© 1984 by the University of Hawaii Press. All rights reserved

The Extinction of Endemic Species by a Program of Biological Control¹

BRYAN CLARKE,² JAMES MURRAY,³ AND MICHAEL S. JOHNSON⁴

ABSTRACT: Land snails of the genus *Partula*, inhabiting the high islands of the Pacific Ocean, have provided exceptional opportunities for studies on the origin and differentiation of species. The endemic taxa of Moorea, in French Polynesia, have been particularly well studied.

In an attempt to control the numbers of the giant African snail, Achatina fulica, which is an agricultural pest, a carnivorous snail, Euglandina rosea, has been introduced into Moorea. It is spreading across the island at the rate of about 1.2 km per year, eliminating the endemic Partula. One species is already extinct in the wild; and extrapolating the rate of spread of Euglandina, it is expected that all the remaining taxa (possibly excepting P. exigua) will be eliminated by 1986–1987.

Euglandina has been introduced into many other oceanic islands, and it appears that more than a hundred endemic species are at risk. These observations point to a serious danger in programs of "biological control."

SINCE THE TIME OF DARWIN, the endemic species of oceanic islands have held a special interest for students of evolution. Archipelagos of volcanic origin, such as the Galapagos and Hawaiian islands, are natural laboratories in which the phenomena of speciation can be studied (Lack 1947, Carson and Yoon 1982). The fauna and flora of such islands are, however, unusually susceptible to the introduction of competitors, parasites, and predators.

In this paper we report the progressive extinction of land snails (genus *Partula*), endemic to the island of Moorea in French Polynesia, by an introduced molluscan predator (*Euglandina rosea* (Ferussac)).

The classic studies of Crampton (1932) and later investigations (Murray and Clarke 1980, Murray, Johnson, and Clarke 1982) have shown that these shails provide exceptional oppOrtunities for study of the origin and differentiation of species. Their unique combination of ovoviviparity, low mobility, short generation time, ease of culture in the laboratory, and extensive genetic polymorphism (at both the morphological and molecular levels) make them almost ideal material for the study of ecological and evolutionary genetics.

Their loss is not merely a tragedy for students of genetics, it is also a warning about the potentially devastating effects of some programs in "biological control"; and it exemplifies a threat to more than a hundred other species. Because the *Partula* of Moorea have been mapped in great detail, we are able to document rather precisely the progress of extinction.

THE Partula OF MOOREA

Moorea is one of the Society Islands and lies about 20 km to the northwest of Tahiti, in almost the exact geographical center of the

¹ Manuscript accepted 10 January 1984.

² Muséum National d'Histoire Naturelle et École Pratique des Hautes Études en Polynésie Française, Centre de l'Environnement de Mooréa, B.P. 12, Mooréa, French Polynesia. Permanent address: University of Nottingham, Department of Genetics, University Park, Nottingham NG7 2RD, England.

³ Muséum National d'Histoire Naturelle et École Pratique des Hautes Études en Polynésie Française, Centre de l'Environnement de Mooréa, B.P. 12, Mooréa, French Polynesia. Permanent address: University of Virginia, Department of Biology, Charlottesville, Virginia 22901.

⁴University of Western Australia, Department of Zoology, Nedlands, Western Australia 6009.

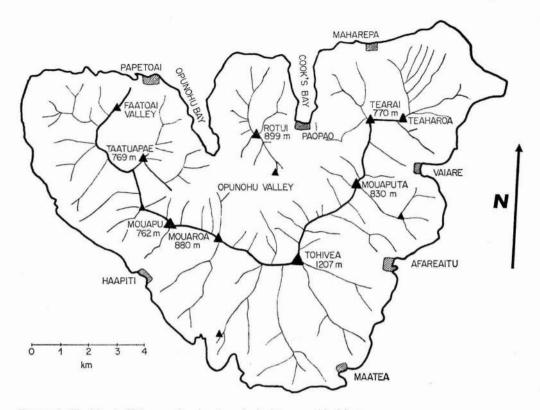


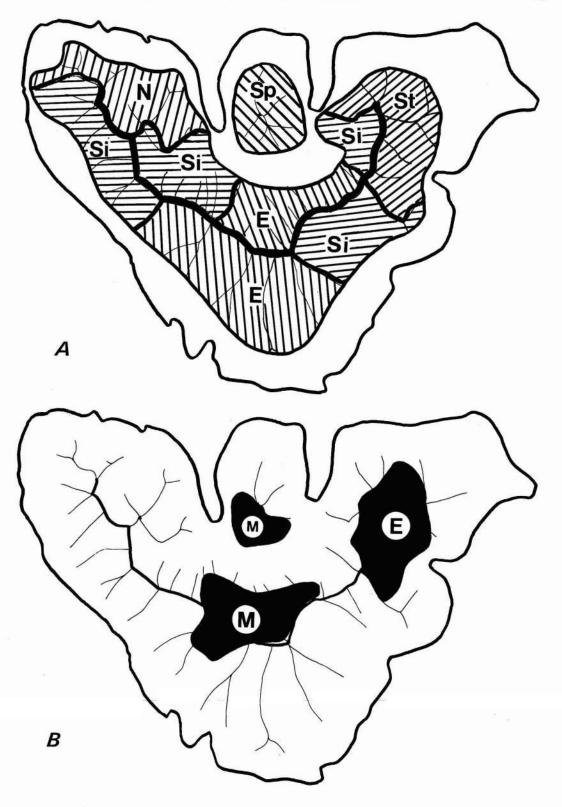
FIGURE 1. The island of Moorea, showing the principal topographical features.

Pacific Ocean. The island is volcanic in origin, and its age is approximately 1.2 million years (Jackson 1976). It is about 12 km in diameter, and its highest peak rises to 1207 m. Nine other peaks exceed 700 m (Figure 1).

Crampton (1932) and Crampton and Cooke (1953) described eleven species of Partula, all endemic to the island. Two of these (Partula solitaria Crampton and Partula diaphana Crampton and Cooke) have since been relegated to the genus Samoana (Kondo 1973). Of the remaining nine, one (P. dendroica Crampton) is clearly a geographical race of P. suturalis Pfeiffer and another (P. olympia Crampton) a geographical race of P. tohiveana Crampton (Clarke and Murray 1969, Murray and Clarke 1980). The number of Partula "species" is thus reduced to seven (P. taeniata Morch, P. exigua Crampton, P. suturalis Pfeiffer, P. tohiveana Crampton, P. aurantia Crampton, P. mooreana Hartman,

and P. mirabilis Crampton). Their status as good biological species is, however, in question because each, at some point on the island, gives evidence of hybridization or intergradation with another. For example, P. tohiveana tohiveana and P. suturalis are the sympatric terminal elements of a ring-species including P. tohiveana olympia. The pattern is such that, potentially at least, genes could flow from any one "species" to any other (with the possible exception of P. mooreana). Nonetheless, at any particular place as many as four of the taxa may coexist without interbreeding. When they do so, they are clearly distinct in genetics, morphology, ecology, and behavior (Johnson, Clarke, and Murray 1977, Murray and Clarke 1980, Murray, Johnson, and Clarke 1982).

The geographical ranges of the taxa prior to the introduction of *Euglandina* are shown in Figure 2 (pages 99 and 100).



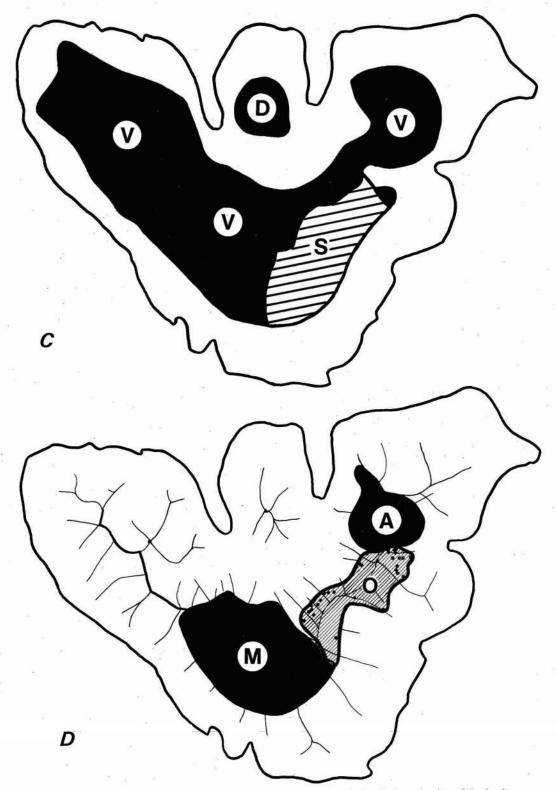


FIGURE 2. The ranges of the different species of *Partula* on Moorea prior to the introduction of *Euglandina rosea*: (A) *Partula taeniata* (N = P. *taeniata nucleola*, Sp = P. *t. spadicea*, St = P. *t. striolata*, Si = P. *t. simulans*, E = P. *t. elongata*); (B) *Partula exigua* (E) and P. *mirabilis* (M); (C) *Partula suturalis* (V = P. *suturalis vexillum*, S = P. *s. strigosa*, D = P. *s. dendroica*); (D) *Partula mooreana* (M), P. *tohiveana* (O), and P. *aurantia* (A).

THE INTRODUCTION OF Achatina AND Euglandina

The giant African snail, Achatina fulica Bowdich, is well known as an agricultural pest (Mead 1961, 1979). It was introduced into Tahiti (by someone who wished to breed it for food) in 1967 and spread rapidly to the other islands in the archipelago. Its numbers increased in Moorea to such an extent that the snails invaded human dwellings, and on one occasion two wheelbarrow-loads of snails were taken from the walls of a single house (R. Brosious, pers. comm.). Because Achatina, unlike Partula, eats living plants, it caused great damage to crops and gardens. The numbers of A. fulica apparently reached a peak on Moorea in 1978, and thereafter declined. The cause of this decline is unknown (see below). but the very large numbers of empty unbroken shells found all over the island suggest an epidemic disease (or perhaps predation by land planarians; see Mead 1979: 70). Living Achatina are still common on Moorea, and still cause damage to crops, but the scale of the problem has greatly diminished.

Euglandina rosea was introduced into Tahiti and Moorea in an attempt at the "biological control" of *Achatina fulica*. *Euglandina rosea*, which is native to Florida and central America, is a carnivorous mollusc that preys upon other land snails. Although it certainly eats *Achatina*, there is, as far as we know, little evidence that it is an effective agent of control (Mead 1979). Nevertheless, it has been widely recommended for this purpose by departments of agriculture in various countries. It is still so recommended by the South Pacific Commission.

Euglandina rosea was introduced into Moorea, with the approval of the Service de L'Economie Rurale and the Division de Recherche Agronomique, at the orange plantation of M. Nardi in Paopao on 16 March 1977 (J. L. Reboul, pers. comm.). It spread into the adjoining forests, and by 1980 its range covered approximately 4km², very nearly a third of the island. Its rate of spread between 1980 and 1982 was approximately 1.2 km per year (Figure 3). If the spread continues at the present rate, *Euglandina* will occupy the whole island by 1986 or 1987.

THE EFFECT OF Euglandina ON Achatina

The decline in the numbers of Achatina fulica on Moorea since 1978–1979 cannot rigorously be ascribed to the effects of Euglandina rosea. Living Achatina are still to be found in the territories occupied by Euglandina, and the decline in the number of Achatina has been observed in parts of the island not yet reached by the carnivore, for example Aareo Valley and Vaihiiaiia Valley. Furthermore, a similar decline has occurred on the island of Huahine, to which E. rosea has not yet been introduced (Pointier and Blanc 1982).

THE EFFECT OF Euglandina ON Partula

Although the role of *Euglandina* in controlling *Achatina* is doubtful, there is unfortunately no doubt at all about its effects on *Partula*. It consumes them with great efficiency. Four individuals of *P. taeniata* were put in a plastic lunch-box with a single *E. rosea*. Within 24 hours they had all been eaten, leaving four empty shells.

During our field studies in 1982 we were unable, with one exception discussed below, to find any Partula in the territories now occupied by Euglandina rosea. Our 1982 surveys specifically included localities (in Paparoa, Mouaputa, Faamaariri, and Puutu Valleys) that had yielded large samples of Partula in 1967 and 1980. Four species (P. aurantia, P. suturalis, P. tohiveana, and P. taeniata) seem to have been entirely eliminated from the northeast of the island. Partula aurantia, which was restricted to this area (see Figure 2), must now be considered extinct in the wild state (the only living examples being those kept alive by James Murray in the laboratory). The subspecies P. taeniata striolata is also, we believe, extinct.

The single exception is *Partula exigua*. This taxon is restricted to the northeast (see Figure 2), although it is closely related to *P. taeniata* and hybridizes with it (Murray and Clarke 1980). Prior to the introduction of *Euglandina* it tended generally to be less common than its sympatric relatives (*P. taeniata*, *P. suturalis*, and *P. aurantia*). In 1982 we found a few scattered individuals of *P. exigua* or

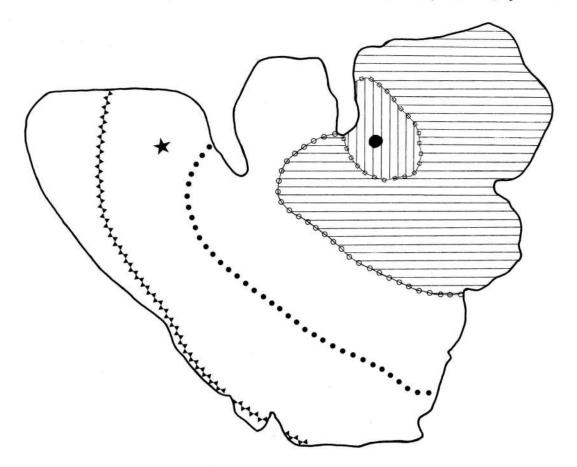


FIGURE 3. The spread of *Euglandina rosea* on Moorea. The black circle represents the site of its introduction in 1977. The vertically hatched area represents its range in 1980, and the horizontally hatched area its range in 1982. The black dotted line represents its expected range in 1984, and the serrated line its expected range in 1986. The star represents the site of a secondary introduction (in Faataai Valley) the success of which is unknown. If it proves successful, the spread of *Euglandina* is likely to be faster than shown in this figure.

taeniata/exigua hybrids surviving where the other Partula were extinct (in Faamaariri and Mouaputa Valleys). We are not yet able to give a reason for the "escape" of some P. exigua, or to tell whether the phenomenon is transient or lasting.

An incidental consequence of the spread of *Euglandina* is the raising of *Partula tohiveana* to the status of a good biological species. Until 1980 *P. tohiveana* and *P. suturalis* formed a ring-species, the zone of intergradation being to the east of Mt. Mouaputa (Murray and Clarke 1980). Populations from this zone have now been eliminated, and the remaining populations of *tohiveana* are sympatric with, and distinct from, *suturalis*.

The rate at which *Euglandina* is spreading (Figure 3), and the known ranges of the *Partula* taxa (Figure 2), allow us to make clear predictions about the years in which the taxa are expected to become extinct in the wild. These are given in Table 1. The majority are expected to die out by 1986.

THE THREAT TO Partula ON OTHER ISLANDS

H. E. Crampton, in addition to his work on Moorea, wrote two further evolutionary monographs, one on the *Partula* of Tahiti (1916), the other on the *Partula* of Guam and Saipan (1925). These snails, too, are under threat. In Tahiti Euglandina rosea was established during 1974 and now occupies the whole of the Temarua Valley, above the village of Papara, and the entire plateau of Taravao, above the village of Afaahiti. In these areas the native Partula appear to have been eliminated (Pointier and Blanc 1982). Because Tahiti, with a diameter of about 30 km, is a larger island than Moorea, some of the Tahitian Partula may survive longer than the Moorean ones, perhaps until the 1990s. The situation is probably worse in Guam and Saipan. Not only is Euglandina rosea well established on both islands, but two other carnivorous snails (Gonaxis quadrilateralis (Preston) and Gonaxis kibweziensis (E. A. Smith)) also have been introduced (Mead 1979).

In view of the rapid spread of *Achatina* among the Society Islands, both by accidental and by intentional transport, it seems very probable that *Euglandina* will reach many other islands within the next few years.

THE THREAT TO OTHER GENERA OF LAND SNAILS

We have not studied the effect of Euglandina on the two Moorean species of Samoana (Samoana diaphana (Kondo) = Partula diaphana Crampton and Cooke, and Samoana attenuata (Pease) = Partula solitaria Crampton), but if they prove to be as susceptible to Euglandina as the other Partulidae we can expect them to be eliminated from the island before 1987. The same is true of the arboreal snail Trochomorpha pallens Pease, which seems now to be absent from the territories occupied by Euglandina.

The introduction of *Euglandina* and other carnivores has been implicated in the extinction of many endemic snails in the Hawaiian islands (van der Schalie 1969, Hadfield and Mountain 1980, Kondo, pers. comm.). *Euglandina* has been successfully introduced into Mauritius, the Seychelles, La Reunion, the New Hebrides, and New Caledonia (Mead 1979). The number of endemic species that are endangered or already extinct as a result of the introductions must now be well over a hundred.

TABLE 1

PREDICTED YEARS OF EXTINCTION OF Partula FROM MOOREA

TAXON	PREDICTED YEAR OF EXTINCTION
Partula taeniata spadicea	1984
Partula taeniata elongata	1986
Partula taeniata simulans	1986
Partula taeniata nucleola	1986-1987
Partula exigua	uncertain (see text)
Partula aurantia	already extinct
Partula tohiveana olympia (P. olympia Crampton)	1983
Partula tohiveana tohiveana	1984
Partula mirabilis	1985
Partula mooreana	1985
Partula suturalis dendroica (P. dendroica Crampton)	1984
Partula suturalis strigosa	1986
Partula suturalis vexillum	1986-1987

REMEDIAL MEASURES

We see no hope of stopping the spread of *Euglandina* on the islands where it has already become established. There is, however, a very good case for discouraging new introductions, whether by governmental programs, by private enterprise on the part of local farmers, or by accident.

In an attempt to preserve the Moorean taxa of *Partula* we have established breeding colonies in our laboratories. Other colonies have been set up by the Jersey Wildlife Preservation Trust and by the Zoological Society of London. However, even if these colonies can successfully be maintained, a valuable genetic resource will have been lost.

We believe that our observations on the effects of *Euglandina* may be worth the attention of the workers and governmental agencies concerned in attempts to control *Achatina* and other pest species. They show that programs of "biological control" may have very dangerous consequences to local faunas.

ACKNOWLEDGMENTS

We are very grateful to Bernard Salvat, Rene Galzin, and Gilbert Vergonzanne for their hospitality, and much practical help, at the Centre de l'Environnement, Moorea; to Jean-Pierre Pointier, Charles Blanc, and Yoshio Kondo for allowing us to mention their unpublished work; and to the Science and Engineering Research Council for financial support. We also thank the Fauna and Flora Preservation Society, and the Onaway Trust, for financial help in setting up breeding colonies of *Partula*.

LITERATURE CITED

- CARSON, H. L., and J. S. YOON. 1982. Genetics and evolution of Hawaiian Drosophila. Pages 207–344 in M. Ashburner, H. L. Carson, and J. N. Thompson, eds. The genetics and biology of Drosophila, Vol. 3b. Academic Press, London.
- CLARKE, B., and J. MURRAY. 1969. Ecological genetics and speciation in land snails of the genus *Partula*. Biol. J. Linn. Soc., 1:31–42.
- CRAMPTON, H. E. 1916. Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Tahiti. Carnegie Inst. Wash. Publ. 228:1-311.
 - . 1925. Studies on the variation, distribution, and evolution of the genus *Partula*. The species of the Mariana Islands, Guam and Saipan. Carnegie Inst. Wash. Publ. 228A: 1–116.
 - . 1932. Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Moorea. Carnegie Inst. Wash. Publ. 410:1–335.
- CRAMPTON, H. E., and C. M. COOKE. 1953. New species of *Partula* from southeastern Polynesia. Occ. Pap. Bernice P. Bishop Mus. 21:135–159.

- HADFIELD, M. G., and B. S. MOUNTAIN. 1980.
 A field study of a vanishing species, *Achatinella mustelina* (Gastropoda, Pulmonata), in the Waianae Mountains of Oahu. Pac. Sci. 34:345–358.
- JACKSON, E. D. 1976. Linear volcanic chains on the Pacific floor. Pages 319–336 in G. H. Sutton, M. H. Manghnani, and R. Moberly, eds. The geophysics of the Pacific Ocean basin and its margin. American Geophysical Union, Washington.
- JOHNSON, M. S., B. CLARKE, and J. MURRAY. 1977. Genetic variation and reproductive isolation in *Partula*. Evolution 31:116–126.
- KONDO, Y. 1973. *Samoana* of the Society Islands (Pulmonata-Partulidae). Malacol. Rev. 6:19-33.
- LACK, D. 1947. Darwin's finches. Harper Bros., New York. 204 pp.
- MEAD, A. R. 1961. The giant African snail: A problem in economic malacology. University of Chicago Press, Chicago.
- ———. 1979. Economic malacology with particular reference to *Achatina fulica*. Pages 1–150 *in* V. Fretter and J. Peake, eds. The pulmonates vol. 2B. Academic Press, London.
- MURRAY, J., and B. CLARKE. 1980. The genus *Partula* on Moorea: Speciation in progress. Proc. R. Soc. Lond. B 211:83–117.
- MURRAY, J., M. S. JOHNSON, and B. CLARKE. 1982. Microhabitat differences among genetically similar species of *Partula*. Evolution 36:316-325.
- POINTIER, J. P., and C. BLANC. 1982. Achatina fulica dans les îles de la Société. Rapport de Mission, Museum Naturelle d'Histoire Naturelle, Antenne de Tahiti, B. P. 562, Papeete, Tahiti.
- VAN DER SCHALIE, H. 1969. Man meddles with nature—Hawaiian style. Biologist 51:136– 146.