ± 0.48	2	5.19 ± 4.96
		1	4	3.25 ± 1.98	3	3.94 ± 3.22
		2	3	1.00 ± 0.58	2	4.15 ± 2.31
		3	3	1.67 ± 0.33	3	4.07 ± 2.34
		4	2	46.50 ± 42.50	2	5.01 ± 3.62
Coenagrion puella	5	0	3	0.00 ± 0.00	0	-
		1	3	0.33 ± 0.33	1	13.23 ± ∞
		2	3	2.00 ± 1.15	2	15.82 ± 4.17
		3	1	0.00 ± ∞	0	-
		4	1	0.00 ± ∞	0	-
	10	0	5	2.80 ± 1.59	3	5.28 ± 1.95
		1	4	0.00 ± 0.00	0	-
		2	4	5.00 ± 2.80	3	3.41 ± 1.48
		3	3	2.00 ± 1.15	2	17.71 ± 12.82
		4	2	0.00 ± 0.00	0	-
		5	1	3.00 ± ∞	1	17.34 ± ∞
	15	0	4	0.50 ± 0.50	1	0.83 ± ∞
		1	4	2.00 ± 1.08	3	10.04 ± 4.01
		2	3	3.33 ± 1.77	2	4.11 ± 2.25
		3	3	8.33 ± 5.24	2	5.22 ± 2.62
		4	1	0.00 ± ∞	0	-
		5	1	0.00 ± ∞	0	-

APPENDIX 35 - Activity Data for damselflies eating *Aedes aegypti* (continued)

Multiple Regressions of Activity Data on No and Ne

damselfly	*Pyrrhosoma nymphula*		*Coenagrion puella*	
measure	mean number of perch changes	mean duration of perch	mean number of perch changes	mean duration of perch
n	36	143	46	94
intercept	-9.27	105783.72	-0.93	48904.36
slope (No)	+0.69	-6186.65	+0.24	-2333.57
F	1.32	30.11	3.01	3.52
α	$\alpha > 0.25$	$\alpha < 0.005$	$\alpha < 0.10$	$\alpha < 0.10$
slope (Ne)	+3.78	-1356.04	+0.31	+2349.13
F	4.31	0.47	0.70	0.54
α	$\alpha < 0.05$	$\alpha > 0.25$	$\alpha > 0.25$	$\alpha > 0.25$

APPENDIX 36 - Strike Success and Capture Success Data, and Linear Regressions on Prey Density (all Data for Predators more than ten days from emergence)

	No = 5				No = 10				No = 15			
	Ind. No.	date	ss	cs	Ind. No.	date	ss	cs	Ind. No.	date	ss	cs
Pyrrhosoma nymphula eating *Aedes aegypti*	41	12/4/76	0.80	0.80	11	11/3/76	1.00	1.00	12	11/3/76	1	0.43
	41	19/4/76	1.00	0.67	30	5/4/76	1.00	1.00	8	22/3/76	1	0.57
					31	12/4/76	1.00	0.18	22	29/3/76	0.80	0.18
					42	19/4/76	1.00	1.00	30	12/4/76	0.33	0.33
Coenagrion puella eating *Aedes aegypti*	10	8/4/76	1.00	1.00	40	8/4/76	0.56	0.56	28	8/4/76	0.75	0.23
	46	6/5/76	1.00	1.00	40	15/4/76	1.00	0.14	34	26/4/76	1.00	1.00
	52	24/5/76	1.00	1.00	55	6/5/76	0.83	0.71	56	6/5/76	1.00	1.00
					45	13/5/76	0.08	0.06	56	13/5/76	1.00	0.20
					52	17/5/76	1.00	1.00				

APPENDIX 36 - Strike Success and Capture Success Data, and Linear Regressions on Prey Density (all Data for Predators more than ten days from emergence) (continued)

Predator-Prey Interaction	*Pyrrhosoma nymphula* eating *Aedes aegypti*		*Coenagrion puella* eating *Aedes aegypti*	
measure	strike success	capture success	strike success	capture success
n	10	10	12	12
intercept	1.07	1.08	0.88	1.03
slope	-0.02	-0.04	-0.00	-0.04
F	0.79	2.80	0.02	1.44
α	$\alpha > 0.25$	$\alpha > 0.25$	$\alpha > 0.25$	$\alpha > 0.25$

APPENDIX 37 -Regressions of FunctionalResponse components on Predator Age

Functional response component	predator	No	n	intercept	slope	F	signi-ficance
a(attack rate) (2 l./min.)	*Pyrrhosoma nymphula*	5	6	0.43	-0.01	0.07	n.s.
		10	8	-0.19	0.01	1.05	n.s.
		15	12	0.52	-0.03	2.30	n.s.
	Coenagrion puella	5	7	0.06	-0.002	0.90	n.s
		10	16	-0.82	0.09	0.16	n.s
		15	12	0.15	-0.01	12.71	**
Th(handling time) (min.)	*Pyrrhosoma nymphula*	5	5	6.17	-0.20	1.10	n.s.
		10	6	9.13	-0.32	3.93	n.s.
		15	10	-0.09	0.16	1.58	n.s.
	Coenagrion puella	5	6	1.72	0.06	0.12	n.s.
		10	13	7.38	-0.16	0.18	n.s.
		15	11	5.02	-0.06	0.02	n.s.
cs (capture success)	*Pyrrhosoma nymphula*	5	2	0.43	0.02	0.01	trivial
		10	4	1.27	-0.02	0.08	n.s.
		15	4	-0.31	0.05	1.79	n.s.
	Coenagrion puella	5	3	1.00	0.00	0.00	trivial
		10	5	-0.80	0.07	1.17	n.s.
		15	4	-1.42	0.12	5.35	n.s.
ss (strike success)	*Pyrrhosoma nymphula*	5	2	1.37	-0.03	0.02	trivial
		10	4	1.00	0.00	0.00	trivial
		15	4	1.40	-0.04	0.23	n.s.
	Coenagrion puella	5	3	1.00	0.00	0.00	trivial
		10	5	1.46	-0.04	0.34	n.s.
		15	4	0.90	0.002	0.006	n.s.

APPENDIX 37 (continued) - Regressional Functional Response components on Predator Age (continued)

Functional response component	Predator	No	n	intercept	slope	F	significance
number of perch changes per capture	Pyrrhosoma nymphula	5	8	2.11	-0.09	0.56	n.s.
		10	12	9.12	-0.36	3.49	n.s.
		15	16	48.28	-2.79	1.24	n.s.
	Coenagrion puella	5	11	0.02	0.04	0.18	n.s.
		10	19	6.89	-0.25	0.60	n.s.
		15	16	8.63	-0.34	0.38	n.s.
duration of each perch (sec.)	Pyrrhosoma puella	5	5	4632.00	-21.00	1.30	n.s.
		10	21	-2146.34	151.94	8.38	**
		15	117	-807.37	74.35	37.26	**
	Coenagrion puella	5	6	267.64	33.18	0.67	n.s.
		10	43	9.02	24.25	0.53	n.s.
		15	45	1572.42	-74.65	3.08	n.s.

The anomalous significant increase in Coenagrion's attack rate with age at prey density 15 is probably not indicative of a more general trend, as the slope (0.01) is low, and dissimilar to the slopes for this relationship at prey densities 5 and 10.

Coenagrion's activity does not change significantly as it ages, but Pyrrhosoma does tend to become more active as it approaches emergence.

The duration of each perch becomes significantly briefer at prey densities of 10 and 15, and the number of perch changes consistently increases with age, for all prey densities, although this is not significant.

This activity is probably symptomatic of confusion, as suggested by Coenagrion's increase in activity at high mosquito densities(Figure 2.17.)

* = significant at the 5% level
** = significant at the 1% level
n.s. = not significant
trivial= $n \leq 3$

APPENDIX 38 - Predicted Numbers of *Aedes aegypti* Eaten by each Damselfly, using the Observed *a*'s and *Th*'s, for a Range of Values of *Tt*

a) *Pyrrhosoma nymphula*

No Tt (min.)	3	5	10	15	20	25	30	35
5	1.00	1.29	1.63	1.77	1.85	1.90	1.94	1.96
10	1.77	2.41	3.18	3.51	3.68	3.79	3.86	3.92
15	2.31	3.33	4.64	5.19	5.48	5.66	5.78	5.86
20	2.64	4.01	5.97	6.81	7.24	7.50	7.67	7.79
25	2.82	4.46	7.14	8.35	8.96	9.32	9.55	9.71
30	2.91	4.72	8.11	9.80	10.63	11.11	11.41	11.62
45	2.99	4.97	9.67	13.21	15.16	16.21	16.82	17.23
60	3.00	5.00	9.96	14.69	18.42	20.63	21.86	22.60
120	3.00	5.00	10.00	15.00	20.00	25.00	29.98	34.89
180	3.00	5.00	10.00	15.00	20.00	25.00	30.00	35.00
240	3.00	5.00	10.00	15.00	20.00	25.00	30.00	35.00
300	3.00	5.00	10.00	15.00	20.00	25.00	30.00	35.00
360	3.00	5.00	10.00	15.00	20.00	25.00	30.00	35.00

APPENDIX 38 - Predicted Numbers of *Aedes aegypti* Eaten by each Damselfly, using the Observed *a*'s and *Th*'s, for a Range of Values of *Tt* (continued)

b) *Coenagrion puella*

Tt (min.) \ No	3	5	10	15	20	25	30	35
5	1.01	1.11	1.19	1.22	1.23	1.24	1.25	1.25
10	1.89	2.17	2.37	2.43	2.46	2.48	2.49	2.50
15	2.56	3.16	3.54	3.64	3.69	3.72	3.74	3.75
20	2.90	4.02	4.68	4.84	4.91	4.95	4.98	5.00
25	2.98	4.64	5.80	6.03	6.13	6.18	6.22	6.24
30	3.00	4.92	6.88	7.21	7.34	7.41	7.46	7.49
45	3.00	5.00	9.50	10.64	10.94	11.08	11.16	11.21
60	3.00	5.00	10.00	13.69	14.45	14.71	14.84	14.93
120	3.00	5.00	10.00	15.00	20.00	24.99	28.58	29.38
180	3.00	5.00	10.00	15.00	20.00	25.00	30.00	35.00
240	3.00	5.00	10.00	15.00	20.00	25.00	30.00	35.00
300	3.00	5.00	10.00	15.00	20.00	25.00	30.00	35.00
360	3.00	5.00	10.00	15.00	20.00	25.00	30.00	35.00

APPENDIX 39 - Regression of *Pyrrhosoma nymphula* Maximum Feeding Rate (Lawton, 1971b) on Age

Data:

y = maximum feeding rate (mg./larva/day)	0.879	0.535	0.412	0.367	0.269	0.138
x = larval age = 10 + no. days before feeding stopped	16	15	14	13	12	11

Results:

n	intercept	slope	r^2	significance
6	-1.32	0.13	0.90	**

** = significant at the 1% level

* = significant at the 5% level

n.s. = not significant

APPENDIX 40 - Raw Data for *Pyrrhosoma nymphula* on mixed prey

Nom = 10; Nod = 40				Nom = 10; Nod = 80				Nom = 20; Nod = 40				Nom = 20; Nod = 80			
Nem	Ned	Ind. No.	date	Nem	Ned	Ind. No.	date	Nem	Ned	Ind. No.	date	Nem	Ned	Ind. No.	date
7	3	15	4/3/76	3	6	12	4/3/76	5	3	11	4/3/76	3	2	17	4/3/76
4	1	16	4/3/76	2	6	13	4/3/76	6	2	14	4/3/76	5	0	18	4/3/76
8	1	41	5/4/76	6	1	19	22/3/76	5	0	19	15/3/76	5	3	8	15/3/76
5	0	1	3/2/77	8	0	39	2/4/76	4	10	38	2/4/76	5	3	19	29/3/76
8	3	12	3/2/77	5	4	13	3/2/77	7	0	39	8/4/76	9	2	42	26/4/76
4	1	14	10/2/77	5	1	13	10/2/77	5	0	14	3/2/77	8	0	15	3/2/76
2	2	2	24/2/77	6	5	15	10/2/77	3	0	1	10/2/77	4	1	12	10/2/76
								2	0	1	17/2/77	3	0	15	17/2/76

APPENDIX 41 - Raw Data for *Coenagrion puella* on mixed prey

Nom = 10; Nod = 40				Nom = 10; Nod = 80				Nom = 20; Nod = 40				Nom = 20; Nod = 80			
Nem	Ned	Ind. No.	date	Nem	Ned	Ind. No.	date	Nem	Ned	Ind. No.	date	Nem	Ned	Ind. No.	date
7	4	10	2/4/76	8	8	33	26/4/76	5	0	33	3/5/76	3	2	34	3/5/76
4	2	29	13/5/76	4	5	32	17/2/77	3	1	57	10/5/76	6	9	29	6/5/76
5	3	30	17/2/77	6	8	38	17/2/77	4	1	35	17/2/77	4	2	46	13/5/76
8	3	34	17/2/77	8	2	43	17/2/77	6	1	26	17/2/77	6	2	42	17/2/77
7	0	23	17/2/77	6	5	5	17/2/77	6	2	9	17/2/77	6	3	25	17/2/77
6	1	4	17/2/77	8	3	40	17/2/77	4	3	41	17/2/77	5	2	10	17/2/77
8	2	24	17/2/77					5	0	45	17/2/77				

APPENDIX 42 - Fit of Mixed Prey Results to Two Prey Random Predator Model

Multiple Regression Equations:

$$\ln\left(\frac{Nom - Nem}{Nom}\right) = -am\ Tt + am\ Thm\ \ Nem + am\ Thd\ Ned$$

$$\ln\left(\frac{Nod - Ned}{Nod}\right) = -ad\ Tt + ad\ Thm\ \ Nem + ad\ Thd\ Ned$$

Results (1976 and 1977 data)

	Pyrrhosoma nymphula	*Coenagrion puella*
-am Tt	0.93	4.08
am Thm	-0.25	-0.79
am Thd	-0.05	0.004
F	0.04	798.77
significance	n.s.	**
-ad Tt	-0.42	0.03
ad Thm	0.07	-0.01
ad Thd	-0.0007	-0.002
F	1009.30	18.64
significance	**	*

** = significance at the 1% level

* = significance at the 5% level

n.s. = not significant

APPENDIX 43 - Regressions of Diet Breadths on Competition Coefficients for *Pyrrhosoma nymphula* and *Coenagrion puella* Aged 20

	Pyrrhosoma nymphula		*Coenagrion puella*	
	Actual Results	Predicted Results	Actual Results	Predicted Results
n	4	4	4	4
intercept	0.16	0.24	-0.08	0.10
slope	-0.09	-0.05	0.14	-0.07
F	0.11	0.98	0.46	0.50
significance	n.s.	n.s.	n.s	n.s.

** = significance at the 1% level

* = significance at the 5% level

n.s. = not significant

APPENDIX 44 - Standard Normal Distribution, Derived from 1975 Emergence Data

Date (1975)	Standard Normal Deviate for *Pyrrhosoma nymphula*	Standard Normal Deviate for *Coenagrion puella*
5/1	-5.4964	-17.77
10/1	-4.1626	-14.25
15/1	-3.3824	-12.05
20/1	-2.8288	-10.49
25/1	-2.3995	-9.15
30/1	-2.0486	-8.29
4/2	-1.7520	-7.45
9/2	-1.4951	-6.72
14/2	-1.2684	-6.08
19/2	-1.0657	-5.4369
24/2	-0.8823	-4.9265
1/3	-0.7149	-4.4605
6/3	-0.5609	-4.0319
11/3	-0.4183	-3.6350
16/3	-0.2855	-3.2656
21/3	-0.1613	-2.9200
26/3	-0.0447	-2.5953
31/3	0.0653	-2.2892
5/4	0.1694	-1.9997
10/4	0.2681	-1.7250
15/4	0.3619	-1.4638
20/4	0.4515	-1.2146
25/4	0.5370	-0.9766
30/4	0.6189	-0.7487
5/5	0.6974	-0.5301
10/5	0.7729	-0.3201
15/5	0.8455	-0.1180
20/5	0.9155	0.0768
25/5	0.9830	0.2647
30/5	1.0483	0.4463
4/6	1.1114	0.6218
9/6	1.1724	0.7919
14/6	1.2317	0.9566
19/6	1.2891	1.1165
24/6	1.3449	1.2717
29/6	1.3991	1.4226
4/7	1.4518	1.5693
9/7	1.5031	1.7121
14/7	1.5531	1.8512
19/7	1.6018	1.9868
24/7	1.6493	2.1190
29/7	1.6957	2.2481
3/8	1.7410	2.3741
8/8	1.7852	2.4972
13/8	1.8285	2.6175

	age 31 and over	age 21-30	age 11-20	age 1-10	(days before emergence)
	1.0	0.0	0.0	0.0	
	1.0	0.0	0.0	0.0	
	1.0	0.0	0.0	0.0	
DEC.	1.0	0.0	0.0	0.0	
	1.0	0.0	0.0	0.0	
	1.0	0.0	0.0	0.0	
	1.0	0.0	0.0	0.0	
	1.0	0.0	0.0	0.0	
	1.0	0.0	0.0	0.0	
JAN.	1.0	0.0	0.0	0.0	
	1.0	0.0	0.0	0.0	
	.999999589	.000000411	.0	.0	
	.999995902	.000004098	.0	.0	
	.999972112	.000027477	.000000411	.0	
	.99986368	.000132222	.000004898	.0	
FEB.	.99946226	.000509852	.000027477	.000000411	
	.9982498	.00161388	.000132222	.000004098	
	.9953388	.00412346	.000509852	.000027477	
	.988989	.0092608	.00161388	.000132222	
	.97725	.0180888	.00412346	.000509852	
	.958185	.030804	.0092608	.00161388	
MARCH	.927855	.049395	.0180888	.00412346	
	.88686	.071325	.030804	.0092608	
	.83646	.091395	.049395	.0180888	
	.77337	.11349	.071325	.030804	
	.70194	.13452	.091395	.049395	
	.62552	.14785	.11349	.071325	
APRIL	.54776	.15418	.13452	.091395	
	.46812	.1574	.14785	.11349	
	.32636	.14176	.1574	.14785	
	.39743	.15033	.15418	.13452	
	.26763	.1298	.15033	.15418	
	.21476	.1116	.14176	.1574	
MAY	.16853	.0991	.1298	.15033	
	.13136	.0834	.1116	.14176	
	.10204	.06649	.0991	.1298	
	.077804	.053556	.0834	.1116	
	.058208	.042832	.06649	.0991	
	.043633	.034171	.053556	.0834	
JUNE	.032157	.026051	.042832	.06649	
	.023295	.020338	.034171	.053556	
	.017003	.015154	.026051	.042832	
	.012224	.011071	.020338	.034171	
	.008894	.008109	.015154	.026051	
	.0062097	.0060143	.011071	.020338	
JULY	.0043965	.0044975	.008109	.015154	
	.003072	.0031377	.0060143	.011071	
	.002186	.0022105	.0044975	.008109	
	.0015382	.0015338	.0031377	.0060143	
AUGUST	.0010703	.0011157	.0022105	.0044975	
	.00073638	.00080182	.0015338	.0031377	
	.00050094	.00056936	.0011157	.0022105	

APPENDIX 44 - Simulated Fraction of *Pyrrhosoma nymphula* Population in Each Age Class, During Spring, 1975
(Continued)

	age 31 and over	age 21-30	age 11-20	age 1-10	(days before emergence)
	1.0	0.0	0.0	0.0	
	1.0	0.0	0.0	0.0	
	.999984088	.000015912	.0	.0	
	.99963757	.00036243	.0	.0	
DEC.	.9976726	.00231149	.000015912	.0	
	.9918025	.00783507	.00036243	.0	
	.979818	.0178546	.00231149	.000015912	
	.959941	.0318615	.00783507	.00086243	
	.933193	.046625	.0178546	.00231149	
JAN.	.89796	.061981	.0318615	.00783507	
	.85769	.075503	.046625	.0178546	
	.81057	.08739	.061981	.0318615	
	.76115	.09654	.075503	.046625	
	.71226	.09831	.08739	.061981	
	.66276	.09839	.09654	.075503	
FEB.	.612175	.100085	.09831	.08739	
	.56356	.09920	.09839	.09654	
	.51595	.096225	.100085	.09831	
	.4721	.09146	.09920	.09839	
	.43251	.08344	.096225	.100085	
	.39358	.07852	.09146	.09920	
MARCH	.35942	.07309	.08344	.096225	
	.32636	.06722	.07852	.09146	
	.29460	.06482	.07309	.08344	
	.26763	.05873	-.06722	.07852	
	.24196	.05264	.06482	.07309	
	.22065	.04698	.05873	.06722	
APRIL	.19766	.0443	.05264	.06482	
	.17879	.04186	.04698	.06873	
	.16354	.03412	.04430	.05264	
	.14686	.03193	.04186	.04698	
	.13350	.03004	.03412	.0443	
	.12100	.02586	.03193	.04186	
	.10935	.02416	.03004	.03412	
	.098525	.022475	.02586	.03193	
	.090123	.019227	.02415	.03004	
	.080757	.017768	.022475	.02586	
	.073529	.016594	.019227	.02415	
	.066807	.01395	.017768	.022475	
	.060571	.012958	.016594	.019227	
	.054799	.012008	.01395	.017768	
	.049471	.0111	.012958	.016594	
	.044565	.010234	.012008	.01395	
	.040930	.008541	.0111	.012958	
	.036727	.007838	.010234	.012008	
JULY	.033625	.007305	.008541	.0111	
	.030742	.005985	.007838	.010234	
	.028067	.005558	.007305	.008541	
	.025588	.005154	.005985	.007838	
AUGUST	.023295	.004772	.005558	.007305	
	.021178	.004410	.005154	.005985	
	.019226	.004069	.004772	.005558	

APPENDIX 44 - Simulated Fraction of *Coenagrion puella* Population in Each Age Class, During Spring, 1975
(Continued)

APPENDIX 45 - Computer Printout of Population Predation Model and Sample Output

```
$JOBW
            DIMENSION YA(200),YB(200),TIM(200)
            DIMENSION N(100,4),M(100,4),P(8,4),B(8,4)
            REAL N,M,K,J,P,B
            READ(5,19)NPT
            READ(5,20)((P(I,L),L=1,4),I=1,8)
            READ(5,20)((B(I,L),L=1,4),I=1,8)
            READ(5,20)((N(I,L),L=1,4),I=1,NPT)
            READ(5,20)((M(I,L),L=1,4),I=1,NPT)
            DO 2 II=1,8
            WRITE(6,22)(P(II,LL),LL=1,4)
            WRITE(6,23)(B(II,LL),LL=1,4)
            SUM=0
            ASUM=0
            BSUM=0
            CSUM=0
            DO 1 L=1,NPT
            TIM(L)=5*(L-7)
            K=N(L,1)*P(II,1)+N(L,2)*P(II,2)+N(L,3)*P(II,3)+N(L,4)*P(II,4)
            YA(L)=K
            J=M(L,1)*B(II,1)+M(L,2)*B(II,2)+M(L,3)*B(II,3)+M(L,4)*B(II,4)
            YB(L)=J
            SUM=SUM+AMIN1(J,K)
            ASUM=ASUM+J+K
            BSUM=BSUM+K
            CSUM=CSUM+J
    1       WRITE(6,21)(N(L,KK),KK=1,4),K,(M(L,JJ),JJ=1,4),J
            WRITE(6,24)SUM
            IF(MOD(II,2).EQ.1)SUM=SUM*2.5
            IF(MOD(II,2).EQ.1)ASUM=ASUM*2.5
            WRITE(6,26)SUM
            SUM=SUM/ASUM
            WRITE(6,25)SUM
            WRITE(6,28)BSUM
            WRITE(6,27)CSUM
    2       CONTINUE
    19      FORMAT(I2)
    20      FORMAT(4F10.5)
    21      FORMAT(1X,4F10.5,4X,F10.7,8X,4F10.5,4X,F10.7)
    22      FORMAT('  P.N. COEFFICIENTS ',4(5X,F10.7))
    23      FORMAT('  C.P. COEFFICIENTS ',4(5X,F10.7))
    24      FORMAT('  ABSOLUTE OVERLAP ',F10.6)
    25      FORMAT('  RELATIVE OVERLAP ',F10.6)
    26      FORMAT('  ABSOLUTE CALORIFIC OVERLAP ',F10.6)
    27      FORMAT('  C.P. TOTAL NE ',F10.6)
    28      FORMAT('  P.N. TOTAL NE ',F10.6)
            STOP
            END
```

```
          $DATA
P.N. COEFFICIENTS          2.7600000        2.5299990        2.0600000        1.2600000
C.P. COEFFICIENTS          7.3999990        4.6400000        2.2299990        0.0000000
  1.00000     0.00000     0.00000     0.00000      2.7600000               1.00000     0.00000     0.00000     0.00000       7.3999990
  1.00000     0.00000     0.00000     0.00000      2.7600000               1.00000     0.00000     0.00000     0.00000       7.3999990
  0.99998     0.00002     0.00000     0.00000      2.7599950               1.00000     0.00000     0.00000     0.00000       7.3999990
  0.99964     0.00036     0.00000     0.00000      2.7599160               1.00000     0.00000     0.00000     0.00000       7.3999950
  0.99767     0.00231     0.00002     0.00000      2.7594560               1.00000     0.00000     0.00000     0.00000       7.3999990
  0.99180     0.00784     0.00036     0.00000      2.7579420               1.00000     0.00000     0.00000     0.00000       7.3999950
  0.97982     0.01785     0.00231     0.00002      2.7542490               1.00000     0.00000     0.00000     0.00000       7.3999990
  0.95994     0.03186     0.00784     0.00086      2.7472720               1.00000     0.00000     0.00000     0.00000       7.3999990
  0.93319     0.04662     0.01785     0.00231      2.7332640               1.00000     0.00000     0.00000     0.00000       7.3999990
  0.89796     0.06198     0.03186     0.00784      2.7106860               1.00000     0.00000     0.00000     0.00000       7.3999990
  0.87577     0.07550     0.04662     0.01785      2.7266870               1.00000     0.00000     0.00000     0.00000       7.3999990
  0.81057     0.08739     0.06198     0.03186      2.6260940               1.00000     0.00000     0.00000     0.00000       7.3999960
  0.76115     0.09654     0.07550     0.04662      2.5593020               1.00000     0.00000     0.00000     0.00000       7.3999870
  0.71226     0.09831     0.08739     0.06198      2.4726800               0.99997     0.00003     0.00000     0.00000       7.3999190
  0.66275     0.09839     0.09654     0.07550      2.3721200               0.99986     0.00013     0.00000     0.00000       7.3996120
  0.61217     0.10009     0.09831     0.08739      2.2554470               0.99946     0.00051     0.00003     0.00000       7.3984460
  0.56356     0.09920     0.09839     0.09654      2.1307230               0.99825     0.00161     0.00013     0.00000       7.3948300
  0.51595     0.09623     0.10009     0.09831      1.9975150               0.99534     0.00412     0.00051     0.00003       7.3857750
  0.47210     0.09146     0.09920     0.09839      1.8627100               0.98899     0.00926     0.00161     0.00013       7.3658850
  0.43251     0.08344     0.09623     0.10009      1.7291590               0.97725     0.01809     0.00412     0.00051       7.3247750
  0.39358     0.07852     0.09146     0.09920      1.5983340               0.95819     0.03080     0.00926     0.00161       7.2541490
  0.35942     0.07309     0.08344     0.09623      1.4700460               0.92786     0.04939     0.01809     0.00412       7.1356560
  0.32636     0.06722     0.07852     0.09146      1.3478090               0.88686     0.07133     0.03080     0.00926       6.9624030
  0.29460     0.06482     0.07309     0.08344      1.2327890               0.83646     0.09140     0.04939     0.01809       6.7240250
  0.26763     0.05873     0.06722     0.07852      1.1246530               0.77337     0.11349     0.07133     0.03080       6.4285840
  0.24196     0.05264     0.06482     0.07309      1.0266110               0.70194     0.13452     0.09140     0.04939       6.0223370
  0.22065     0.04698     0.05873     0.06722      0.9335343               0.62552     0.14785     0.11349     0.07133       5.5679530
  0.19766     0.04430     0.05264     0.06482      0.8477322               0.54776     0.15418     0.13452     0.09140       5.0687970
  0.17679     0.04186     0.04698     0.05873      0.7701447               0.46812     0.15740     0.14785     0.11349       4.5241270
  0.16354     0.03412     0.04430     0.05264      0.6952783               0.32636     0.14176     0.15740     0.11479       3.4238700
  0.14686     0.03193     0.04186     0.04698      0.6315429               0.39743     0.15033     0.15418     0.13452       3.9823330
  0.13350     0.03004     0.03412     0.04430      0.5705662               0.26763     0.12980     0.15033     0.15418       2.9179660
  0.12100     0.02586     0.03193     0.04186      0.5179051               0.21476     0.11160     0.14176     0.15740       2.4231710
  0.10935     0.02415     0.03004     0.03412      0.4677791               0.16853     0.09910     0.12980     0.15033       1.9963960
  0.09852     0.02248     0.02586     0.00319      0.3860854               0.13136     0.08340     0.11160     0.14176       1.6079060
  0.09012     0.01923     0.02415     0.03004      0.3849831               0.10204     0.06649     0.09910     0.12980       1.2846010
  0.08076     0.01777     0.02248     0.02586      0.3467245               0.07780     0.05356     0.08340     0.11160       1.0192400
  0.07353     0.01659     0.01923     0.02415      0.3149593               0.05821     0.04283     0.06649     0.09910       0.7777523
  0.06681     0.01395     0.01777     0.02248      0.2846012               0.04363     0.03417     0.05356     0.08340       0.6008674
  0.06057     0.01296     0.01659     0.01923      0.2583693               0.03216     0.02605     0.04283     0.06649       0.4543537
  0.05483     0.01201     0.01395     0.01777      0.2327531               0.02330     0.02034     0.03417     0.05356       0.3429525
  0.04947     0.01110     0.01296     0.01659      0.2122248               0.01700     0.01515     0.02605     0.04283       0.2542334
  0.04456     0.01023     0.01201     0.01395      0.1912048               0.01222     0.01107     0.02034     0.03417       0.1871807
  0.04093     0.00854     0.01110     0.01296      0.1737685               0.00889     0.00811     0.01515     0.02605       0.1372347
  0.03673     0.00784     0.01023     0.01201      0.1574087               0.00621     0.00601     0.01107     0.02034       0.0985464
  0.03362     0.00730     0.00854     0.01110      0.1428670               0.00440     0.00450     0.00811     0.01515       0.0714855
  0.03074     0.00598     0.00784     0.01023      0.1290310               0.00307     0.00314     0.00601     0.01107       0.0507036
  0.02867     0.00556     0.00730     0.00854      0.1173365               0.00219     0.00221     0.00450     0.00811       0.0364625
  0.02559     0.00515     0.00598     0.00784      0.1058673               0.00154     0.00153     0.00314     0.00601       0.0254966
  0.02330     0.00477     0.00556     0.00730      0.0970210               0.00107     0.00112     0.00221     0.00450       0.0180265
  0.02118     0.00441     0.00515     0.00598      0.0877668               0.00736     0.00080     0.00153     0.00314       0.0616329
  0.01923     0.00407     0.00477     0.00556      0.0801917               0.00050     0.00057     0.00112     0.00221       0.0088360
ABSOLUTE OVERLAP  66.585930
ABSOLUTE CALORIFIC OVERLAP 166.464800
RELATIVE OVERLAP   0.227663
P.N. TOTAL NE  67.172790
C.P. TOTAL NE 225.338300
```

APPENDIX 46 - Age-Related Changes in Diet Breadths and Competition Coefficients for Mixed Prey Densities of 10 Aedes aegypti and 80 Daphnia magna

Pyrrhosoma nymphula age	Coenagrion puella age	Pyrrhosoma nymphula diet breadth	Coenagrion puella diet breadth	α PnCp	α CpPn
35	35	0.3052	0.0108	2.7905	0.2593
35	25	↓	0.0193	1.7489	0.4335
35	15	↓	0.0209	0.9432	0.8093
35	5	↓	0.7972	0.0960	3.2424
25	35	0.2011	0.0108	3.3746	0.2489
25	25	↓	0.0193	2.1002	0.4132
25	15	↓	0.0209	1.1314	0.7706
25	5	↓	0.7972	0.0840	2.2518
15	35	0.1279	0.0108	3.7125	0.2463
15	25	↓	0.0193	2.2988	0.4068
15	15	↓	0.0209	1.2375	0.7581
15	5	↓	0.7972	0.0670	1.6155
5	35	0.0787	0.0108	5.6281	0.1705
5	25	↓	0.0193	3.4713	0.2805
5	15	↓	0.0209	1.8675	0.5224
5	5	↓	0.7972	0.0719	0.7910

APPENDIX 47 - Age-Related Changes in Diet Breadth and Competition Coefficients for Mixed Prey Densities of 20 *Aedes aegypti* and 40 *Daphnia magna*

Pyrrhosoma nymphula age	*Coenagrion puella* age	*Pyrrhosoma nymphula* diet breadth	*Coenagrion puella* diet breadth	α PnCp	α CpPn
35	35	0.3008	0.0525	1.3410	0.5371
35	25		0.0658	0.9360	0.8090
35	15		0.0684	0.4532	1.6882
35	5		0.4444	0.0765	4.0109
25	35	0.2289	0.0525	1.7470	0.4769
25	25		0.0658	1.2106	0.7132
25	15		0.0684	0.5853	1.4860
25	5		0.4444	0.0728	2.6026
15	35	0.1743	0.0525	2.0415	0.4453
15	25		0.0658	1.4070	0.6622
15	15		0.0684	0.6794	1.3782
15	5		0.4444	0.0617	1.7624
5	35	0.1320	0.0525	3.2515	0.2939
5	25		0.0658	2.2315	0.4353
5	15		0.0684	1.0766	0.9050
5	5		0.4444	0.0697	0.8248

APPENDIX 48 - Age-Related Changes in Diet Breadths and Competition Coefficients for Mixed Prey Densities of 20 *Aedes aegypti* and 80 *Daphnia magna*

Pyrrhosoma nymphula age	*Coenagrion puella* age	*Pyrrhosoma nymphula* diet breadth	*Coenagrion puella* diet breadth	αPnCp	αCpPn
35	35	0.3097	0.0227	1.8974	0.3751
35	25	↓	0.0338	1.2853	0.5825
35	15	↓	0.0367	0.6675	1.1355
35	5	↓	0.6400	0.1141	2.7687
25	35	0.2143	0.0227	2.3689	0.3519
25	25	↓	0.0338	1.5923	0.5423
25	15	↓	0.0367	0.8253	1.0551
25	5	↓	0.6400	0.1019	1.8583
15	35	0.1466	0.0227	2.3976	0.3794
15	25	↓	0.0338	1.6030	0.5815
15	15	↓	0.0367	0.8297	1.1298
15	5	↓	0.6400	0.0747	1.4509
5	35	0.1001	0.0227	3.4482	0.2771
5	25	↓	0.0338	2.2960	0.4229
5	15	↓	0.0367	1.1872	0.8209
5	5	↓	0.6400	0.0766	0.7553