

CHAPTER 7

BIOLOGICAL

CONTROL

Since before the turn of the century, the study of the predators and parasites of mollusks has been a matter of at least academic interest. As a consequence, some excellent, detailed, and comprehensive papers have appeared in the literature, including those of Bequaert (1926), Frömming (1954*b*:311–14), Gain (1896), Keilin (1919, 1921), Pelseneer (1928, 1935), Pilsbry and Bequaert (1927: 470–79), Plate (1951), Simroth and Hoffmann (1928), Taylor (1894–1900), and Wild and Lawson (1937). Now that there has arisen a genuine need for a suitable predator or parasite of the giant African snail, however, this study has taken on a very practical aspect. Even more than that, it actually demands an inventory and reassessment of the information on record. With this thought in mind, there has been prepared below a series of discussions, under the subheadings of the main predator or parasitic types, which will bring the subject of biological control more sharply into focus. An examination of this, in turn, will permit of a more accurate evaluation of the biological means of control—especially as it compares with other types of control.

Amphibians Noël (1891) effectively demonstrated the fact that toads and frogs introduced into gardens would have a telling effect upon the slug and snail population. It was knowledge of this sort that persuaded the American authorities in 1937 to introduce the giant Central American toad, *Bufo marinus*, into Guam from Hawaii in an attempt to control the destructive, large, black slug, *Veronicella leydigi*. This biological control measure was very effective and, as a consequence, the Japanese were persuaded subsequent-

ly to introduce the toad into Rota, Tinian, Saipan, and Yap (Townes 1946). In 1938, it was introduced into Mauritius from Puerto Rico in the hopes that it would control the sugar cane pest, *Phytalus smithi* Arrow (Anon. 1939). More recently, this toad has been purposely and in some cases perhaps accidentally introduced in a number of the Micronesian islands. In Ceylon, Bertrand (1928) reported that the only control of *Achatina fulica* in Madagascar was a "big bull-frog." In spite of his recommendation, the Director of Agriculture in Ceylon decided against introducing this giant amphibian predator. Pemberton (1938) announced that Bertrand was apparently in error, that it was Mauritius and not Madagascar, and that the amphibian in question was not a "bull-frog" but probably a "large toad common in Mauritius." Pemberton stated further, "It is probable that *Bufo marinus* would feed on the young snails, should the pest ever become established in regions where the toad occurs." This prediction was shown by the author in 1949 to be correct—at least on the island of Ponape where the stomach contents of this giant toad were examined. Not only were small specimens of *A. fulica* and *Opeas* sp. found, but pieces of the flesh and shell of large specimens of the giant snail were even more commonly encountered (cf. Lever 1939). The presence of dead fly maggots with the latter quickly told the story. The toads were apparently attracted to the crushed larger snail specimens on the roads because of the activity of the maggots. The abundance of the giant snails in all sizes, especially in the Jokaj region of Ponape, and the markedly emaciated condition of the numerous giant toads strongly suggested that *B. marinus* was providing little in the way of biological control. Such were also the conclusions of Lange (1950) on Saipan. More recently, however, Gressitt (1954:90, ICCP 1953) reports that it is believed by some that *B. marinus* is responsible for the decreasing snail population in Ponape. This is questionable, notwithstanding the fact that Jaski (1953) found "with an astonishing frequency" achatinas in the stomachs of a species of toad in Java. Dartevelle (1954) has reported that certain amphibia in the former Belgian Congo seek out the eggs of the endemic achatinas.

Frogs would be even less effective than the toads, as they are less independent of the aquatic environment. Garnadi (1951), however, in Indonesia found the frog *Rana tigrina* Daud. in several instances in the vicinity of egg masses of *A. fulica*; one dissected specimen revealed pieces of achatina egg shell in the stomach. Earlier information from Pilsbry and Bequaert (1927:473) and from Kirkland (1904:8), wherein only 1 per cent of the stomach contents of the

American toad was shown to consist of snails, suggests that amphibians figure in only a minor way in the consumption of snails.

To sum up the effects of introducing *B. marinus*, however, simply by stating that it does effectively control *V. leydigi* but not *A. fulica*, is to ignore the indirect effects, some of which are of considerable importance but infinitely subtle in their connection with the original introduction. As an example on the plus side of the ledger: The great quantity of dead achatinas in a heavily infested area causes the cockroach population to build up often to serious proportions. *B. marinus* will thrive on cockroaches (Pemberton 1949); both are nocturnal. It should be recalled at this point that the toad will also feed on fly maggots. In the absence of experimental evidence, it is quite safe to reason a priori that, even though the introduction of *B. marinus* will not produce an appreciable effect upon the giant snail population, it may reduce substantially some of its side effects of public health importance.

On the other side of the ledger, however, we find an indirect effect which is felt through a wondrously devious chain reaction. The early traders accidentally introduced the pestiferous, disease-carrying rats. In the zoos in Japan, the giant monitor lizard (*Varanus*) fed avidly on rats. The monitor lizard was therefore introduced, as a biological control measure, into the Micronesian islands where it had not earlier become established. Then came an astounding discovery. The monitor lizard is diurnal and the rat is nocturnal. To make matters worse, the biological *faux pas* proved irreversible. The monitor lizard quickly became a pest by consuming eggs and young chickens—precious items indeed in Micronesia, especially since chickens, too, will do their bit in consuming young achatinas. The introduction of *B. marinus*, strangely enough, brought some relief to this problem. The giant toads do not hide as effectively as rats during the day and the monitor lizard would easily find them in its search for food. The toads, however, have potent poison glands in their skin and the meal would prove fatal (cf. Gressitt 1954:142). The prey, paradoxically, was controlling the predator! This was an unexpected benefit which seemed to give further support to the advisability of introducing the toad; in fact, after this was discovered, the toad was purposely introduced into other islands to control the lizard biologically. The benefit, however, was not without serious side effects; for the monitor lizards in the meantime had developed a healthy appetite for the number one agricultural enemy of the Pacific, the grubs of the rhinoceros beetle, which kill the coconut palm—a far more important agricultural item than chickens (Gressitt 1952).

Also, the lizards have been demonstrated to feed on another enemy of the coconut palm—the coconut crab (*Birgus latro*) which incidentally, in turn, feeds on the giant snail, as does the lizard itself (*vide infra*). But the complications did not stop even there. When the barnyard pigs caught the toads and ate them, they became sick or died (Townes 1946). The dogs and especially the cats, as they are largely nocturnal, also discovered the giant toads and similarly were killed when they bit them or attempted to eat them. This was a tragedy, for the dogs and cats were the best rat catchers in the islands! Who could have guessed that introducing *B. marinus* would, in addition to reducing the black slugs, aggravate the rat problem, kill the monitor lizard, reduce natural control of coconut pests and the giant snail, bring some relief to the poultry industry, kill pigs and house pets, and ameliorate a public health problem of cockroaches and flies brought on by the introduction of giant African snails? As a final ironic twist, the native peoples are convinced that their dogs and cats have died from eating the “poisonous” giant African snails!

Ants Green (1910*c*, 1911*b*) was the first to suggest that ants might be a factor in the control of *A. fulica* by reporting that he had observed a predaceous ant “*Phidelogeton affinis* [*sic: Pheidologeton*]” swarming in a batch of eggs that was just hatching.” As it is stated, there is only circumstantial evidence of any attack per se on the snails. This evidence nonetheless has been accepted as fact and even embellished by subsequent investigators (Hutson 1920, South 1926*b*, van Weel 1949). This assumption, however, has proved to be a safe one, for in Indonesia this same species of ant has very recently been shown by Butot (1952*b*) to carry to its nest other species of snail (*Opeas gracile*, *Gulella bicolor*, and *Geostilbia moellendorffi*). Other species of *Pheidologeton* have also been shown to indulge in snail robbing. Meer Mohr (1931*b, c*) reported *P. diversus* was similarly observed carrying away specimens of *Bulimulus* sp. (cf. Rothney 1889). In a letter to the author (Dec. 16, 1949), Professor Silvario M. Cendaña of the University of the Philippines wrote that a species of ground ant common in Los Baños helped check the rapid increase of the giant African snail in that area. Apparently the same species of ant is referred to by Pangga (1949) as *Solenopsis geminata* Fabr.; he reports that they sometimes attack newly hatched *A. fulica*. It is of interest to note that Martinson (1929) reports that in Ghana the worst of the natural enemies of the local achatinids are the “red and black driving ants.”

A number of times during the survey of Micronesia conducted by the author and Kondo ants were seen to be swarming over dead

or dying achatinas. In every case, it seemed quite clear that the snail was either dead before it was attacked by the ants or was dying from overexposure to the hot sun. The same species of ant would completely ignore healthy snails in protected areas. At no time were any ants seen to show the slightest interest in the young snails or the thick-shelled eggs. Occasionally, eggs would be laid in an empty shell and ants were seen to crawl over these to get into the upper whorls of the shell where there still was some decaying flesh. An incautious observer might have been led to believe that the ants were attacking the eggs. It is probable that Lawson (1920*b*) was similarly misled in his observations and that Bequaert's skepticism was justified (1926).

From the evidence accumulated so far, it is questionable that ant raids on young *A. fulica* are producing an appreciable control except under the most limited conditions.

Beetles Several beetle families are notorious for having species that live largely or entirely upon pulmonate gastropods. Bequaert (1925, 1926) has summed up admirably the widely scattered literature on this subject. Significant contributions that have appeared since Bequaert's works, other than those directly pertaining to predation on *A. fulica*, are the following: Cros (1926), *Drilus mauritanicus* consuming *Rumina decollata*; Moore (1934), *Carabus violaceus* killing *Arion hortensis*; Tomlin (1935), *C. violaceus* carrying off *Agriolimax agrestis* (*Deroceas agreste*), *Milax gagates*, and small *H. aspersa*; Ingram (1950), *Calosoma* sp. feeding on *Triodopsis albolabris* and *Ventridens intertextus*; Metteo (1946), *Ablattaria laevigata* consuming *Eobania vermiculata* and *Helicella variabilis*; Fincher (1947), *Lampyrus noctiluca* attacking *Arion ater*; Schwetz (1950), *Luciola* sp. attacking *Planorbis tanganyicensis*. Clausen (1940) reports that *Lampyrus noctiluca* has been imported into New Zealand from England for the control of *H. aspersa*.

Until recently, at least, the beetle most famous for its predation on *A. fulica* is the so-called India glowworm, *Lamprophorus tenebrosus* (Walker) (Lampyridae), endemic in Malaya, Ceylon, and India. Paiva (1919) was the first to draw attention to this nocturnal predator by giving considerable significant information about its life history. Additional studies of this type were reported upon by Hutson and Austin (1924), Austin (1924), Jacobson (1936), Fernando (1952), and Bess (1956). A study of the egg laying of the closely related *L. dorsalis* was made by de Hass (1937). The work of Hutson and Austin, wherein they report that a male larva will consume 20–40 achatinas and a female larva will consume 40–60 achatinas during their development, has in particular been responsible for a

growing optimism as regards the controlling effect the larva of this beetle can and does have. Hutson himself (1920) anticipated this by announcing that it was his belief that *L. tenebrosus* was an important factor in the control of the giant African snail in India. South (1926b), Jarrett (1931), Philbrick (1949), Rees (1950), Somanader (1951), and others, including several of the author's correspondents in southeastern Asia, in the absence of further supporting evidence have continued to add to this optimism until this beetle has been given, in the minds of many, at least the greater share of the responsibility for the increasing sharp decline in the *A. fulica* populations in Ceylon.

Understandably, this whole matter headed the agenda in the author's investigations in Ceylon. Five species of lampyrids were found to be predatory upon both *A. fulica* and the endemic snails. The two most abundant were *L. tenebrosus* and an unidentified species of the genus *Diaphanes*. The other three species were considerably smaller, they were only rarely encountered, and they were not successfully reared to the adult stage and hence could not be identified. Of the two larger species, *L. tenebrosus* (Singhalese: adult is "kalamadiriya"; glowworm larva is "rabadulla") was by far the more common. In contrast to local reports, it was not restricted to the higher altitudes of the interior but was found at a few hundred feet of altitude in Mankulam in the north and Ratnapura in the south. The glowworm of *Diaphanes* sp. was found in drier environments and its ruptive coloration plus its habit of feigning death made it difficult to find. Unlike *L. tenebrosus*, the glowworms of *Diaphanes* not infrequently co-operated in their attack on the snails, as many as five being found feeding at the same time on a single snail.

In both *L. tenebrosus* and *Diaphanes* sp., the attack on the snail was initiated by stabbing and pinching with the long, ice-tongs-like mandibles. The area of attack was invariably the flesh on the left side of the foot near the base of the columella of the retracted snail. When the snail specimen was large or the glowworm was well fed, the attack was limited to the removal of a small amount of flesh in this region. In such cases, the snails would survive the attack and subsequently regenerate the lost flesh. In contrast to the report of Somanader (1951), this suggested very strongly that there was no toxic, proteolytic substance injected into the bite site, as reportedly is the case in *Luciola* (Alicata and Bess 1952). Pieces of flesh lacerated from the snail were seen to be squeezed by the bowed mandibles as one might hug a pillow. The mandibles were seen to be kept in a constant state of alternating with each other, first anterior and then

posterior, after the manner of sharpening two knives together. As this motion continued, the pieces of flesh became smaller and smaller. When no more tissue juices could be extracted, the small wad of flesh was gradually worked onto the dorsal surface of the head and then pushed aside. Once again, then, the glowworm would plunge at the equally rapidly retracting snail, remove another piece of flesh, and work it over as before. This would normally continue until all or nearly all of the snail flesh had been removed. The chances that a snail specimen would be attacked were found to be in inverse proportion to its size.

After feeding, the glowworm apparently crawls only a short distance away before curling up in some shallow refuge to digest its meal. Glowworms in this state were often found in the immediate vicinity of achatina egg masses; but there was no positive evidence that they consumed the eggs. Similarly, there was only circumstantial evidence of cannibalism among the glowworms. Moist snail "retreats" were often found to be harboring several glowworms in addition to a great many snails. During prolonged dry spells, the glowworms sought refuge under rocks and in other deeper retreats. With the advent of the rains, the snails made a noticeably quicker return to activity than the glowworms, hence giving the snails a predator-free period in which to forage. There is strong evidence that *L. tenebrosus* is not limited to the single seasonal cycle suggested by Hutson and Austin (1924). Somanader (1951) reports that the glowworm dies after a straight diet of *A. fulica*. Even when starved, full grown glowworms would not attack specimens of achatina that were larger than 40 mm. in length (Peterson 1957a).

Since 1953, the Board of Agriculture and Forestry in Hawaii has made several attempts to introduce *L. tenebrosus* in Oahu as a biological control agent (Pemberton 1957, Thistle 1957, 1959a, b). Probably the earlier introduction into Hawaii of other lampyrids (*Luciola cruciata*, *L. lateralis*, and *Colophotia praesta*) to control the aquatic snail hosts of disease-producing flukes has done much to encourage further work of this type (Alicata and Bess 1952, Fullaway 1952, Bess and Alicata 1953, cf. Lutz 1927). The first shipment of the live glowworms from Ceylon was kept under subquarantine conditions as attempts were made to rear the specimens to maturity. Eventually, all specimens died (Thistle 1953a, Weber 1954). Subsequent shipments of *L. tenebrosus* from Ceylon were made by Bess (1956). Altogether, he sent over 1,000 glowworms of this species to Oahu for immediate release. Similar shipments directed in 1955 to FOA entomologist Edgar Dresner in Djakarta, Java, were kept un-

der observation and all specimens died before they could be released. Still other shipments were sent to George Peterson, government entomologist of Guam, and during the first few months of 1955, 933 specimens were released on that island (Peterson 1957*a, b*). In October, 1958, additional releases were made on Oahu and Maui (Davis 1959). Considering the nature of the ecological conditions and the extent of the releases, it might be assumed that *L. tenebrosus* has become successfully established both on Oahu and Guam. Subsequent recoveries of specimens in the release areas in Guam lend substance to this assumption; however, to date, no recoveries have been made on Oahu or Maui.

In attempting to evaluate the possible effectiveness of this predator in the control of the giant snail, it might be kept in mind that in Area Seven of the Pallekelle division of the Pallekelle estate in Central Ceylon, both *L. tenebrosus* and *A. fulica* have been together for a minimum of twenty-five years, and yet the giant snail still remains common to abundant (Mead 1955*b*, 1956*a*).

All specimens of the lampyrid *Diaphanes* from Ceylon, intended for release on Oahu, died while under observation in the laboratory; and renewed efforts were not made to determine the value of this species as a biological control agent (Thistle 1957).

Beetles of the family Drilidae also have come into serious consideration in proposed biological control measures. The work of Desmarest (1824), Mielzinsky (1824), and Lucas (1842, 1870, 1871) brought early attention to the pronounced malacophagous¹ proclivities of the drilid beetles. According to Bequaert (1926), further observations of their biology were made by: Bellevoye (1870), Crawshay (1903), Bayford (1906), Rosenberg (1909), Schmitz (1909), and Deubel (1913). The work of Cros (1926, 1930) should be added to this list. It was not until the work of de Peyerimhoff (1914), however, that beetles of this family were known specifically to attack achatinids, at least in East Africa. The observations of Williams (1951), set forth in considerable detail, leave no doubt as to the readiness with which the drilid beetle larvae of East Africa will attack and consume the endemic achatinids, including *A. fulica hamillei*. Achatinas up to 115 mm. in length were observed to be attacked by nearly mature drilid larvae. Living specimens that were sent to Hawaii by Williams failed to multiply and consideration of their use in the biological control of the giant snail was thus abandoned (Pemberton 1954). Entering into this consideration was also the fact that the drilid life cycle is a long one.

¹ Not "malacovorous" of some authors.

In his investigations in East Africa, Williams also found that large, black, voracious beetles of the genus *Tefflus* (Carabidae), in both the larval and adult stages, would consume the giant African snail. Several live adult specimens of this beetle, along with larval specimens of drilid beetles, collected by Williams in and near Mombasa, Kenya, were sent in May, 1948, to the Hawaiian Board of Agriculture and Forestry. The announced purpose for this shipment was to enable the Hawaiian authorities to observe under subquarantine conditions the biology of these beetles so that their worth in the biological control of *A. fulica* might be ascertained (Williams 1953). N. L. H. Krauss, the entomologist of the Board of Agriculture and Forestry, made a second trip in 1951–52 to East Africa and sent back to Hawaii 107 additional live specimens of two species of *Tefflus*. At first, the larger species, ca. 45 mm. long, was reported to be *T. hacquardi*; and the smaller species, ca. 25 mm. long, was reported to be *T. carinatus* (ICCP 1952). Krauss informed the author, however, that P. Basilewsky of the Museum van Belgisch Congo, Tervuren, Belgium, has identified the larger species as *Tefflus zanzibaricus alluaudi* Sternberg and the smaller species as *Tefflus purpureipennis wituensis* Kolbe (cf. Krauss 1955). Q. C. Chock of the Hawaiian Board of Agriculture and Forestry successfully raised in cages several hundred specimens of the smaller species (Lennox 1953). The highlights of their biology have been reported upon by Weber (1954). Of particular interest is their ability to emit an irritant, when disturbed, which will burn the skin if it is not soon removed.

Unfortunately, novel research of this sort, that is, enlisting large beetles to attack, kill, and consume giant snails, has been too much for some overenthusiastic newswriters. The ridiculously humorous article of Milhon (1948, 1949) only inferred that *Tefflus* would be used against the giant snail. But other articles, for example that of Ferguson (1948), treated the matter of their release as a *fait accompli* with such statements as: “. . . and soon Guam resounded with the crunching sound of beetles dining on giant snails.” Efforts were made to correct this misinformation (Mead 1949d). At least partially in response to unrelenting pressure from the people of Hawaii and in spite of earlier decisions to the contrary, it was decided by the Board of Agriculture and Forestry in June of 1952 to release in the giant snail infestation in the Kaneohe area (three-quarters of a mile south of Mahinui) ten marked adult *Tefflus zanzibaricus* (Weber 1953). A few days later, ten more were released (Lennox 1953). The next year, twenty more were released (Thistle 1953a). During 1953 the beetles being raised in cages became less and less thrifty until

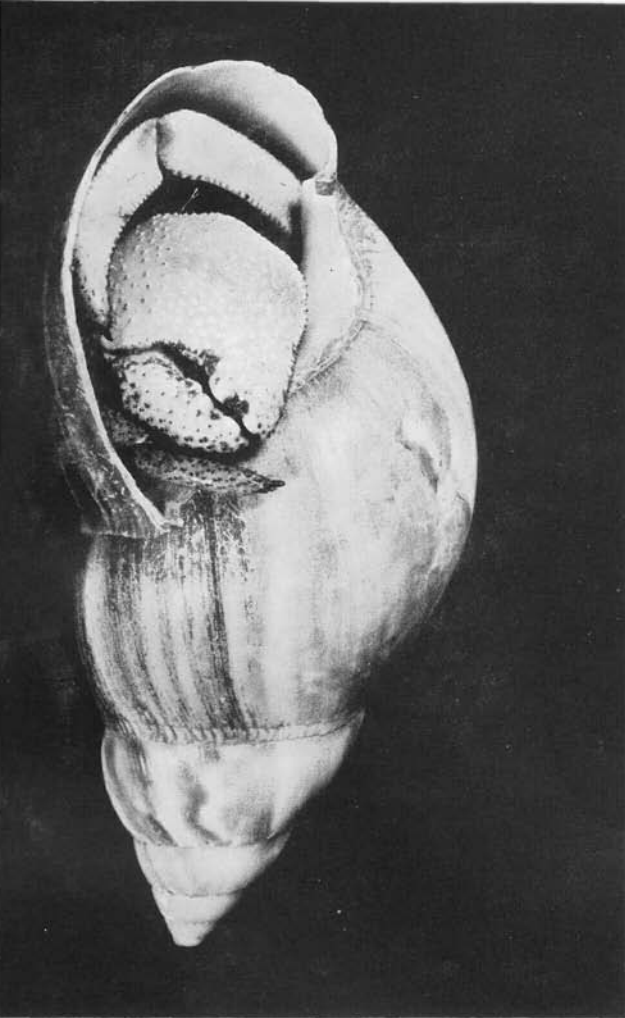


FIG. 9.—The common amphibious hermit crab of Micronesia, *Cenobita perlatus*, not only consumes the flesh of the giant snail, but adds insult to injury by using the shell of its prey as a home. Length of shell ca. 125 mm.

FIG. 10.—*Achatina fulica* from Mahinui, Oahu, Hawaii, showing multiple leuko-dermic lesions of a widespread disease found in high incidence in the older snail populations. The disease is suspected of having a viroid etiology and of being the decisive factor in the observed phenomenon of population decline.

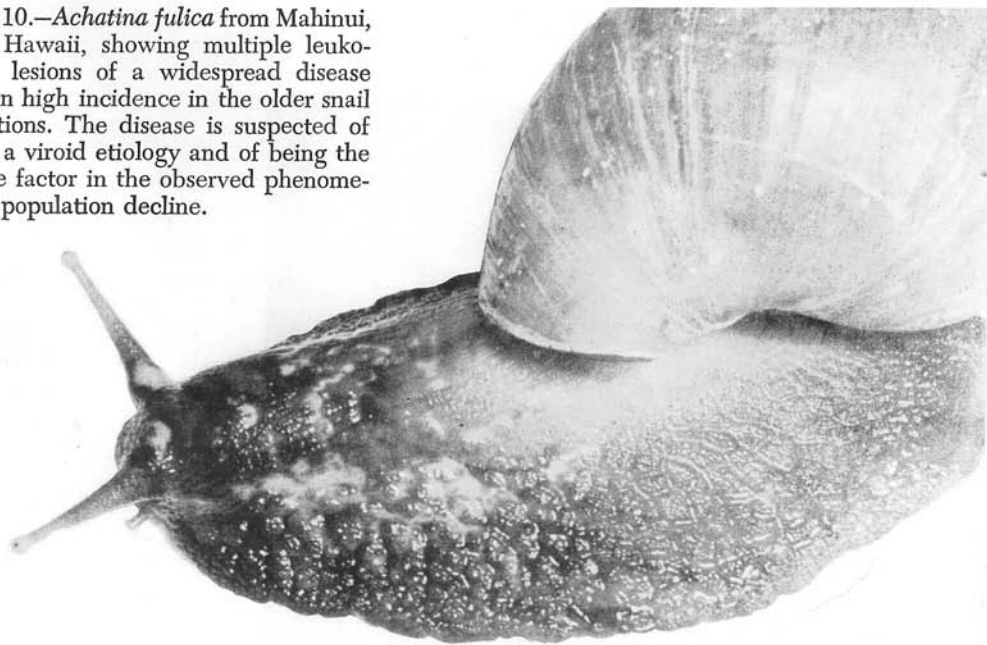




FIG. 11.—Tens of thousands of sun-bleached giant snails in this Rota tomato patch demonstrate several months' cumulative effects of clearing, poisoning with metaldehyde, and erecting a screen barrier. The live snails immediately to the left of the fence and the sparse tomato plants, to say nothing of the need for clearing away the dead shells, suggest that these combined measures have been something less than successful. (Photo courtesy of Yoshio Kondo.)



FIG. 12.—The empty shells of dead giant snails form a tempting source of lime for those that remain, particularly in areas where the soil is acid.

in 1954, it was decided to release all that remained—eleven specimens (Thistle 1954a). During the following several years, only one unmarked adult *Tefflus* was recovered (Chong 1954, Weber 1954); and it was therefore believed by many that the beetle had not become successfully established (Dwight 1955). However, in September, 1959, a second live, unmarked specimen was found (Thistle 1959b). This discovery, nearly five years after the first unmarked specimen was found, has raised new hopes in certain quarters that this beetle has been able to maintain at least a beachhead population. Arrangements have been made with Richard LePelley, senior entomologist of the Department of Agriculture in Nairobi, Kenya, to make additional large shipments of *Tefflus* to Hawaii for immediate liberation in the expectation that they will eventually become firmly established. An earlier tentative decision to introduce *Tefflus* concomitantly with the predatory snail *Gonaxis* in the experimental island of Agiguan was fortunately postponed, in spite of the fact that it was done in Oahu.

More recently, the giant carabid beetle *Damaster b. blaptoides* Kollar from Fukuoka, Kyushu, Japan, has been considered a possibly more suitable predator for achatina because of its spectacularly large size. Specimens under observation in 1958 in Hawaii avidly consumed larger snail specimens than *Tefflus* could manage. On July 3, 1958, fifty specimens were released on the Old Pali Road in Oahu and on July 9, 1958, twenty-five specimens were released in Haiku, Maui. Forty-six specimens of the closely related *D. b. rugipennis* Motchulsky from Sapporo, Hokkaido, Japan, were released on Tantalus, Oahu, on July 28, 1958. Although it is still too soon to determine whether or not establishment has taken place, it should be kept in mind that these beetles come from a temperate zone and the Hawaiian climate may prove inadequate for breaking the diapause. The same may be offered as an explanation for the fact that *Scaphinotus striatopunctatus* (Chaudoir) and *Scaphinotus* sp. from California have not been recovered since their release on Oahu in November, 1956. It is probably too early to determine whether or not specimens of an unidentified species of *Tefflus* from the Congo and *Thermophilum hexasticum* Gerstaecker from Kenya have become established since their release in October, 1956, and May, 1957, respectively (Thistle 1959a).

But, even at this early date, both *Tefflus* and *Damaster* already have become involved in other aspects of the over-all biological program. *Tefflus* is a night feeder, as is its snail prey. This is good. But the introduced toad, *Bufo marinus* is also a night feeder and it

is particularly fond of beetles. Is this the reason why *Tefflus* has been recovered only twice in five years in the release areas? *Damaster* should escape this threat, as it is a day feeder; but at that time, the giant snails characteristically retreat to the tree trunks out of harm's way. It has been suggested that an excessive immediate scattering of a released biological control agent may preclude its establishment. In an effort to offset this, *Damaster* was released in Oahu in a sizable inclosure. The introduced mongoose is also a day feeder and in addition is fond of beetles. One got into the inclosure and put a finish to the experiment. Perhaps the mongoose did a better job on *Tefflus* and *L. tenebrosus* than it did on the rats, for which it was introduced to control. But, as will be shown below, both the mongoose and the rat will consume the giant snail and probably other species, including the introduced predatory snails, for which they may have a preference!

The advisability of releasing any predatory beetle, as will be seen below in the discussion of the predatory snails, is still problematical and therefore pretty much of a controversy. The experiments in rearing *Tefflus* in Hawaii have been carried on for only a relatively short time and have revealed little more than the fact that these beetles can be reared in captivity with difficulty. The extent to which they are possibly effecting a control of achatinas in East Africa has not been determined in the slightest. Even though it can be reasoned that the cause for the achatinas being less abundant in East Africa might rest in the fact that there are also at hand predatory beetles and predatory snails, it is as risky as it is unscientific to reason a priori that the introduction of these predators elsewhere will produce similar results and that therefore introductions are justified in the absence of experimental confirmation. There is already evidence that although the predators do not manifest a high prey-specificity, they do show a preferential selection in what they will attack and consume. The fact that the drilid larvae will apparently more readily attack the East African predatory snails (*Gonaxis* and *Edentulina*, *vide infra*) than they will the achatinas (Williams 1951, Krauss 1951) warns that in a similar fashion, introduced predatory beetles might consume the endemic snails, or even some other invertebrate, in preference to *A. fulica*. Thus a new problem may be created in addition to the unimproved original one. In a partial answer to this problem, the information has been offered that both adult and larval *Tefflus purpureipennis* not only seem to show a preference for *A. fulica*, but they have little proclivity for climbing trees, thus giving a certain degree of immunity to such important endemic, arboreal

genera as *Partula* and *Achatinella*. It should be recalled at this point, however, that it was *T. zanzibaricus*, not *T. purpureipennis*, which was released in Hawaii. In reference to this specific matter, Kondo (1951*b*) has pointed out that what is of infinitely greater significance is the danger to such terrestrial gastropod families as Amastridae, Endodontidae and Zonitidae.

Small, unidentified lampyrid beetle larvae were seen by Williams to feed on quite small and newly hatching achatinas; but their quick dismissal from all but a brief mention suggests that they cannot or are not to be considered in a biological control program. Krauss (1951) similarly gives them only a slight mention in the reports of his East African investigations. A very detailed account of the feeding habits and life history of this type of beetle is given by Newport (1857). A quite common coprine beetle (Scarabaeidae) in East Africa was observed by Williams to frequent the sites of dead achatinas; but since it was only the disintegrating snail flesh which attracted the beetles, they were obviously not a factor in biological control.

Birds The work of Kleiner (1931, 1936) has demonstrated the fact that examination of bird stomachs on an extensive program may show snail remains not only in a majority of cases, but in a great many different avian species. Further, he interestingly demonstrated that in spite of the high frequency of appearance, snails bulk small in the total content of the stomachs (2.69 per cent). Similarly, McAtee (1918) found that mollusks formed only 5.73 per cent of the total food intake of the mallard, and Collinge (1921) found that they formed 6.5 per cent of the animal food ingested by the starling. From these one cannot safely conclude that birds in general find snails uninteresting; for not just the relative degree of appetite for snails but the general availability of snails would determine the percentage consumed. Actually, Kleiner's most important finding is that a wide variety of birds will consume snails, notwithstanding the fact that in some cases the snails may have been taken into the digestive tract accidentally. But this conclusion is independently reached when one surveys the vast literature that has accumulated especially in the past century on the subject of birds consuming snails. In discussing the natural biological control factors of the pestiferous *Theba pisana* in Italy, de Stefani (1913) lists crows, magpies, and owls. To this list, Basinger (1927) in California added the Hudsonian curlew, pigeon, English sparrow, chickens, and ducks.

The domesticated duck has the reputation of being the most avid consumer of snails (e.g., cf. Paños Marti 1952). In fact, there is in correspondence and in the literature the persistent report (e.g.,

South 1923*b*, Jarrett 1931) that the giant African snail was transported into uninfested areas, especially in Malaysia, with the intent that they would provide suitable food for ducks. Just the reverse process is concurrently being undertaken; that is, the ducks are being enlisted in local control measures to keep down the population of the snail. G. A. S. Barnacle (*in litt.* Jan. 15, 1950) states that ducks were "introduced" in this manner in various areas in Ceylon. Essentially the same report was given by R. C. L. Notley (*in litt.* Dec. 5, 1950) with the addition that some ducks got pieces of snail shell stuck in their throats. In Thailand, Ariyant Manjikul (*in litt.* Feb. 14, 1952) states that the giant African snail makes "very good feed and the duck raisers collect them" for this purpose. A similar report comes from Guam (Peterson 1957*b*). In Singapore, R. E. Dean writes (*in litt.* Jan. 17, 1952) that he has been informed that the common practice there is to allow the local strain of domestic ducks free range over the compounds and that they will attack the giant snails with gusto. In that same region, A. F. Caldwell gives supporting evidence (*in litt.* April 23, 1953) in the following statement: "I used to keep a few ducks and fed them a number of these [giant African] snails daily as part of their diet. If the shells are broken ducks eat the snails with obvious relish." A similar report is made by Jaski (1953). The practice of using ducks in an attempt to control *H. aspersa* in California citrus groves, according to Lewis and LaFollette (1941), proved to be of "some value," but it was not recommended. On the other hand, Hely (1946) recommended it as "excellent." In flower and vegetable gardens, however, the ducks may cause more damage than the snails, especially if succulents and seedlings are present.

Not only ducks, but chickens will feed on achatinas (Hutson 1920, South 1926*b*). Lang (1919) also observed this in the Congo. The larger, thick-shelled specimens, however, are not effectively attacked by either ducks or chickens unless they are crushed (van Weel 1949). In South Africa, Joubert and Walters (1951) report that turkeys as well as ducks will eat large numbers of the serious snail pest *T. pisana*. The utilization of the giant snails as a food supplement in poultry has been treated in detail below, under the discussion of control through human use.

As early as 1911, Green proposed the idea that insectivorous birds might be important in controlling *A. fulica*. South (1926*b*) and later Philbrick (1949) announced that *Centropus chlororhynchus*, the "jungle crow" (also called "pheasant crow" or "cockoo") attacks and consumes the giant snail in Ceylon. This was recently verified by the

author during field observations in Ceylon. In areas frequented by jungle crows, shells with characteristic damage were commonly encountered. Of 98 live *achatina* specimens examined on the Warriapolla estate near Matale, 9 (9.2 per cent) were found with diamond- or triangle-shaped wounds. These indubitably were caused by bird pecks. Even in the cases of extensive trauma, tissue regeneration was sufficiently advanced so that it seemed apparent that the snails would survive. Keeping them under observation in the laboratory confirmed this assumption. An explanation for their escaping fatal injury seems to be found in the words of E. Phyllis (*in litt.* Dec. 11, 1950), who states that he has seen the jungle crow in Ceylon hunting for the giant snail for hours on end and that it does not consume more than a part of the snail after it finds one. Introducing the jungle crow into a non-endemic area as a biological control agent to control the giant African snail is completely counterindicated; for this bird is a foraging rogue with the strongest raiding and robbing proclivities, eating in particular the eggs and young of ground-dwelling birds.

Krauss (1952) reports that in the northwestern part of Madagascar, a large native bird, the famakankora ("snail-breaker"), *Anastomus madagascariensis* (Ciconiidae), is said to feed on *achatina* and other animal food. It may have been the anvils of this type of bird which Jaski (1953) saw in South Africa. He reports that scores of *A. achatina* were found hammered to smithereens.

Observing the snail-eating habits of some of the larger birds has persuaded a few people to recommend introducing them into areas infested with the giant African snail. R. S. Gardiner states (*in litt.* Nov. 22, 1949) that in Chile the thick-kneed plovers or so-called "queltehue" birds (*Burhinus superciliaris*), kept in inclosed gardens by clipping their wings, are exceedingly effective in removing all sorts of terrestrial mollusks. Her suggestion that they be used in controlling *A. fulica*, however, is no more practical, for several obvious reasons, than Eyerdam's recommendation (1952a, b) that the New Guinea bush hen or bush turkey (*Megapodius* spp.), the rhea (*Rhea* spp.), and the cassowary (*Casuaris* spp.) be used. With Eyerdam's suggestion in mind. It was of more than passing interest to read in a recent list of offerings of a dealer in live animals that a cassowary could be purchased for a mere \$3,000! Gressitt (1952) and others have reported megapode birds on some of the western Pacific islands (e.g., the northern Mariana Islands) which are not infested with the giant snail. It is possible, though, that both snails and megapodes

have come together in some of the Palau Islands. This is a matter distinctly worth investigating.

Crabs In Micronesia, the ubiquitous hermit crab, *Cenobita perlatus* Edwards (called "humpa" by the Bonin Islanders) has been observed (Mead and Kondo 1949, Mead 1950*b, c*) not only occupying as high as 21 per cent of the empty *A. fulica* shells encountered in beach populations but actually consuming the live snail by pinching off small pieces of the flesh with the chelae. This species spends long periods of time on land; specimens were found in Chichi Jima at an altitude of approximately six hundred feet and over one and a half miles from the nearest seashore. There is, however, an apparently geometrically progressive reduction in their numbers in an inland direction. Even in achatina shells abandoned by the hermit crab, there are unmistakable evidences of their work. The shell becomes highly polished, not just on the underside but all over, due to the rough treatment it gets; and invariably the columellar surface of the ultimate whorl is characteristically abraded away, making more room for the hermit crab. Wilson Savory of Chichi Jima stated to the author that he released half of a flour sack of small achatinas on the tiny island of Higashi Shima, just off the northeast coast of Chichi Jima in 1942. He said that when the island was visited again the following year the hermit crabs were found to have taken over the achatina shells entirely.

A mysterious "achatina-free" area, approximately three-quarters of a mile long and at least five hundred feet wide, bordered by dense populations of *A. fulica* along the east coast of Rota, proved upon examination to be nothing more than a region where the hermit crabs were completely dominant (Mead 1950*b, c*). Conditions along the adjacent coast seemed to be particularly favorable for hermit crab reproduction and existence, and the recent immigrant *A. fulica* had not yet successfully invaded and infiltrated that region. Burning-over the land to plant watermelons, had apparently neutralized the area; but the hermit crabs had relatively rapidly reinvaded the area and kept it free of live achatinas. Paradoxically, the hermit crabs caused greater damage to the melons than did the achatinas; and yet it was the snails which were indirectly responsible for this damage as it was their abundant empty shells that provided vital protection for the soft bodies of a greater population of hermit crabs than otherwise could have built up. A brief reinspection by Kondo (1952) of this achatina-free area and two other similar areas on Rota, emphasized the need for a thorough ecological study to determine what decisive factors are actually operative.

So far as can be determined, no other endemic predator in Micronesia, with the possible exception of the coconut crab, produces a greater kill of the giant snail. Even so, the effect upon the snail population is undoubtedly a minor one, except in localized beach areas or on relatively small islands, where the hermit crabs may have a decimating or even exterminating effect. Davis (1954) concluded that "*Cenobita* was not a predator of *Achatina*." This conclusion, however, was based to the largest extent upon the undependable behavior of caged specimens. Somanader (1951) describes and pictures unidentified hermit crabs which take over the shells of *A. fulica* in the Kalkudah beach area of eastern Ceylon; but he does not suggest that there is predation.

On the island of Auluptagel (Aurapushekaru) in the Palau group, there was found a large, conspicuous cave of a robber crab or coconut crab (*Birgus latro* L.) on the slope of a hill. Well over fifty broken shells of *A. fulica* were found strewn three to four feet below the opening of this cave. Sharp, angular breaks in the very thick, large shells clearly indicated that these had been broken open by the coconut crab. The characteristic droppings gave further convincing evidence. The coconut trees have become virtually extinct on this island because of the work of the introduced coconut beetles (*Oryctes rhinoceros* and *Brontispa mariana*), and it seems obvious that the coconut crab has had to turn to some other source for its food. It is a curious thing that the introduction of beetle pests has predisposed to the destruction of a snail pest! Kondo (1952) reports that on Agiguan, this crab and the rats together kill more than twice as many giant snails as does the predatory snail *Gonaxis*. Direct and indirect evidence of the consumption of achatinas by this crab were reported upon by Davis (1954). Because the coconut crab is so highly prized as an article of food and therefore diligently hunted for by the Micronesians, and because the eating of snails by the coconut crab is only incidental in its catholic diet, *Birgus latro* unquestionably has but the smallest part in the biological control of *A. fulica*.

An unidentified land crab in the Diani Beach area of Kenya was observed by Williams (1951) to consume live achatinas; and, in at least one case, the snail was considerably larger than the crab. Its predation, however, is apparently limited to the peripheral beach zone. Darteville (1954) tentatively identifies this crab as belonging to the genus *Ocypode*.

The so-called "paddy crab" was reported in several instances to feed on the giant snail in Ceylon. Although this was not verified in

the field, it is altogether possible that this crab is of some local, minor value as a biological control agent.

Flies Sarcophagids, sciomyzids, phorids, and other diptera have been reported by a number of observers to come from the dead bodies of various land snails. In by far the majority of the cases, it has been established, or very strongly suggested, that the fly larvae are saprophagous rather than parasitic. And in only a very few instances (e.g., Rostand 1920, Mercier 1921, Mokrzecki 1923, Berg 1953, 1955, Muma 1954, 1955) has there been more than circumstantial evidence of a possible normal parasitic role. Keilin (1919, 1921), Séguy (1921, 1935), Bequaert (1925, 1926), and Pelseneer (1928) have made the major contributions and have surveyed the literature for reports on the general subject of diptera-mollusk associations. With the exception of those that concern the giant snails, more recent works which should be mentioned are those of Bhatia and Keilin (1937), Lopes (1940), Metteo (1946), Berg (1953, 1955), and Muma (1954, 1955). A. R. Main of the University of Western Australia is conducting significant investigations of dipterous parasites which he has reared from the endemic land snails *Bothriembryon* spp.

Muma in particular has done a significant piece of work on the biological control factors apparently operative in keeping down the numbers of a presumed "beneficial" tree snail in Florida citrus groves. He reports that dipteran parasites are the most important agents in reducing the snail population. His rearing experiments convinced him that he had found true parasites and not just saprozoites. From the "parasitized" snails, he raised four sarcophagids, one phorid, and one chloropid, viz., *Sarcophaga lambens* Wd., *S. morionella* Ald., *Johnsonia elegans* Ald., *J. cf. frontalis* Ald., *Megaselia* sp., and *Hippelates dissidens* (Tuck.). As a complication he found that some of the sarcophagids were being attacked, but apparently not seriously, by the epiparasites *Aphaereta auripes* (Prov.) and *Melittobia* sp.

The wingless phorid flies of the genus *Wandolleckia* were apparently first observed on achatinas by Cook (1897) in Liberia, where he saw them running about on the surface of living *Achatina variegata* (i.e., *A. achatina*). The following year, Wandolleck offered the suggestion that the flies feed on the slime of the snails. Bequaert (1919) not only supported this suggestion but advanced the idea that they are perfectly harmless to the snails. He gave further information on the history and biology of this species (*W. achatinae*) and in subsequent papers (1925, 1926), he discussed two other species of this genus, viz. *W. indomita* and *W. biformis* (cf. also Pilsbry and Be-

quaert 1927:472; Brues 1907). The latter species has been shown to live on *A. rugosa chapini* (Bequaert and Clench 1934). Baer (1952) considers the "commensal" *W. biformis* synonymous with *W. achatinae* and reports finding it on *A. achatina* L. and *Archachatina ventricosa* Gould in the Ivory Coast, Liberia, Cameroons, and the former B. Congo. Rodhain and Bequaert (1916) reported a number of larvae of *Mydaea bivittata* Macq. devouring the achatinid *Burtoa nilotica* Pfeiffer.

As far as can be determined, Senior-White (1924) was the first one to report phorid flies from *A. fulica*. These, which were bred from a dead snail, he described as new—*Megaselia achatinae*. Brues (1942) has suggested that it is possible Senior-White actually had the ubiquitous *Megaselia xanthina* Speiser. It was this latter species which Smedley (1928) in Malaya bred from the eggs of *A. fulica*. Because he reports the flies as being capable of producing human intestinal myiasis, Smedley emphasizes the public health implications rather than those of biological control. The phorids bred from a dead specimen of *A. fulica* in Hawaii by Yoshio Kondo were described by Brues (1942) as new—*Megaselia biformis*. At that time, Brues advanced the suggestion that in spite of the lack of experimental evidence, some of the phorids "may be true internal parasites of living snails."

In 1949, Van Emden reported *Ochromusca trifaria* Bigot to attack *A. craveni* E. A. Smith at Fort Johnston, Nyasaland. Captain W. A. Lamborn, the collector of the specimens at Fort Johnston, later reported to Krauss (1951) that the flies were bred from dead snails and had not been observed to come from live individuals. This report removed earlier optimism about the fly being of use as a biological control weapon.

An unidentified fly is described by van Weel (1949) as being a possible parasite of the eggs or young of *A. fulica* in Java. The weak spot in his evidence is that, despite the fact that the "narrow cleft" in the breeding container was not wide enough to permit the adult fly to enter and lay eggs, it was certainly sufficiently wide to allow oviposition within the container at the site of the cleft. Hence it is not possible to determine whether or not the fly larvae had access to the snails or eggs before death from some other possible cause. Hardy (1952) later announced that it was a new species of the phorid genus *Pericyclocera*.

A slightly larger phorid was commonly encountered by the author in the giant snails in Ceylon. Specimens were sent for identification to the British Museum, through the Commonwealth Institute of Entomology. According to D. E. Hardy (*in litt.* April 18, 1956), these

are being described by C. N. Colyer as a new species of *Spinophora*. Under the many circumstances in which these flies were observed, there was never evidence of anything but a saprozoic role with respect to both the endemic and the giant snails. Snails killed in the laboratory would attract in a few hours numerous phorid flies from the nearby bush. Snails killed and being fed upon by the glowworm were observed to contain at the same time female flies busily laying eggs in characteristic patterns on the lip of the shell. Typical larvae were found in insects which had been killed and allowed to decompose. It has been suggested that these phorid flies may be implicated in the transmission of a disease in *A. fulica* (Mead 1956a).

In Saipan, Lange (1950) reared *Sarcophaga gressitti* Hall and Bohart and *S. dux* Thomsen from dying and dead *A. fulica*. Near Diani Beach, Kenya, East Africa, Krauss (1951) found fly larvae and pupae in the shells of *Achatina* "in which the snails were dead and decomposing, and often reduced to a black foul liquid." These were later identified by Van Emden as: *Aethiopomyia steini* Curr., *Alluaudinella bivittata* Macq. (Muscidae); *Sargus* sp. (Stratiomyidae); and *Discomyza similis* Lamb (Ephydriidae). In the same area, Williams (1951) was able to find species of the muscoid genera *Sarcophaga*, *Panaga*, and *Aethiopomyia* in only the dead or dying achatinas. Other saprophagous but unidentified flies were observed on dead achatinas by Pangga (1949) in the Philippines. The large maggots of filth flies were not uncommonly seen by Kondo and the author in several of the islands in Micronesia and especially in the Bonin Islands; unfortunately, a tightly packed itinerary did not permit rearing them for identification. There was, however, absolutely no discernible evidence of parasitism in any of the thousands of snails specimens examined. Krauss similarly found no evidence of dipteran parasitism in his investigations in Kenya, Zanzibar, Tanganyika, and Madagascar.

Recent initial efforts to use *Johnsonia elegans*, which attacks *Drymaeus* in Florida, and a Tetanocerid fly from New York in the biological control of *A. fulica* in Hawaii have failed completely (Thistle 1959a).

Helminths There has been found in the literature no report of helminths of any type being found in the achatinid snails. Pilsbry and Bequaert (1927:472), Pelseneer (1928, 1935), and Adam and Leloup (1943) refer to records of helminths being found in other gastropods. The work of Chitwood and Chitwood (1934) is valuable in that it lists the nematodes encountered in gastropods. An unidentified rhabditoid nematode was encountered by the author during

the examination of the lower one-quarter of the intestinal tract of several specimens of *A. fulica* in Ceylon. However, all evidence suggests that this worm is only an incidental symbiont of low incidence and little consequence. Dying specimens of *A. fulica* found in 1957 in Maui, Hawaiian Islands, by Lew Akaka, were discovered to contain many nematodes; but, in the highest probability, these were saprophagous and not parasitic. Actually the whole subject of gastropod helminthiasis has been seriously neglected and it is hoped that in the near future attention will be given to it by qualified specialists.

Mammals As in the case of bird stomach examinations, the contents of the stomachs of a great many species of mammals have been found to contain the remains of terrestrial or aquatic snails. Without much question, by far the larger share of such cases clearly represent incidental, accidental, or subsistence consumption of the snails. It therefore would be as pointless as it would be misleading to attempt to compile an exhaustive list of mammals known to have consumed snails at one time or another and offer it as a list of the mammalian enemies of snails. There are however certain mammals which have a manifest appetite for snails. Chief among these probably is the shrew (Hamilton 1930, Ingram 1942*b*, 1944), which Clench (1925) brands as one of the worst enemies of land mollusks. Significantly important among the others are: rabbits (Lawson 1929, 1930, Oldham 1929*b*, Wright 1909), mice (Coghill 1909), and rats (Adams 1938, Hoffman 1936, Lawson 1920*a*).

Of the mammals mentioned so far, only the rat has been linked definitely with *A. fulica*. Meer Mohr (1935) illustrated damage to giant African snail shells which was suspected to be caused by rats or birds. Abbott (1951*c*) and Williams (1951), similarly cautious, implicate the rat. The survey in Micronesia conducted by Kondo and the author, however, removed all doubt. Rat nests containing the chewed remains of *A. fulica* shells were found in one or more instances in Guam, Chichi Jima, Haha Jima, and Tinian. In each case, the shells were numerous, fairly small in size, and showed unmistakable evidence of rat work. Numerous arcuate shell flecks in the nest debris indicated that the shells were brought to the nest before being eaten. As the entire columella was destroyed in many specimens, it is probable that all of the soft parts were removed. In northern Saipan (Magpi) two instances were witnessed where rats were feeding on crushed achatinas on the road; but the rats were emaciated and apparently using the snails for subsistence. After considerable field study, Kondo (1952) concluded that on Agiguan the rats are more effective predators of the giant snail than the experimentally introduced carnivo-

rous snails. The report of Davis (1954) was in sharp contrast. However, it is felt in general that, with certain fairly clear-cut, localized exceptions, the over-all controlling effect the rats have on the giant snails is relatively minor. On the contrary, the giant snails are often to be considered contributory to the rat problem by providing themselves as an additional source of food. As an ironic twist, the giant snails on Guam contributed still further to the rat problem by consuming with apparent impunity the warfarin bait intended for the rats (Peterson 1957b).

The omnivorousness of domestic pigs suggests correctly that they will consume the giant snails and that their foraging near habitations provides some small measure of control. South (1926b) lists the wild pig among the enemies of *A. fulica*.

The mongoose, *Herpestes mungo*, is said to eat the giant snail in Ceylon (Philbrick 1949, Rees 1950). While the author was in Ceylon, a great deal of circumstantial evidence was collected implicating this predator in the destruction of achatinas. For example, on several occasions freshly broken snail shells and partly consumed snail carcasses were found in the immediate vicinity of burrows which the local inhabitants declared were those of the mongoose. Equally often, piles of broken shells were found scattered around a prominent rock indicating that the mongoose had used the rock as a "hammer stone." Some of the shells were remarkably broken almost exactly longitudinally. The hepatopancreas or "liver" of the snail not infrequently was left untouched, suggesting that it was distasteful or at least less appetizing than the rest of the snail carcass.

In numerous instances in the field in Ceylon, there were found shells which had been flecked open, hence indicating that they had been attacked by a small mammal of some sort. Informants stated that rats, both the "wild" type and the introduced type, were known to eat the giant snails. In other cases they stated that it was the giant squirrel, "Dondolena" (*Sciurus macrurus* Pennant). In still other cases, for example on the Godahene estate near Kalutara, there was the strongest evidence that it was the Bandicoot, "Uru-miya" (*Bandicota malabarica*) which was breaking the shells and eating the snails.

The "mongoose" of East Africa to which Abbott (1951c) refers is quite probably the civet cat, *Bdeogale tenuis* and *B. crassicauda*, whose snail-eating habits are interestingly described by Williams (1951). The jackal in Ceylon (Philbrick 1949, Rees 1950) and the baboon in East Africa (Abbott 1951c) are also reported to eat the giant snail. In Ghana, an endemic wild cat, referred to by the natives as "odompo," is believed to feed on giant snails. Since the snails are

an important food item to the natives, the "odompo" is hunted and killed at every opportunity. And as an interesting elaboration, a snake—the deadly horned *Cerastes*—is known to attack the "odompo" and has been seen in the company of the giant snails; it is therefore believed by the natives to be the protector of the snails (Martinson 1929).

The large musk shrew, *Suncus murinus* (L.) became established on Guam in 1953 and in two years' time it had spread considerably (Peterson 1959). For a time, it was hoped that this predator would prove to be a potent new biological control agent in the battle against the giant snail; but field and laboratory observations indicated that there was little hope for anything of this sort (Peterson 1957b).

As a strange effect of mammals on snails, Peterson (1954) and Davis (1954) report that the great many feral goats on Agiguan Island are apparently responsible for killing and injuring the giant snails by trampling and crushing them as they get under foot.

Micro-organisms The most neglected aspect in the problem of the giant African snail, and in fact in the entire field of malacological biology, is the study of the role of micro-organisms in molluscan symbiosis and pathology. A search of the literature reveals few references indeed on this important subject, and none of these concerns a virological investigation. The work of Drz (1913), which has not gone unchallenged, reports the presence of bacteria in special cells between the kidney and stomach in *Cyclostoma*. Wurtz and Gray (1939) found in the intestine of *Triodopsis albolabris* what appeared to be eight new species or varieties of bacteria belonging to the genera *Escherichia*, *Alkaligenes*, and *Bacillus*. Edward Steinhaus recently reported to the author that in France an *Aerobacter* infection in colonies of commercially raised *Helix*. Pan (1956) found in tissue sections of the freshwater snail *Australorbis glabratus* an obligate, intracellular, acid-fast bacillus in various organs of the body, and a "fungus spore or yeast-like agent" in the nervous tissue. Spirochetes were found by Fantham (1921) in the hepatopancreas of South African pond snails; their role however was not determined. Dartevelle (1954) similarly reports the spirochete *Borrelia* in the hepatopancreas of 10 per cent of the achatinas examined in a study in the Congo.

For an early basic work on the protozoa of snails, one should turn to that of Kühn (1911). Pelseneer's survey of this portion of the literature (1935) brings the subject more nearly up to date although he does not mention the work of Hegner and Chu (1930), wherein

the ciliate *Balantidium haughwouti* was reported to be found in Philippine fresh water snails. More recently, the species of the sporozoan genus *Klossia*, found in the kidneys of several genera of snails and slugs, have been discussed by Nabih (1938). The contributions of Kozloff (e.g., 1946) on the mastigophoran symbionts of gastropods stand out among the best in this whole field. The mastigophoran *Trypanoplasma isidorae* and an amoeba have been reported from the seminal receptacle of the pond snail *Bulinus (Isidora) tropica*; undescribed amoebae were also found in the slug *Arion fuscus* (Fantham 1923, 1925). As far as can be determined, the only protozoan (and, for that matter, the only micro-organism) that has been described from the giant snails is *Trichodina achatinae* found in the seminal receptacle of *Achatina zebra* (Fantham 1924, Fantham and Robertson 1927); and, although it has been referred to as a "parasite," there is not at present sufficient experimental evidence to warrant such a classification. At two different times, diflagellate protozoans were found in smears of the intestinal tract of *A. fulica* in Ceylon; but contamination could not be ruled out as a possible explanation for their presence. There was absolutely no evidence of pathogenesis.

Gain (1896) refers to Laurent's work wherein the eggs of *Dero-ceras reticulatum* are claimed to have been found infected with a fungus even before they were deposited. The more careful work of Tervet and Esslemont (1938) revealed the fact that the eggs of this slug were infected with the fungus *Verticillium chlamydosporium* Goddard. Even though they felt that this fungus exerted "a strong natural control" of the slug, they considered "impracticable" its use in biological control. The significantly high percentage of infection in the eggs which they collected in the field might find an explanation in the possibility of a sequela of fungous infection subsequent to mechanical injury to the eggs during field collecting and transporting to the laboratory. It is at this instant apropos to point out that Lovett and Black (1920) found fungous diseases "particularly active and virulent" in their breeding cages of slugs; but their field observations indicated that such diseases were "of minor importance under natural conditions."

In looking back over the reports extant in the field of malacological microbiology, it is immediately apparent that the surface of the multifold problems has hardly been scratched. In most cases, the reports have been made by investigators unqualified to do definitive work in microbiology. Hence, if the organism is identified at all, the identification is still very much open to question, as is the particular type of symbiosis (*sensu lato*), that is, whether it is commensalism,

mutualism, or parasitism. Or, for that matter, even the possibility of the association being incidental, accidental, or contaminatory in nature seems hardly or not at all to have been considered. For the problem at hand, however, there is needed not only the information that parasitism exists but that a pathogenesis per se is detectable. Then an investigation of such problems as mode of transmission, epizootiology, methods of culture, possible epiparasitic contamination, and introduction into the field can be undertaken. It is obvious that there is still a long way to go in this phase of the investigations; this notwithstanding, in the long run it will probably prove to be the most practical, productive, and revolutionary method of control. In fact, the possibility of a spontaneous biological control of the giant snail rests almost completely in the field of microbiology.

The possible role of micro-organisms in the so-called "diseased snails" and in the phenomenon of "decline" is discussed under the proper headings below.

Mites Anyone attempting to raise snails or slugs may all too soon find the specimens infested with small, swarming mites. As was the author's experience in raising the giant slug *Ariolimax*, the mites can become so abundant that they even interfere with normal locomotion and feeding. Banks (1915) made early, inconclusive observations on malacophilus mites.

André and Lamy (1930, 1931) have given us our only comprehensive work on the mites of mollusks. There are no known records of mites being found on *A. fulica*. But Bequaert (1925, 1926; Pilsbry and Bequaert 1927:472) reports an unidentified, "ecto-parasitic" mite on a live achatina in the former B. Congo; he also cites from that same area, Stuhlmann's records of mites on *A. schweinfurthi* and *A. stuhlmanni*. Nothing is offered as to the possible parasitic effects upon the snails; however, Turk and Phillips (1946) in their monograph of the slug mite *Riccardoella limacum* (Schränk) (i.e., *Ereynetes limacum*) give convincing evidence that mite and mollusk live together in commensalism of a fairly high order. Baker and Wharton (1952) support this interpretation. On the other hand, a closely related species is believed to be at least contributory to an unthrifty, malformed condition in *Arianta arbustorum* (Oldham 1934). Simroth and Hoffmann (1928) list from the literature a questionable record of the tick *Amblyomma variegatum* being found on the achatinid *Limicolaria adansoni*.

Reptiles In the former B. Congo, the large monitor lizard *Varanus niloticus* (Linne) has been observed by Lang (1919:55) to feed principally upon half-grown achatinas. This observation was

supported by Pilsbry and Bequaert (1927:473) and elaborated upon with the information that the stomach of one specimen was found to contain four large snails. They quote from Schmidt, who earlier pointed out that the teeth of *Varanus niloticus* are adapted for crushing snails. Species of this reptilian genus occur endemically or have been introduced on a number of the snail-infested islands of the Pacific (Loveridge 1945). There has been no adequate examination of the stomach contents of these lizards to determine the extent to which they are feeding upon *A. fulica*. As far as is known, the only studies of the feeding habits of this lizard in the Pacific area are those of Kondo (1952) and Davis (1954); but, unfortunately, negative stomach contents in two specimens and the reluctance of two other captive specimens to feed on achatinas cannot be considered anything but inconclusive. It has already been pointed out however that the lizard, because of its appetite for young chicks and eggs, presents a fair threat to poultry, especially where other food is not available (Mead 1949d). This has caused Eyerdam (1952a, b) to conclude that *Varanus* in the Pacific is at best pretty much of a neutral value. Nor does the fact that the lizard will readily consume the coconut crab (*Birgus latro*) materially change the picture; for, although the crab is a pest of the coconut palm, it will attack and consume the giant snails—undoubtedly far more than will the lizard. But with the recent announcement that the lizard will consume the grubs of *Oryctes rhinoceros* (L.), which is in many respects the most serious agricultural pest in the Pacific, the scales seem to be tipped very much in the favor of *Varanus* (Gressitt 1952). Although *V. monitor* and *V. salvator* were commonly encountered in some snail-infested areas of Ceylon, there was no evidence that they were anything more than of incidental value in controlling the giant snail.

The only chelonian known to attack *A. fulica* is the pond turtle *Nicoria trijuga thermalis* of Ceylon (Green 1911b). During the author's investigations in Ceylon, it was determined that because of the strongly aquatic affinities of this turtle, it was essentially of no value as a biological control agent.

Recently, Vianney (1953) reports that a small Javanese snake *Pareas c. carinatus*, in captivity, fed frequently on very young achatinas, swallowing them shell and all, although somewhat older specimens were "seized in a peculiar way and . . . extracted from their shells by the freely moving mandibles."

Snails In spite of the fact that *A. fulica* will readily and even avidly consume the flesh of injured, dying, dead, and even putrifying individuals of its own species, there is absolutely no evidence of

predation per se. Even the eggs and delicate young are apparently completely safe in the presence of larger individuals. Green (1911*b*) was the first to emphasize this point; and it should be re-emphasized here so that it will be understood that except for competition for food, the giant snails do not provide any direct limiting factor among themselves. It is of real interest to note, however, that an injured or dying snail has a very positive attraction which brings out the latent cannibalistic tendencies of foraging snails. This suggests that there is released in the injured or dying snail some substance which is not apparent in the normal, healthy individual. Many pulmonate gastropod species have been reported in the literature to display occasionally a propensity for cannibalism (e.g., Elliot 1918).

In 1927, Pilsbry and Bequaert (p. 469) indicated that perhaps the most important predacious enemies of the African land mollusks were the rapacious streptaxid snails. Bequaert later reiterated this point (1950*a*). To determine more specifically what the natural enemies of *A. fulica* were in East Africa, where this species is autochthonous, the Pacific Science Board of the National Research Council and the Office of Naval Research in the fall of 1947 sent F. X. Williams to Kenya and Zanzibar for several months. Interesting accounts of the information gathered in the field are on record (L. C. Williams 1949, F. X. Williams 1951, 1953). The following May, live specimens of the two endemic predacious snails in the Diani Beach area of Kenya, *Edentulina affinis* C. R. Boettger and *Gonaxis kibweziensis* (E. A. Smith) (*Streptaxis*), were sent by Williams to the Board of Agriculture and Forestry in Honolulu, Hawaii (ICCM 1948, Bryan 1949). The near maximum length of these species is 50 mm. and 22 mm., respectively. The purpose behind sending these alive was to observe under subquarantine conditions their biology so that the possibility and practicability of using them in the biological control of the giant African snail could be determined.

While these observations were still in progress in the summer of 1949, Kondo and the author made a survey of Micronesia, under the same auspices, to determine among other things what island, infested with *A. fulica*, would be most suitable on which to conduct an experimental introduction of the predatory snails. Reports from these two investigators (Mead and Kondo 1949, Kondo 1949, Mead 1949*a*, 1950*b*, *c*) emphasized the complexity of the problem and recommended that in the selection of an island for the proposed experiments the following factors be kept in mind: size, topography, proximity, available transportation facilities, accessibility, inhabitation, isolation, quarantinability, horticultural and silvicultural crops at

stake, relative abundance of *A. fulica*, types and abundance of indigenous snails, and practicability of possible subsequent eradication of the introduced predatory snails. After reviewing the recommendations in March, 1950, it was determined at the Fourth Annual Meeting of the Insect Control Committee for Micronesia, of the Pacific Science Board, that the small (3 by 1 mi.) uninhabited island of Agiguan (Aguijan), about five miles off the southwest coast of Tinian in the Mariana Islands, would be most suitable (cf. Gressitt 1954:53). Kondo, R. E. Enders of Swarthmore College, and Mead had determined for the first time that *A. fulica* was actually on this island and that for other reasons the island had possibilities. At the same ICCM meeting, it was decided that R. T. Abbott should go to East Africa, collect *Gonaxis* and *Edentulina*, and return to Guam with them for release on the selected experimental island which was to be maintained in quarantine (ICCM 1950). This mission was accomplished during the following May and June (Abbott 1951*b, c*).

On May 31, 1950, and within approximately ten days after 545 living specimens of *Gonaxis kibweziensis* had been sent via air express to Guam by Abbott, about 400 surviving individuals² were released on the first terrace of the southwestern end of Agiguan by Robert P. Owen, entomologist and staff quarantine officer of the Trust Territory of the Pacific Islands (Owen 1950, 1951). On August 30, 1951, Owen returned on the third expedition to Agiguan to determine what progress had been made in the trial field experiment. He was accompanied by George Peterson, Jr., the entomologist of the government of Guam, and J. Lockwood Chamberlin, who was conducting an ecological study of *A. fulica* in Tinian. Due to an unfortunate set of circumstances, they were able to spend only three hours examining the area where *Gonaxis* had been introduced the previous year; but they were able to obtain evidence indicating that this predatory snail had survived, that it was reproducing, and that it had spread at least 300 feet beyond the point of release (Owen 1951). There remained undetermined such important points as: whether or not *Gonaxis* was actually feeding on the giant snail; whether there was being effected any appreciable control of the giant snail; whether any inroads were being made on the endemic snails; and whether any deleterious side effects were being demonstrated as a result of the introduction of *Gonaxis*. The ICCM, which had now become the Invertebrate Consultants Committee for the Pacific, decided at its Sixth Annual Meeting in February, 1952, that these and other points should be investigated over a period of a number of days by Kondo

² This number was later reported to be "229" (Owen 1953) and "407" (Davis 1954).

during the following summer. In accord with the suggestions of the ICCP, Kondo took with him 100 live specimens of *Gonaxis*, raised in Hawaii, for release in a high, forested area near the old village on the third terrace of the east end of Agiguan. At least 95 per cent of these were alive at the time of release. During his seventeen days on Agiguan, in the company of four other assistants and investigators, including Owen and Peterson, Kondo (1952, Anon. 1953a) made a number of discoveries; among the most significant are the facts that *Gonaxis* had actually been feeding on *A. fulica*, that it had effected only about a 19 per cent kill, and that in two years time, the original lot of approximately 400 *Gonaxis* had increased to an estimated 21,750. This great population build-up notwithstanding, Kondo announced that *Gonaxis* could not be considered a strong factor in the biological control of *A. fulica*.

But before this time, Kondo had eminently qualified himself for this field work by spending a number of months in Hawaii making careful observations of the biology of several predatory snails, including *Gonaxis*. The predatory snails sent by Williams to the Hawaiian Board of Agriculture and Forestry were transferred to the laboratory of the Hawaiian Sugar Planters' Association in January, 1950, where Kondo was asked to take charge of them. Their numbers had dwindled considerably and it was thought wise to put them under the care of a trained malacologist. By the spring of 1952, the number of *Gonaxis* had increased from the low of 22 late in 1949 to 439 living specimens.

Under a joint agreement between the ICCP and the Hawaiian Board of Agriculture and Forestry, N. L. H. Krauss, entomologist of the board, was sent to East Africa, Australia, New Caledonia, and adjacent areas for a period of several months in 1950–52 to seek further into the problem of finding a suitable predator or parasite of *A. fulica* (Coolidge 1950, 1951, 1952). Additional live specimens of *G. kibweziensis* and *Edentulina affinis* were sent to the Board of Agriculture and Forestry (Krauss 1951–52, ICCP 1953, Lennox 1953). Besides these and specimens of the beetle *Tefflus*, Krauss sent specimens of several other predatory mollusks so that their potential as biological control weapons might be determined by Kondo. All of approximately two hundred specimens of the omnivorous *Oxychilus cellaria* from Sydney, Australia, died within four months; the cause is attributed by Kondo to the inability of this temperate zone snail to adapt to the summer heat of tropical Hawaii. A similar fate was suffered by eight specimens of *Strangesta capillacea* (*Rhytida*) and 45 specimens of *Paryphanta compacta* (*Victaphanta*), both from Sydney,

as well as eleven specimens of *Rhytida* spp. from the dense rain forests of New Caledonia. Kondo (1950a) reports that, of the latter, *Rhytida inaequalis* (*Ouagapia*) quite unlike the smaller predatory species attacked some of the large specimens of *A. fulica*. When Williams was in East Africa, he found that carnivorous snails belonging to the genus *Gulella* were "probably effective enemies of quite young *Achatina*" (1951, 1953). Their small size, however, eliminated them from consideration. Williams also examined the paryphantids in New Caledonia and found them frequenting moist, dense ravines. G. S. Dun (*in litt.* April 17, 1950) concluded from this that predator and prey might not overlap sufficiently to effect any appreciable control, especially since *A. fulica* tends to be more abundant in the less dense areas frequented by man. As the giant snail is fortunately not in New Caledonia, there is no way of determining what the predator-prey relationships might be. Recently, de Wilde de Ligny (1953) made the following interesting report on the spread of *A. fulica* in New Guinea: "It is believed that this snail is unable to cross the patches of jungle isolating the small farms from the town and from each other. This assumption is supported by the fact that a concentration of empty shells was often found in the outer regions of the forest surrounding the town. In a few cases naked snails, probably parasitic [*sic!*], were observed on the shells of the giant snail. Experiments will be made to ascertain the carnivorous habits of the naked snail."

The *Edentulina* sent to Hawaii by Williams, including an additional 48 specimens sent by Abbott, maintained a steady decline in spite of plenty of food (young *A. fulica*) and moisture until in June, 1951, the colony numbered but eleven individuals (Kondo 1951b). At least in the laboratory, this species proved itself less hardy than *Gonaxis*. Perhaps the same explanation is behind the fact that Williams, Abbott, and Krauss encountered it in the field far less commonly than *Gonaxis*. At any rate, it is not difficult to understand why earlier tentative plans to introduce *Edentulina* in Agiguan, after the establishment of *Gonaxis*, were given up. In June, 1957, a fresh shipment of *Edentulina* was received from Mombasa, Kenya, and was released on Oahu; but to date there have been no recoveries (Thistle 1959a).

At this point, it is appropriate to review the very interesting experiments of McLauchlan (1949), which concerned a biological study of the carnivorous snails *Strangesta capillacea* (Férussac) and *Helicella cellaria* (i.e., *Oxychilus*) in Mosman, New South Wales. The fact that these snails will attack and consume the introduced *Helix*

aspersa is of particular interest in the present discussion. However, it is McLauchlan's belief that a diet made up largely or exclusively of *H. aspersa* causes a high mortality in these predators either because of excessive gorging or because of some toxic factor in the prey. He presents the following additional factors which tend to mitigate against the effectiveness of especially *S. capillacea* as a biological control agent: cannibalism among the predators, a primary preference for the native snails (species of *Paralaoma* and *Egilomen*), a secondary preference for only the young *H. aspersa*, the absence of a tendency for young *Strangesta* to attack young *H. aspersa*, the relatively very slow growth and development of the predator as compared with the prey, the general retiring nature of the predator, and the tendency for *H. aspersa* to move out of the range of *Strangesta*. Benthem Jutting (1952*b*) reports on, but does not elaborate upon, a communication from J. Hope Macpherson to the effect that a similar study was conducted in New Britain to determine the predation of *H. cellaria* and an Australian *Rhytida* on the eggs and young of *A. fulica*.

Kondo (1952) found in field observations of feeding *Gonaxis* that the largest specimens of *A. fulica* which would be attacked were almost never greater than 35 mm. in length. This immediately brings up the question as to whether or not the size of the predator is of any importance. G. S. Dun (*in litt.* Dec. 29, 1950) feels that a small predator is about as effective as a large one since the older specimens in his breeding cages were shown to be sterile. This is not a safe conclusion, however, as it has been found that dietary imbalance in caged specimens of the giant slug *Ariolimax* will invariably produce sterility and genital anomalies (Mead MS). The combination in *A. fulica* of a tremendous reproductive potential and immunity from attack after the first relatively few weeks of growth suggests at least that *Gonaxis* is not an ideal predator and, further, implies that the role of *Gonaxis* might ultimately be reduced merely to that of consuming the multitudinous young which would have been eliminated anyway by other causes. It was reasoning of this sort which encouraged Mead and Kondo (1949) to recommend that if predatory snails are to be used in the biological control of *A. fulica* the larger snail predators should be considered, for example, the giant paryphantids of Australia. Subsequently it was pointed out (Mead 1950*b, c*) that, since in predation the degree of prey-specificity is not as high as is host-specificity in parasitism, the search for a suitable predator of *A. fulica* need not and should not be limited to the area where this snail pest is indigenous, viz., East Africa. That is, merely because the predator has the same endemicity as its prey, it does not

necessarily follow that no better predator can be found. The field work of Krauss and Williams, the observations of Dun, and the reports of Kondo all indicate that the giant predatory paryphantids of the temperate regions are not as promising as hoped. Their inability to adjust to tropical climate suggests automatically that a large tropical molluscan predator might be tried. None is found in the area now occupied by *A. fulica*.

The large species of the voracious, tropical American *Euglandina* would seem to be worth serious consideration if biological control is to be investigated further. The eggs of *Euglandina* are proportionately gigantic and the hatching individuals are therefore so large that by far the majority of the endemic molluscan fauna of the Pacific islands, consisting of small or minute species, would escape their ravages. In addition, the juveniles and adults could attack larger specimens of *A. fulica*, eat more, and live longer than the small endemic predators of East Africa. It is of interest to note that *Euglandina* was imported into France nearly fifty years ago in an attempt to control snail pests of truck crops and was said to confer "immense benefits on market gardeners" (Anon. 1913). *Euglandina rosea* (Férussac) of our own Gulf States area is well known for its vicious attacks upon other snails (Pilsbry 1946:2:1:188). As will be seen below, this relatively small species has already been introduced into Hawaii. Muma (1954, 1955) has observed it feeding upon a reputedly beneficial tree snail *Drymaeus dormani* (Binney) in the citrus groves of Florida (cf. Norris 1952, Nunn 1953). He reports unenthusiastically about it, though, with these words, "Experiments with *Euglandina* . . . have demonstrated that it is not a heavy feeder and probably not of great importance."

The only other frontier in the search for a molluscan predator is in Mauritius. Both *A. fulica* and *A. panthera* have been introduced on that island (Dupont 1878) and there is recent strong evidence that in the ensuing competition the latter species is quite successfully taking over in the areas below 1000–1200 feet in altitude whereas *A. fulica* remains dominant in the area 1200–2000 feet (J. Vinson *in litt.* Dec. 24, 1949). Deep in the interior, where significantly the achatinas have not yet successfully penetrated, there are found about thirty native species of predatory streptaxids. Efforts by G. S. Dun and the author to stimulate by correspondence a scientific investigation of the relationships between the achatinas and the streptaxids have failed. Coolidge (1951) reported that a conchologist, Dorothy Getz, planned to visit Mauritius and would be given assistance to permit her to obtain information there about the problem of the

giant African snail. Her findings, however, have thrown no new light on the possibility of natural biological control being in operation in Mauritius (Coolidge 1952).

On June 3, 1952, while Kondo was still in Agiguan in the process of attempting to determine among other things the nature of precautions which might properly be taken in introducing *Gonaxis* elsewhere, the Hawaiian Board of Agriculture and Forestry made a decision and took action which has stimulated a considerable amount of controversy. The preliminary results of the trial field experiment in Agiguan and the laboratory studies in Hawaii, coupled with extreme pressure from the people of Hawaii to "do something" about the new outbreaks of *A. fulica* in Oahu and Maui, persuaded the Board to introduce *Gonaxis kibweziensis* into the Hawaiian Islands without waiting for additional results from the projected program. Twenty specimens, along with ten specimens of the predatory beetle *Tefflus*, were released near Mahinui in the Kaneohe district of Oahu, where the giant snail has extended its range considerably (Lennox 1953, Weber 1953). Through a singularly unfortunate oversight, however, stones covered with a cement-lime-calcium arsenate bait, scattered there to control the giant snail, proved equally tempting and fatal to all of the introduced *Gonaxis* specimens. A second introduction of 200 specimens of *Gonaxis* was made in this same area in September, 1954. At the time 300 specimens were introduced only a relatively short distance away, near the insane asylum. In January, 1955, this latter site was inspected by the author and there was found to be every evidence of successful establishment of this predatory snail. It was the plan then to move 100 of the specimens from that site to a third location on the east side of Oahu as an initial step in a projected plan to spread *Gonaxis* as rapidly as possible. A few weeks later, specimens were released on Maui (Weber 1956).

In 1953, efforts were made to introduce *Gonaxis* from Kenya into the achatina-infested Seychelles Islands; but because of a prevailing precaution on the part of the administration, the plans were tabled indefinitely.

During the period January 12–16, 1954, G. D. Peterson (1954) accompanied by three assistants, conducted the fifth expedition to Agiguan. He concluded that considerable changes were taking place in the various animal populations on that island, that *Gonaxis* was apparently exacting a greater toll on *Achatina* than estimated by Kondo, and that if the later point could be proved during a subsequent expedition, immediate steps should be taken to establish *Gonaxis* on other infested islands. From July 21 to August 11 of that

same year, Davis (1954), accompanied by Peterson and two assistants, conducted a follow-up survey with the results essentially re-emphasizing and elaborating upon Peterson's earlier conclusions. The elaborations underscored the complexity of the ecological conditions which were obviously in a significant state of flux. The most important announcements were: That the 100 *Gonaxis* released two years earlier by Kondo had increased to an estimated population of 80,800; and that the *ca.* four hundred *Gonaxis* released four years earlier, and which had built up to an estimated 21,750 in two years' time, had died out almost completely. In September, 1954, 88 specimens of *Gonaxis* from Agiguan were marked with plastic paint and introduced by Peterson into Guam (Peterson 1957*a, b*). A few months later, young specimens of the third generation were found, indicating that successful establishment had taken place.

By this time, the authorities in charge of the biological control program in the Pacific area were convinced that a full scale "Gonaxis Program" should be undertaken. Accordingly, a seventh expedition to Agiguan was planned for November, 1955, with the specific mission of obtaining as many *Gonaxis* specimens as possible for introduction into other islands of the Trust Territory, into other areas on Oahu and Maui, and into California as a biological control agent for two introduced helicine pests (Mead 1955*c*, Anon. 1956*b, c*). Reportedly, over 5,000 live *Gonaxis* were collected (Coolidge 1955, Kondo 1956, Anon. 1956*a*). Of these, 2,000 were sent to Hawaii and 200 were sent to California. The remaining specimens were divided into lots and released in one or more sites on Saipan, Tinian, Rota, Ponape, Truk, and the Palaus. Subsequently, specimens were introduced in New Britain. Introductions into still other areas soon followed, as implied in the words of Pemberton (1956), "... our Committee has been besieged from many sources requesting colonies of *Gonaxis*."

G. kibweziensis, however, still has as its main drawback the fact that its small size restricts it to attacking only the smaller achatina specimens. In an effort to improve the situation, the Hawaiian Board of Agriculture and Forestry introduced on Oahu in June, 1957, and subsequently on Maui, the east African *Gonaxis quadrilateralis* (Preston), which is almost exactly twice the size (Thistle 1959*a*). Two years after its release, it was still holding a weak second place; and, in general, the slow, uncertain developments were disappointing.

But even before this, more and more attention had been turned to *Euglandina rosea* as a third possible molluscan predator. A number of live specimens from Florida, collected by Krauss, were sent to

Hawaii in 1955 as the initial step in introducing this species as a biological control agent. Their introduction was speedily approved and 616 specimens were released later that same year in Oahu (Weber 1956, Kondo 1956). In contrast to both species of *Gonaxis*, this aggressive, vigorous, rapacious snail took hold immediately and spread rapidly. By 1957, it was considered clearly the most promising of all biological control agents being used in the giant snail control program. In addition to feeding on *Achatina*, it was found to feed on the snail pest *Bradybaena similaris* and the liver fluke snail, *Lymnaea (Fossaria) ollula* Gould (Thistle 1959a). In both Makiki and Hauula release sites, the snail had moved far afield, even into *Gonaxis* release sites. Ironically, *Gonaxis* have been found in the egg clutches of *Euglandina*. By July, 1958, the Hauula population had built up to the point where it was possible to remove 12,000 specimens for release in many other sites in Oahu, Kauai, Maui, Hawaii, New Guinea, Okinawa, and the Palau, Philippine, and Bonin Islands.

In January, 1956, 25 specimens of a fifth molluscan predator, *Oleacina oleacea straminea* (Deshayes) from Cuba, were released on Oahu (Kondo 1956, Thistle 1957). About four hundred specimens of the predatory snail *Gulella wahlbergi* (Krauss) from South Africa were released in January, 1957, on Oahu and subsequently others were released on Maui. A number of specimens of *Gonaxis vulcani* Thiele and an unidentified species of *Gulella*, both from the former B. Congo, were released on Oahu in November, 1956 (Thistle 1959a). There is no evidence to date that any of these four predators has become successfully established. Similarly, little hope is held that the giant predatory snail *Natalina* sp. (i.e., *Rhytida*), under examination in Hawaii, will prove to be effective enough to warrant its release, in spite of the fact that its body attains a length of 7–8 inches. Another possible candidate, *Varicella similis* from Jamaica, died in the laboratory before it could be decided that it might be released on Oahu. *Gulella bicolor* Hutton from the Philippine Islands proved to be of negative value so far as preying upon *Achatina* is concerned; but it proved to be such an effective predator of the snail pest *Subulina octona*, which is also the host of the cecum fluke of poultry (*Postharmostomum gallinum*), that it was released in large numbers on Oahu and Hawaii in 1957 and 1958 (Thistle 1959a, Davis 1959).

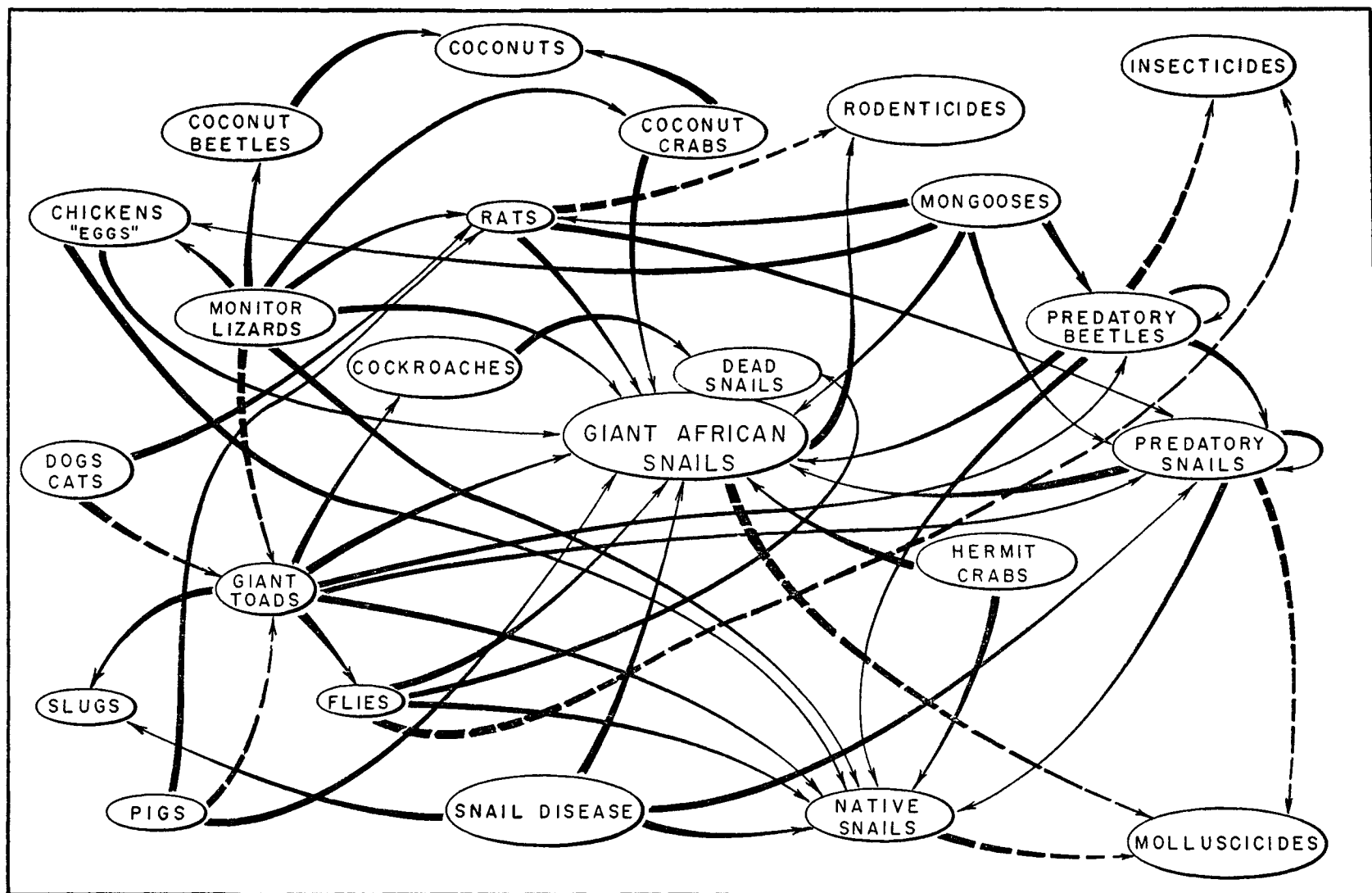
Those absorbed in the economic aspects of the problem have judged this expanded program of predatory snail releases as a strategic, timely, and reasonably safe one, although some naturalists have condemned it as unwise, premature, and irrevocably threatening to the unique native mollusk fauna of the Pacific Islands. For example,

Fosberg (1957) deplores the "almost hysterical program of importations of predators in an attempt to control the giant African snail" in Hawaii and concludes that "these will almost surely bring about destruction of many members of the extraordinary Hawaiian land snail fauna." It undoubtedly will take years to determine positively the actual value of these irreversible introductions. One thing is certain. There is to date absolutely no scientific justification for such a statement as, "The snail [*Gonaxis kibweziensis*] ultimately proved very effective in the control of the giant African snail" (Peterson 1957b).

Miscellaneous In New South Wales, McLauchlan (1949) reports that unidentified "tiny insects in the soil also destroy the eggs" of the predatory snail *Strangesta capillacea* (Férussac).

Biological Control—an Evaluation South (1926b) was probably the first to consider seriously the possibility of attempting to control *A. fulica* by enlisting the help of some of its "natural enemies" from East Africa. He accordingly made contact with authorities in Kenya, Uganda, and Tanganyika; but for some unexplained reason, the program died in its tracks. Since then, the subject has been alluded to from time to time; but it was not until Townes (1946) made his survey of the problem in the Pacific that the matter clearly came out into the open once again with the statement that "the most feasible control for it is to find and introduce a natural enemy." This recommendation was picked up as a keynote by the Pacific Science Board of the National Research Council and subsequently by its Insect Control Committee for Micronesia (Ryerson 1947, ICCM 1947). In this manner, it has influenced to a very great extent the character of the research on the giant snail in the Pacific.

The first major undertaking in the investigation of the biological control of *A. fulica* was the exploration of the native heath of this snail in Kenya by Williams (1951, 1953). The early reports that no parasites but several predators were found brought definitely mixed reactions (ICCM 1948), the record of which might be considered a crystallization of the basic philosophy underlying the current biological control program. Had specific parasites of the giant snail been found, the method of undertaking the project would have been clearly indicated. But with only non-specific predators, some felt that at least a fair amount of precaution was needed. It was this feeling that caused Rees (1950) to announce that "the American authorities are reluctant to release these predators in new countries lest they should become greater pests than *Achatina*." Since that time, however, the program of biological control of the giant African snail has



Representation of the basic environmental interrelationships of the giant African snail and its primary associated organisms. Solid lines represent lines of feeding, predation, or attack; broken lines represent a poisoning effect upon the feeder or predator. Each newly introduced organism or factor inordinately increases the complexity in the existing interrelationships, particularly through ecological chain reactions, and it may be responsible for reversing completely the definitive beneficial or deleterious effect of any other organism or factor. (Drawn by D. B. Sayner.)

become well established. Not one, but nineteen predatory invertebrates have been introduced in the various infested areas. And more apparently are to follow, as there are currently several others under consideration.

As this program continues to develop, there still prevails a mixed feeling as to the element of risk involved. All agree, however, that this so-called "natural control" is exceedingly attractive from the standpoint of its being self-perpetuating. Any other method of control that has been devised requires maintenance; and, at best, maintenance on an indefinite basis is a serious consideration because of the cost, either in money or man-hours of labor, or both.

The literature is replete with reports on the general subject of the dangers of introducing alien species (e.g., Kew 1893; Thompson 1922; Schlesch 1928; Anderson 1934; Storer 1931, 1934, 1949; Hanna 1948; Wodzicki 1950; Rees 1955; and Heim 1956). On the specific subject of the introduction of alien animals to control the giant snail, Aguayo (1950), Clench (1949), Jaski (1953), Mead (1949*b, c, d*, 1950*b, c*, 1955*a, b, c*, 1956*b, c*), Morrison (1950*b*), and others have sounded a warning. Lennox (1949) and Pemberton (1956), in turn, have minimized the dangers and emphasized the importance of continuing with the biological control program. In many ways, Morrison (1950*b*) comes close to the heart of the dilemma with the following words: "The man who introduces a new predator into a country undertakes a grave responsibility. Before it is regarded as safe, it must have been proved conclusively that the candidate for introduction will rather die than touch native fauna or flora or local economic products. Such proofs take a long time to establish, and meanwhile the giant snail is eating its way through the Pacific."

As pointed out earlier, the predatory snails *Gonaxis kibweziensis* and *Euglandina rosea* have taken the limelight almost entirely in the program of the biological control of *A. fulica*. Contrary to various current reports (Anon. 1956*b, c*), there is no evidence that *Gonaxis* effects any real control of the achatinas in East Africa (Abbott 1951*c*). Similarly, the several endemic predators of *A. fulica* in Ceylon have been reported to be of relatively little value as "natural controls" (Fernando 1952, Mead 1955*b*, 1956*a*). But this seems to be the usual story. For example, Ingram (1942*a*) was able to determine that the native carnivorous snail *Haplotrema minimum* in California had an inappreciable effect upon the introduced *H. aspersa* even though it preyed freely upon its young. An explanation for this phenomenon seems fairly simple. It is probable that the foreign species has a biological advantage in that it is in an environ-

ment lacking its own specific natural controlling factors, while the endemic predators continue to be held in check by their own natural controlling factors, despite the increase in acceptable prey. This explanation becomes more tangible if it is assumed that the more effective "natural controlling factors" are specific disease agents that become proportionately more limiting in their effect as the host population increases. Although the idea has not been presented in support of the predatory snail program, it would appear, by extending this same reasoning, that if in a given environment *both* predator and prey are recently introduced foreign species the predator would be at an advantage. If under these conditions, however, disease of *either* the predator or prey should enter the ecological picture, it could be completely decisive in its effects, one way or the other. On the other hand, if disease of *both* prey and predator should enter the picture, the outcome obviously would depend upon the differential of such factors as the severity of the disease, immunity, tolerance, physical hardiness, and a whole host of other factors.

But disease, as a complicating factor, has scarcely entered consideration in the "Gonaxis Program," in spite of its importance. Even without it, the picture is far from simple despite the glib accounts, especially in the more popular articles and newspaper accounts, which suggest that after consuming all the achatinas *Gonaxis* will turn cannibalistically upon its own members and finally exterminate itself (e.g., Mahoney 1955). As an aside, Bodenheimer and Schiffer (1952) have convincingly demonstrated mathematically why there almost never is extermination under natural conditions, even in parasitism. Durham (1920), however, puts over the point more humorously with the following: "I may point the tale with reference to the flea and the louse. With great and enduring pertinacity their 'natural enemies,' the monkey, the dog and cat, nay even on to mice and men, are hunting them day by day and into the night season, but they still abide in their haunts."

Some have pointed out that the predicted predation-to-extinction and self-predation-to-extinction already have taken place on Agiguan Island since all *Achatina* and all *Gonaxis* have been found dead in the area of the first release of the predator. If that is so, how then can one explain the similar disappearance of *Achatina* in other areas on that island where *Gonaxis* has *not* penetrated? (cf. Davis 1954:15, 23) First of all, it should not be forgotten that animal populations under adverse conditions may apparently disappear, only to reappear months or even years later. Hence, merely because specimens could not be found, it cannot safely be assumed that extinction has taken

place in either population. The question, however, does emphasize the fact that in the present case control factors other than *Gonaxis* are effectively operative. If we assume that both *Gonaxis* and *Achatina* have not become extinct, but have been reduced in numbers beyond the point where they can be encountered in the field, we should naturally turn our attention to the factors influential in bringing about a recovery of the populations of both prey and predator. Some of the more obvious of these factors are: general hardiness, versatility in appetite, intraspecific cannibalism (Kondo [1951*b*] has shown this often to be severe in *Gonaxis*), longevity, duration of estivation, reproductive potential, and adaptability to varying types of environment. In every case, *Achatina* has a distinct advantage. From this it can be assumed that at least *Achatina* would make a faster "comeback."

As still another facet in the complex ecological setting in which we find the *Gonaxis*-*Achatina* problem is the role of the endemic snails. Kondo found that *Gonaxis* shows a definite preference for several species of terrestrial and arboreal endemic snails in Oahu (1950*b*, 1951*b*) and for *Omphalotropis erosa* on Agiguan (1952). As long as the arboreal snails remain in the vegetation they will be safe, as *Gonaxis* manifests little tendency to leave the ground. The terrestrial snails, however, would surely suffer (Anon. 1956*d*). This is regrettable; for the terrestrial snails "because of their secretive habits form precious 'keys' indeed for unlocking the vast zoogeographic storehouse of the Pacific" (Mead 1955*c*).

The question has been raised regarding the possibility of *Gonaxis* turning to some other prey, such as earthworms, after the achatinas and the endemic snails have become scarce. Although other carnivorous pulmonate gastropods are known to consume earthworms, Kondo (1950*b*) failed to demonstrate in the laboratory any tendency of this sort in *Gonaxis*. Nothing is known about the extent to which other invertebrates might be attacked. There is strong evidence, however, that certain other terrestrial invertebrate populations may undergo substantial change because of the indirect effects of introducing *Gonaxis*. The reports of Peterson (1954) and Davis (1954) show that four years after *Gonaxis* was introduced on Agiguan, the hermit crabs (*Cenobita perlatus*) decreased in numbers markedly, whereas the coconut crabs (*Birgus latro*) definitely increased. Concurrently, the vertebrate populations went through corresponding changes. The monitor lizard (*Varanus indicus*) went into a definite decline; the rats virtually disappeared; and the ferral goats increased in a very pronounced fashion. The plant communities also under-

went changes, a more significant one of which is the serious increase of the poisonous plants *Jatropha gossypifolia* and *J. curcas* (Peterson 1954). In attempting to explain this whole series of changes, one finds one's self face to face with the exceedingly ramified and little understood subject of ecological chain reactions. Some notable examples of ecological chain reactions have been presented above. A general treatment of the subject as it concerns the biota of the islands of the Pacific is to be published soon (Mead in MS). Because of the high state of flux of the fauna and flora of Agiguan, some have felt that ecological chain reactions are actually in progress and that greater changes are in store before an equilibrium once again is attained. Unfortunately, however, what has happened so far has not met with unanimity of interpretation by the several investigators. For example, when Enders, Kondo, and Mead made the initial survey of Agiguan, there was a manifest abundance of rats; Kondo announced later that the rats in combination with the coconut crabs were killing more giant snails than the predatory snails were; but when Davis and Peterson arrived on the scene, they found such an "extreme scarcity of rats" that they concluded Kondo had "weighed the evidence too strongly in favor of the rats" (Peterson 1957b).

So far, *Gonaxis* has demonstrated twice on Agiguan that in two years it can go from a few dozen individuals to populations estimated to be in the thousands. It is not clear, though, just what takes place following the population buildup. The first population went to an estimated 21,750 in two years; but in an additional two years, practically no living individuals could be found during two different intensive searches. The second population, in another area on that island, went to an estimated 80,800 in two years. At its apparent population peak, over 5,000 individuals were recently removed for introduction into other areas. If this second population is due to continue its increase, the removal of 5,000 individuals should not have any appreciable effect; if however the population has gone into a decline, as the first one had at this stage of its development, then there could conceivably be a very material effect. (It is apropos to recall that hand collecting as a control method for *A. fulica* is most effective after the population has gone into the apparently inevitable "decline.") But we dare not extrapolate from one population to the other; for the populations are not only in different areas, but the populations of the other animals on the island have continued to undergo such pronounced changes that they are bound to cause different repercussions in this second population of *Gonaxis*, and even in the first population, if it is still recoverable.

The "Euglandina Program" similarly is producing in some cases truly remarkable and even enigmatic results. For example, *Euglandina* has been in the Makiki area on Oahu for two years, yet in some of the sections where the giant snail is most abundant, this predator, along with *G. kibweziensis*, is surprisingly only seldom encountered. Specimens that have been collected more often than not are emaciated in spite of the abundance of food. Adult *Gonaxis* have been found consuming the egg clutches of *Euglandina*; but on the other hand, *Euglandina* in the laboratory will often select *Gonaxis* and the small, introduced snail pest *Bradybaena similaris* in preference to the giant snail. In some cases, *Euglandina* steadfastly refused to attack an acceptably small *Achatina* even after fasting two to three weeks. In other cases, specimens which did consume giant snails in the laboratory mysteriously died within a day or two in contrast to others in the same lot that refused to feed. This brings to mind McLaughlan's suggestion of a "toxic factor." The emaciation has suggested the possibility of disease. Individuals have been found with leucodermic lesions apparently identical with those of "diseased" giant snails. It is possible that *Euglandina* is more susceptible to the disease than *Achatina*.

Another differential between these two species is the giant snail's infinitely greater capacity to withstand prolonged estivation with a consequent lack of food and water (Mead 1959b). A protracted dry period could therefore enforce estivation and cause death through starvation in spite of living food being nearby in abundance. Essentially nothing is known of the population dynamics of *Euglandina* and it is altogether possible that this cannibalistic species, as is characteristic of predators in general, will not maintain high populations in limited areas. This may explain why the highest concentrations of this predator have consistently been found at the periphery as an advancing crest in a relatively rapidly expanding population.

Threading through this entire problem as an element of still further uncertainty is the genetic factor. The study of genetics teaches us that each species has its own spectrum of hereditary traits and rate of genetic mutability. From the study of population genetics we learn that different populations of the same species may have different complements of the total possible hereditary traits. In some cases, the differences are great enough so that two populations of the same species may be considered distinguishable as two subspecies. The selecting factors operative in the different environments quite understandably vary in their relative value. It is the sum total of the effects of the selecting factors in a given environment that determines



FIG. 13.—A full-grown larva of the India glow-worm, *Lamprophorus tenebrosus* feeding on a ca. 75 mm. specimen of the giant snail.

FIG. 14.—*Achatina fulica* with two of its natural enemies from East Africa, *Edentulina affinis* (ca. 40 mm. long) and *Gonaxis kibwezensis* (ca. 20 mm. long).

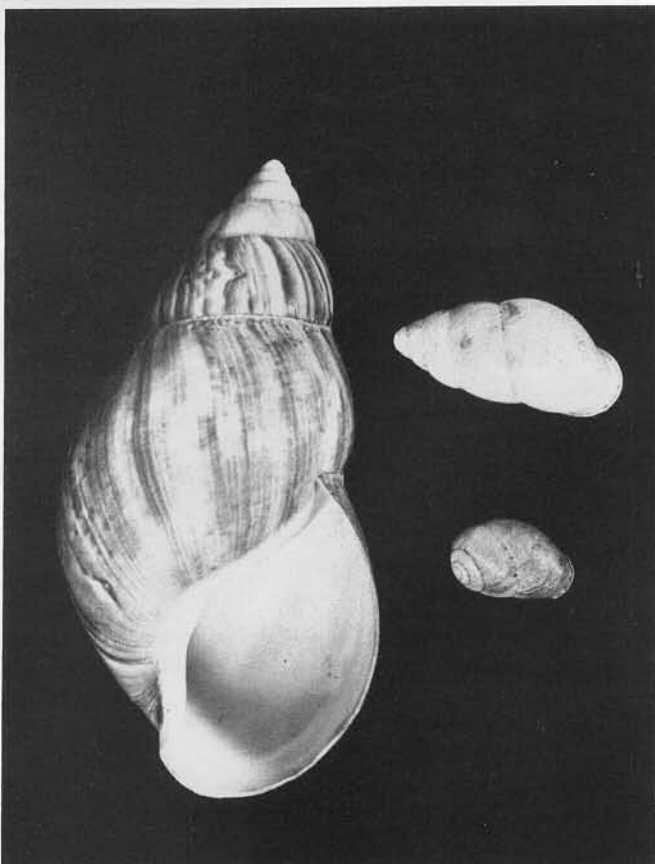




FIG. 15.—California Plant Quarantine inspectors in Los Angeles discover giant snails in a cargo of war salvage material from Guam.

which available hereditary traits will be selected and perpetuated as most suitable in the population in that environment. In the ten to fifteen years that *A. fulica* has been in the western Pacific Islands, it has displayed such a remarkable variability from one population to another, with respect to size, color, thickness of shell, and even as to what plants it will preferably attack, that a taxonomist, unacquainted with the history of this species would be tempted to designate the populations at the very least as those of different "races" (Mead 1951a, 1955b). When these same thoughts are applied to the "Gonaxis Program," we cannot but wonder what this predatory species will do in a like period of time. It has been suggested that even a greater versatility in appetite in *Gonaxis* is not outside the realm of possibility (Mead 1955c, 1956b), notwithstanding the remarks in the literature to the contrary (Pemberton 1956). This carries the disquieting implication that the environment might well select unsuspected and undetectable undesirable traits. There is no way in which this risk can be eliminated; for even though the animals may be "screened" in the laboratory for their feeding proclivities, there cannot be duplicated in the laboratory the population dynamics or the multiplicity of environmental factors operative in a natural population. Therefore, one may not really safely conclude that, merely because all of, say, 2,000 experimental animals refused to eat "*Alpha*" and died when it was their only source of food, "*Alpha*" will not be jeopardized in any way with the release of the experimental animals. The 2,000 experimental animals may have been too small a sample to express the full spectrum of genetic variability in character determiners influencing feeding habits. But grant that this was an adequate sample. How can one anticipate ecological chain reactions which might threaten "*Alpha*" indirectly?

Actually, there have been developed in insect biological control, methods which substantially reduce the greater share of the elements of risk. But these methods demand such an inordinate amount of precious time that, where the life cycle is long or the economic pressure is great, compromise or short-cut measures may be adopted. Such measures have been strongly opposed.

Some have questioned the advisability of introducing multiple predators of the giant African snail in Hawaii. To date, there have been introduced nine predatory beetles, two presumably parasitic flies, and eight predatory snails. In insect biological control, the concurrent introduction of two or more parasites of an insect pest is a common practice (e.g., in the fruitfly control program in Hawaii). The rationale behind this practice is that if one parasite does not

effect a control perhaps another one will; or, together, the multiple parasites will do the required job; or, one parasite may take over in one type of environment and another will take over in a second type of environment. Although these thoughts make good sense, putting the idea into practice introduces new difficulties. In the case where predators instead of parasites are introduced, predators may consume predators, even in preference to the intended prey. Although Peterson (1957a, b) reported that in the laboratory *Lamprophorus* would not attack *Gonaxis* it has been pointed out that *Tefflus* can consume *Lamprophorus*, *Lamprophorus* can consume *Euglandina*, *Euglandina* can consume *Gonaxis*, and *Gonaxis* can consume its own kind (Mead 1955b). In addition, a number of the factors, discussed above in terms of the "Gonaxis Program" and the "Euglandina Program," would also pertain to these other predators. The complexity becomes geometric in its proportions.

Still other difficulties are introduced when different methods of control are concurrently used. Molluscicides and other agents of snail destruction will kill predatory snails quite as quickly as they will *A. fulica*. This was convincingly demonstrated at the time *Gonaxis* was first released in the Hawaiian Islands; and it surely must have been demonstrated again when both *Euglandina* and metaldehyde were used in concentric, contiguous zones of defense in the Mana district of Kauai when the giant snail was first discovered on that island. In the same manner, insecticides used in the field are a threat to the beetle predators of the giant snail. As an apparent "double threat," some snail baits are fortified with insecticides; in other cases, the molluscicides are known to be insecticidal in their effects. And, as a provocative additional thought, there was evidence in Ceylon that a snail dying of metaldehyde poisoning provided a temptingly lethal morsal for the marauding *Lamprophorus*.

It is perfectly obvious at this point that, despite the attractive features of molluscan biological control, the method has more than its share of difficulties. If true specific parasites of *A. fulica* can ever be found, a great share of the intercurrent problems will be removed automatically. The recent works of Muma (1954) and Berg (1953, 1955) on malacophagous fly larvae are also encouraging; but Berg's reference to the fly larvae as "relatively unselective snail predators" seems to sound a familiar note of warning.

The work on diseases of snails (*vide infra*) has only just begun (Mead 1956a); and, although it is exciting to contemplate, it is obviously too early to do more than speculate as to how much promise micro-organisms offer as potential biological control weapons. A

factor distinctly in favor of micro-organisms is their characteristically high host specificity. But at least in one outstanding respect, micro-organisms are potentially more dangerous than the metazoan predators and parasites. It is agreed that their phenomenal biotic potential insures the capacity under favorable conditions to build up rapidly a population capable of causing an epizootic. Ironically, however, it is this same biotic potential which increases the chances of there appearing a mutant type whose metabolism is just different enough to produce undesirable results. The story behind the use of the myxomatosis virus in the biological control of rabbits in Australia is a case in point, particularly with the subsequent appearance of non-virulent, but immunizing, strains in the field (Ratcliffe *et al.* 1952, Fenner and Day 1953, Mykytowycz 1953). It is felt, however, that in the final analysis it is truly the disease-producing agents in an environment which determine both qualitatively and quantitatively the biota the environment will maintain (Mead 1955*b*). In other words, when organisms are in the presence of, and in harmony with, the agents that produce disease, their numbers will not be excessive ecologically and there will be at least a semblance of endemicity. The mission of this phase of biological control, then, is either to bring the foreign species into reasonable balance with the other organisms in the environment through the introduction of a natural disease-producing agent, or to attempt to eradicate the foreign species by introducing an unnaturally virulent disease-producing agent. This mission is a big one and it will not be fulfilled until the biological control man, the malacologist, the microbiologist, and the ecologist all work together on a closely integrated program. Together, they should be able to speed up and intensify the natural process of population decline which sooner or later overtakes an invading species. This decline, it is felt, is nothing more than an indication that the disease factor has finally caught up with the invading species. Disease is the ultimate controlling factor; and it is one that must be recognized and properly evaluated in the problem of the giant African snail.