

## Status of Tree Snails (Gastropoda: Partulidae) on Guam, with a Resurvey of Sites Studied by H. E. Crampton in 1920<sup>1</sup>

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**ABSTRACT:** Tree snails of the family Partulidae have declined on Guam since World War II. One species, indigenous to the western Pacific, *Partula radiolata*, is still locally common along stream courses in southern areas of the island. The Mariana Island endemic *Samoana fragilis* is present but not found in abundance anywhere on Guam. *Partula gibba*, another Mariana endemic, is currently known only from one isolated coastal valley along the northwestern coast, and appears to be in a state of decline. The Guam endemic *Partula salifana* was not found in areas where it had been previously collected by earlier researchers, and is thus believed to be extinct. The decline and extinction of these snails are related to human activities. The single most important factor is likely predation by snails that were introduced as biological control agents for the giant African snail, *Achatina fulica*. The current, most serious threat is probably the introduced flatworm *Platydemus manokwari*. This flatworm is also the likely cause of extinctions of other native and introduced gastropods on Guam and may be the most important threat to the Mariana Partulidae.

TREE SNAILS OF TROPICAL PACIFIC islands have been of interest since early exploration of Oceania and have proven to be useful subjects to organismal and evolutionary biologists (Crampton 1916, 1925, 1932, Clarke and Murray 1969, Johnson et al. 1977, 1986, Hadfield and Mountain 1980, Murray and Clarke 1980, 1984, Hadfield 1986, Hadfield and Miller 1988). Recent work has focused largely on the conservation of these snails (Clarke, pers. comm.) as they disappear from their former ranges for a variety of reasons (Hart 1978; Kondo, pers. comm., 1980; Tillier and Clarke 1983, Clarke et al. 1984, Hadfield 1986, Murray et al. 1988, Meadows 1989). Most of this work has been concentrated on the Hawaiian achatinelline snails and the Partulidae of French Polynesia. However, tree snails of the family Partulidae are widely distributed in Oceania, with five species reported from the Mariana Islands in the western Pacific (Crampton 1925, Kondo 1968,

1970). With the exception of the partulids of the Society Islands, all are lacking study.

The most extensive studies that addressed the endemic and native snails of the Mariana Islands were conducted by early explorers, such as those of the French Freycinet expedition of 1817–1820. More recent collections made by Abbott in 1945 and Langford in 1946 are housed in the U.S. National Museum of Natural History. Kondo (1970) and Easley (1970) provided further information about the biology of the Mariana partulids, based on specimens collected during the Pacific Science Board's survey for the giant African snail, *Achatina fulica*, in 1949.

The most comprehensive study of the partulids of the Marianas was conducted in 1920 by H. E. Crampton. In 2 months of study, Crampton was able to collect specimens of Partulidae on the island of Guam and, to a lesser extent, on Saipan to the north. Crampton's findings were published in a monograph of the Partulidae of the Mariana Islands (Crampton 1925).

Both Guam and Saipan have undergone extensive environmental disturbance since World War II. Recent economic development

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and control programs for agricultural pests have been little monitored with regard to their effects on the native wildlife (Maben 1980) or even on the targeted species in the case of pest control (Nafus and Schreiner 1989). The combined impacts of these factors, especially that of introduced predators, may have had devastating effects on the native snail fauna of these islands (see Clarke et al. 1984). Because of the greatly altered state of the island of Guam since Crampton's work, this study was undertaken to determine the current distribution and status of the species of partulid snails on Guam.

#### METHODS

Thirty-four of Crampton's original 38 collecting sites were visited between 22 April 1989 and 31 December 1989. Thirteen additional sites were surveyed. Most searches were conducted during the rainy season, as was Crampton's study, but conditions were sometimes dry. Timed counts taken of a healthy population during rainy periods and again after several days without rain indicate that the snails can be found readily during dry periods when they are not active. The partulids observed in this study typically occur 1 to 3 m above the ground and spend inactive periods on the undersides of leaves during dry periods, making them readily visible. Visual searches of Crampton's collecting sites were made for 20 min unless partulids were found, at which point more extensive searches were conducted. If snails were present they were generally found within 5 min of searching. If locations visited by Crampton could not be pinpointed on the map, two or three different locations with suitable habitat within the general area were searched. Several of Crampton's sites have undergone extensive development, virtually eliminating all suitable habitat. Despite this, any suitable vegetation present at these altered sites was searched for 20 min. When live snails were located, timed visual censuses were conducted to determine relative abundance. Visual inspections of the ground and leaf litter at these sites were also made for the presence of empty partulid

shells, live specimens, and known snail predators and/or their shells. Introduced snails included *Achatina fulica*, *Bradybaena similis*, *Gonaxis* spp., and *Euglandina rosea*, the last of which is the predatory snail attributed with the extinction of Moorean *Partula* (Clarke et al. 1984, Murray et al. 1988) and Hawaiian achatinellines (Hadfield 1986). The indigenous snail *Pythia scarabaeus* or its shells were also noted. Although not searched for initially, the flatworm *Platydemus manokwari* was later included in the observations. This flatworm is known to prey on some terrestrial snails, such as the giant African snail, *A. fulica* (Eldredge 1988). Habitat descriptions also were recorded for each location. The vegetation or substrate on which partulids were found was recorded.

#### RESULTS

Of the 47 localities surveyed, only 16 supported living partulids, and only 9 of 34 of Crampton's collecting sites were among these (Figure 1). Considerable changes in the species distribution, composition, and abundance have occurred since Crampton conducted his fieldwork 70 yr ago. Following are accounts of the four species found on Guam.

##### *Partula radiolata* (Pfeiffer)

*Partula radiolata* is the most abundant partulid currently found on Guam. It was present at all 16 of the stations that contained snails. Color variation was not site specific where snails were numerous. Small isolated populations show much less variation and in some cases appear to be monomorphic with regard to coloration. Whether this is due to genetic bottlenecking or simply the result of a small sample size is not known.

To date, the largest populations of *P. radiolata* have been located in limestone forest areas, frequently near bodies of fresh water. Only four of the occupied stations were not adjacent to a stream, pond, or marsh. These were the populations at the base of the Anigua cliff line (station 14; station numbers refer to Crampton's original collection locations), Outer Presidio (station 17), Orote Point (sta-

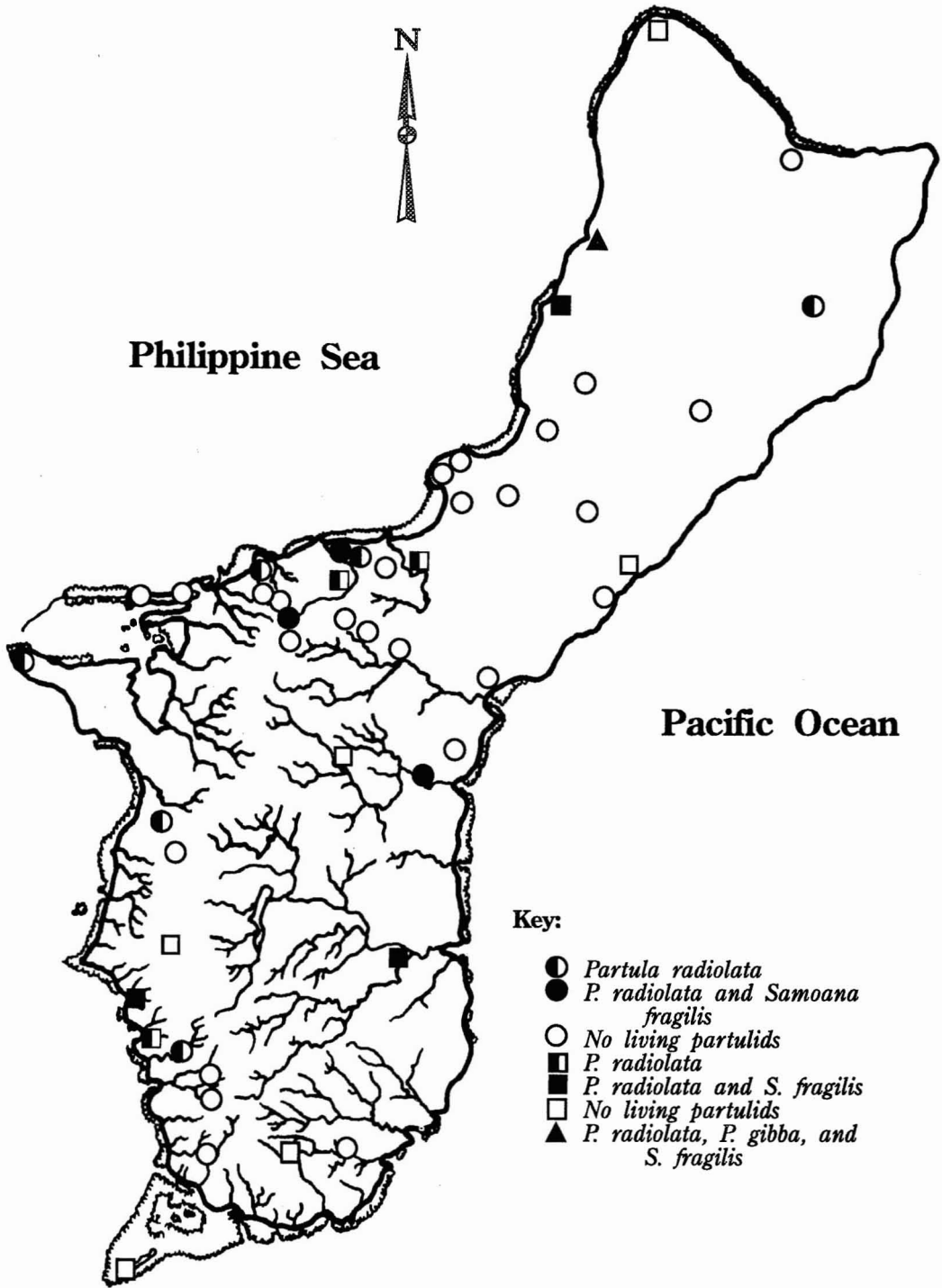


FIGURE 1. Location of sites surveyed for *Partula* spp. and *Samoana fragilis* tree snails. Sites denoted with circles are those of Crampton (1925) that were resurveyed in this study. Squares and triangle are additional sites investigated in the present study.

TABLE 1  
 VASCULAR PLANTS ON WHICH *Partula* SPP. AND *Samoana fragilis* WERE FOUND

PLANT SPECIES	<i>P. gibba</i>	<i>P. radiolata</i>	<i>S. fragilis</i>
<i>Asplenium nidus</i>	+	+	+
<i>Microsorium punctatum</i>	-	+	-
<i>Phymatodes scolopendria</i>	+	+	-
<i>Cycas cercinalis</i>	-	+	-
<i>Heterospathe elata</i>	-	+	-
<i>Cocos nucifera</i>	+	+	+
<i>Pandanus dubius</i>	-	+	-
<i>Musa</i> spp.**	-	+	-
<i>Flagellaria indica</i>	-	+	-
<i>Mammea odorata</i> *	-	+	-
<i>Ficus elastica</i> **	-	+	-
<i>Artocarpus incisus</i>	-	+	-
<i>Guamia mariannae</i> *	-	+	-
<i>Merrilliodendron megacarpum</i>	-	+	-
<i>Barringtonia asiatica</i>	-	+	+
<i>Colubrina asiatica</i>	-	+	-
<i>Triphasia trifolia</i> **	-	+	+
<i>Intsia bijuga</i>	-	+	-
<i>Leucaena leucocephala</i> **	-	+	-
<i>Derris trifoliata</i>	-	+	+
<i>Cynometra ramiflora</i>	-	+	-
<i>Procris pedunculata</i> *	-	+	-
<i>Elatostema calcareum</i>	-	+	-
<i>Hernandia nymphaeifolia</i>	+	+	-
<i>Cananga odorata</i> **	-	+	-
<i>Mikania scandens</i> **	-	+	-
<i>Bidens alba</i> **	-	+	-
<i>Carica papaya</i> **	-	+	-
<i>Passiflora suberosa</i> **	-	+	-
<i>Piper guamensis</i> *	+	+	-

\* Species endemic to Mariana Islands.

\*\* Species introduced to Guam.

tion 31), and Haputo Beach (station B; not visited by Crampton). Populations appear to be well established along the low-elevation river drainages in much of the southern end of the island, although they are absent from some of these drainages (e.g., Geus River). Populations along the southwestern coast are generally found on coconut palms (*Cocos nucifera*) and adjacent vegetation. Except along the southwestern river drainage areas, the snails are narrowly restricted to the riverbanks, and their numbers diminish quickly with increasing distance from the river.

*Partula radiolata* does not appear to show great specificity to plant species. Most areas where it was found in abundance were domi-

nated by coconut palms. Their occurrence on these plants may be an artifact of the great densities of this plant at some locations, because some populations were not in association with coconut palms or the plants were in low abundance. A list of plants on which *P. radiolata* was found is provided in Table 1. At sites where partulids were found on introduced weeds and ornamentals, such plants were found in association with stands of native vegetation.

#### *Samoana fragilis* (Férussac)

Crampton described this species [= *Partula fragilis*] as rare and located most prevalently on the northern limestone plateau. In the

TABLE 2

STUDY SITES OF H. E. CRAMPTON (1925) THAT WERE RESURVEYED AND STILL FOUND TO SUPPORT LIVE TREE SNAILS

LOCATION	n	% SPECIES COMPOSITION	
		1920	THIS STUDY
Mt. Santa Rosa (station 2)	59	100/0/0	0/100/0
Anigua (station 14)	20	84.4/15.6/0	0/100/0
Anigua Cemetery (station 15)	42	92.8/7.2/0	0/97.7/2.3
Outer Presidio (station 17)	15	58.9/41.1/0	0/100/0
Ylig River Lower (station 18)	44	0/100/0	0/72.7/27.3
Fonte B (station 27)	5*	80.0/19.2/0	0/84.0/16.0
Orote Point (station 31)	24	12.7/87.3/0	0/100/0
Agat (station 32)	50	85.7/14.3/0	0/100/0
Umatac Salonga (station 34)	2*	9.8/90.2/0	0/100/0

NOTE: Numbers of adult snails at each location (n) are those observed during timed counts and do not represent the entire population that we found at that site, except for those noted with an asterisk (\*). Percentage composition for the three species is *P. gibba*/*P. radiolata*/*Samoana fragilis*, respectively (site locations from Crampton 1925).

present study *S. fragilis* was only found in the presence of *Partula radiolata* and occurred at six of the sites inhabited by partulids: Anigua Cemetery (station 15), Ylig River Lower (18), Fonte B (27), Lost Pond (C), Sella Bay (J), and Talofofu River (H). As with *P. radiolata*, the snails were more common in limestone habitats, but were found in volcanic areas as well. Morphological similarities of young snails sometimes made it difficult to distinguish between juveniles of the species.

#### *Partula gibba* Férussac

Crampton's description of *P. gibba* as the most abundant of the partulids in some regions of the island is most alarming considering its status as determined in this study. The 1920 collections of adult snails contained 60% *P. gibba*. Crampton described this species as being most abundant in the western upland regions and on the northern limestone plateau. All the stations visited by Crampton in 1920 are now devoid of *P. gibba*, although five of these contained bleached shells of this species. The only extant population of *P. gibba* on Guam was found at Haputo Beach (station B) on the northwestern coast, a location not visited by Crampton. This alluvial coconut forest also supported populations of *P. radiolata* and *Samoana fragilis*. *Partula gibba* was most abundant on the endemic understory plant *Piper guamensis*, but was

also found on coconut palms, the fern *Microsorium punctatum*, and an as yet unidentified fern. Although some vegetation at the Haputo site supported *P. gibba* exclusively, both *P. gibba* and *P. radiolata* frequently inhabited the same plant.

The apparent replacement of *P. gibba* by *P. radiolata* is of particular interest. For some locations, Crampton recorded *P. gibba* as being the only species present. With the disappearance of *P. gibba*, some of these sites are now entirely occupied by *P. radiolata* and *Samoana fragilis* (Table 2). This is discussed in more detail below.

#### *Partula salifana* Crampton

The 1920 collections of Crampton led to the description (Crampton 1925) of a new species of *Partula*, *P. salifana*. This species was found in several locations in the west central highlands region by Crampton, and its presence was verified by Abbott in 1945 (USNM specimen lots 593171, 593391, 573378) and by Langford in 1946 (USNM specimen lot 606976). It was considered endemic to this highland region. The forested slopes where Crampton, Abbott, and Langford collected, as well as other adjacent areas, were searched extensively in the present study. The largest deposits of empty shells were found at these locations. Shells of *P. gibba*, *P. radiolata*, and *P. salifana* were found, but no live snails were

encountered. Our searches of upland habitats in the south included peaks south of and adjacent to Mt. Alifan (the area searched by Abbott in 1945), the western Almagosa area, and the forested areas around Mt. Lamlam. We found no snails in any of these areas but did find weathered shells of partulids. In addition, no snails were found in the isolated interior valleys of southern Guam that were searched.

#### DISCUSSION

##### *Possible Reasons for the Decline and Disappearance of Guam Partulidae*

One of the most noted reasons for the recent decline and extinction of Partulidae is the purposeful introduction of predatory snails, frequently for the control of *Achatina fulica* (Eldredge 1988). The carnivorous snails *Euglandina rosea*, *Gonaxis kibweziensis*, and *G. quadrilateralis* were introduced to Guam in 1957, 1954, and 1967, respectively (Eldredge 1988). Of these, *E. rosea* was the most successful introduction, and its empty shells can be found in most forested areas on Guam. However, no living specimens of *E. rosea* or *Gonaxis* spp. were found during this study. The indigenous land snail *Pythia scarabaeus* was also absent from all locations except Haputo Beach (station B), although its empty shells are often a conspicuous component in the ground litter at other localities. The effects of biological control agents, such as the carnivorous snails, on their target species are seldom considered after they have been introduced (Nafus and Schreiner 1989). Even less studied are the effects on native nonpest species.

In 1978 the terrestrial triclad *Platydemus manokwari* appeared on Guam (Eldredge 1988). It proved to be an effective agent of control on the giant African snail (Muniappan 1983, Eldredge 1988) and has spread over the island, reducing the abundance of *A. fulica* by as much as 95% in some areas (Muniappan 1983). Although predation by *P. manokwari* has not been observed on the other introduced snails, it seems plausible that

the flatworms have played a role in their demise on the island. *Platydemus manokwari*, although largely a ground-dwelling species, will climb trees. At one location in this study, *P. manokwari* was observed 1 m up a tree trunk feeding on a juvenile partulid. In captivity *P. manokwari* will feed on *P. radiolata* and *Pythia scarabaeus* (Hopper, unpublished). This flatworm has also been noted in great abundance in areas where partulids are declining rapidly, as evidenced by the presence of large numbers of freshly dead shells. Controlled experiments to determine the effect of *P. manokwari* on partulids and other native and endemic snails are needed. Until such studies are conducted, introductions of the flatworm to more islands should be strongly discouraged.

The introduction of Eurasian rats to the Hawaiian Islands probably had a damaging impact on the endemic snail faunas there (Hadfield 1986). However, Crampton (1925) reported no evidence of predation by rats on Guam partulids, and there is no evidence of predation by rats in areas where the snails have recently become extinct. Rats are not common on Guam, possibly because of predation by the introduced snake *Boiga irregularis* (Savidge 1987; G. Wiles, Guam Aquatic and Wildlife Resources, pers. comm.).

Although apparently suitable habitat is still present throughout much of Guam, habitat destruction and fragmentation have likely played a role in the reduction of *Partula* populations. Fourteen of Crampton's original collecting locations are now areas of intensive urbanization or sites of industrial complexes. All 14 of these sites, if not occupied by man-made structures, have been greatly disturbed and contain little native vegetation. Five additional sites have undergone the more gradual disturbance of floral replacement by introduced plant species, and most sites visited in this study have undergone some degree of invasion by exotic plants. A major component of the new flora of Guam is the introduced legume *Leucaena leucocephala*. Seeds of this species were widely sown after World War II to reduce soil erosion resulting from loss of vegetation due to bombardment. The replacement of native canopy trees by the more

shrubby *L. leucocephala* has created a more xeric understory, likely less suitable for *Partula* and *Samoana*. There are varying degrees of habitat change resulting from economic development, but some locations that have undergone relatively minor changes still bear populations of partulids.

The degree to which habitat fragmentation has affected or may affect the partulids is not known. Crampton (1925) stated that partulids were not found uniformly around Guam and that certain, apparently suitable, habitats did not contain the snails. Our observations indicate that populations may be patchy and localized, and that even adjacent populations may be isolated from one another. From the historical accounts available, we cannot quantify the degree to which *Partula* were localized and consequently cannot make comparisons. Although the effects of isolation and habitat fragmentation may not be as detrimental to these gastropods as to more intensively studied vertebrates (Wilcove et al. 1986, Lovejoy et al. 1986), possible effects of these conditions should not be neglected. The hermaphroditic condition of these pulmonate snails should effectively double the number of potential mates within a population compared to dioecious species. However, at some sites we found fewer than 10 animals, and such small populations are vulnerable to environmental disturbances and demographic fluctuations.

The use of pesticides on Guam for the control of disease vectors has been intensive in the past (Baker 1946) and has been noted as a possible factor contributing to bird extinctions on Guam (Maben 1980, Savidge 1987). Spraying for disease vector control was also conducted when Vietnamese refugees were residing on Guam in 1975 and is still conducted in some military housing areas (Maben 1980). Whether the use of pesticides has been detrimental to *Partula* spp. and *Samoana fragilis* on Guam is unknown, but negative effects are possible.

Collecting of tree snails has possibly been a major contributing factor to their decline in some regions. Hadfield (1986) reported on the extensive collections made of achatinelline tree snails in Hawaii. Such collecting activities, in combination with the low fecundity of

the snails, habitat destruction, and introduced predators, may have had an increased impact on the snails. The collection of partulids for sale in the shell trade in some regions of French Polynesia is still practiced (Murray et al. 1988). Collection has possibly played an important role in the Mariana Islands as it did in Hawaii. Collection by European explorers likely began with the French Freycinet expedition of 1817–1820. Crampton and his associates collected nearly 4000 snails of the four species from Guam. One whaling captain was reported to have collected “3 bushels of *P. gibba*” from Guam (Crampton 1925). Given the extensive collecting by naturalists and explorers during this period, their combined impact may have been significant, especially on an island as small as Guam.

The virtual replacement of *Partula gibba* by *P. radiolata* remains something of a mystery. In some areas where Crampton reported a majority of *P. gibba*, such as on Mt. Santa Rosa (station 2) or the Anigua cemetery (station 15) (Table 2), *P. radiolata* is the only species present today. The persistence of *P. radiolata* may be indicative of a greater tolerance of environmental perturbations or a reduced susceptibility to introduced predators. The complete replacement of *P. gibba* by *P. radiolata* on Mt. Santa Rosa is puzzling. Crampton did not report finding any *P. radiolata* at that location, so either the present distribution results from subsequent colonization or Crampton’s site has not been correctly located.

However speculative, we believe that the introduced flatworm *Platydemus manokwari* may now be the major threat to the continued existence of Partulidae on Guam, other Mariana Islands, and possibly Oceania as a whole. Although introduced carnivorous snails may have greatly reduced the numbers and species of partulids in the Mariana Islands, the flatworm has probably been a key factor in reducing or eliminating these predatory gastropods. Studies on the feeding behavior of *P. manokwari* are needed to determine if their predation is detrimental to wild populations of partulids and other snails. Given the complete absence of any terrestrial or arboreal snails in some areas, the presence

of the flatworm, and the knowledge that *P. manokwari* will feed on snails other than *Achatina fulica*, the spread of this predator is of extreme concern with regard to the persistence of insular snail faunas. It is also possible that the lack of living predatory snails is due to their starvation after depleting the native snail populations.

The Haputo Beach site is particularly important because it contains the only known population of *Partula gibba* on Guam. Some areas within this location appear to be pristine with regard to snail habitat, but there is evidence of predation in other areas: no live partulids and numerous recently emptied shells. There are no shells of carnivorous gastropods, but *Platydemus manokwari* is present in small numbers. How rapidly the flatworms will spread and how much longer this location will provide good snail habitat remain to be seen. Monitoring of this site has begun, and attempts to propagate *P. gibba* from Guam will be undertaken.

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#### LITERATURE CITED

- BAKER, R. H. 1946. Some effects of the war on the wildlife of Micronesia. *Trans. 11th North Am. Wildl. Conf.* 11:205–213.
- CLARKE, B., and J. MURRAY. 1969. Ecological genetics and speciation in land snails of the genus *Partula*. *Biol. J. Linn. Soc.* 1:31–42.
- CLARKE, B., J. MURRAY, and M. S. JOHNSON. 1984. The extinction of endemic species by a program of biological control. *Pac. Sci.* 38:97–104.
- CRAMPTON, H. E. 1916. Studies on the variation, distribution and evolution of the genus *Partula*: The species inhabiting Tahiti. *Carnegie Inst. Washington Publ.* 228:1–313.
- . 1925. Studies on the variation, distribution, and evolution of the genus *Partula*: The species of the Mariana Islands, Guam and Saipan. *Carnegie Inst. Washington Publ.* 228A:1–116.
- . 1932. Studies on the variation, distribution, and evolution of the genus *Partula*: The species inhabiting Moorea. *Carnegie Inst. Washington Publ.* 410:1–335.
- EASLEY, J. 1970. Quantitative analysis of *Partula langfordi* and *P. gibba* on Agiguan. Pages 83–85 in Y. Kondo. Some aspects of Mariana Island Partulidae. *Occas. Pap. Bernice Pauahi Bishop Mus.* 24.
- ELDRIDGE, L. G. 1988. Case studies of the impacts of introduced animal species on renewable resources in the U.S. affiliated Pacific islands. Pages 118–146 in B. D. Smith, ed. *Topic reviews in insular resources development and management in the Pacific U.S. affiliated islands.* Univ. Guam Mar. Lab. Tech. Rep. 88.
- HADFIELD, M. G. 1986. Extinction in Hawaiian achatinelline snails. *Malacol. Int. J. Malacol.* 27:67–81.
- HADFIELD, M. G., and S. E. MILLER. 1988. Demographic studies on Hawaii's endangered tree snails: *Partulina proxima*. *Pac. Sci.* 43:1–16.
- 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.* 34:345–385.
- HART, A. 1978. The onslaught against Hawaii's tree snails. *Nat. Hist.* 87:46–57.
- JOHNSON, M. S., B. CLARKE, and J. MURRAY. 1977. Genetic variation and reproductive isolation in *Partula*. *Evolution* 31:116–126.



- JOHNSON, M. S., J. MURRAY, and B. C. CLARKE. 1986. An electrophoretic analysis of phylogeny and evolutionary rates in the genus *Partula* from the Society Islands. *Proc. R. Soc. London Ser. B* 227: 161–177.
- KONDO, Y. 1968. Partulidae: Preview of anatomical revision. *Nautilus* 81: 73–77.
- . 1970. Some aspects of Mariana Island Partulidae. *Occas. Pap. Bernice Pauai Bishop Mus.* 24: 73–90.
- LOVEJOY, T. E., R. O. BIERREGAARD, A. B. RYLANDS, J. R. MALCOLM, C. E. QUINTELA, L. H. HARPER, K. S. BROWN, A. H. POWELL, G. V. N. POWELL, H. O. R. SCHUBART, and M. B. HAYS. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257–285 in M. E. Soulé, ed. *Conservation biology: The science of scarcity and diversity*. Sinauer Assoc., Sunderland, Massachusetts.
- MABEN, A. F. 1980. Development of a study to determine the past and present impact of pesticides on Guam's wildlife population. *Aquat. Wildl. Res. Annu. Rep. Dep. Agric. Territory of Guam*.
- MEADOWS, R. 1989. Conservation at a snails pace. *Zoogoer* 18: 30–33.
- MUNIAPPAN, R. 1983. Biological control of the giant African snail. *Alafua Agric. Bull.* 8: 43–46.
- MURRAY, J., and B. CLARKE. 1980. The genus *Partula* on Moorea: Speciation in progress. *Proc. R. Soc. London* 211: 83–117.
- . 1984. Movement and gene flow in *Partula taeniata*. *Malacol. Int. J. Malacol.* 25: 343–348.
- MURRAY, J., E. MURRAY, M. S. JOHNSON, and B. CLARKE. 1988. The extinction of *Partula* on Moorea. *Pac. Sci.* 42: 150–153.
- NAFUS, D., and I. SCHREINER. 1989. Biological control activities in the Mariana Islands from 1911 to 1988. *Micronesica* 22(1): 65–106.
- SAVIDGE, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. *Ecology* 68: 660–668.
- TILLIER, S., and B. C. CLARKE. 1983. Lutte biologique et destruction du patrimoine génétique: le cas des mollusques gastéropodes pulmonés dans les territoires français du Pacifique. *Genet. Sel. Evol.* 15: 559–566.
- WILCOVE, D. S., C. H. MCLELLAN, and A. P. DOBSON. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E. Soulé, ed. *Conservation biology: The science of scarcity and diversity*. Sinauer Assoc., Sunderland, Massachusetts.