THE FEEDING BEHAVIOUR OF A SIT-AND-WAIT PREDATOR - ETHOLOGICAL STUDIES ON *RANATRA DISPAR* (HETEROPTERA : NEPIDAE), THE WATER STICK INSECT

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SUMMARY

The aquatic bugs, Ranatra dispar and Anisops deanei, were used to study ethological and ecological interrelationships in the predatory behaviour of an extreme ambush predator (R.dispar) and its common, mobile prey (A.deanei).

The sequence of behavioural components in the predatory behaviour follows the basic ambush pattern, i.e. initial precapture posture, arousal, orientation, capture, consolidation of grip, exploration, injection of venom/enzymes, feeding, discard of prey, although much variation between components exists. Much of this variation is described, including the predator's defensive and evasive behaviour, along with their effect on the predatory behaviour. The predator's arousal and strike space are described. Both spaces increase with food deprivation.The capture space is dependent on the morphology and reach of the raptorial legs, there being no lunge or pursuit component in the predatory behaviour. Attempts to describe the shape of the arousal space and the effect of hunger using the model designed by Holling (1966) proved reasonably satisfactory, after slight modification, for the horizontal plane but totally unsatisfactory for the vertical plane. This is believed to be due to the unusual eye structure of Ranatra.

The additional effect on predatory behaviour of prey size was investigated. It was found that the hunger level determines whether R.dispar will initially be aroused or not but the distance at which the arousal takes place is influenced by the size of the prey. This is

believed to reflect the capacity and interrelation between visual and mechanoreceptor, sensory organs. The decision to strike at a prey is, although again influenced by hunger, significantly affected by prey size. The distance of the prey when the strike takes place is affected by hunger not the size of the prey. The outcome of the strike is determined by the size of the prey, not the hunger level of the predator. This is believed to reflect the relationship between strike trajectory, leg morphology and prey size. Food deprivation affects all components of predatory behaviour of R.dispar leading up to prey capture, by increasing not only distance of response but also the number of strikes, hits, and captures per unit presentation of prey. It does not affect capture efficiency which remains at about 70 to 80%. Food deprivation also increases the range of prey sizes that R.dispar responds to and attempts to capture. The effect of food deprivation is considered to reflect a motivational change in responsiveness to particular prey stimuli usually described as a sensitization of particular stimulus-response relations rather than the food deprivation affecting the sensory mechanisms. The predatory success in relation to size of model prey suggested an 'optimum' size that could be captured, irrespective of predator motivational level, which is based primarily on the relationship between the shape of the grasping leg and size of prey.

Functional response experiments were performed to examine the effect of prey density on feeding behaviour and to measure attack rates and handling times. In both the temperature and age structure of predator and prey effects, the most generally applicable response seemed to be the Type 2. Progressively more prey were eaten between 15.0°C and 29.0°C. Over the temperature range investigated the attack-rate increases almost linearly while the handling-time increases dramatically between 15°C and 20°C after which it remains constant up to 30°C. Generally the handling-time increases as prey size increases and decreases as the predator size increases. The attack-rate surface is far more complex.The maximum attack rate for instars I and II occurred on the smallest prey size (1 and 2),while as the predator size continued to increase, so the attack-rate on each of the prey sizes increased. Unlike the previously published attack rate surface, with small predators attacking small prey and large predators attacking large prey, the maximum attack-rate stops at the intermediate prey size 3. Predator instar V has the largest attack rate values over all prey sizes. Adult R.dispar have noticeably lower attack-rates for various prey sizes than instars V, IV and to some degree III. The results suggest that small predator instars will usually compete with large instars for prey, unless there is spatial or temporal separation between them. Observations conducted in the field indicate that a distinct age-specific spatial distribution exists in R.dispar (and in the prey A.deanei) with the smallest individuals being found predominantly in the shallow (littoral zone) water while the larger individuals are found in the deeper water.

Related behaviours of the predator were investigated in order to identify factors that were believed to be involved in the observed increase in the numbers of prey eaten at different prey densities.

The feeding behaviour of R.dispar was examined with respect to the prey utilization, 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 the prey item is depleted. The extraction rate was shown to increase significantly during the first 15 minutes before decreasing. Even after 30 minutes 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 and feeding time increased. In conjunction with this the average dry weight extracted per prey also increased. No correlation was found between individual intercatch interval and subsequent feeding time when examined through an 8 prey catch sequence. 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 to the specific level of food in the gut which has resulted from the length of the intercatch interval. The overall effect of the extraction dynamics and duration of feeding on one prey item at different prey densities is that at higher densities, although spending less than half the time on a prey item compared with the low density, the predator still obtains almost 60% of the available prey contents before discarding.

By the use of fluorescent dyes it was shown that during feeding water from the external environment passes into the prey's body, through, it is believed, puncture holes from previous feeding sites. Such a phenomenon, resulting in the diluting of the prey body contents, may be used as a physiological stimulus to detect the quality of the prey which may in turn be used in deciding whether to cease feeding at one site and move to another part of the prey's body or discard the prey.

R.dispar is shown to be able to capture and hold a number of prey simultaneously. Capture of prey characteristically occurs in three distinct patterns, each characterized by a different number of prey caught. The time since last feeding by the predator has a significant effect on whether the predator will capture more than one prey. Once feeding starts there is a critical period during which, if an encounter takes place, the predator will attempt to capture the prey. Once past that period prey are ignored. The critical period is longer the higher the motivational level of the predator. It is suggested that this multi-prey capture behaviour potentially increases the size of a meal as groups or schools of prey move pass the ambush predator.

Particular features of the prey's behaviour believed to be involved in determining its movement patterns, and thus encounter-rate with an ambush predator, were investigated.

Four basic swimming patterns of A.deanei are described. The effects of water temperature and density on movement patterns show that both have a significant effect, with animals moving more at higher temperatures but less as density increases. It is suggested that these intraspecific interactions in groups of A.deanei lead to the formation of groups or schools of individuals, and that this observed behaviour is an anti-predator defence. This aggregating behaviour is strongly supported by data obtained from the field. Additional results indicated that the effect of this aggregating behaviour significantly reduces the encounter-rate with an ambush predator compared with a predicted rate based on the movement of one individual. This trend was repeated over the three experimental temperatures.

Prey density was also shown to influence the choice and duration of stay at an ambush site by R.dispar. It was shown that predators changed ambush sites significantly more frequently when prey density was low compared with when prey density was high. Initially, predators remain at an ambush site for significantly longer than later stays at different sites, irrespective of the presence or absence of prey. There was a tendency, over the three prey densities examined (0, 3, 15 prey per litre), for the duration of stay at a site to become shorter as the experiment progressed. Examination of the angular changes by the predator while at an ambush site showed that R.dispar remained stationary for significantly longer periods when no prey were present, while the incidence of moving through relatively small angular changes occur significantly more often when prey were present.

By using model prey that conferred no nutritional reward it was shown that encountering a prey caused R.dispar to remain significantly longer at a 'potentially' profitable ambush site compared with when no encounter was given. It is suggested that R.dispar uses not only a mean intercatch interval but a prey encounter rate mechanism in assessing the availability of prey. It is predicted that the assessment of prey availability by ambush predators may involved more than one factor and that, depending on the circumstances, predators may switch between different mechanisms or utilize information from several simultaneously.