CHAPTER 3

FACTORS

FAVORING

DISPERSAL

AND SURVIVAL

Man—the Principal Agent of Dispersal   There are many factors, both intrinsic and extrinsic, which either directly favor or otherwise predispose to a greater spread of the giant snail. Chief among these is the human factor—to the extent that man might justifiably be considered the only effective disseminator. There are many references in the literature to wilful introductions of achatinas into uninfested areas. In fact the history of the spread of *Achatina fulica* is in its larger portion little more than a series of one intentional introduction after another. Puteh (1939), for example, relates that "several peasants from the inland [Singapore] who had never seen these snails, came to Cherang Ruku and took some specimens for the purpose of breeding them, saying that they looked very beautiful!" The stories about one of the Oahu introductions (Pemberton 1938) and one of the Djakarta introductions (van Brero 1933) read almost the same way. A check of the literature indicates that to a great extent the intentional introductions of *A. fulica* have been cases of Oriental people introducing the snails for duck feed (e.g., Jarrett 1949). Live specimens of this species were either sent or carried from Siam to Berlin (Boettger 1951); from East Africa to London (Burton 1949); from Rajmahal, India, to London (Godwin-Austin 1908); from Singapore to London (Jarrett 1932); from Mombasa, Kenya, to the Belgian Congo (Anon. 1927a); and from Kenya to London (Rees

1951).[1] In another case, specimens were sent from Singapore to Java in a tin container labeled "flower seeds" (van Leeuwen 1932). This same intent to import the giant snails is reflected in a letter from an Italian correspondent who requested of the author information as to how he might successfully introduce the giant snail into Italy "where food is very dear and scarce."

Specimens of an unidentified species of *Achatina* were sent from Zanzibar to Germany (Semper 1890); and Longstaff (1921) returned to England with three specimens of *A. zebra* from Cape Colony. Andrews (1948) purchased from a Chicago dealer a specimen of the huge *A. achatina* which was kept for some time in his home in Baltimore. It escaped once but was found; shortly afterward it laid a number of eggs which fortunately were improperly cared for and none hatched. He suggested that these snails might be developed in Florida as an additional source of food for us. This drew an immediate sharp rebuke from Hanna (1948). Similarly, the taking of this species into California by Dickinson (1946) was exposed and censured by Hanna (*loc. cit.*) and Mead (1949*b*). At least until a very few years ago, specimens of *A. fulica, A. achatina*, and *A. ventricosa* were to be found alive in the National Zoological Park in Washington, D.C. A similar situation exists in the larger zoölogical parks in Europe and elsewhere.

As for the unintentional introduction of giant snails, Connolly (1912) reports specimens of *A. fulica* arriving in Durban, Natal, in flower pots sent from Mauritius. Other specimens were found in Java in the soil of a shipment of grass plants from Ceylon (Anon. 1925, Leefmans and van der Vecht 1933*a*). Latif (1933*a*) records an instance in Riouw Archipelago in which orchid shipments, apparently bound for Java, were found infested. Many other interceptions of this species are on record. Other species of giant snails have also been taken under similar circumstances. *Archachatina marginata* was found in Berlin on a bunch of bananas originating in the Cameroons (Boettger 1937, 1938). Paravicini (1926) states that *Achatina craveni* was being spread in East Africa through shipments of plants. Still other records of the interception of achatinids have been compiled by Boettger (1947). It would be utterly impossible at this point to give any conception of the multiplicity of reports in the literature of introductions, intentional and otherwise, of live mollusks into

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[1] Dartevelle (1952*b*) reports that a small shell of *A. fulica hamillei* has been found in what was then called the Belgian Congo. Since this species is not endemic in this area, he assumes that the specimen was imported as an amulet from East Africa by one of the natives.

non-endemic areas. This has been going on for years and will continue indefinitely. It thus remains as one of the big forces with which to reckon in setting up control programs.

The reason for most of the unintentional introductions of snails, and of *A. fulica* in particular, may be found in the sheer mechanics of the many diverse and varied activities of man. As one extreme, Campbell (1897) relates in an unintentionally humorous vein how snails even can be "carried about unconsciously by persons on their clothing." The single greatest human factor contributing to the spread of the giant snail is the desire and necessity for members of the human species to be frequently on the move. Coupled with this is the propensity of the snail for crawling back into recesses—recesses which all too often are in the possessions of man. These are carried from place to place and, thus, so are the snails. For this reason, commercial traffic in produce can be particularly threatening and it is therefore the main avenue checked in carrying out quarantines. The author has witnessed in Micronesia the transportation of *A. fulica* in bunches of bananas, a favorite among native peoples for gifts and trading, and this evidence is offered as the most likely explanation for the spread of this species to several islands in the Truk group (Mead 1950*b*, *c*). Shipments of inedible plants or plant products (e.g., grass thatching) provide ideal retreats for the snails (cf. Jarrett 1923). Even soil, especially that containing nursery stock, is not to be overlooked as it may harbor both eggs and snails. It is thus not surprising that Corbett (1933) found the giant snails in the exhibition ground of the Malayan Agri-Horticultural Association. Estivating snails often attach themselves to stored or abandoned war equipment. This helps to explain why war salvage equipment has consistently yielded the greatest share of the giant snails intercepted by quarantine authorities in the United States. Messenger (1952:253–54) has shown illustrations of this type of contamination. This also explains why railroad yards (Corbett 1933), shipyards, and the like have often been found to be the primary site of establishment of new populations. Pereira (1926) has stated that the giant snail was carried into new areas in Ceylon through the agency of motor vehicles. Abortive attempts to effect a control have in some cases succeeded only in spreading the snails still further, for example, attempting to drown the snails in streams (Green 1910*c*). It is significant that the giant snail population on uninhabited Haha Jima in the Bonin Islands was found to be restricted to a relatively small area, whereas the equally old snail population on inhabited Chichi Jima was found

scattered all over the northern part of the island from valleys to mountain tops (Mead and Kondo 1949).

The pronounced appetite for rotting and decaying materials is the main reason that the snails have frequently been reported congregating in garbage dumps and refuse heaps. And for the same reason, the normal accumulation of material of this sort around the habitations of people living in the tropics has fostered the maintenance, spread, and sometimes restriction of these snails to inhabited areas. Abandoned native crops provided a similar situation, particularly when the exigencies of the war caused many to abandon their land just at the crest of the invasion of the giant snail. In other cases, the crops were abandoned because of the depredations of the snails, thus contributing directly to the expanding snail population. One thing is certain: whenever man enters the picture, he introduces undetermined, altering, ecological factors which make the environment more suitable for snail invasion and maintenance. The effect of these factors seems to carry on for some time after man leaves the area; but as the abandoned land gradually returns to native bush, it strangely becomes less and less acceptable to the snails.

Among the more subtle factors operative in man's contributing to the dispersal of the snail is the almost universal strong objection in the non-endemic areas to the very thought of eating snails. But, even more than a matter of innate repulsion, in some areas eating the flesh of such a lowly earth-dwelling animal as a snail is a distinct taboo. The dominance of the Buddhist and Hindu religions in many of the Far Eastern snail-infested areas is directly responsible for the actual "protection" of these pestiferous snails. One good Buddhist acquaintance of the author complained that even in the city where she lived, the snails were so abundant that every night she collected two baskets full, and by the next night, there were as many more in her small garden. Knowing that she certainly had not killed the snails, I asked what she does with the baskets of snails after they are collected. To this, she answered, "Oh, I just take them across the street and dump them on the other side." If her Buddhist neighbor across the street is as fastidious as she, it can be imagined that these two ladies have been trading snails for a long, long time! As one might guess, attempting to set up any sort of control program in these Far Eastern countries is frustrating in the extreme; for even though one may have the co-operation of the well-educated local official, the most orthodox laborers steadfastly refuse to be parties to the crime. Hence, if control measures are set up at all, they more often are half-hearted and ineffectual. It can be seen, then, that al-

though man is basically the single greatest factor known in the "natural" control of the giant African snail, there are whole areas of the world where this factor has virtually been eliminated. Man, therefore, once again has unwittingly fostered the spread of the giant snails.

Longevity The specimen of *A. fulica* which van Leeuwen (1932) kept in captivity for nine years is clearly the record for this species. It is very possible, however, that his specimen spent a large portion of its life in estivation. Because the body processes are at their lowest ebb during estivation, it is altogether logical to reason that the resultant economy in the physiological mechanisms delays the normal gerontologic changes that bring on senescence and death. Longevity could thereby conceivably be extended by an amount comparable to the capacity to withstand estivation, although excesses in frequency or duration in estivation could produce just the opposite effect. As is shown below, this species will readily retreat into quiescence for protracted periods. It is felt, therefore, that van Weel (1948) was probably correct in assuming that van Leeuwen's specimen represents "an exceptional case." But as a case it does seem to emphasize the fact that estimates of the longevity of this species have probably been on the low side.

According to Pelseneer (1935:620), Gibbons reported that *A. fulica* lives for at least two and a half years. The closely related *A. zebra,* however, lived for six and a half years in captivity in London (Longstaff 1921). The only other record for an achatinid is that of Flower (1922), who states that a small *Limicolaria* from Sudan lived in captivity for one year and twenty-one days. In strong contrast are the records of longevity of much smaller pulmonates (e.g., twelve years for *Rumina decollata* [Vignal 1919], thirteen years for *Helix spiriplana* [Vignal 1923] and twenty-three years for *Oxystyla capax* [Baker 1934]). Considering the length of life in other pulmonate gastropod species (cf. Woodward 1880, Pelseneer 1935), it is felt that an average life span of five to six years is a conservative estimate for *A. fulica.* Where specimens are in areas perennially offering optimum conditions for protracted activity, the normal life span possibly may be shortened by a year or more.

Reproductivity In determining the reproductive potential of *A. fulica,* one must know how long it lives, how soon it begins to lay eggs, how often it lays eggs, and how many eggs are laid at a time. One additional factor has been well known from the first: This animal is hermaphroditic and therefore each individual is a pro-

ducer of eggs; further, any two sexually mature individuals have the capacity for being mutually receptive in cross fertilization.

Van der Meer Mohr (1949*b*) reported that he had repeatedly observed "self-fertilization" in *A. fulica* in Sumatra. Rees (1951) interpreted the report as a warning with the words, "This means that the introduction of a single snail to a new country is enough to start a colony." In correspondence with the author, van der Meer Mohr later stated that his conclusions had been based on the fact that snails of seven and a half whorls kept in isolation for as long as 382 days still laid viable eggs. To check his conclusions, van der Meer Mohr (*in litt.* Nov. 5, 1951) kept "virgin" specimens in isolation for two years. None laid eggs. He therefore retracted his original conclusion and reinterpreted his data to mean that a single copulation was sufficient for the fertilization of a number of batches of eggs laid intermittently over a period of many months. It would now appear that van Leeuwen's specimen kept in captivity for nine years without laying eggs had apparently never copulated. In the absence of autofertilization, Rees's warning still is to be taken almost as seriously as it was given; for a single, fertilized, young specimen is capable of laying a great many viable eggs, even after months of estivation.

Information regarding the period necessary for attaining sexual maturity was given by G. S. Dun (*in litt.* Nov. 25, 1949), who reported that snails raised by him from the egg laid their first batch of eggs at the tender age of five to eight months. This concurs almost exactly with the unpublished findings of Daniel B. Langford in Guam. Garnadi (1951) independently reports it as eight months. Earlier, Leefmans (1933*c*) stated that with an abundant supply of CaCO₃ the first eggs were laid in six months; and without it, nine months were required.

According to observations in Micronesia, the number of eggs laid at a time by the average, normal appearing adult snail was found to be close to 300. In Ceylon, the number was found to be nearer 200. Mature pygmy individuals in the Isley Field population in Saipan, however, produced only 30–60 eggs at each laying. Kondo has indicated that the maximum number may go over 500 eggs. Atoda's maximum of 733, as reported by Hatai and Kato (1943), quite probably represents total productivity during the period of observation as his largest snail specimen was only 66 mm. long from base to apex. The whole question of total productivity of *A. fulica* still rests very much in the realm of speculation as the existent figures are based on specimens held in captivity for only a portion of their life or

until they happened to die. Field observations, however, indicate strongly that under optimum conditions, this species will lay a batch of eggs every few weeks for apparently an indefinite period of time or until the advent of unfavorable conditions. There probably is a natural tapering-off in productivity with advanced age; but this also has not been determined for certain.

Green (1911b) assumed that *A. fulica* lived two years and that it laid 100 eggs the first year and 200 the second. From these pure assumptions, he estimated that one gravid individual would give rise to 10,930,442,400, or approximately 11 billion snails, in a period of five years. This figure has been quoted many times in the literature. Van Weel (1949), however, points out that the annual output of eggs would actually be nearer 900–1200; but he makes no estimate as to how these higher figures would alter Green's total. Morrison's estimate (1950b) was ten times that of Green, but it is still too conservative. In the light of our present knowledge of the life history of this snail, and figuring very definitely on the conservative side, let it be assumed that the snails mature in nine months after hatching, produce four batches of eggs a year of 150 eggs each, and live for at least five years. At the end of a three year period, the progeny from one gravid individual, if all lived, would total 7,783,764,301 or nearly 8 billion. With numbers building up exponentially in multiple geometric series, another two years would show an increase to 16,-121,432,399,695,050 or somewhat over 16 quadrillion!

In order to grasp fully the significance of the latter figure, it is almost necessary to interpret it in terms of time and distance. Thus, if we conservatively assume that each individual is 4 inches long and that all the progeny is arranged in a straight line, there would be 15,840 snails per mile for 1,017,767,196,950 miles. This distance would be equivalent to over 2,130,494 round trips to the moon or over 5,477 round trips to the sun. And with light traveling 186,300 miles per second, it would take well over two months for it to travel the distance from the first to the last individual. On the other hand, if one were to count these 16 quadrillion snails, day and night, at the rate of one a second, it would take over half a billion years. This in reverse would take the counter back to the mid-Cambrian, during which period most of our oldest fossils were formed. And as a final comparison: This number of snails would permit each man, woman, and child in the world today to have over 80 million all to himself —or somewhat over 125 acres of snails packed just as closely as possible in a single layer.

This prodigious reproductive potential of *A. fulica* significantly is

in strong contrast to that of predatory snails. According to Kondo (1951*b*), the predatory snail *Gonaxis kibweziensis* gives rise oviparously to only three or four encapsulated, advanced embryos at a time. These are brought forth at an apparent maximum average rate of every ten days during the breeding season for a "reproductive potential of 11 maximum per year (in laboratory)" (Kondo 1956).

Variability   Among the most striking impressions one gets as one examines the various populations of *A. fulica* is the pronounced difference in appearance of the snails. This point has been emphasized and elaborated upon by both Kondo (1950*a, c*, 1952) and Mead (1950*b, c*). Jaski (1953) has been so impressed with the variability in the specimens in Java that he has suggested an explanation might be found either in "recent spontaneous mutation" or "cross-breeding" of the Japanese introduced stock with the stock issuing from the original infestation.

In the Santa Rita and Laguna populations on Guam, the shells are commonly close to six inches in length and are exceedingly thick. Not far away, giant specimens have been found that have exceeded seven inches in length. Probably the record specimen was found by G. D. Peterson; it measured just one-eighth of an inch under eight inches! In contrast, the Isley Field population in Saipan, in the midst of an abundant supply of calcium carbonate, was made up largely of "pygmy" but mature specimens in a size range of two to three inches in length. Shells from Anguar Island in the Palaus were found to have a deep, rich, contrasting color pattern, a thick periostracum, and a high nacreous gloss. Farther north, on Koror Island, a large share of the snails had shells that were dull, chalky, devoid of a periostracum, and so pale that they appeared almost white. One out of every three or four shells in the Army Hill population in Saipan were also pale and devoid of a periostracum; in addition, however, they not only had an arcuate axis, which gave them a "bent-nose" appearance, but had so many lamellate layers of calcareous material deposited around the aperture that the snail could withdraw only partway into its shell. The average specimen encountered in Micronesia was found to be of moderate size ($3\frac{1}{2}$–$4\frac{1}{2}$ inches), to be so thin that they could be broken with ease, and to have a body whorl that was unicolorous olivaceous-tan. Specimens from Manila and India have the proportionately larger body whorl as does *A. fulica hamillei* from East Africa. On the other hand, specimens from some populations in Ceylon and Hawaii, besides being considerably darker in color, have such a long axis and reduced body whorl that they always roll with the aperture upward when they are placed on a flat surface. Nearly all

populations have a small percentage of anomalous forms; Germain (1921) has made an interesting study of these.

An explanation for these and other apparent differences is not difficult to discover. Environmental influence, of course, is being expressed; but the extent has not been determined. In particular, the works of Moore (1936), Ino (1949), and Wagge (1952) bring forth convincing evidence to demonstrate that diet has a pronounced effect upon the appearance, and especially the color, of the snail shell. Because some variable physical characters persist in the same expression in individuals of populations under wholly different environmental conditions, it is assumed that these characters are of genetic origin. The genetic makeup of a given population is predetermined to the largest extent by the genetic complement possessed by the invariably few specimens which started the population. As these first few specimens give rise to subsequent generations, the various genetic combinations make their appearance. The environment, in turn, has its own complement of variable ecological factors. This complement will literally "select" from the genetically variable snails the combination of genetic characters which is best suited to it. Had the original first few snails been of a different genetic makeup, other genetic combinations would have been available, and the environment might therefore have selected differently. Another environment would have selected still differently. The many different appearing snail population types, then, would seem to be explained by the simple combination of small initial population, isolation, inbreeding, considerable genetic variablity, phenomenal reproductivity, and environmental diversity. Variability thus is of survival value and it helps to explain the success this species has had in becoming established in the many different environments in which it now is found. We do not know the limits of genetic potentiality in producing still different and still more hardy individuals.

Estivation and Hibernation   In 1930 Duval made a significant finding when he determined that the freezing point was lower in hibernating *Helix pomatia* than in active individuals of the same species. This work was followed quickly by that of von Brand (1931, 1932) confirming the predictable fact that the H_2O content of *H. pomatia* is actually lower during hibernation than during periods of normal activity. Kamada (1933) corroborated with the report that the blood of hibernating *H. pomatia* was isotonic with 0.69 per cent NaCl whereas that of active individuals was isotonic with 0.50 per cent NaCl. These findings meant to Howes and Wells (1934a, b) that hibernation as a physiological phenomenon requires "elaborate met-

abolic preparations," whereas estivation, which is also a resting phase, is a comparatively simple physiological phenomenon. The two phenomena are elaborated upon by Pelseneer (1935).

Estivation in *A. fulica* is of the commonest occurrence. In fact, of the great many populations of this species that have been examined by the author in almost every conceivable type of environment there never has been one in which an estivating individual could not readily be found. A direct correlation between estivation and reduced moisture in the environment has been independently arrived at by a number of investigators. But it was not until the observations of Howes and Wells (1934*a*, *b*) that an interpretation was advanced to explain the presence of estivating individuals even under optimum conditions for snail activity. It was their conclusion that "there was a tendency for phases of estivation to alternate with phases of activity during the life of any one individual, even under approximately constant external conditions, so that at any time some of the animals would be in either phase." They concluded further "that estivation is the result of a low water content, and that the latter may be brought about either by dryness of the environment or else by the natural hydration cycle of the animals." The significance of these conclusions is tremendous; for in them is found the explanation for the fact that no combination of even the most rigorous control measures, under apparently ideal conditions, have ever been effective in eradicating *A. fulica*. In other words, it is the well-secreted, estivating individuals that are responsible for restocking an infested area after the effects of normal or man-made adverse conditions have dissipated.

Although estivating snails are most often found under protective conditions that are very superficial, some individuals work their way into remarkably inaccessible niches. They have been found far under sizable rocks, deep in hollow trees, in the center of rotten logs, high in the crotches of trees, far into plant debris, and under many protective layers of man-made litter. The inhabitants of Chichi Jima stated that during the winter months *A. fulica* specimens are found four to five inches below the ground. In the former Belgian Congo *A. rugosa* has been found four inches below the surface of the ground in a dry, open, sunny spot (Bequaert 1919). Others have been found "several inches" in the ground (Lang 1919). In Ceylon it was observed that during mildly adverse conditions, such as a brief dry spell during the rainy season, specimens of *A. fulica* to a great extent tended to remain in a quiescent state on the tree trunks. Usually they were in a range of 3–9 feet from the ground, although specimens were observed to be as high up as 30–35 feet in the dadap trees. At

these times the ground-dwelling predators remained active and it was therefore a temptation to ascribe a protective function to this behavior of the snails. When environmental conditions were favorable, a large percentage of the snails would make nocturnal visits to the ground but would retreat to the tree trunks with the approach of day. Under prolonged adverse conditions, however, the snails would leave the tree trunks to seek normal estivation sites on or in the ground. At such times many of their predators, significantly, also were inactive.

During estivation a thin, fragile, muco-calcareous epiphragm is formed over the aperture of the shell. This epiphragm is normally complete except for a thin grooved slit over the pneumostome permitting the reduced respiration to take place. The slightest disturbance may cause the estivating snail to withdraw farther into its shell. This invariably ruptures the epiphragm. The snail may then repair it, replace it with a new one, or go into a period of activity. The general subject of epiphragm formation has been treated by Hora (1928) and Hora and Rao (1927). The epiphragm of *A. immaculata* has been described by Smith (1899); and Williams (1951) has described the epipragm of *A. albopicta*. Of particular interest is his description and illustration of the tubular epiphragm formed by specimens estivating on tree trunks. This apparently has never been observed in *A. fulica,* although specimens adhering to vertical surfaces have very often been observed to attach themselves at the aperture by a more parchment-like secretion before forming the normal, flat, complete epiphragm.

It is definitely not known whether *A. fulica* can actually undergo hibernation with all its attendant complex physiological adjustments. In Hong Kong, Herklots (1948) stated, "In the cold, dry winter months they hibernate. . . ." It is possible, though, that the quiescent individuals to which he referred were really in a continuing state of estivation which had been initiated by the dryness of the late fall months. Specimens in that area examined by the author in January, 1955, behaved no differently from those known to be in estivation in other areas. The most northerly, well-established populations of this species are in Ani Jima and Chichi Jima of the Bonin Islands. The "shivering cold" weather in those islands, however, is quite comparable to that of Hong Kong inasmuch as weather records for Chichi Jima indicate a low of 45° F. during a recent thirty-year period (Kondo *in litt.* Jan. 6, 1950; cf. Clayton 1927). But irrespective of whether it is hibernation or estivation, the fact remains that *A. fulica* in these cooler areas not only survives, but thrives.

Hardiness   Coupled with the phenomena of estivation and hibernation is the physiological faculty of being able to survive prolonged periods without food or water. There is strong evidence that the duration of a period of quiescence is closely correlated with temperature. Under tropical conditions, *A. fulica* has been reported to have survived periods of estivation, without food or water, for 5½ months (Lange 1950), 7 months (Mead 1950*b, c*), 10 months (Corbett and Pagden 1941), and 12 months (G. S. Dun *in litt.* Nov. 25, 1949). G. S. Butler in Hawaii placed 27 specimens in a jar without food or water in November, 1958; 10 months later, 10 specimens remained alive. *Archachatina degneri* was still living after having been kept under similar conditions for nearly 6 months (Mead 1950*a*). In the literature, the record for duration of estivation is 15 years for an unnamed snail species (Bingley 1829); the scientific accuracy of this record, however, is open to question. The classical example, often referred to, is that of *Xerarionta veatchii* which estivated for 6 years (Stearns 1868). Other records worth noting are *Paludestrina ulvae* (a freshwater snail), 5 years (Quick 1924); *Helix desertorum,* 4+ years (Baird 1850); *Otala lactea,* 4+ years (Gaskoin 1850); "many Helices," 3+ years (Calkins 1877); *Bulimulus pallidior,* 2+ years (Stearns 1877); and several common European helicine species, approximately 1 year (Hartley 1898, Lockwood 1880, Sivers 1872, Ward 1879). Kew (1893) gives a general treatment of the subject. Even though the record so far for *A. fulica* lines it up with the lesser lights in the literature, the faculty for estivating for a whole year without food or water equips this species well for surviving even the slowest, most devious trip to an uninfested land.

Dun (*loc cit.*) stated that after twelve months in estivation his specimens of *A. fulica* had lost approximately 60 per cent of their original weight. Specimens emerging from estivation were observed both in the Pacific islands and in Ceylon to "drink" water by rasping at drops. In this manner, other species have been reported to take up 80–100 per cent of their weight in water in a short period of time (Zimmerman 1931). Anatomical examinations of estivating *A. fulica* have shown that several of the organ systems are drawn upon for sustenance. One of the first to be affected is the reproductive system; this becomes atrophied and proportionately attenuated, resembling superficially the condition in the juvenile specimen (Mead 1950*a, b, c*). This same phenomenon has been reported in other species (Laviolette 1950). The general subject of resistance to desiccation has been ably elucidated by Gebhardt-Dunkel (1953). Important as a consideration in the present study is the classical work of Shelford

(1913) which establishes the fact that the rate of evaporation in an environment is the result of the combined action of wind, temperature, isolation, and dryness of the air. It is this rate of evaporation which closely determines, inversely, the rate of activity of terrestrial gastropods in general; and *A. fulica* is manifestly no exception. In fact, it was observed innumerable times in Ceylon and in the Pacific islands that this species is extremely sensitive to even a slightly elevated evaporative rate.

Food, as a vital factor in the environment, is quantitatively and qualitatively infinitely more flexible in the life of *A. fulica* than in almost any other animal that could be mentioned. As pointed out below, this snail has a tremendous range of acceptable foods; now it is apparent that it can go without all food, including water, for months on end.

The environmental factor of temperature operates apparently in a much more limited range than the factors of food and water. *A. fulica* dies quickly when exposed to the direct sunlight; however, a humid, tropical climate in general seems to offer the nearest to optimum conditions for this species. Such a climate is also conducive to typically luxuriant plant growth which affords ample protection for the giant snail during the daylight hours. As this snail has rapidly extended into many new areas in the past few years, it has "taken hold" in some environments which seem far indeed from what might have been predicted as acceptable. For instance, beach populations were encountered in the Bonin and Mariana Islands, which had such formidable barriers as open stretches of barren, hot sand, and adjacent vegetation covered with fine salt crystals from the constant ocean spray (Kondo 1950c). The fact that this snail was able to crawl over salt-covered vegetation with apparent impunity attests to its remarkable adaptability and hardiness. But as far as the excessively high temperature of the beach areas is concerned, it was the normal nocturnal habits of the snail which permitted it to forage under the suitable conditions of reduced temperatures and concomitantly higher relative humidity. This, incidentally, is a point completely overlooked by those who are prone to preconception in deciding whether or not a given environment will be acceptable to the giant snail. As a parallel, Jarrett (1922) announced on the basis of a small amount of empirical evidence that the European *Helix aspersa* could not take hold in Malaya. Others had similarly predicted that this species could not survive in the Sonoran southwestern part of the United States; yet it was recently found to be well established in southern Arizona (Mead 1952a, 1953a).

The capacity of *A. fulica* to withstand reduced temperatures is an almost completely unknown quantity. The experiments of Chock and Nakao (1951) provide the only information extant on this subject; but even these were very limited in their scope and, therefore, misleading. Their experiments consisted of placing snail and egg specimens in "standard refrigerators of various models" set at 20° F. at r.h. 52–56, 30° F. at r.h. 55–65, 40° F. at r.h. 35–40, and 45° F. at r.h. 40–50. Specimens were set up in the following groups: eggs on the surface of soil, eggs buried in one inch of soil, active adults on the surface of soil, active adults buried with three inches of soil around them in every direction, and dormant adults on the surface of soil. The groups were exposed to a given reduced temperature for a varying number of hours or days. The lethal minimum exposure for 45° F. was reported as 4 days for active snails on soil, 4 days for active snails in soil, and 7 days for dormant snails. The eggs proved to be very susceptible to all reduced temperatures. Some investigators unfortunately have accepted the reported results of these exploratory experiments as definitive and have speculated as to just where in the world *A. fulica* could become successfully established. Both as a note of caution and as a guide in future experiments in the problem of reduced temperature tolerance, certain points should be emphasized.

In the experiments of Chock and Nakao, there are some inconsistencies in results which seem significant. Nineteen out of 20 dormant snails, exposed to a temperature of 40° F. for 24 hours, remained alive after 5 days; 7 out of 10 active snails, exposed to a temperature of 30° F. for 8 hours, remained alive after 5 days; and 1 out of 10 dormant snails, exposed to a temperature of 20° F. for 8 hours, remained alive after 5 days. The inference is that larger samples might have told a somewhat different story, especially regarding survival at the population level. In strong contrast to these survival rates in the preliminary series of experiments, the supplementary series conspicuously showed consistently complete killing throughout the experimental results. No explanation was given for this. Although humidity was controlled to an extent, it was not treated as a constant; and this fact doubtless has influenced the results as another variable.

An important consideration which was apparently overlooked in the experiments is the distinction between estivation and hibernation. The "dormant" specimens were obviously in estivation; yet they were subjected suddenly to conditions demanding a hibernation response. Although it should have been the dormant specimens rather than the active specimens that were buried in soil during these experiments, burying them in the manner that they did, with

three inches of soil all the way around, did not duplicate conditions in the field where heat loss takes place essentially from a single plane. Naturally, there would be in the field an additional insulating effect produced by superincumbent logs, rocks, plant debris, rubble, and the like.

The most important factor which has not been taken into consideration in these experiments is that which concerns the acclimatization or *conditioning* of the animal as it *gradually* is exposed to lower and lower temperatures. Actually, after a snail has been feeding actively for several days, it extends so far beyond the lip of its shell in the fully contracted condition that it cannot possibly form the protective epiphragm even though sudden adverse conditions may demand it. Normally, a period of less favorable conditions will effect a gradual water loss which, among other things, will permit of epiphragm formation. The entomologists have demonstrated many times that certain insects will adjust to remarkably low temperatures if they are arrived at slowly enough. Cockroaches put suddenly in a cold chamber will die in a short time; and yet if several days are taken to reach gradually the temperature in the cold chamber, these insects will undergo physiological changes, including the alteration of the water content of the cells, and withstand successfully the lower temperatures for prolonged periods of time (Wigglesworth 1953). It therefore brings no surprise that many insect pests are infinitely more abundant after a mild winter than they are after an unseasonably sudden cold snap. It doubtless is this phenomenon of a physiological adjustment that permits the giant snail to maintain vigorous populations in the Bonin Islands despite the relatively cold winters. Apropos of this, it has been suggested that a possible sensitivity to the greater diurnal-nocturnal fluctuations in temperature at altitudes above 5,000 feet have kept *A. fulica* conspicuously only at the lower altitudes (see p. 197).

As an interesting and possibly significant sidelight, Longstaff (1921) kept specimens of *Achatina zebra* in London for six and a half years, during which time the temperature in the conservatory where they were kept "did not fall below 45° F." He observed that during the colder months, they remained buried for many weeks at a time.

The faculty of *A. fulica* to withstand trauma and even an extensive loss of its shell attests still further to its general physical hardiness. Particularly in the islands of the Pacific, specimens are frequently encountered that have shells almost unbelievably damaged. On inspection, it can be seen that the shells have suffered many breaks. Some-

times the broken shell pieces are not dissociated and are repaired in place. But, more often, the pieces break off completely or become badly dissociated; under such conditions, repair produces an unsightly shell that gets progressively worse with each subsequent break. Occasionally the mantle becomes damaged and this adds to the distortion through malformation of the new shell. Kondo (1950c) has reported instances where specimens have survived the loss of the lower 2–2½ whorls of their shell; and that is considerably over half the bulk of the shell. As might be expected, there is a direct correlation between the instances of damaged shells and the barren, hard, or rocky nature of the terrain. If there is a cover of humus or a thick undergrowth to break the fall of the foraging snail, there will be little or no damage to the shell even though it is relatively thin.

In the regions in Ceylon where the jungle crow was commonly encountered, it was not unusual to find giant African snail specimens which had sustained a considerable loss of flesh as a result of pecks by these malacophagous birds. Most often, it was the posterior portion of the foot, that is, the last part to be withdrawn into the shell, that was amputated and regenerating. Occasionally, however, specimens were found with one or both ommatophores removed, including a portion of the head. Specimens were also found that were regenerating tissue lost in unsuccessful or incomplete attacks by the predatory glowworms.

The large, heavy shell and the generous supply of mucus of a mature giant African snail affords considerable protection both from the adverse physical factors in the environment and from natural enemies. Even such avid snail feeders as ducks and geese are unable to handle the snails if the specimens are more than a few months old.

As will be seen in the discussions below, this species has demonstrated a remarkable capacity to withstand submersion in both fresh and salt water. The typhoon and flood in Manila (Pangga 1949), the flood in Babelthaup (Esaki and Takahashi 1942), and the tidal wave in Chichi Jima (Mead and Kondo 1949), if anything, seemed to speed up the increase and spread of the giant snail population after the initial, temporary setback.

Paucity of Natural Enemies   As one reviews the entire topic of the biological control of *A. fulica*, one is left with the profound conviction that this animal has remarkably few natural enemies indeed. Even the natural enemies it does have are of questionable value in effecting any real control. And this is one of the reasons that some investigators are now in the process of attempting to discover and import foreign predators which promise to become new "nat-

ural" enemies of the giant snail. *A. fulica* even seems insensitive to competition from the endemic species of snails in the areas it has invaded (e.g., the large *Rhysota* in the Truk Islands). On the contrary, it is felt that some of the endemic species, such as *Partula gibba*, are actually losing in the competition for the gastropod niche in the environment (Kondo 1950c).

Period of Activity   The facts that *A. fulica* is normally nocturnal and crepuscular in its habits, and that it will become active in the daytime when it is raining or overcast, indicate that light, as well as temperature, moisture, and food, is a vital factor in its activity. To a great extent, activity during these periods permits the giant snail to escape a number of basically unfavorable environmental factors operative under normal diurnal conditions. A definite homing instinct appears to be present in this species. The experiments of Hatai and Kato (1943) indicated that this may be demonstrated by as much as 70 per cent of the active members of a giant snail population. Such an instinct is of survival value in that it permits the snail to locate readily a protective retreat.

Availability of Calcium   In a study of the relationships of snails to soil, Van Cleave (1953) concluded that "the presence of the snails is an indicator of available lime supply. . . ." Usually, the malacologist looks at the correlation from the other direction, namely, that if a good lime supply is present, snails will be found. With respect to the achatinas in particular, Pilsbry and Bequaert (1927) found in the former Belgian Congo a direct correlation between limy soil and abundance of snails. Similarly, Oughton (1948) concluded that the sole nutritional factor limiting the distribution of snails is the availability of calcium. It is not understood why the findings of Hagen (1952) were in direct contrast. Adding calcium to the diet of snails was demonstrated by Oldham (1929a, 1934) to produce in several European snails a shell somewhat larger and heavier by three to four times.

With information of this type coupled with the knowledge of the diversified eating habits of *A. fulica*, it is understandable why the coralline islands of the Pacific have managed to support inordinately large populations of this snail pest. The mineral soils of these islands is reported to have a pH range that is on the alkaline side (e.g., pH 7.2–8.7 in the Arno Atoll [Stone 1951]). $CaCO_3$ in such soils would be stable. This is precisely the explanation for the findings of Atkins and Lebour (1923a, b) wherein snails showed a preference for slightly alkaline soils, being most abundant in the pH range of 7.0–8.0.

These facts, however, made it all the more difficult to understand

how the strongly acid soils of Ceylon could support equally large populations of *A. fulica*. The soil in the tea-growing areas, for example, is characteristically near a pH of 4.5. $CaCO_3$ could not possibly last long in such acidity, especially in the presence of the usual abundant moisture. The calcium which is present is locked up in silicates and combinations of iron and aluminum. Plants are able to "unlock" this calcium as manifested by the fact that plant leaf analyses in the acid soil areas of Ceylon revealed as much as 40 per cent calcium in the ash. When the nocturnally feeding *A. fulica* were seen to feed extensively on fallen leaves in these areas, it was then understood where they were obtaining the lime for their shells. But of even greater importance was the fact that here were snails independent of an "available" supply of lime in the soil.

The calcium cycle continues as shells of dead snails are rasped completely away by those that survive. Even the living snails will rasp their own shells, especially along the lip of the shell, and particularly right after a period of estivation. In the Pacific islands, specimens were encountered with the surface of the shell, which had been exposed during estivation, rasped by other snails until it was paper-thin. Snails deprived completely of an external source of calcium are able to draw upon their own shell for their calcium needs for a long period of time (Wagge 1952).

Acid soils and a concomitant lack of available $CaCO_3$ in the soil, then, are no real deterrents to *A. fulica*. Ironically, man in Ceylon unwittingly converts a situation which is tolerable for the giant snail into one that is distinctly favorable. Cacao is being grown more and more in that country because on the world market it is more dependable than rubber. Cacao, however, requires a less acid soil (i.e., in a pH range of 6.0–7.0). Alkalizing the soil is accomplished by adding dolomitic lime. This increases the productivity of the cacao; but it also makes the environment more favorable for the giant snails. Little wonder that the largest populations of this snail in Ceylon were encountered in cacao plantations!

Escape Reaction and Migration Cycle Specimens of *A. fulica* from the Mahinui population in Oahu were marked with white paint and after a period of confinement were released in their home area under essentially the same weather conditions in which they were collected. Observations over the following hours and days revealed an unmistakable "escape reaction" of sustained crawling to the periphery of the experimental area in surprisingly near-equal numbers in all directions of the compass. Further experiments are being conducted. On the basis of what has been observed, however,

it has been suggested (Mead 1959*b*) that there exists a "migration cycle" comparable to the "hydration cycle" of Howes and Wells (1934). It is proposed that even under essentially ideal conditions, specimens from time to time will undergo sustained movement out of the home area. Stimuli adequate to invoke this reaction may be less intense in an inverse proportion to the time element since the last "migration." The most subtle stimulus may be sufficient to initiate the reaction in some individuals that have been sedentary for a protracted period of time. On the other hand, a sufficiently strong stimulus might surpass the threshold of a large segment of a snail population in an erstwhile reasonably stable environment and precipitate a "mass migration." Such migrations have been observed many times in the field by a number of investigators, but they have continued to remain essentially unexplained. It is more than likely that intercurrent stimuli (e.g., prevailing wind [Chamberlin 1952*a, b*]), would have a directive influence on the movement.

Proof of the existence of a "migration cycle" would throw much light on the factors of dispersal and population density.