Penetration of the Shell and Feeding on Gastropods by *Octopus*

JEROME WODINSKY

*Department of Psychology, Brandeis University,
Waltham, Massachusetts 02154*

SYNOPSIS. The behavior of the octopus when feeding upon shelled molluscs is described in four steps: selection of prey, boring a hole in the shell, secreting into the borehole, and pulling out the body of the mollusc and eating it. Selection of some gastropod prey is determined by a firm, deep, either partial or complete obstruction in the aperture of the shell. Selection of other prey, gastropods, pelecypods, and amphineurans, may be based upon resistance by the mollusc to the application of force by the octopus. Drilling of the hole is done by the radula. Since the octopus will drill and secrete into empty shells with obstructions in the apertures, metabolites from a live mollusc are unnecessary. This technique can be used to collect the secretion. The frequency of occurrence and the effect of the secretion are discussed. The hypothesis that the octopus first tries by force to pull out the body and, failing to do so, drills a hole in the shell is experimentally supported.

The conditions under which the octopus drills or pulls out the body of the mollusc are incompletely understood. The octopus may drill two or more shells in succession without feeding upon the previously drilled and weakened snail. No two steps in the behavioral sequence are necessarily linked to each other. The drilling-feeding patterns are complex and plastic.

The octopus normally preys upon shelled gastropod and pelecypod molluscs and in addition on crustaceans, fishes, and other octopuses. Two independent investigators discovered that the octopus drills a hole in the molluscan shell (Fujita, 1916; Pilson and Taylor, 1961). Shell-drilling by

the octopus was based upon inference by Fujita, and by observation in laboratory tanks by Pilson and Taylor. In neither case was the behavior of the octopus described. The work of Arnold and Arnold (this Symposium), from whom I learned of the phenomenon, and the present report are, therefore, the first descriptions of the drilling and feeding behavior. The description presented in this paper is based upon extensive field and laboratory observations and experiments on the behavior of *Octopus vulgaris* Lamarck, in which the prey were several species of gastropod.

The behavioral sequence consists of at least four steps: (1) recognizing and selecting the prey; (2) drilling a hole in the shell; (3) ejecting a secretory substance into the drilled hole; and (4) removing the mollusc from its shell and eating it. This is not a rigid sequence.

STEP 1. RECOGNIZING AND SELECTING THE PREY

There are two distinct problems: that of recognizing the species of prey, and that of recognizing that an individual shell contains an edible object.

TABLE 1. *Molluscan prey of the octopus.*

Species Drilled	Common Name	Reported by
Acanthopleura granulata Gmelin	Fuzzy chiton	Wodinsky
Astraea phoebia Roding	Long-spined star shell	"
A. tecta americana Gmelin	Imbricated star shell	"
Cassis tuberosa Linnaeus	King helmet	Arnold and Arnold (this Symp.)
C. madagascariensis Lamarck	Emperor helmet	" "
C. flammea Linnaeus	Flame helmet	" "
Chione fluctifraga Sowerby	Smooth Pacific Venus	Pilson and Taylor (1961)
C. undatella Sowerby	Frilled California Venus	" "
Cymatium femorale Linnaeus	Angular triton	Wodinsky
Cypraea zebra Linnaeus	Zebra or measled cowrie	"
Cypraecassis testiculus Linnaeus	Reticulated cowrie-helmet	"
Fasciolaria tulipa Linnaeus	True tulip	"
Haliotis fulgens Philippi	Green abalone	Pilson and Taylor (1961)
H. cracherodi Leach	Black abalone	" "
Ischnochiton conspicuus Carpenter	Conspicuous chiton	" "
Leucozonia nassa Gmelin	Chestnut latirus	Wodinsky
Livona (Cittarium) pica Linnaeus	West Indian top shell	"
Murex pomum Gmelin	Apple murex	Arnold and Arnold (this Symp.)
M. florifer Reeve	Burnt rock or lace murex	Wodinsky
Mytilus edulis Linnaeus	Blue mussel	Pilson and Taylor (1961)
M. californianus Conrad	Californian mussel	" "
Nassarius fossatus Gould	Giant western nassa	" "
Nerita peloronta Linnaeus	Bleeding tooth	Wodinsky
N. versicolor Gmelin	Four-toothed nerite	"
Oliva reticularis Lamarck	Netted olive	"
Pecten spp	Scallop	Fujita (1916)
Pinctada spp (probably *P. margaritifora* Linnaeus)	Japanese pearl oyster	"
Protothaca staminea Conrad	Common Pacific littleneck	Pilson and Taylor (1961)
Purpura patula Linnaeus	Wide-mouthed purpura	Wodinsky
Strombus raninus Gmelin	Hawk-wing conch	Arnold and Arnold (this Symp.)
S. gigas Linnaeus	Queen conch	" "
S. gallus Linnaeus	Rooster-tail conch	" "
S. costatus Gmelin	Ridged or milk conch	" "
Tectarius muricatus Linnaeus	Beaded periwinkle	Wodinsky
Tegula funebralis A. Adams	Black tegula	Pilson and Taylor (1961)
Thais deltoidea Lamarck	Deltoid rock shell	Wodinsky
T. rustica Lamarck	Rustic rock shell	"
Xancus angulatus Solander	Lamp shell, West Indian chank	"

Recognizing the Species of prey

A review of the range of species used for prey will aid in delineating the problem. Table 1 lists the species of molluscs which the octopus has been known to drill, or suspected of drilling, in the field or in the laboratory. There are representatives of (1) gastropods, pelecypods, and amphineurans, (2) sedentary and mobile species, (3) among the mobile species, those that adhere to a substratum such as rocks, and those that move freely over the bottom, (4) diurnal and nocturnal species, (5) herbivorous and carnivorous species, and, (6) among the gastropods, those which do not possess an operculum and

those whose operculum either completely or partially seals the aperture.

When ontogenetically an octopus first attacks an individual shell of any of these species, the stimuli eliciting this response might be any of the following: shape, position, movement, texture, odor, or chemical secretions, emanating from the mollusc. They might also result from the changing resistance of the mollusc to an accidental touch by the octopus during its movements, causing, for example, a snail to retract into its shell, to adhere tightly to the substratum, or an oyster to close its valves. The stimulated sensory modality of the octopus might be visual, chemical, tactual, or proprioceptive. On the second and subse-

quent attacks upon shells of a given species, the same stimuli and sensory modalities, or others, may be utilized. In addition, the effects of the previous experience(s) may exert a selective influence upon which stimuli to focus.

Since sedentary species such as the oyster are preyed upon, stimuli from locomotion may be unnecessary. Likewise, since nocturnal species are also prey, visual stimuli may not be necessary, although original predation may be correlated with lunar phases, and thus vision would not necessarily be eliminated. Fujita (1916), for example, reported that six adult octopuses ate an average of seven oysters between 6 PM and 7 AM, whereas three octopuses ate an average of 0.7 oysters between 8 AM and 6 PM.

The octopus appears to be unable to integrate the sensory input from vision and local arm-sensitivity (tactual and chemical summation), "...since neither has a modifying effect upon a response produced by the other" (Maier and Schneirla, 1935, p. 113). Young (1964) reported that there are no anatomical connections between the brain lobes subserving vision and touch. Therefore, if both vision and touch are implicated in the original selection of the prey species, it would appear that they must originate separately. Transfer from one modality to the other would not be expected.

Also relevant to the problem of species-recognition is Fujita's (1916) report that the octopus drilled holes in pelecypods (the Japanese pearl oyster, *Pinctada spp*, and in pectens). I imported the common American oyster, *Crassostrea virginica* Gmelin, from Florida, U.S.A., to Bimini, Bahamas, and presented them to a dozen octopuses, none of which had been drilling or eating pelecypods. During a three-month period none of the oysters was drilled. On the other hand, these octopuses, which had been drilling and eating gastropods, readily accepted New England periwinkles. Thus, abundance of a species may lead to its becoming a prey, and predatory experience subsequently determines

the direction of appetite. The absence or scarcity of a species need not be a deterrent to acceptance provided it is similar to familiar species of prey.

These observations suggest that several sensory modalities may be implicated initially in the discovery of prey species. Individual learning may be a necessary prerequisite to recognition of the species to be drilled and eaten. It is unknown how this comes about ontogenetically, and what stimuli and sensory modalities form the basis of this learning.

Individual Recognition

Gastropods may be roughly classified as unattached, free-moving, bottom-dwelling, or as adhering to hard substrate. This is not a precise classification, for most snails behave in both ways. It is useful in investigating the problem of prey-recognition to ask whether the stimuli responded to, the sensory modalities used, and the behaviors of the octopus are different with respect to these types of snail.

With unattached, freely-moving snails, such as *Strombus raninus*, the octopus, immediately upon contact with the gastropod, reaches into the aperture with a tentacle and moves it over the operculum, or over the body of the snail if there is no, or only a partial, operculum. This behavior was described incidentally as "customary procedure" by Abbott (1955, p. 54).

With gastropods which adhere to substrate, such as *Livona pica*, the octopus climbs on top of the shell. It may pull the shell off the substratum, following which its behavior is the same as just described. If the snail is not dislodged, the octopus may proceed to Step 2, drilling a hole in the shell.

Given that these species, *qua* species, are already recognized as prey, what stimuli determine that an experienced octopus will accept an individual shell? I have now completed two groups of studies concerned with identifying the stimuli for the initiation of drilling and feeding. The first group involved presentation of single

shells, and the second group involved discriminative experiments. In both groups of experiments, drilling was used as the criterion that the individual shell was acceptable to the octopus. Another operational definition of individual recognition emerged from the experiments, and will be noted shortly.

Studies on single shells. Boycott (1954) reported that the octopus ate hermit crabs, *Eupagurus bernhardus,* but did not report how they were gotten out of their shells. I presented *Pagurus* sp. in a variety of shells to the octopus in laboratory tanks. The octopus drilled 28 out of 33 (85%) of the shells. The fact that the octopus treated hermit crabs as though they were molluscs by drilling the shell, indicates that stimuli for drilling may not be specific to molluscs but may also be shared by crustaceans under these circumstances. One obvious characteristic shared by living hermit crabs and molluscs is blockage of the aperture.

To test the influence of this factor, I blocked the aperture of shells in a number of ways. The operculum of *L. pica* (which completely closes the aperture) was sealed with epoxy into an otherwise empty shell. For weight control the shell was filled with seawater approximating the weight of the snail. For weight and odor controls the shell was filled with juice from freshly killed snails. I also sealed the aperture of both *Strombus gigas* and *S. raninus* with Lang's dental plastic (used for casting human dentures); and the apertures of different *S. raninus* were sealed or blocked with loose sand, sand cemented upon the dental plastic, paper towelling, cotton, and $\frac{1}{4}''$ or $\frac{1}{2}''$ strips of plexiglass. The dental plastic either completely or imperfectly sealed the aperture. The dental plastic strips only partially sealed and were cemented either deep into the aperture, or near the top of the aperture flush with the lip of the shell. Empty shells with no blockage of the aperture were also presented.

Some of each of the shells with blocked apertures were drilled. Exceptions included shells whose aperture contained loose sand, and shells partially blocked with plexiglass strips flush with the lip of the shell. Empty shells with no blockage of the aperture were never drilled.

Although almost any blockage of the aperture invites drilling, experiments to date do not justify an ordering of the types of blockage in a quantitative continuum relative to their effectiveness. This is because preparation of the blockages was not standardized, and because the octopuses were not equated for adjustment to laboratory conditions. The following preliminary ordering is thus presented: complete blockage with Lang's dental plastic, 46 to 87% drilled; sand cemented upon plastic, 39%; cotton, 38%; discontinuous plastic, 36%; paper towelling, 27%; strips of plexiglass deep in the aperture, 16%; strips of plexiglass flush with the lip, 0%; empty shells with no blockage, 0%.

Discriminative studies. The question was asked, how effective is the stimulus provided by the blocked aperture? Can the octopus discriminate between aperture-blocked empty shells and normal shells containing a live snail; if not, can the octopus learn to make this discrimination? In one experiment, both the live and experimental shells were *L. pica.* In a second, they were both *S. raninus.* In a third, an attempt was made to increase discriminability between live and aperture-blocked shells by using different species of shell. Thus, in half of the cases the blocked aperture was of the preferred prey, *S. gigas,* and was pitted against a live, but less-preferred prey, *S. raninus.* In the other half, the live snail was *S. gigas* and the blocked aperture was of *S. raninus.* The aperture was completely sealed in the experimental shells.

The data, based upon daily observations for as long as two weeks, suggest that the octopus does not discriminate between the aperture-blocked and live snail shells, and that it is incapable of learning to make this discrimination. Approximately equal numbers of both aperture-blocked and live shells were drilled during the testing peri-

od. For example, when a live *S. raninus* and an aperture-blocked *S. gigas* were presented daily to four octopuses, 20 *S. raninus* and 16 *S. gigas* were drilled during the first six days of testing. During the next six days, 20 *S. raninus* and 16 *S. gigas* were drilled. No decrease in the drilling of the blocked shells was found with continued testing. The data indicate that blocking of the aperture seems to be a highly effective stimulus, equivalent to that presented by a live snail, or a live hermit crab.

Stimulus for initiating of drilling. I conclude that stimuli for initiation of drilling are provided by obstruction of the aperture of the shell. The obstruction may be complete or partial, but if partial, it must be deep within the aperture. It must also be firm.

There are empty shells on the floor of the bays and seas. Some of these shells are impacted with sand, or have smaller shells wedged into the aperture. While it seems unlikely and inefficient from an evolutionary point of view that the octopus would drill these shells, the data presented above suggest that an occasional mistake might be made if there were a firm blockage deep in the aperture, though sand-filled shells would not be drilled.

The sensory discrimination made by the octopus appears to be tactual. The octopus does not require a metabolite from a live prey in order to drill the shell. In this it differs from the boring oyster drill, *Urosalpinx cinerea* (Say), and *U. cinerea follyensis* Baker (Carriker, Scott, and Martin, 1963). Other factors which do not seem to be necessary for the initiation of drilling include the position or locomotion of the animal prey, weight (within the limits tested), hardness and roughness of the blockage, and changing resistance due to the retraction of the snail into the shell following insertion of the tentacle of the octopus. Vision also seems unnecessary since the octopus drills in light-sealed tanks. The firmness of the blockage may be the critical determinant whether the octopus will drill or whether it will pull out

whatever is blocking the aperture (this factor will be discussed further under Step 4). In this regard it may be noted that when shells with blocked aperture were given to the octopus, frequently the material (loose sand, cotton, paper towelling, epoxy-sealed operculum, and on one occasion even the dental plastic) was pulled out, either before or after the shell was drilled. This observation indicates that the criterion of pulling out the blockage, as well as drilling, may be used where feasible to test whether an individual shell is acceptable to the octopus.

While the factors named do not seem to be necessary for the initiation of drilling, they may be facilitatory. However, the discriminative studies do not support such an interpretation, since the incidence of drilling shells with blocked aperture was the same as with live snails. The studies with single shells on the other hand, indicate that other factors may exert influence, but those factors regulating the quantitative continuum of effectiveness have not yet been evaluated.

These conclusions must be restricted to the cases of unattached freely-moving snails, and to those of adhering snails which are pulled off the substratum. The conclusions do not seem readily applicable to adhering snails which are not dislodged but are drilled while adhering, nor to pelecypods in general, and amphineurans which are not dislodged. The latter may be viewed as discriminations of resistance by the mollusc to the application of force by the octopus. The distinction between species and individual recognition should not be confused in any of these cases. Initiating stimuli and sensory modalities may be quite distinct in the two problems, and for different classes of molluscs.

Behavior after tentacular insertion. After exploring with a tentacle, the octopus may behave in one of several ways. (1) It may reject the shell, because the shell is empty and the blockage is loose, or can easily be pulled out, or is incomplete and not deep into the aperture; the octopus may not be sufficiently hungry; the species

offered may not be a preferred food source, or it may not be "familiar" and therefore not a "prey"; in laboratory tanks, the octopus may be disturbed by what it sees outside of the tank (even if deprived of food for a long time); or because of other unknown reasons. (2)The octopus may hold the shell for a while before commencing to feed or to drill, or having rejected the shell, it may return to it later. (3) The octopus may begin immediately either to drill the shell or to pull the snail out of the shell.

These alternative behaviors suggest that while the blocked aperture may be a necessary stimulus for drilling, it does not specify the precise timing of the onset of the response.

STEP 2. DRILLING A HOLE

The second step in the behavioral sequence may be the drilling of a hole in the shell.

Characteristics of Hole

Fujita (1916), Pilson and Taylor (1961), and Arnold and Arnold (this Symposium) have described the size, shape, and location of the boreholes. Pilson and Taylor (1961) reported that a 48-g octopus drilled a hole in *Haliotis fulgens* 1.4 mm deep, 0.8 mm $\times$ 0.6 mm outside (top) dimensions, and 0.3 mm $\times$ 0.2 mm at the bottom. Fujita (1916) reported a range of sizes in the holes drilled in the Japanese pearl oyster without reporting the sizes of the octopuses. At the top these ranged from 1.2 to 2.0 mm $\times$ 0.7 to 1.4 mm (largest value 3.2 $\times$ 1.9 mm) and at the bottom from 0.2 to 0.3 mm $\times$ 0.1 to 0.2 mm (largest value 0.6 $\times$ 0.4 mm). In agreement with those of previous workers, my measurements suggest that the size of the hole varies with the species, thickness, and hardness of the shell, and with the size of the octopus. Thus, for a given species and age (or size) of shell, the size of the hole varies with the size of the octopus; for a given octopus and size of shell the hole varies with the species of shell; and for a

given octopus and a given species of shell, the size of the hole varies with the age (size) of the individual shell. In general, with octopuses weighing from 40 to 1500 g, the smallest holes, of dimensions comparable to the smaller of those reported above, occur in *Oliva reticularis, Nerita peloronta, Purpura patula,* and *Fasciolaria tulipa.* Larger holes, comparable to the larger values reported by Fujita, are found in the shells of *Strombus, Cassis, Murex,* and *Xancus angulatus.* Still larger holes, up to 4.0 mm in outer diameter, are found in large, thick-shelled *L. pica, S. raninus,* and *S. costatus.*

Location of the hole on the shell is nonrandom. Measured clockwise from a line drawn between the apex of the spire and the beginning of the lip, the favored position is within the first 90°, between the parietal wall and the apex of the spire. Out of 677 boreholes in *S. raninus,* made by more than 30 octopuses in three different years, 498 (74%) were located 0 to 90° from this reference line; 100 (15%) were 100 to 180°; 30 (4%) were 190 to 270°; and 49 (7%) were 280 to 360°. There are also predictable individual preferences. There are, thus, both inter- and intra-individual preferences which suggest the influence of learning. This is in agreement with the findings of Arnold and Arnold (this Symposium). Fujita (1916) also found inter-individual consistencies in the placement of the holes in the Japanese pearl oyster, predominantly within the pallial line and over the adductor muscle.

Arnold and Arnold (this Symposium) indicated that the lip of the shell in *S. raninus* may be a major reference point with which the octopus orients the location of the borehole. Whether other reference points are involved, such as the aperture, the spire, and the siphonal canal, is unknown, but suspected as gastropod shells without prominent lips (such as *Cypraea zebra*) as well as pelecypod and amphineuran shells are drilled. The fact that the octopus drills empty shells with blocked aperture provides an opportunity for test-

ing these potential factors on artificial shells.

The hole was occasionally drilled in a nonsensical place by very small octopuses, as in the lip of the shell, so that secretion would go directly into the seawater. This did not occur more than once with a given animal in my limited sampling, and suggests that the octopus may learn rapidly where to drill.

The number of holes per prey shell seems to vary as a function of species of shell. Fujita (1916) reported that more than two holes per shell in the Japanese pearl oyster were rare. I found that the number of holes is generally one for *Strombus*, *Oliva*, *Purpura*, *Nerita*, and *Livona*. In an experiment with *L. pica*, for example, only five out of a total of 78 drilled shells had two drill holes. A median number of two holes is the case in *Fasciolaria* and *Murex* shells, and three or more holes may occur per shell. The larger number of holes is associated with the carnivores rather than with the herbivores. This may be a function of the relative strength of the snails, size of the aperture, whether the operculum completely seals the aperture, or a combination of factors.

The presence of multiple holes raises the questions of whether drilling and secreting occur in an invariant sequence or are dissociable, and whether characteristics of the prey determine repetitive drilling. Evidence will be presented in Step 3 which suggests that drilling and secreting are separable.

The angle of orientation of the borehole is not necessarily perpendicular to the surface of the shell. This is in agreement with the findings of Arnold and Arnold (this Symposium). The easiest route may not necessarily be the perpendicular one.

Viewed from the exterior surface, shapes of octopus boreholes vary from oval, circular, cross-shaped, and multi-sided polygon, to extremely irregular. Pilson and Taylor (1961) and Fujita (1916) described the boreholes as oval. It may be difficult to detect these patterns in small boreholes, but the largest give clear exam-

ples. The hole may decrease in diameter like a triangle with apex down, and may have a bend in it; the inner end may be extremely minute, and of just sufficient diameter to permit the octopus to pass its secretion into the prey. The thicker the shell, the wider is the outer portion of the hole. These observations are in agreement with those of Arnold and Arnold.

The variable shapes of the boreholes suggest that the octopus rasps in a straight line, then rotates its buccal mass, its odontophore, or the shell, and again rasps in a straight line. This maneuver may be repeated in several different directions.

The inner walls of the octopus' borehole may be smooth, but may also possess vertical striations strongly reminiscent of rasp marks made by radular teeth. This observation was also made by Fujita (1916) and Arnold and Arnold (this Symposium).

Fujita (1916) reported that the octopus on the average ate 5.7 oysters per day, of which 2.6 had boreholes. As many as nine holes were sometimes drilled per day. In experiments with *L. pica*, I found that the mean number drilled varied from 2.16 to 3.33 per octopus per day: five octopuses drilled four holes; 13 octopuses drilled three holes; 15 octopuses drilled two holes; and nine octopuses drilled one hole. Octopuses were deprived of food approximately one day before the experiments.

In further experiments with *S. gigas* as prey, in which each octopus was tested after 0, 1, and 4 days without food, the mean number of holes drilled per octopus per testing day was 3.0, 3.5, and 4.5, respectively, for the three periods of deprivation. For all testing periods, 11 octopuses drilled five holes per day; five octopuses drilled four holes; four octopuses, three holes; and two octopuses one and two holes each.

Similar experiments with *S. raninus* as prey in which the periods of deprivation were 1, 2, 4, and 7 days, produced means of 2.6, 2.6, 3.2, and 3.1 holes drilled per octopus per testing day, respectively. Six octopuses drilled five holes; two octopuses, four holes; 15 octopuses, three holes; eight oc-

topuses, two holes; and five octopuses drilled one hole per testing day.

The characteristic borehole of gastropods is smooth-walled, circular, perpendicular to the surface, and decreases in diameter at the inner end (Carriker and Yochelson, 1968). Only the last characteristic is common to the octopus' borehole. If only a single octopus-hole is examined, its most striking aspect is the small size of the interior opening. The function of the hole, apparently, is merely to provide an entrance for secretion from the octopus.

Characteristics of the Drilling Process

Sounds of drilling may be heard with an underwater hydrophone with suitable amplification. They resemble high-pitched rasps, and sonographic analysis indicates that they have frequency components up to about 16,000 cycles, with dominant frequencies between 2,000 and 6,000 cycles.

The individual rasp is 0.3 to 0.4 second in duration. Of several thousand rasps that have been analyzed, only a few have been more than one second in duration. The number of rasps per minute shows a negatively accelerated function. Starting from a mean of about 10 rasps for the first two minutes (with a range from one to 22 rasps), the number rapidly decreases within five to 15 min to a stable rate of two to four per min for the duration of the drilling period. There may be a burst of more rapid rasping when the final layer of the shell is pierced. Since the rate of drilling is more or less continuous, there are rarely long silent intervals between rasps. In some cases a second sound may be heard, which may be described as a "pick", "pluck", or "chip". The sound has a sudden and steep onset, a very short duration of about 0.1 to 0.2 seconds, and a rapid decline. That decrease in rate of rasping is not due to muscular fatigue is supported by the fact that a second shell may be drilled immediately upon completion of the first, with a high initial rasp rate for the first few minutes.

The total time that the octopus takes to penetrate the calcareous shell can be determined by listening to the rasping sounds. The time may be estimated independently by observing the gross behavior of the octopus (Step 4). Upon completing drilling, the octopus may turn the aperture of the shell toward the buccal mass, or it may drop the shell entirely. Examination of the shell at this time indicates that the hole is complete. Preliminary analysis indicates that octopuses drill *O. reticularis* in about 20 to 30 min; *S. gigas* in about 40 to 60 min; *S. raninus* in about 60 to 80 min; and *L. pica* in about 90 to 120 min. For purposes of comparison, it may be noted that the following values have been published for *U. cinerea*: duration of individual rasp, 1.0-1.5 sec; rasping period, few seconds to five minutes; interrasping (silent) interval, between 10-90 mins (common range, 25-30 min); rate of boring, about 0.5 mm per day. (Carriker and Martin, 1968; Carriker, this Symposium).

It is not clear whether the mechanical penetrating of the shell is aided by chemical weakening or dissolution. In this regard the following should be kept in mind: (1) If there is chemical action, it must either be rapid in its action, since the interrasp intervals are short, or it must be continuously present during the rasping. (2) Although the sides of the borehole may be lined with striations, suggesting tooth marks, some holes may be smooth. (3) When a borehole is made on the nacreous portion of the shell, a patch of discoloration results on the nacre surrounding the hole. It is not clear whether this discoloration is produced by radular action, chemical action associated with drilling, or chemical action associated with the postdrilling secretion that is ejected into the hole. (4) Efforts to measure the hardness of the radular teeth with the diamond test for hardness, were not successful, as the teeth are smaller than the point of the diamond. If it could be shown that some shells which the octopus drills are harder than the radular teeth, the likelihood of the involvement of chemical action would be substantially increased. The octopus'

beak may be eliminated as the hole-boring instrument because of the correlation of the size and structure of radular teeth with the sizes, shapes, and vertical striations of the holes, and because the beak is much softer than any of the shells whose hardness has been measured. Fujita (1916, p. 256) was unable to scratch oyster shell with the octopus' radula and assumed that chemical action is responsible for weakening the shell. Fujita also concluded that the most likely gland whose secretion might perform this dissolution is the anterior salivary gland, the extract of which he found is slightly acid. Analysis of these glands was begun recently (Gennaro, Lorincz, and Brewster, 1965).

STEP 3. POST-DRILLING SECRETION

A transparent mucus is frequently present at the site of a freshly drilled hole. Often, after the snail has been eaten, a large mass of transparent mucus can be shaken from the shell. It is not miscible with sea water.

When an empty shell with a blocked aperture has been drilled and is cut open, a strand of mucus leading from the site of the borehole into the shell can be collected. This is the octopus' secretion which is ejected into the hole. The secretion stretches for several inches, is viscous, and winds around the column of the shell. I have collected amounts varying from 1.65 cc to more than 4.0 cc.

This technique of collection will be valuable for pharmacological studies, since one can "milk" the octopus daily and collect large amounts of this secretion in the natural proportions of its many constituents. This technique is preferable to the two standard techniques currently used: sacrifice of the animal to homogenize the glands, and electrical stimulation of the glands to secrete (Hartman, Clark, Cyr, Jordon, and Leibhold, 1960; Ghiretti, 1960). Out of 24 aperture-blocked shells which I have cut open after the octopus drilled them, only about 40% have contained this secretion. This may mean that

at some point after drilling the octopus detects an abnormality about the shell, which inhibits secretion. Perhaps greater care in preparing aperture-sealed shells would increase the proportion of cases with secretion. On the other hand, these observations might mean that under normal circumstances there is not a rigid coupling of drilling and secreting. This would require determining the conditions under which drilling is followed by secreting. In the absence of a fixed drilling-secreting sequence, the occurrence of multiple drill holes in the same shell might be easily understood. The fact that crustaceans are killed with secretions from the posterior salivary glands without being drilled indicates that there is no obligatory relationship between drilling and secreting. Pilson and Taylor (1961) reported that an abalone which had just been drilled was weaker than normal, but that it recovered within two weeks when removed from the octopus. My observations support this finding. The amount that the octopus normally secretes weakens the snail, but does not typically kill it, and it recovers when removed from the predator. I have collected living, apparently healthy *S. gigas* in the field which have an octopus' hole in the shell. This may mean only that not all drilling is followed by secretion. Normally, however, the secretion does immobilize, paralyze, or weaken the snail.

I investigated a second technique in an attempt to estimate the length of time that the secretion exhibits its effects on prey. In the first series of experiments, snails that were drilled, and into which the octopuses presumably secreted, were removed while the snails were still alive. At various times thereafter (immediately, one, two, or seven days later) the snails were given to octopuses other than the ones which initially drilled them. The new octopuses ate 90% of the snails without redrilling the shell, when given the prey immediately after it had been drilled. Incidence of eating without redrilling declined to 50% within one day, and remained at this level from two to seven days. The fact that the octo-

pus will drill 85% to 90% of its normal snail prey, pulling the previously drilled snail out of its shell 50% of the time a week after it had been drilled, indicates that the weakening effects of the secretion last in some cases at least that long. Pilson and Taylor (1961) injected the abalone with an extract from the posterior salivary gland of *O. bimaculoides*. In the dosage given, the subjects died within two days. Fujita (1916) reported that similar extracts killed crabs and rabbits instantly, and frogs within 5-10 min.

It is not known how the secretion penetrates the snail. The wide variation in location of boreholes in shells suggests that the secretion is not injected into any specific part of the snail's body, but rather is ejected into the shell-mantle interface.

STEP 4. REMOVING THE MOLLUSC FROM ITS SHELL

Five behavioral patterns occur after drilling and secreting; four of these involve removing the mollusc from its shell. It has also been reported that the octopus may remove the mollusc from its shell without first drilling and secreting (Fujita, 1916; Pilson and Taylor, 1961).

Behavior After Drilling and Secreting

(1) After drilling, the octopus may proceed immediately to pull out the snail and eat it. It holds the shell with some of its suckers, pulls out the snail with other suckers, and pushes it into its buccal mass. *O. reticularis* is consumed in 20-30 min, and *S. gigas* is eaten in 40-60 min. A discrete movement terminates feeding which involves spitting out the unconsumed prey to a considerable distance from the home area. (2) The octopus may hold the shell with its tentacles for a period of time before proceeding as in (1). (3) The shell may be dropped by the octopus, which then moves a short distance away into its home area and waits. After some time, the octopus retrieves the shell and proceeds as in (1).

It is not clear in the last two cases whether the octopus waits for a specified period of time for the secretion to take effect, thus making a temporal discrimination, or whether it periodically returns and samples the pull of the snail until it is capable of drawing it from the shell. On the basis of the experiments reported below, it is clear that the octopus is indeed capable of, and likely to make, a discrimination of force. However, I have no experimental evidence to support a hypothesis of temporal discrimination.

When a number of shells are available to the octopus, a fourth behavioral pattern in exhibited. The octopus, after drilling and secreting into a shell, may drop the shell as in (3), pick up another shell, insert its tentacle into the aperture (Step 1), and start to drill it (Step 2) without eating the snail from the shell already drilled. My data indicate that the octopus may drill at least six shells in succession without eating any of the snails from the previously drilled shells. I hesitate to call this behavior "hoarding" because of the implication, which has not yet been independently demonstrated, of anticipation and purposefulness that the term suggests. If "hoarding" is defined as the accumulation of food supplies beyond the normal amount consumed, it does not completely describe the situation for the octopus, since in some cases it may drill repetitively and not eat at all for 10 or more days. The drilling seems to become independent of feeding. The data clearly indicate a separation of drilling and secreting from immediate feeding upon the weakened snail. A grouping of the data from the previously described deprivational studies reveals that in 31 out of 72 instances (43%) the octopuses drilled two or more shells in succession before eating, meeting the criterion of repetitive drilling. This phenomenon also occurs naturally. In at least one instance I caught an octopus which held onto and carried into captivity with it two *C. zebra*, both of which were drilled, alive and uneaten.

Removal of Mollusc Without First Drilling and Secreting

When a number of live snails are available to the octopus, a fifth behavioral pattern is exhibited. The octopus, after drilling and secreting into one of the shells, may drop it, and pick up another snail from which it will pull out the body and eat it even though this new shell has not been drilled. Both Fujita (1916) and Pilson and Taylor (1961) noted the same phenomenon. Pilson and Taylor (1961) reported that the octopus can open a bivalve, or pull an abalone off the substratum by force. They hypothesized that the octopus may try force first and, failing in this, may then drill a hole (p. 1367). Fujita (1916) reported that each of his octopuses on the average ate 5.7 oysters, of which 2.6 oysters had holes (p. 253). He also considered the hypothesis of force to explain consumption of undrilled prey. Fujita (1916) also hypothesized that the octopus might inject its secretion between the valves of the oyster, without boring a hole in the shell. There is no evidence to support this hypothesis.

I observed octopuses pull adhering snails, *L. pica*, off the side of a laboratory aquarium, and off rocks in the field by force, and many cases have occurred in the laboratory of feeding without the shell being drilled. Among octopuses kept in the laboratory, there seem to be individual preferences either for drilling shells, or for forcibly pulling out the snail and eating it without drilling. The number of octopuses which prefer using force is very much smaller than the number which drill, but almost all will use force on rare occasions.

I performed the following experiments in order to test the hypothesis that the octopus may try force first and if this fails may then drill a hole.

(1) A small break was made in the shell of live *S. gigas*, and the columellar muscle was cut through it. The break was sealed with dental plastic, and the snails were given to octopuses. In 100% of the snails

(N=16) the body was pulled out and eaten without the shell having been drilled. If the live snail was removed from the shell and given to the octopus, it was always eaten.

(2) Snails (*S. gigas*) in the shell were killed by deep freezing, allowed to thaw to ambient temperature, and one group was given to octopuses after three, and a second group after 24 hours. After both time intervals, 100% of the bodies were pulled out and eaten (N=21), in whole or in part, and none of the shells was drilled.

(3) The spire of the shell of *S. raninus*, where drilling usually occurs, was covered with dental plastic which is harder than most gastropod shells. No hole was drilled in the plastic (N=20). Fifty-five percent of the octopuses shifted drilling locations to new sites just below the plastic covering; and 35% pulled out the bodies without drilling. The remainder neither ate nor drilled. I place particular importance on this experiment because (a) the snails were undamaged, (b) the technique gives the experimentor control over the behavior of the octopus, depending upon the area of the shell covered with the plastic, and (c) the technique provides a basis for investigating what coatings the octopus will drill through, and what tactual discriminations it is capable of. Different areas of the shell can be covered with different materials and the octopus can be tested in locating the uncovered areas of the shell to which to shift its drilling location.

(4) The following series of replacement experiments was made using live *S. gigas*: (a) after the octopus had completed drilling the shell (but not eating the snail), I removed the snail and gave the octopus a new undrilled live snail. In 100% of the cases (N=10) the new shell was drilled. (b) Using the same procedure, I gave the octopus a new live snail, whose shell had just been drilled by another octopus which had presumably secreted into it. In 90% of the cases (N=9) the new shell was not redrilled, but the body was pulled out and eaten. In 10% of the cases (N=1), the new

shell was redrilled. (c) I repeated procedure (b) with snails which had been drilled the previous day, two days before, or one week before. The shells were not redrilled in 53%, 37.5%, and 50% of the cases, respectively, but the body was pulled out and eaten. (d) In a variation on procedure (b), the previously drilled snails were given to octopuses as their first snails. Similar results were found. Thus, previous drilling by a given octopus is not a necessary prerequisite for its pulling the mollusc out of its shell and eating it.

These experiments indicate that the octopus discriminates between healthy and weakened or paralyzed snails. Snails drilled two or more weeks prior to being given to new octopuses, were almost always redrilled, indicating that the presence of a drill hole in the shell is not the relevant factor determining whether the shell will be redrilled or the body pulled out.

(5) Results of individual recognition studies are cited here. In one of the discriminative studies in which L. pica was the experimental gastropod, the octopus was given a choice between a live snail and an empty shell in which the operculum was sealed in place with epoxy. In 39 out of 90 cases the epoxy-sealed operculum was pulled out of the aperture of the shell. In 10 of these 39 cases, the shell was not drilled, and in the other 29 cases the shell was drilled. Furthermore, when the aperture was blocked with paper towelling or cotton, both of these materials were pulled out, sometimes when the shell had been drilled, and sometimes when it had not been drilled. These results throw new light on the behavior of the octopus. The resistance of the epoxy-sealed operculum does not weaken in a few hours though it may harden with time; nor is it weakened by the posterior salivary secretion. It thus seems unlikely that the octopus is discriminating a change in the resistance of the blockage. Sometimes the epoxy-sealed operculum is pulled out without drilling, and sometimes after drilling. The data indicate that the octopus is capable of exerting force to clear the aperture, that weaken-

ing is unnecessary for this, and that the factors determining when it drills or when it pulls are incompletely understood.

The hypothesis that the octopus tries force first is strongly supported by these experiments. Although some of the data might be interpreted in terms of sensitivity of the octopus to biochemical stimuli, indicating that the snail is damaged or abnormal in some way, other data cannot be so interpreted. The fact that some individual octopuses manifest a preference for forcefully removing the prey indicates that the octopus is indeed capable of pulling a live, apparently healthy snail from its shell and eating it.

Trueman and Packard (1968) measured the holding tensions of O. vulgaris with the animal pulling on a nylon thread stitched through the cranial cartilage. Tension was considered maximal when the thread was broken. Apart from difficulties of the method, which remain to be assessed, data were presented only for octopuses weighing from 1 to 15 g. A negatively accelerated function was fitted to the data without rationale, although a linear function appears to be an equally good fit. I have extrapolated both functions to a 1-kg octopus which yields holding tensions of about 13 lb for the negatively accelerated function, and about 55 lb for a linear function. Since the tension must be related to the duration of time during which it is exerted, and since we do not know the force-time functions required to pull various molluscs off substrate, nor the body out of various shells, these values are not particularly helpful. Starfish open bivalves, and observation indicates that octopus is capable of exerting far greater holding tensions.

The results of my experiments were somewhat unexpected in view of the data and interpretations of Wells (1961, 1962). He reported that the octopus is incapable of learning to distinguish between different weights of at least a nine-fold difference (5 versus 45 g), and interpreted his data to mean that the octopus is unable to make a discrimination based upon the force or

muscular tension it must exert. The failure to demonstrate a capacity, however, may merely represent the selection of an inappropriate testing situation. In other situations the capacity may be easily demonstrated. Furthermore, the octopus may indeed be making the discrimination in Wells' testing situation, but may be responding naturally to the discrimination that it makes. In order for the octopus to eat (as opposed to drill) shelled molluscs, the body must be pulled out. Resistance by the mollusc does not mean that the octopus should abandon the task, but may merely mean that it should try harder or longer. The pulling out of epoxy-sealed opercula may be relevant here. Viewed in this fashion and from the adaptive standpoint of feeding upon shelled molluscs, Wells' data are not necessarily contradictory. I should like to know whether his octopuses try to drill his cylinders. They do try to drill the underwater hydrophone inserted into the tank to record the drilling of shells. I conclude that the octopus does indeed make discriminations of effortfulness or force based upon the muscular tension it must exert.

Since the octopus may pull the mollusc's body out of its shell, it may be asked why it drills at all. No definitive answer can be given.

The Probable Generic Nature of the Drilling Behavior

Drilling has been reported for six species of octopus: *O. (polypus) vulgaris, O. ocallatus, O. macropus* (Fujita, 1916); *O. bimaculoides, O. bimaculatus* (Pilson and Taylor, 1961); and *O. joubini* (Arnold, personal communication). It has now been reported from both the Atlantic and the Pacific Oceans.

Table 1 lists the species of molluscs which the octopus has been known or suspected of drilling either in the field or in the laboratory. In my experience, only two species of gastropods have not been drilled under laboratory conditions, nor have I found their empty shells in the field

with drill holes: the triton *Charonia tritonis nobilis* Conrad (*C. variegata* Lamarck), and the flamingo tongue, *Cyphoma gibbosum* Linnaeus. The triton may secrete a great deal of mucus which, in a laboratory tank with relatively slow circulation of water, may clog the gills of the octopus, killing it. More than a dozen octopuses have been lost for this reason. Other snails that have been responsible for this include large *Cassis tuberosa, C. madagascariensis,* and *Cypraea zebra.* That this is a laboratory phenomenon is indicated by the fact that (1) drilled *Cassis* and *Cypraea* shells are commonly found in bays, and that (2) fishes and other gastropods were also killed in tanks in which large amounts of mucus were secreted, with the exception of adhering snails such as *L. pica,* which climbed out of the mucus-filled water into the air along the side of the tank. No interpretation can be offered for the refusal of the octopus to drill and eat *C. gibbosum.*

I have found empty shells of the reticulated cowrie-helmet, *Cypraecassis testiculus* Linnaeus, in the field, often with what appear to be octopus' drill holes. I have never seen a live snail of this species. Through the courtesy of Dr. William Clench, formerly Curator of the Department of Mollusks, Museum of Comparative Zoology, Harvard University, the Museum's collection of *C. testiculus* shells was made available for examination. Most of the shells were empty when collected. Out of 333 shells examined, 124 had what appered to be drill holes of the octopus. This may represent a natural rate of predation of 37% due to the octopus. These shells were collected from an area covering Mexico to Ascension Island, and Brazil to Florida. Predation by the octopus may pose serious commercial problems. Fujita (1916) noted that pearl oyster beds suffered great damage.

The wide geographic distribution of species of octopus which drill, and the large number of species of molluscs preyed upon, suggest that the drilling and feeding pattern investigated may be typical of

the octopus. As a soft-bodied invertebrate, the octopus leaves little record of the dates of its appearance paleontologically. A permanent record may be available in the drill holes occurring in fossil molluscan shells.

CONCLUSION

The octopus feeds upon shelled molluscs. It is a behavior typical of the species. The pattern as described by observations and experiments in the field and in the laboratory consists of four recognizable steps: selection of the prey, drilling a hole in the shell, secreting into this hole, and pulling out the body of the mollusc and eating it. Close examination indicates that no two steps in this process are necessarily or inextricably linked to each other. Thus, selection of the prey may lead to (1) drilling a hole in the shell, or to (2) pulling out the body, or to (3) selecting another prey, if more than one are available. Drilling of a hole in the shell may lead to (1) ejecting the secretion, or to (2) pulling out the body, bypassing secretion, or to (3) selecting another prey. The ejection of the secretion may lead to (1) pulling out the body, or to (2) selecting another prey. Since the octopus presumably kills crustaceans with the secretion from the posterior salivary glands, drilling and secreting are not necessarily linked. Whether the octopus attempts to eject its posterior salivary secretion directly into the aperture of a gastropod shell, or between the pelecypod valves, without first drilling a hole is unknown. This was not observed, but remains a possibility. Drilling of the hole is clearly produced by the radula. Chemical action responsible for either the dissolution of, or the weakening of the shell has not yet been demonstrated. The function of the anterior salivary glands remains unknown.

The drilling-feeding behavioral patterns are remarkably complex and plastic. If the usual site for drilling is blocked, the octopus may either drill in a new atypical location, or it may resort to pulling out the body without drilling. There is not one behavioral pattern, but rather there exist many behavioral routes to achieve the end of feeding. The phenomenon of repetitive drilling without feeding upon the drilled molluscs divorces the drilling behavior from the act of feeding. The fact that the octopus first tries forcefully to pull out the body and sometimes succeeds, divorces the act of feeding from the drilling process. Ordinarily, the sequence of drilling and ejecting secretion serves the function of weakening the mollusc so that the octopus may feed more easily upon it.

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