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Achatina fulica Bowdich and Other Achatinidae as Pests in Tropical Agriculture

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Achatinidae are native to Africa. The family is represented by about 200 species in 13 genera. Several species have attained pest status within their native African range when the habitat is modified for human habitation and cropping. Furthermore, associated with the increased mobility of humans and globalization of travel and trade, several achatinids, the most notable of which is *Achatina fulica* Bowdich, have been accidentally or purposefully transported to areas outside their native range in Africa and further afield. In these new areas Achatinidae can cause significant economic and ecological impacts. This chapter provides a synopsis of Achatinidae as pests in tropical agriculture, focusing primarily on *A. fulica*, but also bringing together the relevant information on other pestiferous achatinid species.

Origins

The dominant features of the vegetation in Africa today are the tropical forest and the savannah. Most of the diversity in African terrestrial gastropods is concentrated in the forest and its isolated outliers, and indeed the forest is generally regarded as the centre of gastropod evolution on the continent. Van Bruggen (1986) recognized four sub-Saharan centres of endemism among African terrestrial gastropods, namely: (i) southern Africa; (ii) East Africa; (iii) north-east Africa; and (iv) Central/West Africa. Each centre was assumed to have functioned as an important refugium during periods of forest contraction in the Holocene.

The margins of the forest have never been permanent: throughout the climatic history of Africa the forest has waxed and waned in response to changing rainfall patterns. In the arid or interpluvial period *c.* 18,000

years BP the forest was reduced to a number of major blocks, which may have functioned as refugia for the tropical, forest-dependent biota (Diamond and Hamilton, 1980; Hamilton, 1981; van Zinderen Bakker, 1982; Mayr and O'Hara, 1986; van Bruggen, 1989). The East African forest in particular suffered the vicissitudes of climatic variation in the past due to the varied topography. Verdcourt (1984) and van Bruggen (1986) indicated that even fairly minor changes in rainfall and temperature have given repeated opportunities for vicariant speciation. However, this view may be an oversimplification of the evolutionary setting in Africa, particularly if the primary adaptive radiation(s) and the greater part of the speciation that led to the extant fauna predate the Holocene (which is highly probable in the case of the terrestrial gastropods) and if we accept that the savannah was or is not the biological desert that it is often purported to be.

The earliest fossil record for the Achatinidae is from the Pleistocene in Africa (Solem, 1979a,b) but the family clearly evolved much earlier. Mead (1950a, 1995, 1998) has postulated that the earliest achatinids originated north of the Zambezi, in the Lower Guinea of Cameroon and Gabon, with subsequent dispersive radiation into the southern parts of the subcontinent, in both the arid and the subarid areas, and in the moist parts east of the great watershed. Mead thus considered that the temperate species were in the main directly derived from tropical ancestors. Van Bruggen (1969, 1970, 1978) concurred with Mead in regarding the fauna of southern Africa as being derived from southward dispersal. None the less, the evolutionary history of the achatinids remains unknown. While much anatomical information is available (Pilsbry, 1906/7; Mead, 1950a, 1979b, 1988; van Bruggen, 1965, 1966, 1968, 1985; van Bruggen and Appleton, 1977; Sirgel, 1989) (much more is purported to be at hand but remains unpublished – A.R. Mead, personal communication, 2000), compelling data have yet to be presented to demonstrate that the nominal supraspecific taxa are in fact monophylogenetic units, and no quantitative character analysis has been presented to date to elucidate the phylogenetic relationships within the family. Thus the evolutionary history of the Achatinidae remains largely unkown.

Today the Achatinidae occupy practically all of sub-Saharan Africa, from Senegal (15°N) in the west, the region of Lake Chad (about 14°N) and the southern Egyptian Sudan (about 8°N) in the centre, and southern Ethiopia (about 7°30′ N) and Somaliland (about 5°N) in the east. They extend to South Africa, where species are to be found in the Orange River area on the west coast and in the District of George on the south coast of Cape Province. Central/West Africa is remarkably rich in achatinids, as is the East African centre. Achatinid diversity is considerably lower in southern Africa and north-east Africa (van Bruggen, 1969, 1986). São Tomé, a remote island off the Central/West African coast, has at least one endemic genus, the monotypic *Atopocochlis* Crosse & Fischer, while Príncipe and São Tomé share the monotypic subgenus *Archachatina* (*Archachatina*) Albers s.s. In contrast, the continental and little distant

island of Fernando Poo (distance to continent 32 km) does not harbour any endemics among the Achatinidae.

Species richness among the achatinids is concentrated in two main genera, *Achatina* de Lamarck and *Archachatina.* J. Bequaert in Pilsbry (1919) considered *Archachatina* to be West African, being present on the islands of the Gulf of Guinea and in the coastal belt from Monrovia to the Kuilu River (Gabon). *Achatina* is widely distributed in sub-Saharan Africa. In West and Central Africa species of *Achatina* are confined to humid areas, while species of *Archachatina* are distributed in less humid areas (Hodasi, 1984). According to J. Bequaert in Pilsbry (1919), *Achatina* are essentially 'of the lowlands; in the mountains and on the plateaus of Central Africa the number of species and individuals decreases at about 1200 m and the genus is not found above 1500 m'. This points to a tropical origin. The majority of species in these genera are naturally confined to forested areas. However, as noted by H. Lang in Pilsbry (1919) in relation to species of the Belgian Congo, achatinids are often scarce in unmodified forest. Indeed, several achatinids, such as *Achatina achatina* (Linnaeus), have exhibited great adaptation to environmental change brought about by human encroachment and modification of the forests and in many of these modified areas Achatinidae occur in great numbers.

In East Africa a number of achatinid species are confined to humid, tropical forests. Further species are temperate forest dwellers, with *Achatina mulanjensis* Crowley & Pain, *Achatina tavaresiana* Morelet and *Archachatina bequaerti* Crowley & Pain occurring at high altitude in Malawi. However, as in West and Central Africa, a number of species are prevalent in forest-margin habitats. *A. tavaresiana* and *A. fulica*, for example, occur in large numbers along the margins of forest in East Africa (Crowley and Pain, 1964). *A. fulica* is present naturally from Natal and Mozambique in the south to Kenya and Italian Somaliland in the north. It extends 250–830 km from the coast, going farthest inland in the northern section of the range (Mead, 1949; J. Bequaert in Lange, 1950).

Numerous species of Achatinidae occur in humid, tropical–subtropical south-eastern Africa. The family is also well represented in temperate zones in South Africa: *Archachatina ustulata* (de Lamarck), *Archachatina marinae* Sirgel and *Achatina zebra* (Bruguière) are lowland species, while *Archachatina machachensis* (Smith), *Archachatina montistempli* van Bruggen and *Archachatina omissa* van Bruggen are confined to areas over 1300 m in the Drakensberg Range. *A. machachensis* occurs at altitudes of 1600–1800 m in Lesotho and the neighbouring plateau of southern Africa, areas that have cold winters with frosts and snow. The animals hibernate over winter. Elsewhere in Africa achatinids have a montane existence as well, but as rule only under temperate conditions. Furthermore, there are species of southern Africa that occur in less humid areas. The South African *Archachatina zuluensis* (Connolly) is restricted to dune and other coastal forests. *Achatina immaculata* de Lamarck is an example of a savannah-adapted species, occurring as large morphs in the savannah in southern Africa but as a somewhat smaller

morph in the forests of the Rhodesian eastern escarpment (van Bruggen, 1978), possibly indicating a better adaptation to the savannah environment than to the forest. Bechuanaland of South Africa and the adjoining Botswanian deserts support five species of Achatinidae, namely *Achatina ampullacea* Böttger, *Achatina dammarensis* Pfeiffer, *Achatina passargei* von Martens, *Achatina schinziana* Mousson and *Achatina tracheia* Connolly (van Bruggen, 1969, 1978). These desert taxa have comparatively small shells compared with their more northern, forest-dwelling relatives, possibly indicating a gradient of selection pressure opposite to that operating on *A. immaculata*.

The genus *Limicolaria* Schumacher, represented by about 17 species (Crowley and Pain, 1970), extends from the southern limits of the Sahara south to the northern part of Malawi. According to Crowley and Pain (1970, p. 1), '*Limicolaria* are common everywhere on the west coast but are not found in maritime areas to the east.' Crowley and Pain (1970) regarded these animals as 'tropical' and to 'live equally in the forest and the veld country'. However, on both points these authors provide erroneous generalizations. First, a number of species are confined to montane habitats (to about 3000 m in the case of *Limicolaria turriformis* von Martens on Mt Mweru and *Limicolaria saturata* Smith on Kivu), and are more correctly to be regarded as temperate. Secondly, while a number of species occur in both forest and savannah, the majority are evidently confined principally to one or the other type of habitat. Many of the forest species occur in abundance in modified forest, at the forest edge and in plantations (e.g. Owen, 1965; Crowley and Pain, 1970; Tattersfield, 1996). In open country, *Limicolaria* spend long periods of time in soil, often at appreciable depths. These open-country species often also favour cultivated land and are found on the outskirts of settlements and farms.

Burtoa Bourguignat, as recognized by Crowley and Pain (1959) in their revision, comprises a single species (*Burtoa nilotica* (Pfeiffer)) widely distributed from the Sudan, south of 10°N, throughout the region of the Great Lakes to the Amanze Inyama River in the south, and into the upper Congo, upper Kasi and Lake Chad regions in the west. In Central Africa, *B. nilotica* occurs as a large, silvicolous form, often at high elevation, and is rarely seen in modified areas (H. Lang in Pilsbry, 1919). However, to the south, a smaller, savannah-adapted form is present (Crowley and Pain, 1959; van Bruggen, 1978). Crowley and Pain (1959) assigned subspecific status to seven regional variants of this taxon.

Among the minor achatinid genera, *Perideriopsis* Putzeys is restricted to the forests of the Congo basin. The genus *Limicolariopsis* d'Ailly occurs widely in Central and East Africa, represented by a small series of species of high-elevation forests. *Callistopepla* Ancey, a probable composite genus, has apparently been found only in the West African and equatorial rain-forest belt. *Callistopepla nyikaensis* (Pilsbry) occurs at high altitude in Malawi. J. Bequaert in Pilsbry (1919) considered *Cochlitoma* de Férussac to be restricted to South Africa, south of the Orange River on the west coast and of the Zambezi in the east. *Metachatina* Pilsbry is

restricted to south-east Africa, predominantly in the coastal lowlands of Natal and southern Mozambique, but also occurring at 600–1300 m in the Lebombo escarpment and Drakensberg Range of Natal. Restricted to humid habitat in shrubland and forest vegetation, this monotypic genus, represented by *Metachatina kraussi* (Pfeiffer), is apparently a comparatively new development in a submarginal but none the less warm and humid area of the family.

Many achatinids are able to secrete a protective epiphragm in order to temporarily close the shell aperture, which for species living in the drier parts of Africa is considered of great survival value. H. Lang in Pilsbry (1919) notes, for example, that the species of the open-plain areas of Central Africa aestivate over the dry season, buried 'several inches below the surface, their aperture closed by a strong epiphragm some distance in from the edge of the shell'. None the less, the occurrence of aestivation varies among and within species (Hodasi, 1982) and even species living in moist rainforest, such as *A. achatina*, may aestivate during the drier months. Van Bruggen (1969) considered the absence of the capacity to produce an epiphragm, evident in a number of forest-dwelling achatinid species, to be a secondary phenomenon. This implies that at least some of the extant Achatinidae were derived from species that primarily inhabited the open veld country, which is contrary to the hypothesis of origin in the tropical forest.

Humans have long been part of the African biota and have had a profound influence on the African environment, particularly at the margins of the tropical rainforest (e.g. Boughey, 1963). As noted above, a number of achatinid species are evidently well adapted to this human-induced disturbance of the rainforest and can be locally abundant in plantations. There are occasional reports from various parts of Africa of achatinids causing damage to crop species (Table 3.1). However, many such situations are often short-lived, as the achatinids are collected for their meat, especially by peoples of West and Central Africa (Bequaert, 1950a). Hodasi (1989) reported that the increase in the human population in West Africa, coupled with the increasing cost of animal proteins, such as beef, pork and chicken, has meant that achatinid meat is an increasingly popular source of protein and iron for the rural poor.

Von Stanislaus *et al.* (1987) considered predation by humans as currently important in population regulation of forest-dwelling species, such as *A. achatina*, *Achatina monochromatica* Pilsbry, *Achatina balteata* Reeve, *Archachatina marginata* (Swainson), *Archachatina degneri* Bequaert & Clench and *Archachatina ventricosa* (Gould). The peoples in West Africa have different preferences for achatinids: in Nigeria the species of choice is *A. marginata*, while in Ghana *A. degneri* is preferred (Hodasi, 1989; Olufokunbi *et al.*, 1989). Coupled with habitat destruction through deforestation, the high rates of human predation are leading to a general decline in Achatinidae in West Africa (Hodasi, 1989). Consequently there is increasing interest in commercial production of achatinids to supply the lucrative urban gourmet trade (Elmslie, 1982;

Table 3.1. Crop plants in Africa recorded as being susceptible to feeding damage by Achatinidae.

Country in which damage was recorded	Crop species	References
Achatina achatina (Linnaeus)		
Ivory Coast	Cabbage (*Brassica oleracea* Linnaeus; Brassicaceae)	Otchoumou
	Cassava (*Manihot esculenta* Crantz; Euphorbiaceae)	*et al.* (1989/
	Lettuce (*Lactuca* Linnaeus spp.; Asteraceae)	90), Tra
	Papaya (*Carica papaya* Linnaeus; Caricaceae)	(1994)
	Sweet potato (*Ipomoea batatas* (Linnaeus)de Lamarck; Convolvulaceae)	
	Yam (*Dioscorea alata* Linnaeus; Diascoreaceae)	
Ghana	Lettuce (*Lactuca* Linnaeus spp.; Asteraceae)	Hodasi (1975,
	Oil palm (*Elaeis guineensis* von Jacquin; Arecaceae)	1979)
	Orange (*Citrus sinensis* (Linnaeus) Osbeck; Rutaceae)	
	Papaya (*Carica papaya* Linnaeus; Caricaceae)	
	Pear (*Pyrus communis* Linnaeus; Rosaceae)	
Achatina albopicta Smith		
Kenya	Papaya (*Carica papaya* Linnaeus; Caricaceae)	Williams (1951)
Achatina craveni Smith		
Tanzania	Coffee (*Coffea* Linnaeus spp.; Rubiaceae)	Salaam (1938),
	Sesame (*Sesamum orientale* Linnaeus; Pedaliaceae)	van Dinther (1973)
Achatina fulica Bowdich		
Tanzania	Coffee (*Coffea* Linnaeus spp.; Rubiaceae)	Mead (1961)
Achatina zanzibarica Bourguignat		
Tanzania	Cotton (*Gossypium herbaceum* Linnaeus; Malvaceae)	Tomaszewski
	Sisal (*Agave sisalana* Perrine; Agavaceae)	(1949), van Dinther (1973)
Archachatina marginata (Swainson)		
Nigeria	Banana (*Musa paradisiaca* Linnaeus; Musaceae)	Imevbore &
	Lettuce (*Lactuca* Linnaeus spp.; Asteraceae)	Ajayi (1993)
	Papaya (*Carica papaya* Linnaeus; Caricaceae)	
Limicolaria aurora (Jay)		
Cameroon	Oil palm (*Elaeis guineensis* von Jacquin; Arecaceae)	Spence (1938)
	Leguminous cover crops	
Limicolaria flammea (Müller)		
Nigeria	Apple (*Malus* × *domestica* Borkhausen; Rosaceae)	Egonmwan (1991)
Limicolaria kambeul (Bruguière)		
Sudan	Maize (*Zea mays* Linnaeus; Gramineae)	Salaam (1938),
	Groundnut (*Arachis hypogaea* Linnaeus; Fabaceae)	Godan (1983)
Limicolaria martensiana (Smith)		
Uganda	Cabbage (*Brassica oleracea* Linnaeus; Brassicaceae)	Owen (1965)
	Lettuce (*Lactuca* Linnaeus spp.; Asteraceae)	
Nigeria	Carrot (*Daucus carota* Linnaeus; Apiaceae)	Egonmwan
	Lettuce (*Lactuca* Linnaeus spp.; Asteraceae)	(1991)
	Potato (*Solanum tuberosum* Linnaeus; Solanaceae)	
Limicolaria numidica (Reeve)		
Cameroon	Oil-palm (*Elaeis guineensis* von Jacquin; Arecaceae)	Spence (1938)
Limicolaria zebra Pilsbry		
Cameroon	Oil-palm (*Elaeis guineensis* von Jacquin; Arecaceae)	Spence (1938)

Awesu, 1988; Hodasi, 1989; Olufokunbi *et al.*, 1989; Awah, 1992; Monney, 1994). Most commercial interest in Africa is in *A. achatina*, *A. marginata*, *A. degneri* and *A. ventricosa*.

A number of Achatinidae are naturally restricted to virgin rainforest and decline markedly in abundance when the forest is replaced by second-growth vegetation. An example is the Liberian *Archachatina knorrii* (Jonas).

As Invasive Species in Africa

H. Lange in Pilsbry (1919, p. 55) remarks on the probable role of human agencies in the wide distribution of various Achatinidae in the Congo region of Africa. There is no reason to suspect that this does not also apply to other places on the continent. Bequaert (1950a, p. 41) raised the possibility that the disjunct distribution evident in *A. balteata* of Guinea was due to 'accidental or perhaps intentional introduction by man'. *A. zebra* occurs naturally in the south-eastern and southern coastal regions of South Africa. A colony of this species in the Hout Bay area of Cape Town, significantly further westwards, is believed to have been transported by humans (Sirgel, 1989).

A. marginata has evidently been dispersed by human agencies in West Africa, having recently invaded the south-west parts of Ghana (Monney, 1994). This species has also been introduced on to Annobón and São Tomé in the Gulf of Guinea (Gascoigne, 1994). On São Tomé it has become widespread and Gascoigne (1994) suggested that competitive interactions, along with habitat destruction, may have contributed to the decline in the indigenous *Archachatina bicarinata* (Bruguière).

The natural range of *A. fulica* is generally regarded to be the coastal area of East Africa, including its many islands (Pilsbry, 1904; Bequaert, 1950a), but at least part of this range in East Africa may be due to introductions by humans (Verdcourt, 1961). *A. fulica* now occurs in the southern part of Ethiopia and Somalia, throughout Kenya and Tanzania and into northern Mozambique. Very recently this species has been recorded in Morocco (van Bruggen, 1987), on the Ivory Coast (de Winter, 1988; Zong *et al.*, 1990) and in Ghana (Monney, 1994) of West Africa.

There is at present little information on the economic status of *A. fulica* in areas invaded in Africa. However, within a short period of its introduction, *A. fulica* achieved dominance in the achatinid community in Ivory Coast and Ghana and achieved significance as a crop pest (von Stanislaus *et al.*, 1987). *A. fulica* distributes in its faeces spores of *Phytophthora palmivora* (Butler) Butler, the cause of black pod disease in cacao (*Theobroma cacao* Linnaeus; *Sterculiaceae*) plants in Ghana (Evans, 1973). Since the local people do not accept *A. fulica* as an edible species, this alien species is allowed to go unchecked, while predation pressure is maintained on species such as *A. achatina*.

As Invasive Species Out of Africa

Pilsbry (1919) and van Bruggen (1981) treat the occurrence of Achatinidae in Madagascar as natural. None the less, Pilsbry (1919) admitted the possibility that the occurrence in Madagascar and several other islands off the African mainland were due to human importation. Van Bruggen (1981) considered *A. immaculata* (usually treated as *Achatina panthera* (de Férussac)) to be shared between south-eastern Africa and Madagascar, although the possibility was admitted that the occurrence in Madagascar is due to introduction through human agencies. Other authorities have considered that there exists no sound argument to consider Madagascar within the original geographical range of Achatinidae. Because of the absence of achatinid shells in Late Pleistocene deposits, both Dollfus (1899) and Germain (1921) considered the present occurrence of *Achatina* in Madagascar to be the consequence of introduction by human agency in the recent past. Bequaert (1950a) considered *A. fulica* to be an introduction to Madagascar. The presence of the East African *A. immaculata* in Rodrigues, Mauritius, Réunion, the Comores and the Seychelles (Bequaert, 1950a), clearly outside the realm of Africa, lends support to the idea that the Achatinidae have been dispersed to Madagascar and beyond by human agency.

The dispersal of *A. fulica* out of Africa has been discussed by a number of authors, including van Weel (1948/49), Lange (1950), Bequaert (1950a), Rees (1951), Mead (1961, 1979a), Wolfenbarger (1971), Lambert (1974), Srivastava (1992), Civeyrel and Simberloff (1996) and Cowie (2000). Bequaert (1950a, p. 73) concludes:

> that the spread of *Achatina fulica* from its original continental African home and Madagascar to the islands of the Indian Ocean, India, the Orient, the East Indies and the Pacific is entirely due to transport by man, usually deliberate, in a few cases accidental. Furthermore all later importations may be traced back ultimately to the first introduction from Madagascar into Mauritius, some 150 years ago.

A. fulica was evidently introduced to Madagascar prior to 1800 from Kenya, but was not accepted as an edible species. It assumed pest status through damage to crop plants. However, the species was attributed medicinal properties and, on these grounds, was introduced to Mauritius and thence to many island groups in the Indian Ocean. From there naturalists introduced them to India and Sri Lanka. By the 1930s *A. fulica* had been spread throughout tropical and subtropical East Asia. Subsequent further penetration of Asia and dispersal into the Pacific was aided by the Second World War and postwar commerce and by deliberate introductions for a variety of reasons. *A. fulica* had reached the outer islands of Papua New Guinea by 1946, New Ireland and New Britain by 1949 and mainland Papua New Guinea by 1976/77. *A. fulica* had invaded Tahiti by 1967 and New Caledonia and Vanuatu by 1972 and was reported from other areas in French Polynesia in 1978, the year in which it reached

American Samoa (Fig. 3.1). *A. fulica* continues to spread; for instance it was first reported on Upolu, Samoa, in 1990 and in Kosrae, Federated States of Micronesia, in 1998.

Small, incipient populations of *A. fulica* have been eradicated at various times from California, Florida, Queensland in Australia, Fiji, Western Samoa, Vanuatu and Wake Island (Abbott, 1949; Mead, 1961, 1979a; Colman, 1977, 1978; Muniappan, 1982; Waterhouse and Norris, 1987; Watson, 1985).

Bequaert (1950a) and Wolfenbarger (1971) had predicted the establishment of *A. fulica* in the New World tropics, based on the evident eastward dispersal of the species and the likely favourability of the Caribbean and American tropics as a habitat. This prediction was realized when, in 1984, *A. fulica* was found established in Guadeloupe, French West Indies (Frankiel, 1989). By 1987 it had spread to other parts of the island, and in 1988 was recorded in Martinique, about 200 km to the south of Guadeloupe (Schotman, 1990; Mead and Palcy, 1992).

With the advent of Achatinidae as a tradable commodity on the world market, captive breeding has been established for various species in different parts of the world (Mead, 1982; Upatham *et al.*, 1988; Runham, 1989; Monney, 1994), heightening the potential for further spread of *A. fulica* and related species. Considerable quantities of *Achatina* meat are exported to Europe and America from Taiwan, China and other Asian countries (Mead, 1982). Escapes and undoubtedly purposeful releases from these breeding facilities have certainly contributed to the naturalization of *A. fulica* in new areas in Asia. Furthermore, the continuing interest in achatinid meat has led to expansion of the industry into South America and was responsible for the very recent establishment of feral populations of *A. fulica* in many regions of Brazil, including São Paulo, Rio de Janeiro, Minas Gerais, Parana and Santa Catarina (Teles *et al.*, 1997; J. Coltro, personal communication, 2000).

Being of African origin, it has generally been assumed that *A. fulica* will be confined as an alien species to tropical environments. However, *A. fulica* exhibits wide environmental tolerances. The species is now well established in the temperate environs of Bonin and Ryūkyū Islands in the southern regions of Japan, and in the São Paulo region of Brazil. It also poses a serious threat to crops in the Coochbehar, Gauhati, Imphal, Nongpoh, Kumarghat, Chaibasa, Darbhanga, Dumka and Purnea districts of India, where temperatures down to 2°C occur during the winter months and the animals go into hibernation. Furthermore, published records indicate establishment in temperate environments imposed by altitude in low-latitude areas, such as at 350 m in Hawaii, 400 m in the Philippines, 600 m in Mauritius, 1166 m in India, 1200 m in Sri Lanka and 1500 m in Malaya (South, 1926; Mead, 1955, 1961, 1979a; Raut, 1983a). It is therefore apparent that *A. fulica* has the potential to occupy areas at 40° latitude, or the environmental equivalents at higher altitudes nearer the equator (Raut, 1983a).

Fig. 3.1. Dispersal of *Achatina fulica* Bowdich (Achatinidae) out of Africa.

Over much of its introduced range, *A. fulica* has a predilection for modified environments, such as plantations and gardens. The emergence of *A. fulica* as an important crop pest within a decade or two of establishment has been repeated over much of its naturalized range. Van Benthem Jutting (1952) notes that *A. fulica* has not been found in truly undisturbed conditions in Java, or in tropical rainforest. Cowie (1998a) notes that *A. fulica* is primarily found in disturbed low- to mid-elevation sites in Hawaii. However, *A. fulica* has also been observed as an invader of primary or secondary forest in the Hawaiian Islands, Bonin Islands, India, Java, Sumatra and New Caledonia (Mead, 1979a; Tillier, 1982; Raut and Ghose, 1984; G.M. Barker, personal observation).

It is generally thought that animal species do not attain marked elevation in abundance and thus status as an environmental pest in their natural range, other than short periods of eruptive population behaviour. If this is so, in the case of introduced species, such as *A. fulica*, how many years are needed to develop an association with the local fauna such that the exogenous species can be regarded as endogenous with respect to the nature of its population dynamics? After an initial period of high abundance, do populations in their naturalized range decline due to the regulatory effects of natural enemies? Mead (1979a, p. 83) expressed the opinion that 'the phenomenon of decline in populations of *Achatina fulica* appears to be inevitable. The timing of its earliest manifestation, rate of progress and the ultimate degree of expression are functions of the environment.' Mead presented evidence for the principal role of disease in the decline. From information such as that presented in Fig. 3.1, it is possible to estimate the length of time that *A. fulica* has been resident in an area as an alien. It is evident that, in some areas of India, *A. fulica* has been thriving for a period of 100–150 years, with no clear evidence of abatement in its pest status (Raut and Ghose, 1984). None the less, there are situations where, after a period of remarkable abundance and environmental effects, *A. fulica* populations have declined. There is evidence, for example, that *A. fulica* became a lesser problem after only 20 years on Moorea in French Polynesia (Clarke *et al.*, 1984) and after some 60 years in Hawaii (Cowie, 1992) and Ogasawara (K. Takeuchi, personal communication, 2000).

Little information is currently available on the pest status of *A. immaculata* in its naturalized range in the islands of the Indian Ocean. It is of interest that this species has not been more widely dispersed by the human agencies responsible for the spread of *A. fulica*. Indeed, the great majority of achatinid species have not been dispersed to become feral outside Africa. A recent exception is the West African *Limicolaria aurora* (Jay), recorded for the first time outside Africa in 1989 when discovered in Martinique (Mead and Palcy, 1992; Palcy and Mead, 1993). According to Mead and Palcy (1992), the infestation probably arose from purposeful introduction as an edible species direct from Africa, some time after 1986. Mead and Palcy (1992) reported that *L. aurora* occurred in considerable numbers in the infested area of Martinique, causing damage to yam

(*Dioscorea alata* Linnaeus; Diascoreaceae), kidney bean (*Phaseolus vulgaris* Linnaeus; Fabaceae), black pepper (*Piper nigrum* Linnaeus; Piperaceae), Jerusalem artichoke (*Helianthus tuberosus* Linnaeus; Asteraceae), cucumber (*Cucumis sativus* Linnaeus; Cucurbitaceae), okra (*Abelmoschus esculentus* (Linnaeus) Moench; Malvaceae), rose-mallow (*Hibiscus* Linnaeus sp.; Malvaceae) and sweet potato (*Ipomoea batatas* (Linnaeus) de Lamarck; Convolvulaceae) within 8 months of being first recorded there.

In addition to farming for meat, several species of Achatinidae, including *A. fulica*, *A. achatina* and *A. marginata*, are maintained in temperate regions outside Africa as laboratory animals (e.g. Nisbet, 1974; Plummer, 1975; Pawson and Chase, 1984; Tranter, 1993).

Biology

The biology of some Achatinidae has been extensively studied. That of the great majority is hardly known at all. Two important books by Mead (1961, 1979a) bring together and appraise most of the literature on *A. fulica*. In this chapter we provide a synopsis of information relevant to the pest status and management of achatinids in tropical agriculture.

Achatinidae are nocturnal. Like other terrestrial gastropods they are dependent on the availability of moisture. Accordingly they are active under high-humidity conditions. In many tropical areas, activity is thus restricted to the monsoon season and the following moist summer period. Usually achatinids spend the daytime hours under protective cover. When populations are high, many *A. fulica* are to be found resting on exposed walls and tree trunks, indicating that under these conditions there may be a shortage of home sites. Activity generally commences with the approach of darkness at sunset. Takeda and Ozaki (1986) demonstrated an endogenous circadian rhythm in the activity of *A. fulica* that is independent of temperature and light conditions but regulated by hydration effects on haemolymph osmolality. Further, these authors showed that *A. fulica* only becomes active when the ambient relative humidity rises above 50%. In Calcutta, India, Panja (1995) found that foraging *A. fulica* spent on average 338 min (55%) of their nightly activity crawling, 95 min (15.5%) feeding and 180 min (29%) resting. Panja (1995) found that the distance travelled by *A. fulica* in a single night of activity decreased during the season irrespective of the age structure of the population, with an average of 1429 cm in June reducing to 912 cm by October. The distance travelled in a single night varies with the size of the animal. Tomiyama (1992) found that, in Chichi Jima, Japan, immature *A. fulica* dispersed up to a distance of 100 cm (standard deviation 34 cm), while mature animals moved an average distance of 161 cm (standard deviation 44 cm). It was observed that, in the course of searching for food, *A. fulica* typically moves some distance from the daytime resting site before commencing feeding. The animals may be active for over an hour

before locating a favourable host plant. Foraging patterns are suspended when *A. fulica* is engaging in mating activity.

The length of feeding time at one site depends on the quality and quantity of the food, but invariably feeding is interspersed with periods of rest. Once the animals have satisfied their hunger or at the approach of dawn, *A. fulica* typically seek suitable daytime resting sites. In Chichi Jima, Tomiyama (1992) observed that mature *A. fulica* return to the same resting site after each night's activity, while immature *A. fulica* tend to use different resting sites each day. Similarly, Panja (1995), working in Calcutta, recorded the absence of homing activity in *A. fulica* of 20–29 mm shell size, but frequency of homing was 20% in animals of 40–49 mm shell size and 78% in animals of 70–79 mm shell size. Homing in terrestrial gastropods has been shown to be mediated by directional trail-following and chemoreception of airborne odours from the home site (Chelazzi, 1991; Cook, 2001). That animals are able to return to home sites despite being experimentally transplanted up to 30 m (Tomiyama, 1992) suggests that distant chemoreception is involved in the homing behaviour of *A. fulica*. Chase and Boulanger (1978) have shown that mucus trail-following behaviour can occur in *A. fulica* but, because snails do not crawl along old mucus trails on their way back to their home sites, Tomiyama (1992) concludes that mucus trail-following is not important in the homing of this species.

Any site that provides adequate protection from light and desiccation will be used by *A. fulica* for daytime sheltering and for aestivation. In the rain forest this need is evidently not so urgent and the animals will frequently rest on the bare ground or the litter (Dun, 1967). During the rainy season *A. fulica* will often ascend considerable distances up tree-trunks or the walls of buildings, embankments, etc. to rest during the day.

That many achatinid species aestivate during the dry season in Africa has been noted above. Throughout its naturalized range, *A. fulica* undergoes aestivation with the onset of dry weather. In the monsoonal tropics, such weather conditions occur in winter, when temperatures are typically 15–28°C but in some regions may fall below 10°C. As *A. fulica* is able to maintain activity at temperatures below 10°C (Mead, 1979a; Raut and Ghose, 1984), the cue for aestivation is evidently the humidity of the air. Raut and Ghose (1984) have reported aestivation when maximum temperatures reach 28–30°C at a humidity of 80–82%. Raut and Ghose (1983a) observed *A. fulica* feeding on fleshy and succulent food plants prior to aestivation, evidently as a body hydration strategy. *A. fulica* prefers to aestivate in moist soil, but will also aestivate at sites above the ground. Although aggregation (Chase *et al.*, 1980) and homing are well developed in *A. fulica*, there exists no affinity for particular aestivation sites in these animals. They aestivate singly or in aggregations of as many as 100 or more animals (Raut, 1978; Srivastava, 1992), with the shell aperture oriented downwards and sealed with an epiphragm (Raut and Ghose, 1984). In the aestivatory state there is considerable physiological change, including reduction of the heart rate from 52 to 8 beats min^{-1}

(Raut and Rahman, 1991). While the epiphragm functions to reduce loss of body water, the animals do gradually dehydrate during aestivation. The dehydrated animals periodically retract further into their shell and in doing so secrete a further epiphragm, which places further demands on body moisture. As many as six to 12 epiphragms may be produced (Raut and Ghose, 1984). The longer the aestivatory state is maintained, the greater the potential for body dehydration to reach a critical threshold for survival. In Calcutta, Raut and Ghose (1981) recorded 100% mortality over an aestivation period of 7 months (November to May) for *A. fulica* that were 10–15 days old at the onset of aestivation. These authors noted that the rate of mortality declined with increasing age of the animals at the commencement of aestivation, with 33–45% mortality in animals of the 100–105 day age-group. Aestivation in *A. fulica* lasts from 2 to 10 months, depending on the climatic zone (see Raut and Ghose, 1984).

Raut and Ghose (1984) state that more than 50 mm rainfall can terminate aestivation at any time. Often in the tropics the dry season can be interrupted by occasional, brief periods of rainfall. While these rains may not be sufficient to induce *A. fulica* to terminate their aestivation, the temporary restoration of humidity provides an opportunity for the animals to rehydrate. This rehydration can be critical to their survival over the long aestivatory period.

Nisbet (1974) found that achatinids exhibited a tendency to bury themselves in the soil, even in the absence of aestivation.

Achatinids are hermaphrodites. Mead (1949) recorded male sexual maturity in *A. fulica* before the animals are a year old; development of female organs and egg deposition takes a few months longer. Tomiyama (1991, 1993) demonstrated that *A. fulica* has determinate shell growth, with thickening of the shell peristome occurring after cessation of shell growth. During the shell growth phase the animals also develop sexually, but producing only male gametes. In the later part of the male phase, the animals begin to engage in copulation. At or shortly after cessation of shell growth, the animals complete reproductive development and enter a phase where both male and female gametes are produced. If there is no prolonged interruption by aestivation or hibernation, the animals mature within 1 year. *A. fulica* generally attains sexual maturity at the age of 5–8 months under field conditions (Leefmans, 1933; van Weel, 1948/49; Mead, 1949, 1961; van der Meer Mohr, 1949a; Bequaert, 1950a; Kondo, 1964; Pawson and Chase, 1984; Raut, 1991). Ghose (1959) reported that *A. fulica* attained sexual maturity within 6 months in the laboratory, consistent with the data of Pawson and Chase (1984), which indicated that this species laid the first eggs at the age of 5 months under controlled laboratory conditions of 20–24°C and 12 : 12 h light/dark photo regime. In subtropical areas, such as the Ryūkyū and Ogasawara Islands of Japan and certain regions in India, growth of *A. fulica* is interrupted by winter dormancy and the first eggs are not produced until the age of 12–15 months (Ghose, 1959; Sakae, 1968; Suzuki, 1981; Numasawa and Koyano, 1987; Tomiyama, 1993). *A. achatina* typically take 18 months to mature in

West Africa (Hodasi, 1979), while some animals that experience two intervening seasons of aestivation take 21 months to reach maturity (Hodasi, 1982).

Stievenart (1992) showed that *A. marginata* also has determinate shell growth, but, unlike *A. fulica*, the peristome is produced as a reflected lip after cessation of shell whorl growth. Furthermore, *A. marginata* was shown to reach sexual maturity and to produce eggs prior to peristome lip formation. *A. marginata* requires about 9–10 months under laboratory conditions (Plummer, 1975). Owen (1964) presented evidence for year-round reproductive activity of the Ugandan *Limicolaria martensiana* (Smith), but with peaks of activity in January–February and July. This bimodality was apparently associated with alternating wet and dry seasons.

Achatinidae are generally outcrossing and therefore require allosperm to produce fertile eggs. Olson (1973) summarizes the situation with respect to the possibility of self-fertilization in *A. fulica*: 'for all intents and purposes, cross fertilization is necessary for the laying of a sufficient quantity of eggs to ensure perpetuation of the species'. He states that self-fertilization does occur but that virgin animals provide clutches comprising fewer than ten eggs, that most of these eggs are sterile and that progeny arising from these eggs rarely survive through to sexual maturity.

In the case of *A. fulica*, individuals receptive to a mate can be distinguished by their dilated genital orifice and the occasional protrusion of the phallus (Raut and Ghose, 1984). Courtship is initiated by these animals immediately on encountering a prospective partner, and they often take an aggressive role in the courtship (Raut and Ghose, 1984; Tomiyama, 1994). The sequence of events in the courtship of *A. fulica* has been described by Raut and Ghose (1984) and Tomiyama (1994), and in that of *A. marginata* by Plummer (1975). Mating is generally reciprocal, and generally pairing occurs between animals of similar size. Mating generally occurs during the hours of darkness, although courtship may be initiated late in the afternoon (Lange, 1950). Tomiyama (1994) observed that, while 'young' adult *A. fulica* will initiate courtship at any time between 6.30 p.m. and 4.30 a.m., mating in the older animals was initiated only between 10 p.m. and 12.30 a.m. The duration of copulation in *A. fulica* is typically 6–8 h but can vary from 1 to 24 h (van Weel, 1948/49; van deer Meer Mohr, 1949a; Lange, 1950; Raut and Ghose, 1984; Tomiyama, 1994), and in *A. achatina* may continue for 12 h (Hodasi, 1979). Raut and Ghose (1984) reported that a small percentage of matings in *A. fulica* were not reciprocal.

In *A. fulica* one individual initiates courtship and the other may accept courtship. These initiators and acceptors exhibit different behaviours during the courtship process. Tomiyama (1994) describes the mating process. First, one animal (the initiator) approaches another from behind and mounts its shell. Generally, the phallus is extruded by the initiator during the shell-mounting phase. If the acceptor animal wishes to accept and proceed with courtship, it bends its head backward and

rocks the whole body. Responding to this behaviour, the initiator bites the body of the acceptor in the cephalic region and then proceeds to rub its extruded phallus against the now extruded phallus of the acceptor animal. Finally, reciprocal intromission occurs with phallic penetration into the vagina of the partner. With intromission established, the con-joined animals fall to the ground side by side and remain in this position for the duration of copulation.

Tomiyama (1994) suggested that the courtship initiators are essentially 'male-behaving' and the courtship acceptors 'female-behaving'. Asami *et al.* (1998) have demonstrated that the shell-shape bimodality evident in stylommatophoran snails, where snails either carry a high-spired (height : diameter > 1) or a low-spired (height : diameter ≤ 1) shell (Cain, 1977), is associated with discrete mating behaviours. In general, flat-shelled species mate reciprocally, face to face, while tall-shelled species, such as Achatinidae, mate non-reciprocally: the 'male' copulates by mounting the 'female's' shell. Asami *et al.* (1998) categorized mating in achatinids as non-reciprocal, with one animal functioning as the 'male' and achieving copulation by mounting the 'female's' shell, consistent with Tomiyama's (1994) interpretation. The duration of courtship behaviour in *A. fulica* observed by Tomiyama (1994) was less than 5 min, i.e. less than *c.* 1.8% of the whole duration of successful mating. Copulation duration was much shorter in mating among young *A. fulica* than among relatively older animals.

Tomiyama (1994) found that, in *A. fulica*, courtship progressed successfully to copulation in only 10% of observed courtships. The rejection was usually made by the acceptor ('female-behaving') animal.

While eggs may be deposited within 8–20 days of mating in the case of *A. fulica* (Lange, 1950), the reproductive strategy of Achatinidae includes the capacity for long-term storage of allosperm. Owiny (1974) recorded production of viable eggs in *L. martensiana* 520 days after mating, while van deer Meer Mohr (1949a) and Raut and Ghose (1979b) record egg production 382 and 341 days, respectively, after mating in *A. fulica*. Allosperm viability is evidently maintained over lengthy periods of aestivation (Raut and Ghose, 1982). Allosperm storage provides achatinids with the capability to produce eggs at any time of the year given favourable environmental conditions. It is quite clear that intro-duction of a single allosperm-bearing specimen is sufficient for the establishment of a colony in a previously non-infested area.

A. fulica is oviparous, as evidently are most Achatinidae. Bequaert (1950a) presented information indicating that *Achatina zanzibarica* Bourguignat and *Achatina allisa* Reeve are ovoviviparous. Tompa (1979) indicated that all Achatinidae are egg retainers of one form or another. Delayed oviparity or ovoviviparity may, in some species, be associated with occupancy of a strongly seasonal habitat (van Bruggen, 1985). The reported duration of the egg stage in *A. fulica* varies from 1 to 17 days. Mead (1949) has reported retention of eggs in the spermoviduct so that hatching occurs within a few hours of oviposition. Ghose (1960, 1963)

points out that eggs with embryos in different stages of development are laid; hence the period to hatching varies, with some eggs hatching within a few days of being laid. This has been confirmed by Pawson and Chase (1984) for *A. fulica* in laboratory culture. Such egg retention apparently has not been observed by others (e.g. Lange, 1950), indicating that egg retention in *A. fulica* may vary with environmental conditions. The incubation period for eggs of the oviparous *A. marginata* is approximately 30–40 days (Plummer, 1975; Plummer and Mann, 1983).

Achatinids produce shelled eggs. There is insufficient calcium in the albumen to allow for body-shell formation so the embryo utilizes calcium from the eggshell. Plummer and Mann (1983) found that *A. marginata* embryos use 33% of the calcium initially present in the eggshell. Eggs of *Archachatina* are larger than those produced by *Achatina* of comparable size. This is reflected in the bulbous, protoconch of *Archachatina* species. The eggs of Achatinidae are generally deposited in 'nests' excavated in the soil by the gravid animal, but occasionally may simply be deposited in moist crevices among plant litter, stones and other debris on the ground. The West African *Pseudachatina* Albers species, such as *P. downesii* (Sowerby) from Fernando Poo, deposit their eggs in the axils of the branches of the trees they inhabit. Tryon and Pilsbry (1904) mention a similar behaviour in *A. marginata.* The sites chosen by *A. fulica* for oviposition are similar to the resting sites on the ground, although if the cover is too sparse the gravid animals may turn some loose soil and deposit the eggs 25 mm or so below the surface.

The frequency of oviposition varies with the duration of the period favourable for activity. Mead (1961) stated that, in the field, *A. fulica* will lay a batch of eggs 'every few weeks' as long as favourable conditions prevail. In reality, however, the frequency of oviposition in the field does not approach this level. According to Dun (1967), egg laying by *A. fulica* in New Guinea occurs in two pronounced peaks each season, the first shortly after resumption of activity following the onset of the rainy season and the second 2–3 months later. Thus each reproductive animal typically produces two clutches of eggs each year. In Oahu, Hawaii, only five to six clutches of eggs are produced by *A. fulica* per season (Kekauoha, 1966). In Calcutta, India, where *A. fulica* is active for only 4 months in the year, 1.9, 4.2, 3.9 and 2.0 egg clutches were produced on average per animal in the first 4 years following attainment of reproductive maturity (Raut, 1991). Pawson and Chase (1984) showed that fecundity was maximal in *A. fulica* aged between 210 and 270 days under laboratory conditions. After that, the production of eggs declines markedly, with almost no clutches produced by animals older than 1 year. A similar pattern is evident in animals in the field, although the time to peak oviposition activity and the rate of subsequent decline is delayed commensurate with the slower growth rates. While data on *A. fulica* fecundity have not been collected by standardized methods for different regions, some estimates are available: 100 eggs in the first year and 500 eggs in the second year in Sri Lanka (Green, 1911); 100 eggs in the first

year and 200–300 eggs in the second year in Hong Kong (Jarrett, 1931); 900–1200 eggs annually in Oahu (van Weel, 1948/49); 677–1817 eggs annually in Oahu (Kekauoha, 1966); 160–1024 eggs annually in Calcutta (Raut, 1991). Clutch size varies from ten to 400. Tomiyama and Miyashita (1992) demonstrated great variability in clutch size and egg size in *A. fulica*, with both parameters positively correlated with the size of the parent animals. The limited available data, summarized by Tomiyama and Miyashita (1992), indicate a considerably higher reproductive potential in *A. fulica* than in other *Achatina* species and in *Archachatina* species. Lange (1950) noted the discrepancy between high viability among eggs deposited in laboratory animals and the low rates of recruitment into feral populations. None the less, an enormous potential for recruitment into the population is indicated by the reproductive strategy in *A. fulica*.

Plummer (1975) reports an average longevity of 4.5 years for *A. marginata* kept in captivity in London, although specimens occasionally lived for 7.5–10 years. *A. fulica* can live as long as 9 years in captivity (van Leeuwen, 1932) but under field conditions maximum longevity is usually in the order of 3–5 years (Mead, 1979a; Suzuki and Yasuda, 1983; Tomiyama, 1993). Thus, these animals evidently persist long after their peak reproductive fitness. However, van Bruggen (1985) remarks that early maturity, possibly combined with a long life and a steady increase in clutch size, seems to be the key element in the reproductive strategy in *A. machachensis*.

After emerging from the egg, achatinids generally remain underground with other members of the clutch for several days. During this time the hatchlings consume their eggshells, sometimes the eggshells of unhatched siblings and soil organic matter. This eggshell-eating behaviour has been observed frequently, both in *A. fulica* (Rees, 1951; Pawson and Chase, 1984) and in other achatinids (e.g. Owiny, 1974; Plummer, 1975; Hodasi, 1979). Lange (1950) reported that the young of *A. fulica* feed on the eggshells for 3–4 days. In the field Rees (1951) determined that *A. fulica* hatchlings remain below the surface of the soil for 5–15 days, while for laboratory colonies of this species Pawson and Chase (1984) found hatchlings to remain in the soil for 4–7 days. Plummer (1975) stated that *A. marginata* hatchlings remain underground for 7–14 days before surfacing. On emergence from the soil the young snails display exploratory and voracious feeding behaviour.

Observations in India clearly indicate that emergent juvenile *A. fulica* typically do not disperse great distances. They initially remain near the site of hatching, feeding on decaying plant matter and preferred host plants. After about 2 weeks the juveniles begin to range further, but none the less still tend to be aggregated and forage on palatable plant species. While their small size limits the quantity of plant material consumed per animal, the aggregated nature of the infestations can lead to severe damage in infested plants. As the *A. fulica* grow, they progressively disperse, seeking out and inflicting substantial damage on susceptible

plants. After about 2 months the snails establish home sites, from which they leave at dusk to forage and to which they return at or before dawn. A typical behavioural pattern is that, following emergence from their home sites, *A. fulica* move directly to the sites of preferred food plants in the garden or crop. Such behaviour in adults, possibly reinforced by entrained long-term memory (Croll and Chase, 1977) and selective feeding, can lead to severe damage in susceptible plant species. The behavioural sequence of sedentary early juveniles, dispersive juveniles and then home-site-bound adults can lead to progressive elimination of susceptible and vulnerable plant species from a localized area. This herbivory is most pronounced where the abundance of susceptible species is low and thus the selective pressure is greatest.

Achatinidae are generally regarded as herbivorous, feeding primarily on living and decaying vascular plant material. Van Weel (1948/49) reported that young of *A. fulica* feed on decaying matter and unicellular algae. Animals with shells between 5 and 30 mm height were observed to prefer living plants. It was during this period that *A. fulica* was found to be most injurious to plantations and gardens. Although not entirely neglecting living vegetation, the maturing snails were found to largely return to a scavenging, detritivorous habit. Olson (1973) refers to *A. fulica* as an opportunistic, omnivorous and carpophagous feeder. He considered this species to be basically a scavenger as 75% of its food is detritus. Das and Sharma (1984) comment on the necrophagous habit of *A. fulica*.

A considerable number of plant species susceptible to *A. fulica* are to be found listed in the popular and scientific literature. The information pertaining to economically important plant species is reviewed in a later section of this chapter. There are few reports on damage in indigenous plant species in areas where *A. fulica* has been introduced. This undoubtedly reflects a preoccupation with cultivated plants among investigators, rather than the absence of damage to the natural vegetation. Dun (1967) reports the virtual local extinction of the indigenous *Pipturus argenteus* (Forster) Weddell (Urticaceae) in parts of the Gazelle Peninsula, New Britain.

The literature on *A. fulica* is conspicuous for the scarcity of quantitative data on feeding preferences and impacts on plant communities. Generally, observations support the hypothesis of Waterhouse and Norris (1987) that the preference for particular food plants exhibited by *A. fulica* at a particular locality is dependent primarily on the composition of the plant communities, in respect to both the species present and the age of the plants belonging to the different species. Most severe damage is likely to be observed in susceptible species when they predominate in the plant community. In the absence of quantitative sampling methods, substantial damage to the less abundant plant species may often go undetected. Moreover, the extent of damage varies according to the age structure of the *A. fulica* population, which in turn will relate to the stages of the crop in relation to the phenology of *A. fulica* recruitment (Jaski, 1953; Raut, 1982).

The herbivory damage inflicted by *A. fulica* varies substantially between seasons, due to variation in plant occurrence in the habitat and variation in climatic favourability for gastropod activity. Of 22 plant species offered by Raut and Ghose (1983a) to *A. fulica* in outdoor cages in India, 13 plant species suffered damage during the monsoon and summer and only eight during the winter (Fig. 3.2).
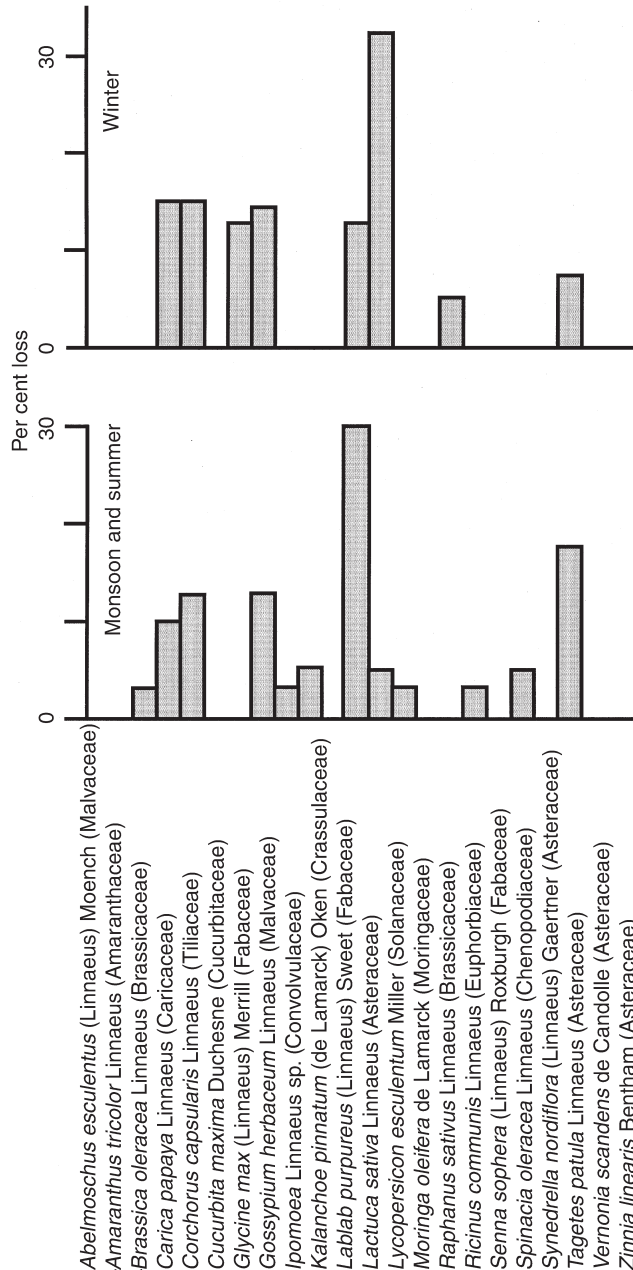

Fig. 3.2. Differential losses among 22 plant species due to feeding preferences by *Achatina fulica* Bowdich (Achatinidae) in field cages during two seasons in Calcutta, India (from Raut and Ghose, 1983a).

Ahmed and Raut (1991) demonstrated that *A. fulica* had higher growth rates on *Trichosanthes anguina* Linnaeus (Cucurbitaceae) and a mixed diet than when maintained on single-species diets comprising *Lactuca sativa* Linnaeus (Asteraceae), *Lablab purpureus* (Linnaeus) Sweet (Fabaceae), *Cucurbita maxima* Duchesne (Cucurbitaceae) or *Basella rubra* Linnaeus (Basellaceae). These differences occurred irrespective of the temperature regime at which the *A. fulica* were maintained (constant 20, 25 or 30°C; ambient 24.5–32.8°C), but were accentuated at 20°C. These results suggest that food-plant availability and feeding preferences may have important effects on the population dynamics of *A. fulica* by regulating growth rates and their subsequent effects on survival, fecundity and population recruitment. Egonmwan (1991) demonstrated that food preferences in *Limicolaria flammea* Müller varied between animals in somatic growth and those sexually active.

Ghose (1963) observed that young *A. fulica* denied access to soil 'did not thrive well'. He suggests that soil may be important in the provision of certain requirements of the juveniles in the early stages of postembryonic development. Nisbet (1974) subsequently found that ingestion of soil was important to the health of achatinids maintained in the laboratory.

A. fulica occurs across a range of soil pH and calcium conditions (summarized by Srivastava, 1992). By controlling the amount of available calcium in different soil types, Voelker (1959) was able to demonstrate environmentally induced variation in shell growth rate, size, weight, shape and colour in *A. fulica*. Schreurs (1963) conducted similar experiments in which he demonstrated the importance to normal development in *A. fulica* not only of calcium, but also of certain physical properties of the soil, the presence of adequate decaying organic material and the ample availability of green plant material. He found that, when many animals were kept together in a small space, the stress of 'crowding' was manifested in retarded growth, even though an abundance of food was available. This crowding effect is consistent with that observed in other terrestrial gastropod species (Cook, 2001).

According to Mead (1961), *A. fulica* persists but does not flourish at temperatures of 6–7°C. On the basis of observations in Hawaii, F.J. Olson (quoted in Mead, 1979a) established an optimal temperature for *A. fulica* of *c.* 26°C and predicted a maximum high temperature of *c.* 29°C and a minimum low temperature of 9°C for activity, and therefore feeding and growth, in this species. Singh and Birat (1969) recorded activity of *A. fulica* at a temperature of 8.8°C in Bihar. Raut and Ghose (1984) have stated that *A. fulica* will survive within the temperature range of 0 to 45°C, but for population increase a temperature range of 22–32°C is required. The latter authors found that hatching of *A. fulica* from eggs did not occur at temperatures below 15°C.

In the Bonin Islands winter temperatures are typically as low as 7°C and, according to Mead (1961), *A. fulica* persist there by winter

hibernation 100–125 mm below the soil surface. Raut and Ghose (1984) reported that, despite favourable humidity during winter in India, at a temperature of 8°C about 58% of *A. fulica* go into hibernation. As a result of observation over several years, Raut and Ghose (1984) found that the timing and duration of hibernation and aestivation vary in different parts of India, reflecting seasonal variation in temperature and rainfall. Srivastava *et al.* (1987) observed that hibernation is initiated in New Delhi populations of *A. fulica* when temperatures declined to 11°C. By the time the temperature was down to 5.5°C and relative humidity was below 65%, all *A. fulica* had gone into hibernation. Larger animals were observed to hibernate earlier than small animals.

Modelling indicates that, under conditions of unrestricted growth, a group of 100 hatchling *A. fulica* is theoretically capable of producing a population in excess of 10^{12} individuals in the space of 2700 days (S.K. Raut, unpublished; Fig. 3.3). Under favourable field conditions, *A. fulica* can indeed reach high densities and biomasses. Tillier (1982), for example, recorded a biomass of up to 780 kg ha^{-1} in New Caledonia. Raut and Ghose (1984) record population densities of up to 46 m^{-2} in mainland India and up to 56 m^{-2} in Andaman and Nicobar. On the Philippine island of Bugsuk, Muniappan *et al.* (1986) estimated that 45 million *A. fulica* were collected and destroyed on 1600 ha (mean = 2.8 m^{-2}) over a 7-month period. In the Maldives, Muniappan (1987) reported 73 *A. fulica* m^{-2} for the island of Male. On Christmas Island, Lake and O'Dowd (1991) recorded a mean of 10 *A. fulica* m^{-2} in the heavily infested areas. As pointed out by Civeyrel and Simberloff (1996), there is almost invariably considerable variance in population density within infested areas.
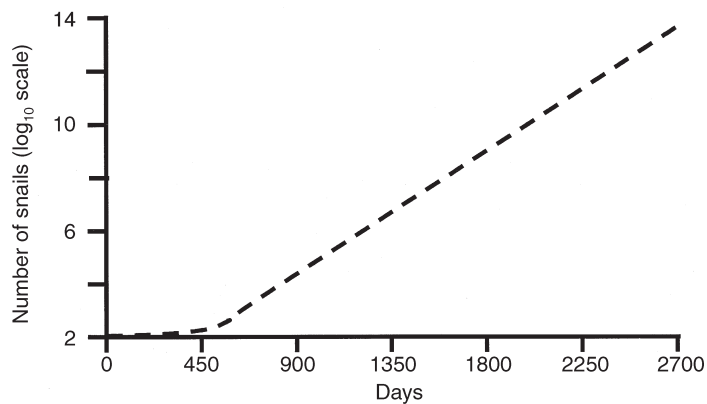
Fig. 3.3. Modelled growth rate in *Achatina fulica* Bowdich (Achatinidae) population size under abiotic environmental conditions pertaining to Calcutta, India. The model assumed an initial (Day 0) population of 100 0-day-old *A. fulica*, and incorporates growth, fecundity and mortality parameters derived from the literature and laboratory experimentation.

Pest Status

In tropical agriculture the cost of *A. fulica* is threefold. First, there is the loss of agricultural productivity caused by herbivory on crop plants, either through damage to the crop itself or to other plants that provide shade or soil enrichment in key elements such as nitrogen. Damage may also take the form of transmission of plant pathogens. Secondly, there is the cost of labour and materials associated with the management of the pest in such crop situations. Thirdly, there are the opportunity losses associated with enforced changes in agricultural practice, such as limiting the crop species to be grown in a region to those resistant to *A. fulica.* While outside the scope of this chapter, we may add the costs to the natural environment that arise from: (i) herbivory on native plant species; (ii) the altered nutrient cycling associated with the large volumes of plant material that pass through the achatinid gut under conditions of heavy infestations; (iii) the adverse effects on indigenous gastropods that may arise through competition for resource and fouling of the habitat with faeces and mucus; (iv) the adverse effects on indigenous gastropods that may arise through the non-target predation by malacophagous or genera-list animals introduced as biological control agents of the achatinids; and (v) the adverse effects on indigenous gastropods that may arise through the non-target poisoning of chemical pesticides applied against the achatinids. Also beyond the scope of this contribution, but none the less a significant cost in many Asian, Pacific and American societies, is the role of achatinids in the transmission of the metastrongylid causative agents of eosinophilic meningoencephalitis, *Angiostrongylus cantonensis* (Chen) and *Angiostrongylus costaricensis* (Morera & Céspedes).

Estimates of costs to agricultural production associated with infest-ation by *A. fulica* are exceedingly scarce. Mead (1979a) argues that damage is characteristically localized and restricted to vegetable and flower gardens and that both the popular and scientific media have greatly exaggerated it. He expressed the opinion that the sheer numbers of snails, their slime trails, their excreta and even their decaying corpses have led observers to overestimate the threat to agriculture. Mead (1979a, p. 27) stated:

> by and large, the greatest damage caused by *Achatina fulica* is to be found either in new infestation sites or at the crest of expanding populations, with the amount of damage decreasing proportionately towards the epicentre. Even with the great numbers characteristic of young populations, however, the damage is fairly localized, and not catastrophic or devastating on a broad scale.

In a review of the economic importance of infestations, Mead (1979a) makes little mention of *A. fulica* as a crop pest. Civeyrel and Simberloff (1996) suggest that the apparent inevitable population decline that occurs in the wake of the invasion argues against a long-term threat to agricultural production. These views obviously do not accord with those

of farmers whose land is infested by *A. fulica* and do not take into account the altered economy of farming that results from pest-enforced changes in agricultural practice. While it must be accepted that *A. fulica* populations have often declined after an initial period of severe infestation, we have already noted above that there are areas where *A. fulica* has persisted at pestiferous levels for many decades. While the constraints on agriculture imposed by infestations of *A. fulica* are well highlighted in the popular and scientific literature, there is little attention given in the literature to changes in farming practice following a decline in the pest. We thus have little information on the resilience of agricultural systems that have been subject to pest infestation for extended periods.

A. fulica has a reputation as a voracious herbivore. Schreurs (1963) determined that, in general, specimens up to 60 mm in shell length consume *c.* 10% of their own weight daily. From the literature it is well established that, in the agricultural landscapes of its naturalized range, this species feeds extensively, if not primarily, on cultivated and adventive, ruderal plant species. The species will persist on weeds and various indigenous vascular plants during periods in which cultivated plants are scarce. The list of cultivated plants reported to be susceptible to *A. fulica* is extensive, and is summarized in Tables 3.2 and 3.3 for economic and ornamental/medicinal plant species, respectively. Damage also extends to ground-cover and shade species grown in conjunction with cultivated shrub and tree species, such as cacao, tobacco (*Nicotiana tabacum* Linnaeus; Solanaceae), tea (*Camellia sinensis* (Linnaeus) Kuntze; Theaceae), rubber (*Hevea brasiliensis* (von Willdenow ex de Jussieu) Müller; Euphorbiaceae) and teak (*Tectona grandis* Linnaeus; Verbenaceae).

Irrespective of the crop, the seedling or nursery stage is most preferred and most vulnerable. In some situations, infestations of crops in the seedling or nursery stage are so severe as to demand changes in the crop species cultivated. In Guam, Indonesia and Malaysia, for example, *A. fulica* infestations made it uneconomic to grow vegetables, at least during the period of peak infestations (South, 1926; Kondo, 1950a; Mead, 1961). A similar situation was experienced by the growers of water melon (*Citrullus lanatus* (Thunberg) Matsumura & Nakai; Cucurbitaceae) in Mariana Islands and papaya (*Carica papaya* Linnaeus; Caricaceae) in Mariana Islands and India (Chamberlin, 1952; Raut and Ghose, 1984). Thus production of some crops has proved unsustainable in certain infested areas.

In more mature plants, the nature of the damage varies with the plant species, sometimes involving defoliation and in others involving damage to stems, flowers or fruit.

Waterhouse and Norris (1987) noted the differences in crop species reported to be susceptible in different regions. For example, in Sri Lanka (Green, 1910b), the Philippines (Pangga, 1949), Saipan (Lange, 1950), Rota (Kondo, 1952) and India (Raut and Ghose, 1984) it has proved difficult to produce yam and yet in Mariana Islands damage to this crop has proved

Table 3.2. Economically important plants recorded as being subject to losses through damage by *Achatina fulica* Bowdich (Achatinidae) in regions outside of Africa.*

Amaranth (Amaranthaceae)	*Amaranthus* Linnaeus spp., including *A. blitum* Linnaeus, *A. tricolor* Linnaeus and *A. viridis* Linnaeus
Banana (Musaceae)	*Musa* Linnaeus spp., particularly *M. acuminata* Colla and *M. paradisiaca* Linnaeus
Basella (Basellaceae)	*Basella alba* Linnaeus
Beans and peas (Fabaceae)	*Arachis hypogaea* Linnaeus; *Glycine max* (Linnaeus) Merill; *Lablab purpureus* (Linnaeus) Sweet; *Pisum* Linnaeus spp., particularly *P. sativum* Linnaeus; *Vigna radiatus* (Linnaeus) Wilczek and *V. unguiculata* (Linnaeus) Walpers
Blimbi (Oxalidaceae)	*Averrhoa bilimbi* Linnaeus and *A. carambola* Linnaeus
Breadfruits (Moraceae)	*Artocarpus* Forster & Forster spp., including *A. altilis* (Parkinson) Fosberg and *A. heterophyllus* de Lamarck
Brinjal/aubergine (Solanaceae)	*Solanum melongena* Linnaeus
Brassicas (Brassicaceae)	*Brassica oleracea* Linnaeus cultivars; *Raphanus sativus* Linnaeus
Cacao (Sterculiaceae)	*Theobroma cacao* Linnaeus
Carrot (Apiaceae)	*Daucus carota* Linnaeus
Cassava (Euphorbiaceae)	*Manihot esculenta* Crantz
Castor (Euphorbiaceae)	*Ricinus communis* Linnaeus
Chillies and peppers (Solanaceae)	*Capsicum* Linnaeus spp., particularly *C. annuum* Linnaeus and *C. baccatum* Linnaeus
Citrus (Rutaceae)	*Citrus* Linnaeus spp., particularly *C. sinensis* (Linnaeus) Osbeck and *C. reticulata* Blanco
Coffee (Rubiaceae)	*Coffea* Linnaeus spp., especially *C. arabica* Linnaeus and *C. canephora* Pierre ex Froehner
Corm (Araceae)	*Amorphophallus paeoniifolius* (Dennst.) Nicolson
Cotton (Malvaceae)	*Gossypium* Linnaeus spp., especially *G. herbaceum* Linnaeus
Drum stick (Moringaceae)	*Moringa oleifera* de Lamarck
Erythrina (Fabaceae)	*Erythrina* Linnaeus sp.
Eucalyptus (Myrtaceae)	*Eucalyptus* L'Héitier de Brutelle spp., especially *E. deglupta* Blume
Figs (Moraceae)	*Ficus hispida* Linnaeus
Gourd/pumpkins/ cucumber/melons (Cucurbitaceae)	*Citrullus lanatus* (Thunberg) Matsumura & Nakai; *Cucumis* Linnaeus spp., including *C. melo* Linnaeus and *C. sativus* Linnaeus; *Cucurbita* Linnaeus spp., including *C. maxima* Duchesne and *C. pepo* Linnaeus; *Edgaria darjeelingensis* Clarke; *Lagenaria* Seringe spp., including *L. siceraria* (Molina) Standley; *Luffa* Miller spp., including *L. acutangula* (Linnaeus) Roxburgh and *L. aegyptiaca* Miller; *Momordica* Linnaeus spp., principally *M. cochinchinensis* (de Loureiro) Sprengel
Jute (Tiliaceae)	*Corchorus capsularis* Linnaeus
Kokko (Fabaceae)	*Albizzia* Durazzini spp., including *A. lebbeck* (Linnaeus) Bentham; *Falcataria moluccana* (Miquel) Barneby & Grimes
Lettuce (Asteraceae)	*Lactuca* Linnaeus spp., including *L. sativa* Linnaeus and *L. indica* Linnaeus
Mahogany (Meliaceae)	*Swietenia mahagoni* (Linnaeus) von Jacquin
Mulberries (Moraceae)	*Broussonetia papyrifera* (Linnaeus) L'Héritier de Brutelle ex Ventenat; *Morus alba* Linnaeus

Table 3.2.   Continued

Okra (Malvaceae)	*Abelmoschus esculentus* (Linnaeus) Moench
Onion (Liliaceae)	*Allium cepa* Linnaeus
Palm nuts (Arecaceae)	*Areca catechu* Linnaeus; *Elaeis quineensis* von Jacquin
Papaya (Caricaceae)	*Carica papaya* Linnaeus
Passion-fruit (Passifloraceae)	*Passiflora* Linnaeus sp.
Potato (Solanaceae)	*Solanum tuberosum* Linnaeus
Rubber (Euphorbiaceae)	*Hevea brasiliensis* (von Willdenow ex de Jussieu) Müller
Shishu (Fabaceae)	*Dalbergia sissoo* Roxburgh ex de Candolle
Soursop (Annonaceae)	*Annona muricate* Linnaeus
Spinach (Chenopodiaceae)	*Spinacia oleracea* Linnaeus
Sunflower (Asteraceae)	*Helianthus annuus* Linnaeus
Sweet potato (Convolvulaceae)	*Ipomoea batatas* (Linnaeus) de Lamarck
Taro (Araceae)	*Alocasia* (Schott) Don spp., including *A. macrorrhizos* (Linnaeus) Schott; *Colocasia esculenta* (Linnaeus) Schott; *Xanthosoma braziliense* (Desfontaines) Engler
Tea (Theaceae)	*Camellia sinensis* (Linnaeus) Kuntze
Teak (Verbenaceae)	*Tectona grandis* Linnaeus
Tobacco (Solanaceae)	*Nicotiana tabacum* Linnaeus
Tomato (Solanaceae)	*Lycopersicon esculentum* Miller
Vanilla (Orchidaceae)	*Vanilla* Miller sp.
Yam (Diascoreaceae)	*Dioscorea alata* Linnaeus

*Sources of information include: Green (1910b), Charmoy and Gébert (1922), South (1926), Bertrand (1928, 1941), Corbett (1933, 1937), Latif (1933), Leefmans and van der Vecht (1933a,b), Riel (1933), van Benthem Jutting (1934, 1952), Beeley (1935, 1938), Fairweather (1937), Heubel (1937, 1938), Cotton (1940), Feij (1940), Esaki and Takahashi (1942), Hatai and Kato (1943), Townes (1946), Anonymous (1947), Otanes (1948), van Weel (1948/49), Hes (1949, 1950), Pangga (1949), Rappard (1949), van der Meer Mohr (1949b), Altson (1950), Kondo (1950a,b, 1952), Lange (1950), Rees (1951), Chamberlin (1952), Holmes (1954), van Alphen der Veer (1954), Weber (1954a), Behura (1955), Mead (1961, 1979a), Chiu and Chou (1962), Dun (1967), Singh and Birat (1969), Ranaivosoa (1971), Olson (1973), Raut (1982), Raut and Ghose (1983a, 1984), Srivastavsa (1992), Jahan and Raut (1994).

negligible (Chamberlin, 1952). Similarly, Srivastava (1992) mentioned the bitter gourd (*Momordica charantia* Linnaeus: Cucurbitaceae) being grown free from *A. fulica* herbivory in the Andamans and yet there have been records of some damage to this crop species in various provinces in India (e.g. Raut and Ghose, 1984; Jahan and Raut, 1994). Other crop species for which there are conflicting reports of damage from different regions include tea, coffee (*Coffea* Linnaeus spp.; Rubiaceae) and various taro species (*Alocasia macrorrhizos* (Linnaeus) Schott, *Colocasia esculenta* (Linnaeus) Schott, *Xanthosoma brasiliense* (Desfontaines) Engler;

Table 3.3. Ornamental and medicinal crop species recorded as being subject to damage by *Achatina fulica* Bowdich (Achatinidae) in regions outside Africa.*

Aloe (Aloeaceae)	*Aloe indica* Royle
Alsophila (Cyatheaceae)	*Alsophila* Brown sp.
Amaranth (Amaranthaceae)	*Comphrena globosa* Linnaeus
Spleenwort (Aspleniaceae)	*Asplenium nidus* Linnaeus
Bauhinia (Fabaceae)	*Bauhinia acuminata* Linnaeus
Boatlily (Commelinaceae)	*Tradascantia spathacea* Swartz
Bouganvilles (Nyctaginaceae)	*Bougainvillea* Commerson ex de Jussieu spp., particularly *B. spectabilis* Willdenow
Buckhorn (Cactaceae)	*Opuntia* Miller sp.
Cactus (Cactaceae)	*Cereus* Miller sp.
Calophyllum (Clusiaceae)	*Calophyllum inophyllum* Linnaeus
Canna (Cannaceae)	*Canna* Linnaeus spp., particularly *C. indica* Linnaeus
Chrysanthemums (Asteraceae)	*Chrysanthemum* Linnaeus sp.
Clitoria (Fabaceae)	*Clitoria ternatea* Linnaeus
Cosmos (Asteraceae)	*Cosmos* Cavanilles spp.
Crinums (Liliaceae)	*Crinum* Linnaeus spp.
Dahlias (Asteraceae)	*Dahlia* Cavanilles sp.
Dumbcane (Araceae)	*Dieffenbachia seguine* (von Jacquin) Schott
Gardenias (Rubiaceae)	*Gardenia angusta* (Linnaeus) Merrill
Impatiens (Balsaminaceae)	*Impatiens balsamina* Linnaeus
Indian bark (Lauraceae)	*Cinnamonum tamala* (Buchanan-Hamlin) Nees & Eberm.
Jasmine (Oleaceae)	*Jasmin sambac* (Linnaeus) Aiton
Kalanchoe (Crassulaceae)	*Kalanchoe pinnatum* (de Lamarck) Oken
Marigold (Asteraceae)	*Tagetes* Linnaeus spp., including *T. erecta* Linnaeus and *T. patula* Linnaeus
Moth orchids (Orchidaceae)	*Phalaenopsis* Blume spp.
Oleander (Apocynaceae)	*Nerium* Linnaeus spp., including *N. indicum* Miller and *N. oleander* Linnaeus
Perwinkle (Apocynaceae)	*Catharanthus roseus* (Linnaeus) Don
Pothos (Araceae)	*Epipremnum pinnatum* (Linnaeus) Engler
Purslane (Portulacaceae)	*Portulaca grandiflora* Hooker
Rose-mallow (Malvaceae)	*Hibiscus* Linnaeus spp., including *H. rosasinensis* Linnaeus and *H. mutabilis* Linnaeus
Roses (Rubiaceae)	*Rosa* Linnaeus spp.
Sanseviera (Liliaceae)	*Sansevieria trifasciata* Prain
Snake gourd (Cucurbitaceae)	*Trichosanthes anguina* Linnaeus
Spiderwisp (Capparaceae)	*Cleome gynandra* Linnaeus
Sunflower (Asteraceae)	*Helianthus annuus* Linnaeus
Vanda (Orchidaceae)	*Vanda* Jones sp.
Zinnia (Asteraceae)	*Zinnia linearis* Bentham

*Sources of information include: Green (1910a), Jarrett (1923), South (1926), Dammerman (1929), Latif (1933), Leefmans and van der Vecht (1933a,b), Riel (1933), van Benthem Jutting (1934, 1952), Feij (1940), Otanes (1948), Pangga (1949), Lange (1950), Mead (1961), Olson (1973), Raut (1982), Raut and Ghose (1984), Manna and Raut (1986), Srivastava (1992), Jahan and Raut (1994).

Araceae). In the case of taro, part of the variance in damage reports undoubtedly relates to the different crop species grown in different regions. There are also several cases in the literature where reports from within one region are at variance. For example, Hutson (1920) reported no damage to cacao in Sri Lanka, but Mead (1961) reports damage to this crop there. Likewise, occasional damage to impatiens (*Impatiens balsamina*

Linnaeus; Balsaminaceae) has been recorded in India (e.g. Raut and Ghose, 1984; Jahan and Raut, 1994), but it is one of few ornamental species that have been reported to survive in infested gardens there (Srivastava, 1992).

That plant susceptibility can vary depending on the composition of the plant community suggests that the extent of damage to crop species will vary between agricultural systems based, at one extreme, on production in monocultures and those based, at the other extreme, on multiple land uses and crop species mixtures. This could well explain the feeding behaviour of *A. fulica* on the ornamental plant species *Canna indica* Linnaeus (Cannaceae). In the presence of many kinds of preferred food plants, Raut and Ghose (1984) noted that *A. fulica* rarely attack *C. indica*, but often use this species for daytime shelter. In contrast, *C. indica* was completely defoliated within a few days when the preferred host plants were no longer available (Manna and Raut, 1986).

Lange (1950) and Srivastava (1992) list observations on non-preferred plant species but, as noted earlier, there is no quantitative information available on the effect of *A. fulica* on the ecology of plant communities. At present there is little understanding of the chemical or physical traits that confer different levels of susceptibility among plant species or indeed as to whether any particular phylogenetic clades of vascular plants are more or less susceptible. As summarized by Schotman (1989), from the literature we may conclude that the economic crops generally suffering little damage from *A. fulica* include sugar cane (*Saccharum officinarum* Linnaeus; Gramineae), maize (*Zea mays* Linnaeus; Gramineae), rice (*Oryza sativa* Linnaeus; Gramineae), coconut (*Cocos nucifera* Linnaeus; Arecaceae), pineapple (*Ananas comosus* (Linnaeus) Merrill; Bromeliaceae) and screw pine (*Pandanus tectorius* Parkinson ex Zuccarini; Pandaceae). Onion (*Allium cepa* Linnaeus; Liliaceae), garlic (*Allium sativum* Linnaeus), yam-beans (*Pachyrhizus tuberosus* (de Lamarck) Sprengel; Fabaceae) and betel (*Piper betel* Linnaeus; Piperaceae) are particularly remarkable among crop species in that they are evidently immune to the attentions of *A. fulica* everywhere (Godan, 1983; Srivastava, 1992).

That *A. fulica* feed on a variety of plant species and the extent of damage varies temporally, spatially and with the compositional structure of the vegetation poses significant difficulties for the standardization of sampling and the development of economic thresholds in crops. This is accentuated by the generally small area of individual fields devoted to particular crops, the frequent intercropping within fields and the small-scale mosaic of dwellings, cultivated fields and primary and secondary forests that characterize much of the agriculture landscape in tropical regions. Undoubtedly the economics of infestations and appropriate action thresholds have been established for the more extensive crops, such as plantation banana (*Musa* Linnaeus spp.; Musaceae), but the relevant information is not available in the plant protection or malacological literature.

A. fulica has been implicated in transmission of plant diseases – *P. palmivora* in black pepper, betel pepper, coconut, papaya and vanilla (*Vanilla* Miller spp.; Orchidaceae), *Phytophthora colocasiae* Racib. in taro and *Phytophthora parasitica* Dastur in aubergine (brinjal; *Solanum melongena* Linnaeus: Solanaceae) and tangerine (*Citrus reticulata* Blanco; Rutaceae) (Mead, 1961, 1979a; Turner, 1964, 1967; Muniappan, 1983; Schotman, 1989). However, while the importance of these disease organisms is well established, the relative importance of *A. fulica* as a transmission agent in the epidemiology of these diseases under usual cropping conditions has not been well established.

While the pest status of achatinids has generally focused on *A. fulica* outside Africa, as outlined earlier in this chapter, various achatinid species can assume pest status in Africa. The achatinids feed on both dead and living plant tissues in their natural habitat, but, when that native habitat occurs adjacent to or is converted to sites of human habitation, they can assume pest status because of their predations on cultivated plants. Crop species damaged by Achatinidae under these circumstsances are listed in Table 3.1. Since some of these Achatinidae are edible, there is often a reluctance to regard them as pests (Hodasi, 1979, 1984; von Stanislaus *et al.*, 1987). Furthermore, the recent establishment of *L. aurora* as a crop pest in Martinique illustrates the potential for species in addition to *A. fulica* to adversely affect agricultural crops outside Africa (Mead and Palcy, 1992; Palcy and Mead, 1993).

Control

Physical, chemical and biological strategies have variously been used to manage infestations of *A. fulica*. However, the great variety of cropping and socio-economic environments in which infestations have occurred has prevented planned, coordinated and integrated approaches to the development of control methods. Most of the literature relating to the control or eradication of the pest predates the 1960s, primarily in relation to attempts to control infestations that developed as the pest was dispersed throughout the Indo-Pacific region. The published information pertaining to chemical control almost solely relates to that period. Mead (1979a, p. 8) noted in the Indo-Pacific:

> [a] growing attitude of resignation and even indifference – an acceptance of this pest as one of the many unfortunate facts of life. This attitude is explained in part by the fact that in most areas . . . where this snail is found, the people have learned to live with it.

Mead (1979a, pp. 8–9) goes on to suggest that the:

> overall picture that emerges . . . is one in which the snail continues to be a serious pest in the peripheral areas but is becoming less so in the older infested areas, to the point, in some cases, where it essentially ceases to be a

pest. In many areas, indeed if not most, there are virtually no organized efforts to control this snail.

Physical control strategies

Physical control relies primarily on the collection and destruction of the snails and their eggs from infested sites. The strategy has been effective in providing relief from *A. fulica* infestation in crops, albeit temporary, as reported from Guam (Peterson, 1957c), Hawaii (Olson, 1973), Japan and Sri Lanka (Mead, 1961). Schotman (1989) maintains that manual collection and destruction of the snails can be an effective control strategy when practised on a small scale or in organized campaigns involving the public or farmer groups. Collection and destruction of snails and their eggs have also played a significant part in eradication of incipient infestations in Japan (Mead, 1961), Australia (Colman, 1977), Arizona and Florida (Mead, 1961, 1979a).

The establishment of physical barriers that prevent or reduce movement of snails has long been practised as a control strategy for *A. fulica*. These barriers may simply be a strip of bare soil as a headland around the crop or may be a fence that comprises a screen of corrugated tin or security wire mesh. Schotman (1989) recommends that ditches be dug around the field and the snails collected and destroyed each day.

Protection of valuable horticultural plants can be provided during their vulnerable seedling stage by ringing them with a strip of cardboard that has been dipped in a suspension of metaldehyde, the dispersion of the latter being aided by the addition of a detergent (Bridgland and Byrne, 1956; Dun, 1967).

Chemical control strategies

Most early attempts at chemical control employed baits containing metaldehyde and/or calcium arsenate. A considerable number of toxicants and repellents have been evaluated at various times and locations for activity against *A. fulica* (summarized by Mead, 1979a; Raut and Ghose, 1984; Srivastava, 1992), but the great majority of these evaluations have not yielded significant advances over bran-based baits containing metaldehyde, which were initially developed in the 1930s for gastropod control in temperate regions. In many cases the evaluations were undertaken under experimental, laboratory conditions and the effectiveness of many materials under field conditions has not been demonstrated. Subsequently methiocarb baits also became available. In recent years the situation has not dramatically changed, although a number of new molluscicidal chemicals are now available, albeit rarely developed or registered specifically for use against *A. fulica*.

Bait formulations can be rendered ineffective by rain, which obviously poses constraints on the effectiveness of baits applied during the rainy season, when the gastropods are most active. Cement briquette formulations containing metaldehyde have provided for greater persistence and have enabled control in remote areas where repeated applications were not practicable (e.g. Dun, 1967; Watson, 1985). Many current commercial bait products have been formulated to persist, at least for a time, under moist field conditions. However, there is little published information on their effectiveness under tropical conditions.

Because a proportion of *A. fulica* occur arboreally and is thus not readily controlled by ground-applied baits, there has been interest in the efficacy of molluscicidal dusts or sprays. Nair *et al.* (1968), for example, demonstrated the effectiveness of kaolin dusts containing 1% metaldehyde and suspensions containing 1–4% metaldehyde.

Because of continuing concern about the environmental effects of synthetic chemicals, there is currently much interest in naturally occurring chemicals as molluscicides. Panigrahi and Raut (1994), for example, have demonstrated that an extract of the fruit of *Thevetia peruviana* (Persoon) Schumann (Apocynaceae) has activity against *A. fulica*. However, evaluations under field conditions are yet to be made.

Cropping strategies

Rees (1951, p. 585) noted that *A. fulica* 'does not appear to like aromatic plants, and it may be profitable to pursue this subject further to see whether judicious planting is likely to have some effect on its activity in gardens'. This strategy has not been seriously investigated. Relative to losses in monoculture crops, however, Raut and Ghose (1983b) demonstrated that planting selected non-crop species in headlands or guard rows can reduce economic losses within the crop (Fig. 3.4). As a strategy for the management of *A. fulica*, such mixtures of crop and non-crop species are not yet widely practised, although the approach is compatible with the current interest in the potential benefits of increased biological diversity in agriculture.

Biological control strategies

A. fulica, as with other Achatinidae, are subject to pathogens, parasites and invertebrate predators in their natural range in Africa. Those that are known are listed in Table 3.4. In addition, various vertebrates are recognized predators of Achatinidae in Africa (e.g. Rees, 1951; Williams, 1951, 1953; van Bruggen, 1978; Hodasi, 1989). None the less, the importance of these natural enemies in the regulation of *A. fulica* populations in Africa has not been studied, and much of the information on natural enemies stems from anecdotal observation made in the course of
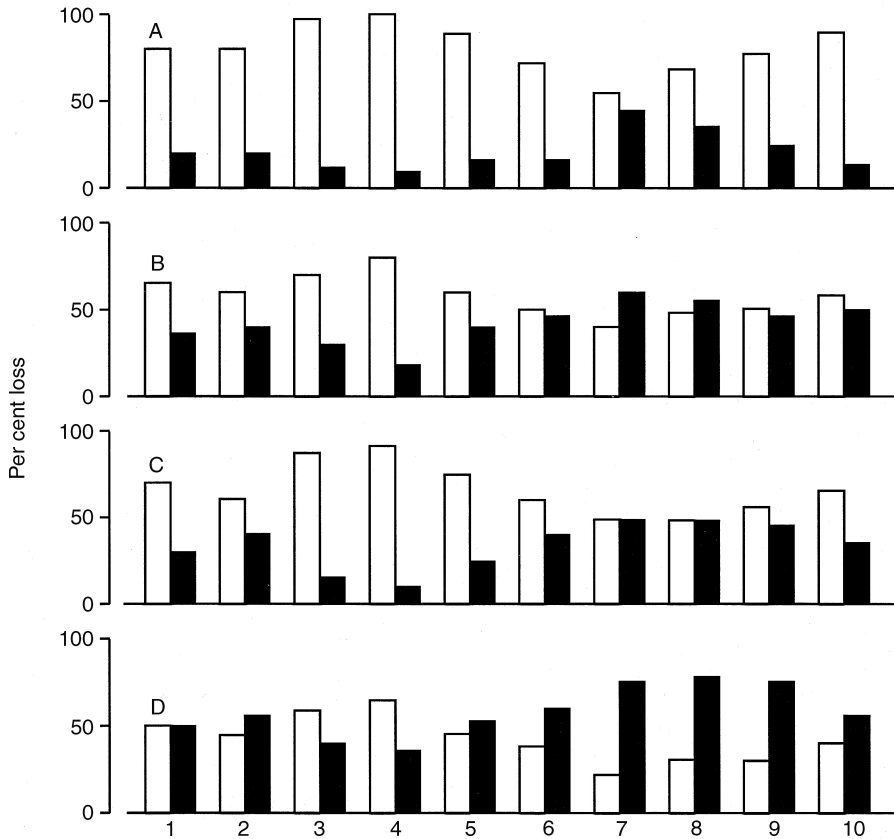
Fig. 3.4. Level of loss inflicted in ten crop plant species by *Achatina fulica* Bowdich (Achatinidae), in the presence of one of four non-crop species (black bar), namely: A. *Senna sophera* (Linnaeus) Roxburgh (Fabaceae). B. *Kalanchoe pinnatum* (de Lamarck) Oken (Crassulaceae). C. *Synedrella nordiflora* (Linnaeus) Gaertner (Asteraceae). D. *Tagetes patula* Linnaeus (Asteraceae). The crop species were: 1. *Lactuca sativa* Linnaeus (Asteraceae); 2. *Brassica oleracea* Linnaeus (Brassicaceae); 3. *Glycine max* (Linnaeus) Merrill (Fabaceae); 4. *Lablab purpureus* (Linnaeus) Sweet (Fabaceae); 5. *Cucurbita maxima* Duchesne (Cucurbitaceae); 6. *Carica papaya* Linnaeus (Caricaceae); 7. *Lycopersicon esculentum* Miller (Solonaceae); 8. *Gossypium herbaceum* Linnaeus (Malvaceae); 9. *Abelmoschus esculentus* (Linnaeus) Moench (Malvaceae); 10. *Ricinus communis* Linnaeus (*Euphorbiaceae*).

field surveys and searches for agents that may be employed in biological control outside Africa.

It is also evident that, when introduced into new areas, *A. fulica* is not without some level of population regulation from pathogens, parasites and predators naturally resident there, as evidenced by the suite of organisms reported to attack this gastropod species outside Africa (Table 3.5). That *A. fulica* almost invariably assumes pest status when introduced to areas of favourable climate clearly points to the lack of significant population regulation by pathogens, parasites and predators, at least in the early phases of invasion by the pest.

Table 3.4. Invertebrate natural enemies of Achatinidae in Africa, with observation on utilization in biological control programmes for *Achatina fulica* Bowdich outside Africa.*

Microspora	*Plistiphora husseyi* Michaud	Recorded from *Achatina zebra* (Bruguière)
Acari	Indeterminate sp.	Belgian Congo. Recorded from *Achatina scheinfurthi* von Martens and *Achatina stuhlmanni* von Martens
Decapoda	Undetermined sp.	East Africa. Recorded attacking *Achatina* de Lamarck sp.
Diptera: Phoridae	*Wandolleckia achatinae* Cook	Evidently widespread in Africa. Ectoparasitic. Recorded from *Achatina variegata* Roissy, *Achatina achatina* (Linnaeus), *Archachatina ventricosa* (Gould), *Achatina* de Lamarck sp. and *Lignus* Gray sp.
Diptera: Tachinidae	*Mydeae* sp. nr *bivittata* (Macquart)	Central Africa. *Burtoa nilotica* (Pfeiffer)
Diptera Muscidae	*Ochromusca trifaria* Big.	Malawi. Recorded from *Achatina craveni* Smith
Coleoptera: Carabidae	*Tefflus carinatus* Klug	Introduced into Hawaii. Apparently not established
	Tefflus zanzibaricus alluaudi Sternberg	Both adult and larval stages predacious on phytophagous terrestrial gastropods in Kenya. Introduced and established in Hawaii, but no demonstrated impact on *Achatina fulica* Bowdich
	Tefflus purpureipennis wituensis Kolbe	Kenya. Released in Hawaii. Apparently not established
	Tefflus raffrayi jamesoni Bates	Republic of the Congo. Released in Hawaii. Apparently not established
	Tefflus tenuicollis (Fairmaire)	Republic of the Congo. Released in Hawaii. Apparently not established
	Tefflus planifrons (Fabricius)	Nigeria. Released in New Britain but failed to establish
	Tefflus megerlei (Fabricius)	Nigeria. Introduced into Hawaii. Apparently not established
	Thermophilum hexastictum Gerstaecker	Kenya. Released in Hawaii. Apparently not established
Coleoptera: Drilidae	Undetermined species	West Africa
	Undetermined species	Morocco. Introduced into quarantine in Hawaii but evidently not released
	Undetermined species	Kenya. Introduced into quarantine in Hawaii but evidently not released
	Selasia unicolor (Guérin)	Nigeria. Introduced to New Britain. Apparently not established
Stylommatophora: Streptaxidae	*Gonaxis quadrilateralis* (Preston)	East Africa (Kenya). Introduced to India, parts of Asia, and many islands of the Pacific and Indian Oceans. Often failed to establish. Where established effect on *Achatina fulica* Bowdich when known, generally marginal. Generally preys on eggs and juveniles of *A. fulica*
	Gonaxis kibweziensis (Smith)	East Africa (Kenya). Established in Sri Lanka, Bermuda, and many islands of the Pacific, but impact on *Achatina fulica* Bowdich demonstrated only on Agiguan and Guam. Generally preys on eggs and juveniles of *A. fulica*
	Gonaxis vulcani Thiele	West Africa (Zaïre). Attempted introduction to Hawaii unsuccessful
	Gulella Pfeiffer sp.	South Africa. Released in Hawaii

Table 3.4. Continued

	Gulella Pfeiffer sp.	Republic of the Congo. Released in Hawaii
	Gulella Pfeiffer sp., nr *planti* (Pfeiffer)	South Africa
	Gulella bicolor (Hutton)[†]	Established as a tramp species in many tropical areas. Also introduced purposefully to Andaman Islands for control of *A. fulica* Bowdich but with no effect. Attempted introduction to Hawaii unsuccessful
	Gulella wahlbergi (Krauss)	South Africa. Established in Hawaii, but no demonstrated impact on *A. fulica*
	Edentulina affinis Boettger	East Africa (Kenya, Tanganyika). Released in Hawaii but failed to establish
	Edentulina obesa bulimiformis (Grandidier)	East Africa (Kenya, Tanzania). Attempted introduction to Hawaii unsuccessful
	Edentulina ovoidea (Bruguière)	Endemic to Mayotte. Preys on phytophagous gastropods. Introduced to Madagascar, Comores and Réunion. Attempted introduction to Hawaii unsuccessful
Stylommatophora: Rhytididae	*Ptychotrema* Mörch sp.	Belgian Congo. Introduced to Hawaii but establishment success and impact on *A. fulica* Bowdich unknown
	Ptychotrema walikalense Pilsbry	West Africa (Zaïre). Introduced to Hawaii but establishment success and impact on *A. fulica* Bowdich unknown
	Species complex	Twenty-two species, confined to eastern South Africa. Prey principally comprises achatinids and subulinids
	Natalina cafra (de Férussac)	South Africa. Predation on *Metachatina kraussi* (Pfeiffer). Attempted introduction to Hawaii unsuccessful

*Sources of information include: Stuhlmann (1894), Cook (1897), Wandolleck (1898), Brues (1903), Schmitz (1916, 1917, 1928, 1929, 1958), Bequaert in Pilsbry (1919), Bequaert (1925, 1926, 1950b), Pilsbry and Bequaert (1927), Williams (1951, 1953), Kondo (1952, 1956), Baer (1953), Weber (1953, 1954a,b, 1957), Davis (1954, 1958, 1959, 1960a,b, 1961, 1962, 1971, 1972), Pemberton (1954), Krauss (1955, 1964), Mead (1955, 1961, 1963a,b, 1979a), Peterson (1957b,c), Anon. (1961), Davis *et al.* (1961), Davis and Krauss (1962, 1963, 1964, 1965, 1967), Schreurs (1963), Simmonds and Hughes (1963), Davis and Butler (1964), Kim (1964), Dun (1967), Robinson and Foote (1968), Srivastava (1968b, 1976, 1992), Davis and Chong (1969), van Bruggen (1969, 1977, 1978), van der Schalie (1969), Ranaivosoa (1971), Etienne (1973), Lambert (1974, 1977), Sankaran (1974), Nakao *et al.* (1975), Nishida and Napompeth (1975), Srivastava *et al.* (1975), Lai *et al.* (1982), Muniappan (1982, 1983), Godan (1983), Backeljau (1984), Christensen (1984), Lionnet (1984), Nakamoto (1984), Raut and Ghose (1984), Howarth (1985, 1991), Nakahara (1985b), Waterhouse and Norris (1987), Eldredge (1988), Funasaki *et al.* (1988), Hodasi (1989), Nafus and Schreiner (1989), Naggs (1989), Napompeth (1990), Schreiner (1990), Herbert (1991), Cowie (1992, 1997, 1998a,b, 2000), Tillier (1992), Disney (1994), Civeyrel and Simberloff (1996), Sherley and Lowe (2000).
[†]Native range unknown. Possibly Africa or the Mascarene Islands (Solem, 1989) or Asia (Naggs, 1989).

Faced with infestation of *A. fulica*, many countries were eager to develop biological control strategies. Not only were natural enemies introduced from East Africa, in many cases introductions of polyphagous enemies were made from other parts of the world. Many introductions did not lead to the establishment of viable populations, as is typical for introduced species generally, but a great many of these introduced species were successful in naturalization. Unfortunately, the eagerness to effect biological control of *A. fulica* was not matched by consideration of environmental effects, particularly the impact on the indigenous

Table 3.5. Naturally occurring invertebrate enemies of terrestrial gastropods, utilizing the introduced species of Achatinidae in regions outside Africa, with observation on importance to regulation of achatinid populations.*

Bacteria	*Aeromonas hydrophila* (Chester) Stainer (= *Aeromonas liquifaciens* (Beijerinck))	Recorded in Sri Lanka, Singapore, Hong Kong, Thailand, Bangkok, Hawaii, India, Andaman Islands. Causing leucodermic lesions and epizootic disease in *A. fulica* Bowdich. Implicated as a causative agent in the decline of *A. fulica* observed in sectors many of the pests' naturalized range
Ciliophora: Peritrichida	*Trichodina* Ehrenberg spp.	India, recorded from *A. fulica* Bowdich. Germany, recorded from *A. zebra* (Brugière). Probably little effect on parasitized animals
	Pallitrichodina rogenae van As & Basson	Recorded from *A. fulica* Bowdich in Mauritius and Taiwan. No evidence of pathological effect. Regarded as a symbiont
	Pallitrichodina stephani van As & Basson	Recorded from *A. immaculata* de Lamarck in Mauritius. No evidence of pathological effect. Regarded as a symbiont
Nematoda: Rhabditidae	Unidentified sp.	Recorded from *A. fulica* Bowdich in India. Effect on *A. fulica* populations not known
Nematoda: Metastrongylidae	*Angiostrongylus cantonensis* (Chen)	Widespread in Asia and the Pacific. Definitive hosts are *Rattus* Fischer spp. (Muridae). Utilizes *A. fulica* Bowdich and other gastropods as intermediate hosts
	Angiostrongylus costaricensis (Morera and Céspedes)	Widespread in Americas. Definitive hosts are *Rattus* Fischer spp. (Muridae). Utilizes *A. fulica* Bowdich and other gastropods as intermediate hosts
	Anafilaroides rostratus Gerichter	Widespread. Definitive host *Felis* Linnaeus sp. (Felidae). Utilizes *A. fulica* Bowdich and other gastropods as intermediate hosts
Turbellaria: Geoplanidae	*Endeavouria septemlineata* (Hyman)	Hawaii. Important regulatory agent in *A. fulica* Bowdich. Also adversely affecting indigenous terrestrial gastropods, and the streptaxids and oleanicids introduced for biocontrol
	Undetermined sp.	Ogasawara. Observed attacking *A. fulica* Bowdich
Turbellaria: Rhynchodemidae	*Platydemus manokwari* de Beauchamp	New Guinea. Importance unknown but suspected as a contributory factor in decline in *A. fulica* Bowdich at some sites
Bipaliidae	*Bipalium indica* Whitehouse	India. Predation on juvenile *A. fulica* Bowdich. Effect on *A. fulica* populations not known
Coleoptera: Lampyridae	*Bipalium* Stimpson sp.	Ogasawara. Observed attacking *A. fulica* Bowdich
	Lamprophorus tenebrosus (Walker)	Sri Lanka and India. Important predator of *A. fulica* Bowdich
Hymenoptera: Formicidae	*Solenopsis geminata* (Fabricius)	Native to Central America. Invasive species, widely dispersed accidentally. Observations in New Britain, mainland New Guinea and Christmas Island suggest species can exert considerable mortality in young *A. fulica* Bowdich
	Oecophyllus Smith sp.	India. Predation on newly hatched *A. fulica* Bowdich. Importance in population regulation not known
	Pheidologeton affinis (Jerdon)	Sri Lanka, India. Mainly attacks the eggs of *A. fulica* Bowdich. Invasive species, widely dispersed accidentally. Importance of predation in *A. fulica* populations unknown
Diptera: Phoridae	*Megaselia javicola* (Beyer)	Asia. Recorded from *A. fulica* Bowdich

Table 3.5. Continued

	Spiniphora Malloch sp.	Recorded from *A. fulica* Bowdich
Diptera: Sarcophagidae	*Sarcophaga* Meigen sp.	India. Parasite of *A. fulica* Bowdich and other terrestrial gastropods
Diplopoda: Paradoxosomatidae	*Orthomorpha* sp.	Andaman Islands. Observed attacking *A. fulica* Bowdich
Chilopoda	Unidentified sp.	New Guinea. Occasional predation on *A. fulica* Bowdich
Decapoda: Coenobitidae	*Coenobita cavipes* Stimpson	East coast of Africa to Ryūkyū Island and Bismarck Archipelago. Confirmed predator of *A. fulica* Bowdich in Andaman Islands
	Coenobita perlatus Milne Edwards	Aldabra and Madagascar to Line and Gambier Islands. Confirmed predator of *A. fulica* Bowdich in various Pacific Islands
	Coenobita brevimanus Dana	East coast of Africa to Line and Tuamotu Archipelago. Confirmed predator of *A. fulica* Bowdich in Ogasawara, and member of a complex of *Coenobita* species implicated in control of *A. fulica* in Andaman Islands
	Coenobita purpreus Stimpson	Ogasawara. Predator of *A. fulica* Bowdich
	Coenobita rugosa Milne Edwards	East coast of Africa to Line Islands and Tuamotu Archipelago. Among a complex of *Coenobita* species implicated in control of *A. fulica* Bowdich in the Andaman Islands
	Birgus latro (Linnaeus)	East coast of Africa through to Malay Archipelago and Pacific Islands. Confirmed predator of *A. fulica* Bowdich, but level of control effected generally minimal
Decapoda: Grapsidae	*Geograpsus grayi* (Milne Edwards)	East coast of Africa to Japan and Society Islands. Confirmed predator of *A. fulica* Bowdich in Ogasawara
	Metopograpsus messor (Forskål)	Red Sea and east coast of Africa to Japan. Confirmed predator of *A. fulica* Bowdich in Ogasawara
	Sesarma dahaani (Milne Edwards)	Confirmed predator of *A. fulica* Bowdich in Ogasawara
Decapoda: Ocypodidae	*Ocypoda cordimana* Latreille	Red Sea and east coast of Africa to Japan and Society Islands. Confirmed predator of *A. fulica* Bowdich in Ogasawara
Decapoda: Gecarcinidae	*Gecarcoidea natalis* Pocock	Christmas Island. Confirmed predator of *A. fulica* Bowdich

*Sources of information include: Green (1910b, 1911), Annandale (1919), Paiva (1919), Hutson (1920), Austin (1924), Fantham (1924), Hutson and Austin (1924), South (1926), Jarrett (1931), Mead and Kondo (1949), Lange (1950), Mead (1950b, 1956, 1958a,b, 1961, 1963a, 1969, 1979a), Rees (1951), Kondo (1952), Davis (1954, 1971), van Zwaluwenburg (1955), Peterson (1957a), Seneviratna (1958), Beyer (1959), Ash (1962, 1976), Schreurs (1963), Alicata (1964, 1965a,b, 1966, 1969), Davis and Butler (1964), Davis and Krauss (1964), Cheng and Alicata (1965), Srivastava (1966, 1968b, 1970, 1976, 1992), Dun (1967), Srivastava and Srivastava (1967, 1968), Nair (1968), Robinson and Foote (1968), Davis and Chong (1969), van der Schalie (1969), Wallace and Rosen (1969a,b), Dean *et al.* (1970), Crook *et al.* (1971), Pradhan and Srivastava (1971), Raut and Ghose (1977, 1979a, 1984), Raut (1980, 1983b, 2001), Iga (1982), Godan (1983), Muniappan (1983), Nakahara (1985a), Higa *et al.* (1986), Waterhouse and Norris (1987), Raut and Panigrahi (1989), Schotman (1989), Kaneda *et al.* (1990), Lake and O'Dowd (1991), Raut (1993), van As and Basson (1993), Eldredge (1994), Ogren (1995), Teles *et al.* (1997), K. Takeuchi (personal communication, 1997), Kadirijan and Chauvet (1998), Cowie (2000), Sherley and Lowe (2000).

Fig. 3.5.   A pair of *Achatina fulica* Bowdich (Achatinidae) in copulation.

molluscan biodiversity. Tests of host specificity preceding introductions of control agents have often been perfunctory or non-existent. More adverse effects on indigenous faunas, including species extinctions, can be attributed to species importation for biocontrol of *A. fulica* than can be attributed to the much more maligned chemical control. Despite some claims to the contrary (e.g. Tauili'ili and Vargo, 1993), the devastation wrought on indigenous terrestrial faunas by the polyphagous predator *Euglandina rosea* (de Férussac) (Oleacinidae) in the islands of the Pacific and India Oceans has been widely recognized and canvassed in the recent scientific literature (e.g. Tillier and Clarke, 1983; Civeyrel and Simberloff, 1996) and the popular media (e.g. Wells, 1988). Ironically there is no evidence that *E. rosea* or any other purposefully introduced pathogen, parasite or predator has effected population regulation in *A. fulica* (e.g. van der Schalie, 1969; Tillier, 1992; Tillier and Clarke, 1983; Clarke *et al.*, 1984; Pointier and Blanc, 1985; Cowie, 1992; Hopper and Smith, 1992; Griffiths *et al.*, 1993; Hadfield *et al.*, 1993; Civeyrel and Simberloff, 1996). The ecological effects of the great number of introduced agents remain to be investigated.

Populations of *A. fulica* have often been observed to pass through three phases following establishment in a new area (Mead, 1961, 1979a; Pointier and Blanc, 1985): (i) a phase of exponential increase, with the population typified by large, vigorous individuals; (ii) a stable phase of variable duration; and (iii) a phase of decline, with the population typified by small individuals. Thus naturalized populations of *A. fulica* often eventually decline greatly. There has been a widespread belief among local peoples that introduced biological control agents, particularly *E. rosea*, were responsible for the declines (Wells, 1988). The Hawaiian islands were often viewed as a pilot study that served as a model for other biological control projects and it is mainly from the Hawaiian islands that *E. rosea* and other predatory gastropods, such as

Table 3.6.   Invertebrate enemies of terrestrial gastropods, naturally occurring outside Africa, introduced to different regions for biological control of *Achatina fulica* Bowdich (Achatinidae) and observations on importance to regulation of *A. fulica* populations.*

Turbellaria: Rhyncho- demidae	*Platydemus manokwari* de Beauchamp	Native range not known. Accidentally introduced to Guam and northern Mariana Islands. Subsequent purposeful introduction to Bugsuk Island (Philippines) and Maldives and thence to many Pacific islands. Providing some regulation of *A. fulica*, and attributed with eradication in some areas. Probable adverse effect on indigenous gastropod faunas
Coleoptera: Lampyridae	*Lamprophorus tenebrosus* (Walker)	Native to Sri Lanka. Introduced to various Pacific and Indian Ocean islands, but did not establish
	Colophotia concolor (Olivier)	Native to the Philippines. Introduced to Hawaii, but not released
	Pyrophanes quadrimaculata bimaculata (Olivier)	Native to the Philippines. Introduced to Hawaii, but not released
	Diaphanes sp.	Native to Sri Lanka. Introduced to Hawaii, but perished in the laboratory prior to release
Coleoptera: Carabidae	*Damaster blaptoides* Kollar (includes sub-species *D. b. rugipennis* Motschulsky)	Native to Japan. Introduced to Hawaii but did not establish
	Scaphinotus striatopunctatus (Chaudoir)	Native to western North America. Introduced to Hawaii but did not establish
	Scaphinotus ventricosus (Dejean)	Native to western North America. Introduced to Hawaii but did not establish
Stylommatophora: Oleacinidae	*Euglandina rosea* (de Férussac)	Native to south-east USA. Introduced to India, parts of Asia and many islands of the Pacific and India oceans. Often failed to establish. Where established, no demonstrable regulatory effect on *A. fulica* but with adverse effect on indigenous fauna
	Euglandina singleyana (Binney)	Native to south-east USA. Introduced into quarantine in Hawaii but not released
	Salasiella Strebel sp.	Native to West Indies (Cuba). Introduced to Hawaii but did not establish
	Oleacina oleacea Deshayes	Native to West Indies (Cuba). Introduced to Hawaii but did not establish
	Oleacina Röding sp.	Native to West Indies (Cuba). Introduced to Hawaii but did not establish
Stylommatophora: Streptaxidae	*Streptaxis contundata* de Férussac	Native to South America (Brazil). Introduced to Hawaii but did not establish
Stylommatophora: Rhytididae	*Victaphanta compacta* (Cox & Hedley)	Native to Victoria, Australia. Imported into Hawaii but did not survive to be released
	Ptychorhytida ferreziana (Crosse)	Native to New Caledonia. Imported to Hawaii but evidently not released
	Ptychorhytida inaequalis (Pfeiffer)	Native to New Caledonia. Imported to Hawaii but evidently not released
	Austrorhytida capillacea (de Férussac)	Native to New South Wales and Victoria, Australia. Imported into Hawaii but did not survive to be released

Table 3.6. Continued

Stylommatophora: Zonitidae	*Oxychilus cellarius* (Müller)	Native to Europe. Purposefully introduced into New Britain. Early attempts at introduction into Hawaii unsuccessful, but accidentally introduced and established there. No evidence of effect on *A. fulica* populations
Stylommatophora: Haplotrematidae	*Haplotrema vancouverense* (Lea)	Native to north-west USA and western Canada. Imported into Hawaii but did not survive to be released
Decapoda: Coenobitidae	*Coenobita cavipes* Stimpson	East coast of Africa to Ryukyu Island and Bismarck Archipelago. Inundative releases in Andaman Islands provided control of *A. fulica*

*Sources of information include: Rees (1951), H. Macpherson in van Benthem Jutting (1952), Thistle (1953), Weber (1954b, 1956, 1957), Kondo (1956), Peterson (1957a,b,c), Davis (1958, 1959, 1960b, 1961, 1962, 1971, 1972, 1973), Chiu (1960), Mead (1961, 1979a), Chiu and Chou (1962), Schreurs (1963), Davis and Butler (1964), Krauss (1964), Davis and Krauss (1967), Dun (1967), Srivastava (1968a, 1976, 1992), Davis and Chong (1969), Mitchell (1969), van der Schalie (1969, 1970), Pradhan and Srivastava (1971), Ranaivosoa (1971), Etienne (1973), Lambert (1974, 1977), Sankaran (1974), Nishida and Napompeth (1975), Hart (1978), Hadfield and Mountain (1980), Hadfield and Kay (1981), Leehman (1981), Severns (1981, 1984), Whitten (1981), Muniappan (1982, 1983, 1987, 1990), Tillier (1982a), Godan (1983), Howarth (1983, 1985), Tillier and Clarke (1983), Wells *et al.* (1983), Backeljau (1984), Christensen (1984), Clarke *et al.* (1984), Nakamoto (1984), Raut and Ghose (1984), Pointier and Blanc (1985), Hadfield (1986), Muniappan *et al.* (1986), Waterhouse and Norris (1987), Eldredge (1988, 1992, 1994), Funasaki *et al.* (1988), Lai (1988), Gerlach (1989, 1993), Howarth and Medeiros (1989), Murray (1989), Nafus and Schreiner (1989), Schotman (1989), Cowie (1990, 1992, 1993, 1997, 1998a,b, 2000), Napompeth (1990), Schreiner (1990), Solem (1990), Hadfield and Miller (1992), Hopper and Smith (1992), Kawakatsu *et al.* (1992, 1993), Kinzie (1992), Smith (1992), Griffiths *et al.* (1993), Hadfield *et al.* (1993), Miller *et al.* (1993), US Congress (1993), Eldredge and Smith (1994), Griffiths (1994), Kobayashi (1994), Asquith (1995), Kay (1995), Obata (1995), Bauman (1996), Civeyrel and Simberloff (1996), Simberloff and Stiling (1996), K. Takeuchi (personal communication, 1997), Sherley and Lowe (2000).

Gonaxis quadrilateralis (Preston) (Streptaxidae), were introduced to other regions for control of *A. fulica*. There has thus been continued purposeful introduction of polyphagous enemies by people blissfully unaware of or blatantly dismissive of the ecological catastrophes unfolding in areas to which these same agents had earlier been introduced.

It is evident that lessons from the disastrous biological control effects of the past have not been well heeded. Generalist predators such as *E. rosea*, *G. quadrilateralis* and, more recently *Platydemus manokwari* de Beauchamp (Rhynchodemidae), continue to be dispersed to new areas in an attempt to control *A. fulica*.

The factor(s) causing the decline in *A. fulica* remains to be fully elucidated. Periods of high population densities of *A. fulica* are frequently followed by a high frequency of leucodermic lesions, evidently caused by the bacterium *Aeromonas hydrophila* (Chester) Stainer (Mead, 1979a). The disease has been considered a significant regulatory factor in declining *A. fulica* populations (Mead, 1961, 1979a; Raut and Ghose, 1984; Raut and Panigrahi, 1989). Exactly what triggers this epizootic disease is uncertain, but Mead (1979a) argues that various stresses associated with high populations lead to a breakdown in the natural resistance,

while Civeyrel and Simberloff (1996) postulate that increasing density facilitates its transmission. Srivastava and Srivastava (1968) were successful in initiating disease outbreaks in *A. fulica* by spraying field populations with fluids derived from diseased animals. Undoubtedly, other natural enemies have also contributed to regulation of *A. fulica* in some areas, but the agents involved have not been studied.

Some island systems have evidently proved to be resistant to invasion by *A. fulica*. Schotman (1989) attributes the low abundance of *A. fulica* on some Pacific atolls to the sandy soils and predation by hermit crabs *Coenobita perlatus* Milne Edwards and *Birgus latro* (Linnaeus) (Coenobitidae). Lake and O'Dowd (1991) demonstrated that the omnivorous crab *Gecarcoidea natalis* Pocock (Gecarcinidae) provided biotic resistance to invasion by *A. fulica* on Christmas Island.

Future Prospects

A. fulica is a serious pest of agriculture in many tropical regions. Despite the decline in its abundance after long residence in many regions, *A. fulica* continues to impose severe economic constraints on agricultural productivity. Thus there is continuing demand for the development of effective, sustainable control strategies. There has been little advancement in the development of sustainable controls for *A. fulica* over the past 30 years. Further, this invasive species continues to spread. For those countries currently free from *A. fulica*, the most prudent control strategy is clearly the implementation of barriers to importation of unwanted organisms through apppropriate border security. Prevention of entry, rather than later control, is the most important means of mitigating the agricultural impacts of *A. fulica* and other invasive achatinids.

By reaching enormous numbers and invading native ecosystems *A. fulica* additionally poses a serious conservation problem. Not only do they eat native plants, modifying the environment, but they probably also outcompete native gastropods. However, the more insidious conservation problem they cause is that they tempt agricultural officials and individual farmers to initiate putative biological control measures. The best publicized of these measures is the introduction of generalist predators, most notably *E. rosea*. It cannot be stressed enough that these introductions of putative biological control agents against *A. fulica* are extremely adverse from the perspective of the conservation of native gastropod faunas. And, in any case, there is no good evidence that such generalist predators can indeed control *A. fulica* populations.

There is increasing awareness internationally of the adverse ecological and economic impacts of invasive species. Coupled with this is the recognition that mitigation of the effects of invasive species on biodiversity is best coordinated regionally, and agencies such as the International Union for the Conservation of Nature (IUCN) are coordinating development of biosecurity policies and operational procedures.

Examples are the *IUCN Guidelines for the Prevention of Biodiversity Loss caused by Alien Invasive Species* (IUCN, 2000) and the draft *Invasive Species Strategy for the Pacific Region* (Sherley *et al.*, 2000). There is a good case for integrating consideration of both agricultural and environmental pests in such strategy developments, given that impacts on agriculture result in a heavy demand for the introduction of biocontrol agents, which, by their very nature, involve further introductions of alien species. A coordinated effort among countries at the regional level is needed to prevent further spread of *A. fulica* and for the development of environmentally sustainable controls of current infestations.

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