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PREY CAPTURE BY THE CUTTLEFISH (SEPIA OFFICINALIS L): AN EXPERIMENTAL STUDY OF TWO STRATEGIES

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ABSTRACT

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This study shows that the size of the prey (Carcinus maenas) relative to the predator (Sepia officinalis) is of importance in the choice between two types of attack: either capture by ejection of the two extensible tentacles, or capture by jumping on the prey. Small crabs are preferentially captured by the first method and large crabs by the second. Other factors which may explain the observed variations, include previous experience of the predator and the behaviour of the prey.

INTRODUCTION

The cuttlefish, Sepia officinalis L., is a very active predator able to catch comparatively large living prey: shrimps, fishes and crabs. Various studies (Wilson, 1946; Boulet, 1964; Messenger, 1968, 1977) have shown that there are two methods of attack: an attack involves either the ejection of the prehensile tentacles or the use of all the arms without the tentacles once the animal has jumped upon its prey ("jump"). Some authors (Wilson, 1946; Boulet, 1964) think that each type of capture is characteristic of a certain kind of prey. Messenger (1968) was the first to show that crabs could be seized by either of these two methods of capture. However, his observations remain fragmentary as regards this question, and we thought it would be interesting to study thoroughly the problem set by the choice of capture method and to try to answer two questions which have been asked lately (Chichery, 1980):

- Is the choice of method of capture linked to the locomotory characteristics of the prey (swimming, creeping, moving fast or slowly) or is it related

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simply to the size of the predator and the size of the prey?

- Does an individual animal preferentially use one method of capture or the other?

MATERIAL AND METHODS

The animals used in this study had been caught by local fishermen few miles away from Luc-sur-Mer between May and October. The animals ranged from 140 to 1700 g according to the age of the different individuals (from eight months to thirty months). The captivity life varies from few days to ten months. The floating animals do not take preys any more and are moribund. They were never considered in our study. We also used animals bred in the laboratory of Luc-sur-Mer and weighing from 30 to 70 g. The behaviour of some individual animals was followed over several weeks to see whether their strategies changed with experience.

The observations were made through an aquarium made of glass (80x45x30 cm) containing filtered fresh circulating seawater. Several series of experiments were carried out:

- In the first, different types of prey were caught by the cuttlefish in nearly natural conditions. Thus, we used crabs (Carcinus maenas) of various sizes. For each crab the surface of the cephalothorax was measured approximately (width x length). 270 captures were observed and 197 of them were filmed with a video-camera for a detailed study of the capture. We calculated the relation between the weight of the cuttlefish (in g) and the size of the crab (in mm^2). Weight is a parameter easy to measure for Sepia, and the exponential relation size-weight is now well known (Richard, 1971). We use the quotient R which designates the weight of the cuttlefish divided by the surface of the crab. The smaller is R, the bigger is the crab, compared to the cuttlefish. We also studied 179 attacks on shrimps (Crangon crangon, Palaemonetes sp.) and observed 11 attacks on fishes (young Mugil sp.).
- In the second series of experiments we altered the locomotory characteristics of the prey (crab) to determine whether this changed the type of catch. Large crabs (relative to the Sepia, $R<0.3$) were fixed by the anterior part of the cephalothorax to an electromechanical system. This apparatus allowed us to move the crab backwards very quickly (8 cm in about 200 ms). The time of the displacement was selected by the experimenter at the beginning of the "jump" or at the ejection of the tentacles. At the end of four trials the cuttlefish was allowed to eat the crab, whatever the last type of capture attempt used. This procedure avoids a positive reinforcement of one or other type of capture.
- The third series of experiments included only young cuttlefish bred in laboratory. These experiments were specifically designed to study the factors in-

volved in the attack on shrimps. Ten animals aged 8 months had the extremities called "clubs" (which are the only parts with suckers) of both tentacles removed under alcohol anaesthesia (2% alcohol in seawater). Afterwards these animals were regularly fed with shrimps. We followed the behaviour of all ten animals for four weeks, and 4 of them for eight weeks.

RESULTS

(1) Rate of successful captures

Our results indicate that the rate of success of the captures at the first attempt (87.7%) can be compared with those obtained by Messenger (1968) for the capture of shrimps by the prehensile tentacles.

The analysis of the catches of crabs (n = 197) recorded with a videotape has allowed us to reckon the rate of successful attacks on the first attempt. Of the two types of capture, the "jump" seems to be more efficient (96.2% for the "jump" and 84.6% for the ejection of tentacles; accuracy of attacks was significantly higher for the "jump" strategy, $X^2 = 6.71$, $P \leqslant 0.01$).

(2) The importance of prey size (quotient R)

(a) Choice of capture method for crabs in relation to R (Fig.1)

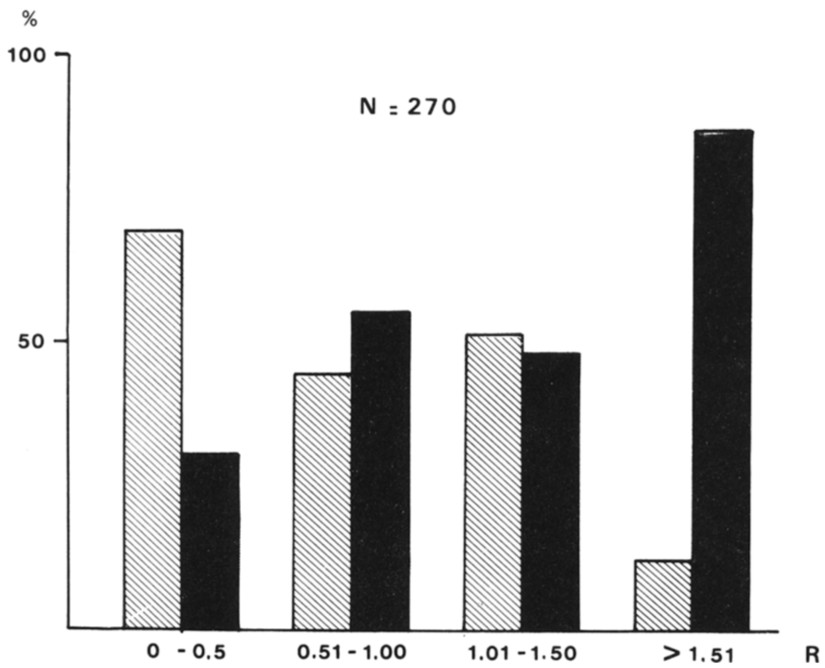

Fig.1. Choice of the capture method for crabs in relation to prey size: quotient R (R is a measure of the relation between crab size and cuttlefish size - a small R means that the prey is large compared with the predator).
: "jump" : tentacles

Fig.1 represents the frequencies observed for both types of capture for the different classes of R over the whole of the population studied (270 captures). We can note:

- on the one hand, a reduction of the frequency of the "jump" with the increase of R; crabs which are small in relation to the size of the cuttlefish are preferentially captured by the ejection of the tentacles.

- on the other hand, the existence of a central area (R values between 0.5 and 1.5) where the frequencies of the two types of capture seem to be balanced.

(b) Study of some individual diagrams (Fig.2)

We were able to observe some animals over a period of a few weeks. The study of individual diagrams shows, just as for the whole population, an increase in the frequency of captures using the tentacles with an increase of R. The absence of results in the high classes of R for the small cuttlefish (individuals 1 and 2) may be explained by the fact that they do not catch crabs which are too small (carapace width < 5 mm); the profitability is probably too small. Once we were able to observe an animal (unfortunately for only 5 days) which seemed always to use the tentacles whatever the value of R.

(3) The role of previous experience and the behaviour of the prey

Because we were able to follow the catches of an individual animal over several weeks we gained an impression of the part played by other factors.

(a) Changing the jumping strategy as a result of a quick displacement of the crab

A temporal analysis of the "jump" allowed us to develop an hypothesis of the intervention of a closed loop control (with visual feedbacks) in the execution of this behaviour (Chichery, work in progress). The second series of experiments was undertaken to test this hypothesis. Although the results obtained were fragmentary and although the six animals studied behaved rather differently we can still draw one conclusion. An animal that has failed to capture a rapidly displaced crab begins to use the tentacle attack (with a ratio $R < 0.3$ usually inducing catches by the jumping method). Fig.3 illustrates this result with an individual profile. Then, an animal resorts to the tentacle method of capture after the "jump" has failed many times.

(b) Changing the tentacle strategy as a result of ablation of the tentacle tips

We noticed 1359 attempts to catch shrimps, distributed as follows:

- 1123 attempts by ejection of the tentacles (failing because of the lack of suckers).

- 236 attempts by "jump".

Fig.4 shows the change with time in the rate of "jump" related to the to-

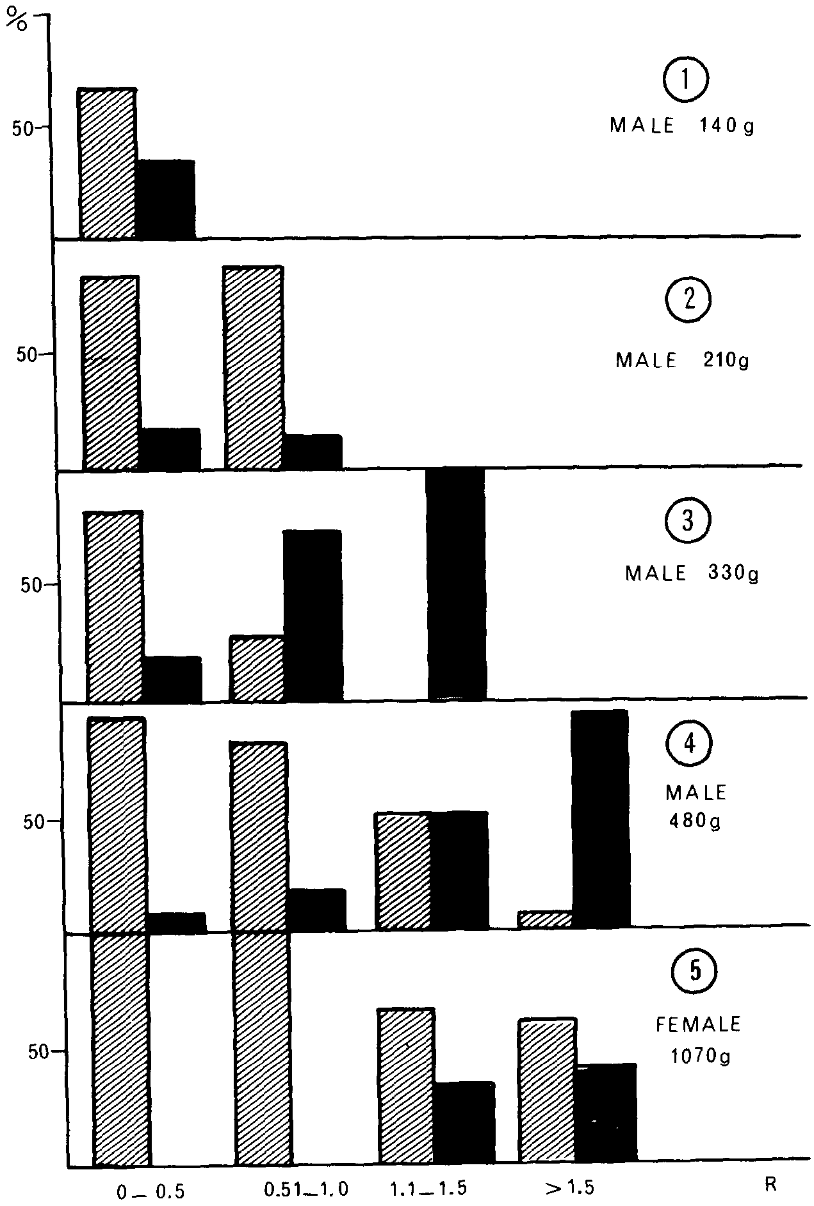

Fig.2. Individual diagrams: choice of the type of capture for crabs
: "jump" : tentacles.

tal attempts (on the first day after the operation, the average of the first week after the operation, the 2nd week, 3rd, 4 th and 8th week).

Among the 236 jumps we noticed 100 failures and 136 successes (57.6%); only 96 attempts were successful at the first try (40.6%). However we must stress the point that these animals are perfectly able to catch crabs of the appropriate size by the jump technique with a standard rate of success.

We observed that the last animals studied (8 weeks) showed, at that time, a very obvious regeneration of the extremities of the tentacles, with small suckers just visible (but not yet functional). This result confirms those obtained by Feral (1978, 1979).

DISCUSSION

Our results on the success rate of capturing shrimps at the first attempt (87.7%) confirm those obtained by Messenger (1968): 81% in a white tank and 91% in grey tanks probably without reflection.

The rate of success of catching fishes by ejection of the tentacles was not methodically studied. Our results, obtained on only a few captures, show a low rate of success. The small fishes used in this study (*Mugil* sp.) move in schools. Neill and McCullen (1974) have already made a thorough study of the protective role of these social structures in relation to the efficiency of different predators (*Sepia, Loligo*).

The duration of the ejection of tentacles is less than 30ms. The hight speed of this motor act precludes its control by visual feedback and it seems that it is under "open loop" control (Messenger, 1968). A study in preparation shows that the central control of the "jump" also includes a closed loop system. Indeed, after a very quick displacement of the whole animal, the "jump" possesses a terminal stage which has a variable duration ($>$100ms) characterized by an active braking of the animal. These stages might allow the use of visual feedbacks and ensure the possibility of terminal corrector adjustments. This difference in central control might explain the observed dissimilarities in the efficiency of the two strategies (84.6% for the ejection of tentacles and 96.2% for the "jump"). The more frequently noted mistakes in the strategy "tentacles" reside in an under-estimation of the attacking distance.

The most important result of this study affords an answer to the two questions posed earlier. It shows the importance of the size of the prey in relation to that of the predator, particularly in the case of extreme values ($R < 0.5$ and $R > 1.5$). The quotient, size cuttlefish/size prey, plays a definite part in the process of determining between the two types of capture. For the central values of R relative sizes of predator and prey appear to be less important, as the frequencies of the two types of capture are more equally

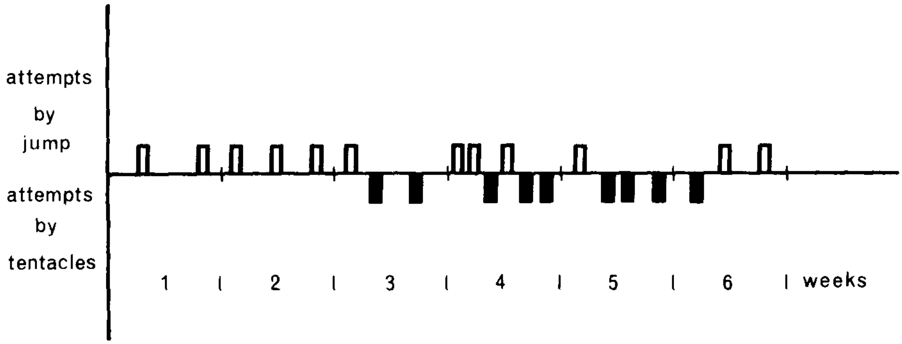

Fig.3. Changing the jumping strategy as a result of a quick displacement of the crab: an individual profile.

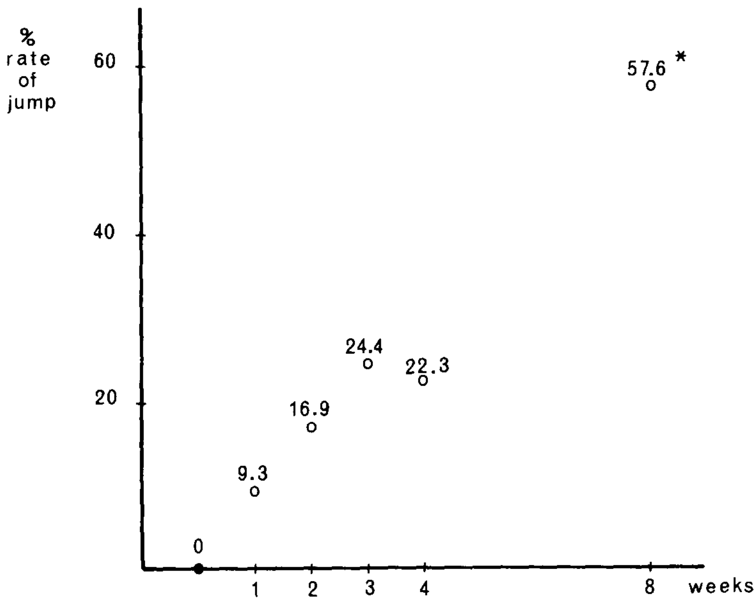

Fig.4. Increasing the jump strategy as a result of ablation of the tentacle tips.
* : Result obtained on only four animals.

divided. Therefore, it is necessary to take into account the existence of other factors relating to the prey or to the predator. An examination of the behaviour of individuals over some weeks shows that individuals do not have particular strategies and use the two strategies.

The part of previous experience is well demonstrated in the experiment on the capture of crabs mechanically displaced. In spite of a quotient $R < 0.3$ we quickly noted numerous attempts to catch the prey with the tentacles. Then, the cuttlefish returns to the "jump" with a change in the speed of its execution (Chichery, in preparation). The visual perception of the quick displacement of the prey induced by the apparatus may also explain why the cuttlefish resorts to ejecting its tentacles, the method normally used for fast prey. It is well known that memory processes are particularly well developed in Cephalopods (Young, 1965; Messenger, 1973), and so it is interesting to see here how flexible the programming of the attack is. This individual experience and the different levels of hunger might explain the relative disparity of the individual diagrams (cf. Fig.2.).

The results obtained after ablation of the extremities of the tentacles support earlier interpretations. The repeated failures of the strategy "tentacles" induce progressively more attempts with the alternative "jump". However, two results must be emphasized:

- Even after very many tries the cuttlefish still show very numerous attempts to eject the tentacles.
- The rate of successful captures of shrimps by the "jump" method is very inferior compared on the one hand to those usually obtained by the ejection of tentacles and on the other hand to those of the catches of crabs. We must stress that these young cuttlefishes (about 8 months) are quite able to catch the crabs by jumping on them. The last experimental series shows very well (considering the persistence of the technique "tentacles") that the ejection of the tentacles is particularly well adapted to catching rapidly escaping prey. We must stress that the shrimps with their giant fibres and the fishes with the Mauthner cells are able to escape very quickly. The "jump" which is slower (200-1000ms) than the ejection of tentacles (< 30ms, cf. Messenger, 1968) might not be adapted to catching such quick prey; hence the numerous failures noted in the last series of experiments.

In summary this work shows the importance of the ratio between predator and prey size in the choice of the type of attack on crabs, and presents evidence that the type of attack employed may change with experience. Our experiments have also shown decisively that the ejection of tentacles is nearly always used to capture small fast prey.

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