Oecologia (Berlin) (1986) 68:291–297

Oecologia

The feeding behaviour of a sit-and wait-predator, *Ranatra dispar* (Heteroptera: Nepidae): optimal foraging and feeding dynamics

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Summary. The feeding behaviour of *R. dispar* was examined with respect to the proportion of prey contents used, the time between successive captures (intercatch interval) and the feeding time. The feeding process consisted of three stages. (1) Injection of venom, (2) breakdown of tissue/digestive stage and (3) extraction of food. The rate of extraction from an individual prey decreases as its contents are depleted, but was shown to increase significantly during the first 15 min before decreasing. Even after 30 min the extraction rate was still marginally higher than the initial extraction rate. This phenomenon is quite different to what has previously been reported for sucking bugs.

There was a negative relationship between increasing prey density and prey depletion, with the predators being significantly more 'wasteful', (i.e. prey were discarded before all extractable food was removed) at the two higher prey densities compared with those at the lower densities. As the prey density decreased from 60 to 1 prey per container, so the resultant intercatch interval, feeding time, and the average dry weight extracted per prey increased. No correlation was found between individual intercatch interval and subsequent feeding time when examined throughout a sequence of eight captures. This is taken to support the optimal feeding model in which the predator reacts to the average profitability of the environment (i.e. mean intercatch interval) rather than as reflected by the amount of food in the gut. The effect of the changing rate of extraction of food during a meal allows *Ranatra*, when exposed to high prey density, to feed for less than half the time on each prey item that it spends at low densities, and yet still obtain 60% of available food.

The way in which a sucking bug like *R. dispar* feeds on a single prey can be likened to the way in which a predator uses a patch of resource. As food is removed, so the quality of the patch decreases as the amount of food left in the patch (prey) and thus its ease of harvesting (extraction) declines. Recently, two classes of models have been used to examine the amount of food extracted from the prey (patch), the time spent in feeding and the effect of prey density. These are based on notions of optimal foraging and gut-limitation respectively.

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Optimal foraging theory predicts that natural selection will favour those behavioural processes that maximize the net rate of energy intake per unit time spent feeding (Pyke et al. 1977). This theory has been used to examine the allocation of time to patches, that is, how long a foraging predator should spend in a patch of resource of certain profitability (Schoener 1971; Pyke et al. 1977; Krebs 1978, 1979). Recently, Cook and Cockrell (1978) extended this theory to include the amount of food extracted from a prey and the time spent in the extraction. They proposed that if some parts of a prey were easier (or more nutritious) to consume than others a predator could maximize the net rate of energy intake at high prey densities by selectively feeding on these parts. The mechanism suggested by Cook and Cockrell (1978) involves the predator's ability to 'measure' the intercatch interval, that is, the time between successive prey captures. The handling-time for each prey will be determined by this intercatch interval, such that each prey will be discarded when the ingestion rate reaches the average rate of injestion (i.e. similar to the marginal value theory of Charnov 1976). Cook and Cockrell's (1978) hypothesis has been used further to explain the variance in the allocation of time per patch and the partial consumption of prey in a number of different organisms (Giller 1980; Griffiths 1980a, b, 1982; Hodges 1981; Hodgers and Wolf 1981; Kruse 1983; Sih 1980).

Alternatively, variability in feeding times and the partial consumption of prey can be explained by a 'gut-filling' model (Gelperin 1971; Johnson et al. 1975; Cook and Cockrell 1978) in which a predator continues feeding until particular regions of the gut are full. During the intercatch interval food passes through the gut into a second region. The space in the first region, the fore-gut, at the start of the next feeding determines how much food can be taken in and hence the feeding time.

Ranatra dispar (Heteroptera: Nepidae) is an aquatic, sit-and-wait, predatory bug that feeds by injecting a mixture of venom and enzymes into prey and extracting the liquified contents (Bailey in press a and b). In farm ponds in Adelaide, South Australia, they are important predators of the backswimmer, *Anisops deanei* (Heteroptera: Notonectidae) (Bailey 1984) and, consequently provided an ideal opportunity to investigate factors controlling the allocation of time to individual prey. In particular, the experiments reported in this study were designed to explore the relationships between feeding time, ingestion rate, prey depletion and prey

density in order to differentiate between the optimal foraging and gut-limiting models.

Materials and methods

General

Adult predators, *R. dispar*, and prey, *A. deanei*, were collected from the ponds in Hahndorf, South Australia. In the laboratory each species were housed separately in large plastic tubs and fed various aquatic organisms (mainly mosquito larvae, *Daphnia*, corixids and small notonectids).

Measurement and weighing of prey

Individual prey were placed on their sides under a Zeiss binocular microscope fitted with a calibrated eye-piece. Body length was measured from the anterior outer curvature of the eye to the tip of the wing.

To estimate the wet weight of an animal it was carefully removed from the water, blotted on absorptive tissue, placed into a small petrie dish, covered with a gauze lid, and left for 5 min. It was then placed onto the weighing tray of an electric microbalance (Beckman Ltd Model LM600) and the weight read immediately. This procedure followed the construction of a standard drying curve for *A. deanei* to compensate for any water clinging to the external surfaces following blotting. For dry weight estimation, individual animals were dried at 105° C for 48 h, transferred in desiccator jars over silica gel and weighed within 15 min. The dry weight (mg) was related to the length (mm) of prey by the relationship:

$$\text{Dry weight} = -7.893 + 1.692\ \text{Length}$$
$$(r = 0.95,\ P < 0.001,\ n = 250)$$

The estimated initial dry weights ($\pm$error) of individual prey were then used to predict the loss of body weight due to feeding by *R. dispar*. Adult female *R. dispar* and adult *A. deanei* (Table 1) were used as predator and prey respectively in all the following experiments. No predator was used more than once and new prey individuals were used in each experiment.

Basic experimental method

Individual predators were transferred from the holding tubs into 1.0 l beakers and fed an abundance of medium sized notonectids for 24 h. They were then placed into 3.5 l plastic jars filled with 3.0 l of aged, dechlorinated tap water. Predators were then fasted for between 48 and 54 h, depending on the duration of the experiment.

Individual, adult *A. deanei* were blotted, weighed and measured as outlined previously. Following the feeding experiments, dead, partially digested *A. deanei* prey were removed from the experimental containers and their sizes, wet and dry weights obtained as described.

Both predators and prey were assigned randomly to the treatments and all experiments were carried out in the jars in a room at constant temperature (22 ± 1.5° C water temp.), and 1.5 m beneath a bank of 3 'daylight' fluorescent tubes. A diffuser filter provided an even flooding of light of intensity 1200 lux at the water surface.

Feeding time was defined operationally as the time from the initial insertion of mouthparts into the prey until their withdrawal and the subsequent discarding of prey. Because *R. dispar* can capture additional prey while feeding (Bailey in press c) the term intercatch interval has been defined here as the time between successive captures rather than the time from termination of one feeding to the beginning of the next as proposed by Cook and Cockrell (1978). The term ingestion rate (weight of prey ingested/unit feeding time) is used for those predators interrupted during their feeding activities. All times were measured with an electronic stopwatch.

Table 1. Size characteristics of adult *A. deanei* used in feeding experiments

	$\bar{x}$	Std. Dev.	Range	N
Body length (mm)	6.81	0.43	5.73 to 7.92	120
Wet weight (mg)	12.674	2.702	8.100 to 20.204	120
Dry weight (mg)	3.626	0.770	2.390 to 5.991	120

Experiment 1. To investigate the initial feeding behaviour (injection of toxins and digestive enzymes) and subsequent extraction of prey tissue, predators were allowed to feed on individual prey for fixed periods. Similar-sized prey animals ($\bar{x} = 13.37$ mg, SD = 2.98) were selected and individually hand fed to adult *R. dispar* by placing the notonectid close to the *Ranatra* with forceps. Meals were interrupted after 5, 15, 30, 60 and 105 min by either grasping the prey carcass with forceps and removing it from the rostrum or grasping the predator gently and removing it from the water. This treatment always terminated feeding and the prey could be removed.

Experiment 2. The effect of the initial density of prey on depletion (as measured by percent of maximum dry weight available per prey eaten) was also determined. Six densities (8, 12, 20, 24, 32, 40 prey/container) were tested. Notonectids were captured by individual *R. dispar* and the experiment ended after the first eight prey at every density had been consumed. Prey were removed, measured, weighed and dried as outlined previously. There were three replicates at each density.

Experiment 3. As the density of the prey increases the interval between catches should decrease. Both the optimal foraging and gut-limiting hypotheses predict a decrease in the time spent feeding on each prey when this happens. Therefore the effect of prey density on both intercatch interval and feeding time was examined. Four prey densities (1, 10, 30, 60 prey/container) were tested. Predators of density 1 were hand fed as outlined in Experiment 1, whereas *Ranatra* of densities of 10, 30 and 60 prey captured their own prey. As prey were captured they were replaced immediately with a similar-sized individual to maintain a constant density. Discarded prey were immediately removed, measured, weighed and transferred to a glass vial for drying. Data were collected over an 8-prey catch sequence at each density with five replicates.

Results and discussion

Experiment 1. For a sucking predator like *Ranatra*, feeding can be broken down into three stages: (1) the injection of ven-

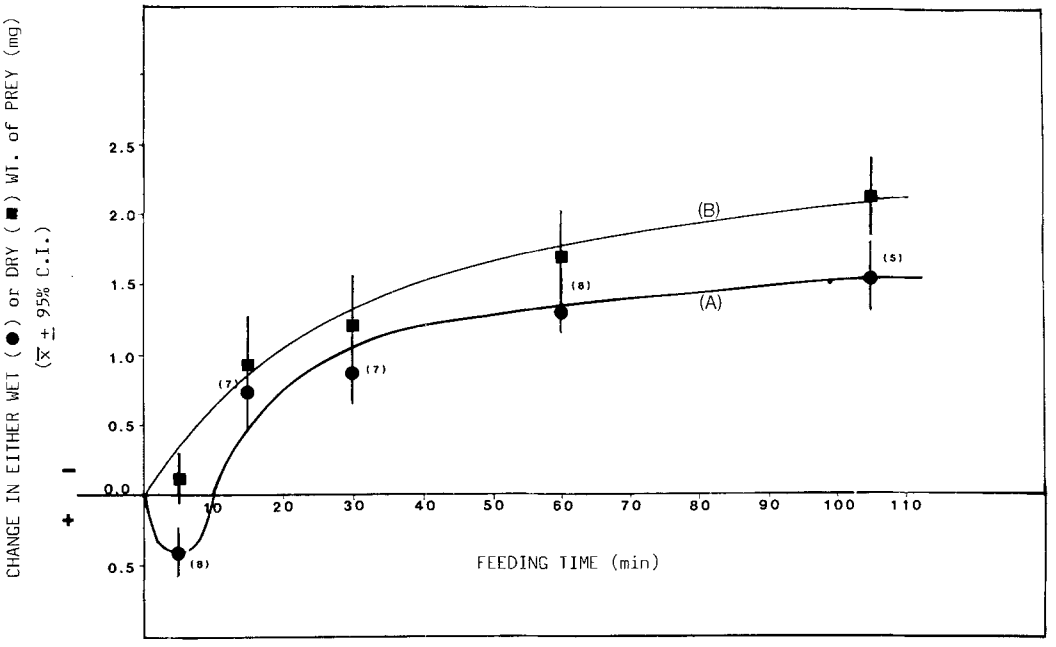

Fig. 1. A comparison of the weight change in individual prey during feeding by *R. dispar* as measured by both (*A*) wet and (*B*) dry weight. Values given are mean ±95% confidence interval. Figures in parenthesis indicate number of replicates. Both curves are fitted by eye. ● Change in wet weight; ■ Change in dry weight; + Increase in weight; − Decrease in weight

om and enzymes, (2) a pause while enzymes act, and (3) extraction of the liquefied food (Griffiths 1982). The results illustrated in Fig. 1 A showing changes in wet weight of prey support this hypothesis. However, changes in dry weight of the same prey individuals suggest that the contents of the body are extracted from the onset of feeding (Fig. 1 B). In their studies of *Notonecta glauca* feeding on mosquito larvae, Cook and Cockrell (1978) used changes in dry weight to demonstrate an immediate extraction of food from the prey. In contrast, Griffiths (1982) measured changes in wet weight of prey, following their capture by antlion larvae, and argued that the observed increase in prey weight was due to the injection of venom and enzymes. He pointed out that Cook and Cockrell's (1978) results for *N. glauca* were probably due in part to their use of dry weights, making enzyme injection difficult to detect.

My results show that both these phenomena may be seen in the same animal. In *R. dispar*, two processes probably work simultaneously. Enzymes and venom are injected into the prey while samples of the prey tissue, presumably haemolymph, are withdrawn. In my experiment the first artificial interruption of feeding did not occur until 5 min after the onset of the feeding period and the injection/extraction dynamics within this period remain obscure. However, prey contents may be extracted within the first few seconds (see references in Pollard 1973) and continue to be 'sampled' in a cyclical fashion. In contrast, the observed reduction in dry weight may indicate a modified probing response, (Hennig 1968; McLean and Kinsey 1968; Zettler 1967) which is used by the predator to ascertain the type and quality of the prey and stimulate the release of enzymes and saliva (Miles 1972; Pollard 1973). Furthermore, because *R. dispar* is an aquatic predator, it may be necessary for it to sample the potential food source to allow identification via appropriate chemoreceptors in the mouthparts and to cause adequate salivation.

Examination of the amounts extracted as measured by both wet and dry weights (Fig. 1) shows the dry weight curve exhibiting higher values at the different interrupt times. This is because external water passes into the prey as the feeding session continued, (Bailey in press d).

The ingestion rate decreases with time (Fig. 1) and supports the findings of Cook and Cockrell (1978), Giller (1980) and Kruse (1983). This result suggests that prey contents initially are ingested quickly, but that the yield per unit time decreases as the predator continues to feed. A one-way ANOVA suggested that the mean rates of extraction at different times were not the same ($F=6.72$, df 5,26; $P<0.0004$) (Fig. 2). The Student Newman Kuel's (SNK) Multiple Range Test ($\alpha=0.05$) showed that extraction rate did increase significantly during the first 15 min before decreasing and, even after 30 min feeding, the rate of extraction was still marginally, although not significantly, higher than the initial extraction rate. The rate of extraction then decreased almost linearly as the feeding session continued. This phenomenon is quite different from what has been reported previously for sucking insects and the significance of it is discussed below.

Experiment 2. There was a negative relationship between increasing prey density and prey depletion (Fig. 3). After an arcsine transformation of the data, a one-way ANOVA showed that the mean percentages eaten differed significantly ($F=7.745$, df 5,12, $P<0.05$) among the six densities. Mean comparison tests (SNK Multiple Range Test, $\alpha=0.05$) showed that *R. dispar* feeding on prey at the two highest densities were significantly more 'wasteful' than those fed prey at the lower densities, whereas the remaining mean percentages eaten at the lower densities were not distinguishable (Fig. 3).

Experiment 3. The effect of density on feeding time was explored because it was suspected that the results from Experiment 2 may relate to differences in feeding time per prey among the six densities.

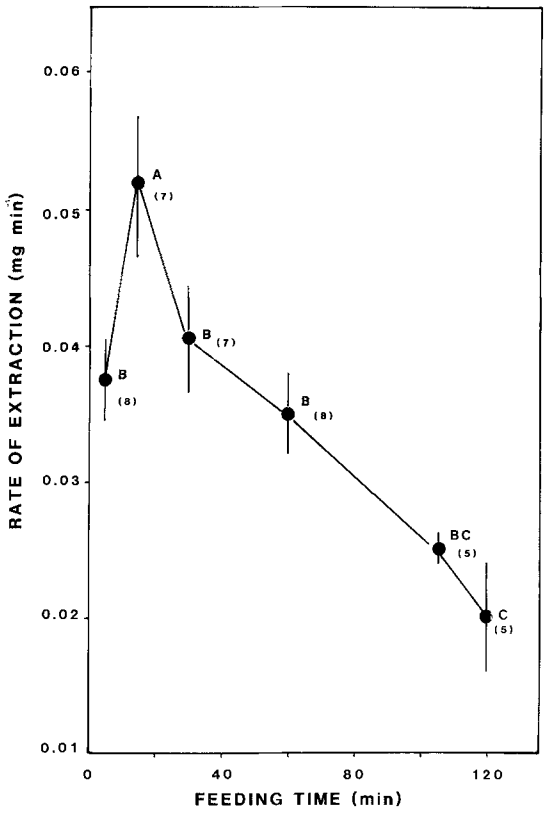

Fig. 2. The change in mean rate of dry weight extracted from a single prey with time spent feeding by *R. dispar*. Value given is mean ± standard error. Means with same letter are not significantly different (SNK Multiple Range Test, $\alpha = 0.05$). Figures in parenthesis indicate number of replicates

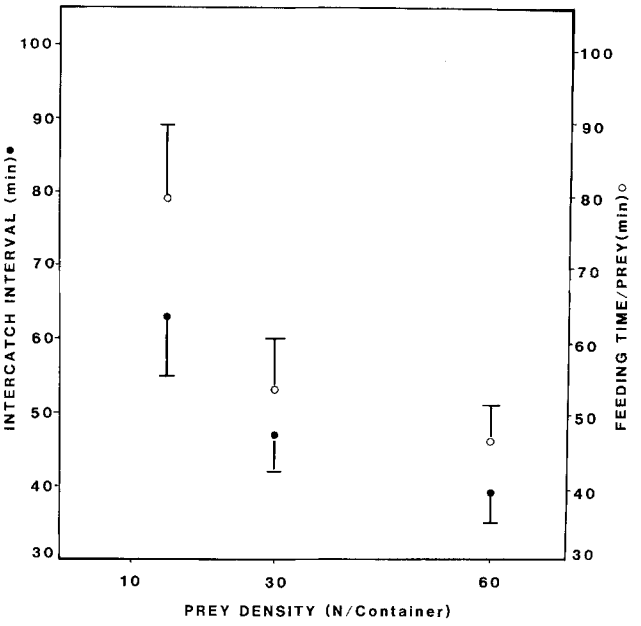

Fig. 4. The effect of prey density on the mean feeding time per prey (o) and mean intercatch interval (•). Value given is mean ±95% confidence interval. (For clarity, only the upper half of the confidence interval is given for the feeding time mean, and lower half of the intercatch interval mean.)

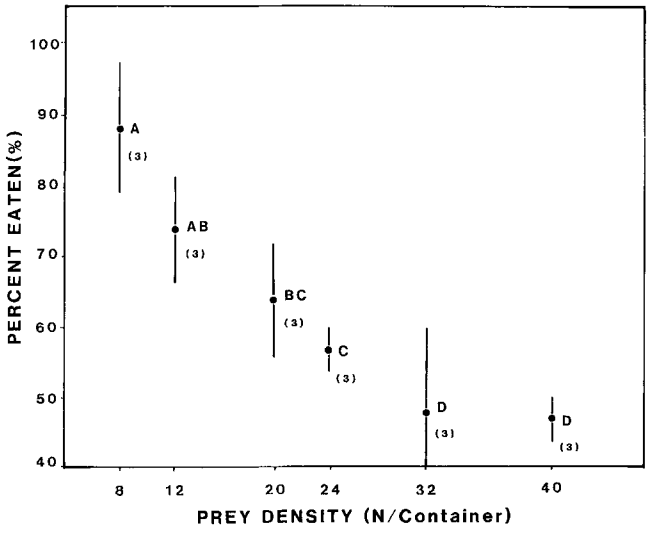

Fig. 3. The relationship between initial prey density and prey depletion as measured by percentage consumed (i.e. dry weight left/initial dry weight × 100). Value given is mean ± standard deviation. Figure in parenthesis is number of replicates. Means with same letter are not significantly different (SNK, Multiple Range Test, $\alpha = 0.05$). The percent consumed was calculated from the first 8 prey eaten at each density

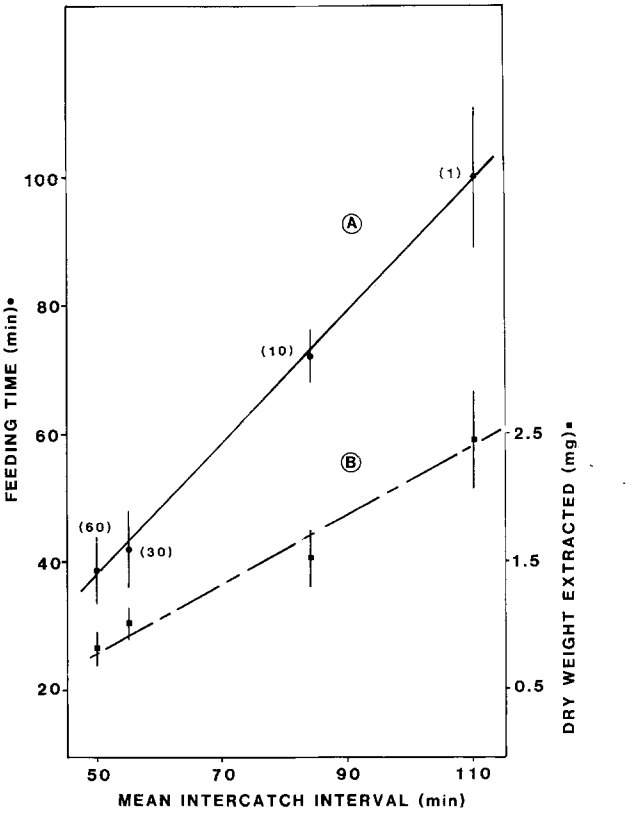

Fig. 5. The effect of mean intercatch interval on (*A*) the time spent feeding (• mins.) and (*B*) the dry weight of prey extracted from each prey (■ mg). Values given are mean ± standard error. Figure in parenthesis indicates prey density (number/container). Both slopes are significantly different from zero. *A:* $t = 30.6$, $P < 0.01$; *B:* $t = 11.33$, $P < 0.01$)

Table 2. Correlation between individual intercatch interval and individual feeding time as assessed by spearman rank correlation coefficient test

Density	r_s	p
10	0.0175	0.47 NS
30	−0.1077	0.28 NS
60	0.1464	0.21 NS

Figure 4 shows the relationships among mean feeding time, mean intercatch-interval and prey density, where mean intercatch interval and feeding time per prey both decreased as prey density increased. These findings support those of Cook and Cockrell (1978) and Giller (1980). In addition, Fig. 5 shows the relationships between the mean dry weight extracted per prey and the feeding time with the intercatch interval. As the prey density decreased from 60 to 1 prey per container, the resulting intercatch interval and feeding time increased and the average dry weight extracted per prey also increased.

Both the 'optimal foraging' and the 'gut-filling' model predict these quantitative trends. In order to distinguish between the hypotheses, the individual feeding times were plotted against their corresponding intercatch interval, as suggested by Cook and Cockrell (1978). There was no correlation between intercatch interval and feeding time using the Spearman Rank Correlation Coefficient (Table 2), and, tends to support the optimal foraging model.

Examination of the feeding times on each prey through the capture sequence (Fig. 6A) showed that the mean feeding time per prey decreased at all prey densities tested. Prey density was shown to affect significantly the values for mean feeding times ($F=4.11$, df 3, 156, $P<0.01$). This result differs from that reported by Giller (1980).

The relationship between mean feeding time per prey and prey density (as shown in Fig. 4) can be explained by a combination of two components: (1) the decline in mean feeding time through the catch sequence (Fig. 6A), and (2) the number of prey killed and eaten at each prey density (Fig. 6B) (Giller 1980). The form of the relationship (Fig. 6B) is much like the functional response curve as discussed by Bailey (in press e). At low prey densities, only

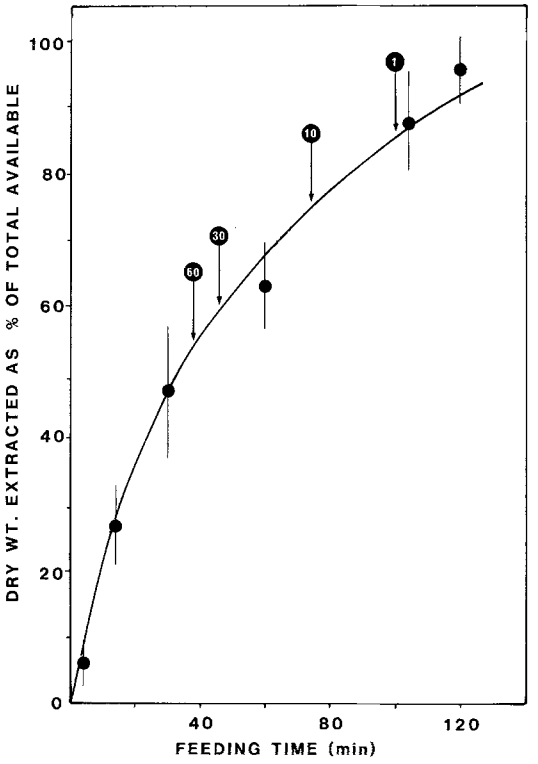

Fig. 7. The change in mean (±standard error) amount of dry weight extracted from a single prey with feeding time of *R. dispar*. Weight extracted is expressed as a percentage of total dry weight of prey available. The *arrows* indicate the mean feeding time per prey at four different prey densities. Prey density is shown on (●)

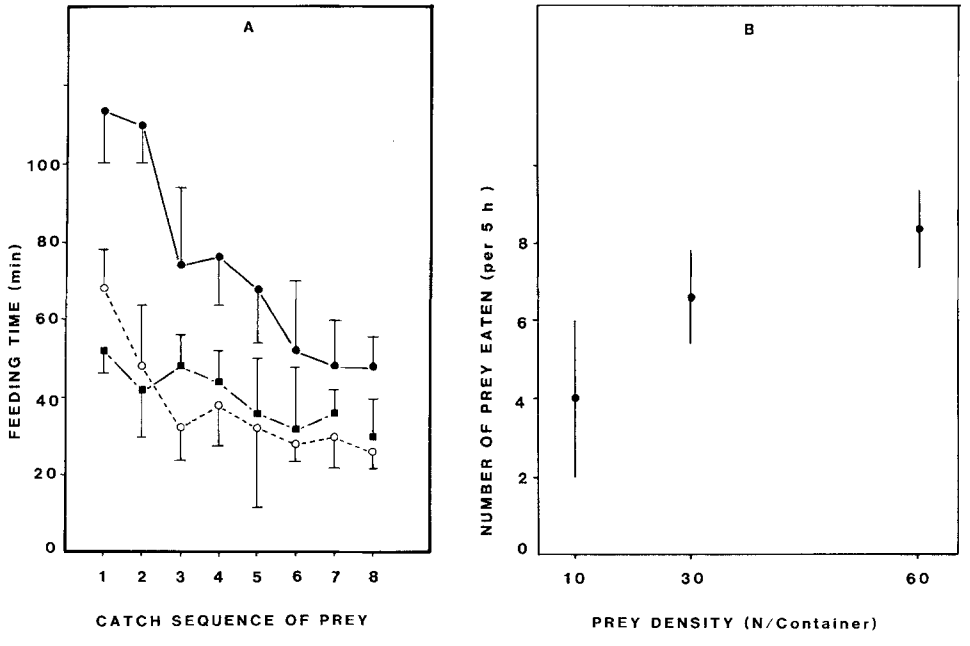

Fig. 6A. The decay in mean ±95% confidence interval feeding time per prey through an 8 prey catch sequence at three different prey densitites.
● Prey density of 1 per container;
o Prey density of 30 per container;
■ Prey density of 60 per container.
For clarity, only the top or bottom half of the confidence interval has been given for each mean. (The curve for the 10 prey density followed the same trend but has been left out of the figure to prevent overcomplication).
B The relationship between the number of prey eaten during the first 5 h of the experiment and prey density. Value given is mean ±95% confidence interval

the first few prey in sequence were caught, resulting in a high mean feeding time for that density. As the density increased more prey were caught, and correspondingly lower mean feeding times resulted. Similar declines in feeding times through a sequence of prey captures have been reported by Ellis and Borden (1970), Fox and Murdoch (1978) and Giller (1980) for notonectids.

Figure 7 shows the overall effect of the extraction rate and duration of feeding on one prey at different prey densities. Despite spending only about a third of the time feeding on a prey item, when prey density was high, the predator was able still to obtain almost 60% of the available food before discarding the prey. This extraction process, coupled with *R. dispar's* ability to capture a second and third prey while feeding on the first (Bailey in press c), results in a rapid, processing of prey items when prey are available.

General discussion

My results support strongly the optimal foraging model. Overall, the ingestion rate of *R. dispar* adults feeding on individual prey decreases as the prey is consumed. This decrease agrees with those reported for the other heteropteran predator *Notonecta*, by Cook and Cockrell (1978) and Giller (1980) and for larvae of the beetle *Dytiscus fasciventris* (Kruse 1983). Because the ingestion rate decreases with time spent in a patch, optimal foraging theory predicts that as the probability of capturing a prey increases (reflecting increasing prey density in this case) the feeding time on individual prey will decrease and the ultimate result will be an overall increase in the rate of food intake. In my experiments predators fed individual prey had consistently longer feeding times (and, therefore, lower marginal ingestion rates per prey) than did predators which captured prey naturally from constant densities of 30 and 60 per container (see Fig. 6). These results support those of Kruse (1983) and agree with one of the predictions of optimal foraging theory (Charnov 1976; Parker and Smith 1976); that is, the richer the habitat, the shorter the handling or feeding time per 'patch'. Unlike Kruse (1983), however, the results shown in Fig. 5 and Table 2 suggest that the mean intercatch interval may be the mechanism responsible for this optimization process in *R. dispar*. It suggests that the predator is reacting to the average profitability of the environment rather than to the specific level of food in the gut which has resulted from the length of the intercatch interval. This does not mean necessarily that the capacity of the gut is never limiting and that hunger is not affecting the feeding time but, rather, that gut capacity defines the limits within which the optimal feeding strategy operates (Cook and Cockrell 1978).

Because the ingestion rate at first increases and then decreases (Fig. 3) with time spent feeding on an individual prey, the amount of food taken per unit feeding-time is increased when each prey is not exploited fully. One way the predator could assess the prey density is to monitor the prey swimming nearby. This has been suggested by Kruse (1983) and demonstrated by Bailey (1984).

Acknowledgements. The work reported in this study forms part of a Ph.D thesis conducted under the supervision of Professor T.O. Browning and Dr. Roger Laughlin, University of Adelaide. Their advice, discussions and constructive, critical examination of the first draft is gratefully acknowledged.

Carol Wallace kindly read a later draft, and her helpful suggestions and comments improved the final manuscript, as did those of Jane Hughes, Roger Kitching, Tom White and an annonomous referee. I would also like to thank Duncan McKay for statistical advice and who, along with George Hoffman, provided generous amounts of discussion, ideas and constructive critical comments.

The project was completed while in receipt of a Commonwealth Postgraduate Research Award, and various drafts of the manuscript were kindly typed by Janis Wedge.

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Received July 29, 1985