

SURVEY OF ENDANGERED TREE SNAILS ON NAVY-OWNED LAND IN GUAM

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INTRODUCTION

The land snail faunas on islands of the tropical Pacific exhibit spectacular evolutionary radiations (Cowie, 1996), although they are dominated by relatively few families. Despite this diversity, native land snail faunas of the Pacific islands are composed almost entirely of narrow-range endemics. The same factors that favored rapid evolution of endemic land snail biotas from colonists dispersing successfully to islands also imposed extreme sensitivity to environmental disturbances and high rates of extinction on the resulting populations. These constraints among insular endemic species are consequences of small geographic ranges and small populations (Diamond, 1984; Tracy and George, 1992).

These unique native snail faunas are now disappearing rapidly (Lydeard et al., 2004). In the Mariana Islands, Bauman (1996) recorded at least 39 native species of land snails in Rota, and Kurozumi (1994) recorded at least 16 species on the islands north of Saipan. Sixty-eight percent of the Rota snail species are extinct or declining (Bauman, 1996). These and other data suggest that overall perhaps 50% of the land snail fauna has disappeared throughout the Pacific islands as a whole, mostly in recent times (Lydeard et al., 2004).

The family Partulidae consists of predominantly arboreal snails that are limited in geographic distribution to volcanic high islands of the tropical Pacific, ranging from the Marquesas and Austral Islands in the east to the Mariana Islands and Belau in the west (Kondo, 1968; Cowie, 1992). Members of the most primitive order of pulmonate snails, the Partulidae is speciose; Kondo (1968) recognized 126 species. Partulids are also highly endemic, with most species restricted to single islands. Only one species occurs in more than one island group (Cowie, 1992; Johnson et al., 1993).

Partulid populations have declined throughout their range in recent years, in some cases to extinction (Clarke et al., 1984; Murray et al., 1988; Hopper and Smith, 1992; Miller, 1993). In Guam, the endemic Mt. Alifan tree snail, *Partula salifana*, is thought to be extinct (Hopper and Smith, 1992). The tree snail *Partula gibba* has disappeared from historical locations in Guam and Saipan studied by Crampton (1925) in 1920 and by Kondo in 1949 (Smith and Hopper,

1994). No living *Partula gibba* were found in previously reported habitations in Rota, Tinian, and Aguiguan, as well (Smith and Hopper, 1994; Smith, 1995, In Review). Major factors contributing to this broad decline include loss of habitat to agricultural and urban development and introductions of invasive species, including predators intended as biological controls for the giant African snail *Achatina fulica* (Smith and Hopper, 1992; Cowie, 2000, 2001).

The objectives of this survey are to determine the location of Guam tree snails on Navy-owned lands in Guam and to identify the location of suitable habitat and inventory areas that have the highest probability of supporting snail populations. The areas of interest are on NCTS and the Ordnance Annex. Three species of Guam's native tree snails—*Samoana fragilis*, *Partula gibba*, and *Partula radiolata*—are candidate species under the federal Threatened and Endangered Species Act (Federal Register, 1994). All four species, including *Partula salifana*, are listed as endangered species under the Endangered Species Act of Guam (5 GCA, Section 63205.(c)).

TAXONOMIC REVIEW

The Mariana Archipelago (Figure 1) historically supported five species of partulids scattered across seven small islands lying at the northwestern limit of the geographical range of the Partulidae. In the first systematic study of the distribution of Mariana partulids, Crampton (1925) reported four species of partulids from Guam and Saipan. Kondo (1970) added five smaller islands to the range of partulids in the Mariana Islands and described a fifth species endemic to the tiny island (<3 mi²) of Aguiguan [also known as Aguijan]. However, recent surveys indicate that as many as three of the five Mariana species are either extinct or on the brink of extinction (Hopper and Smith, 1992; Smith and Hopper, 1994; Smith, In Review).

Partula gibba Férussac, 1821 (FIGURE 2)

Synonymy:

Partula mastersi Pfeiffer, 1857

Partula bicolor Pease, 1872

Description: Shell dextral or sinistral, conic-ovate, perforate, pellucid. Spire acute, 4 to 4½ whorls, the last gibbous. Sculpture of spiral striae, crossed by weak longitudinal growth striae; suture slightly adpressed, white or brown. Aperture oblong-ovate, subquadrangular; peristome reflexed, broadly dilated, white. Background color variable, chestnut brown to whitish-yellow; also purple. Adult length 14 to 18 mm, width 10 to 14 mm.

Range: *Partula gibba* is the most widely distributed tree snail in the Mariana Islands, occurring on nine islands. This species is known from Guam, Rota, Aguiguan, Tinian, Saipan, Anatahan, Sarigan, Alamagan, and Pagan.

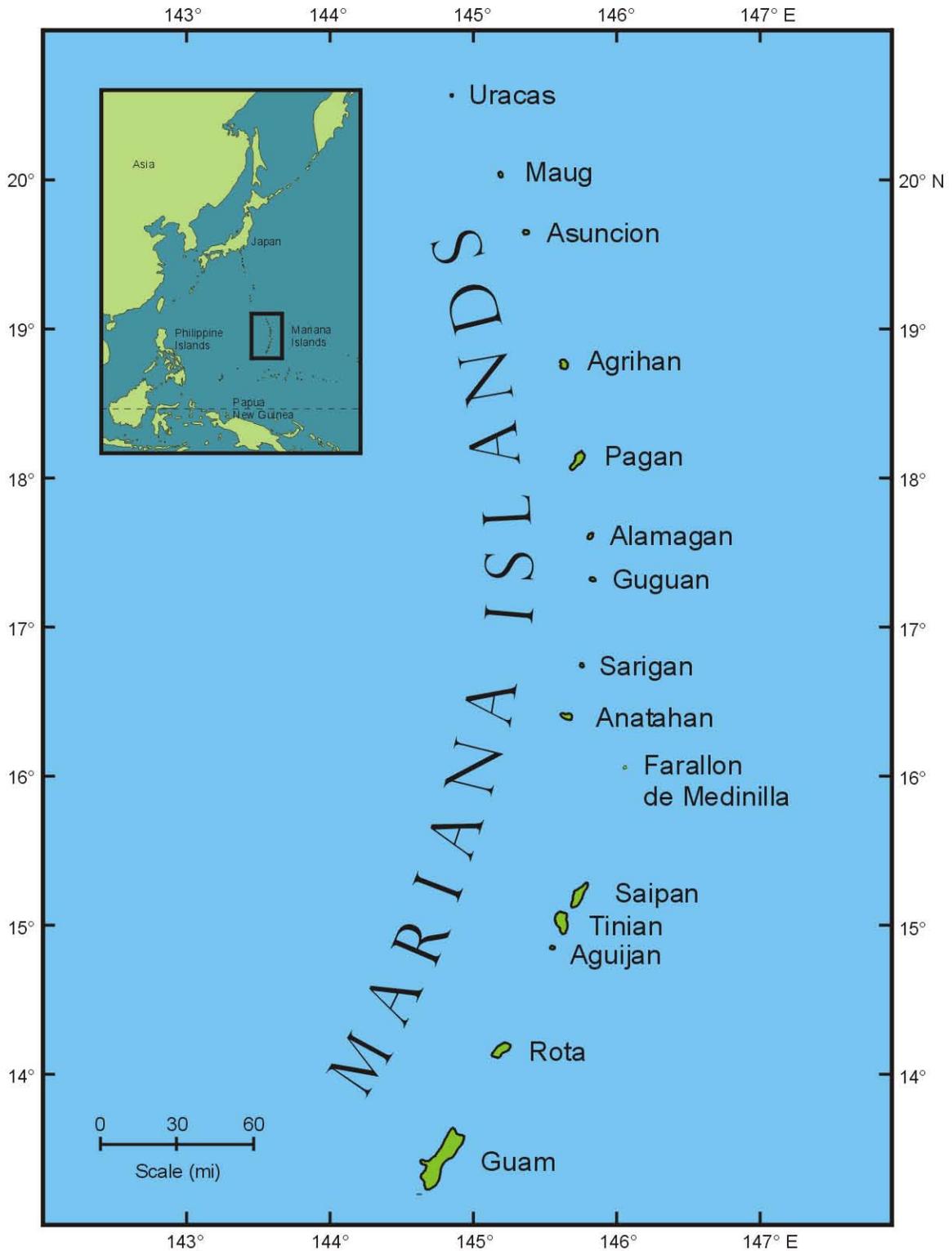


Figure 1. Map of the Mariana Islands. Inset shows the position of the Mariana Islands in relation to Asia and the western Pacific.



Figure 2. *Partula gibba* on *Alocasia macrorrhiza* leaf at Haputo, Guam.

Partula radiolata (Pfeiffer, 1846) (FIGURE 3)

Synonymy:

Bulimus (Partula) radiolata Pfeiffer, 1846.

Description: Shell dextral, oblong-tapering, subperforate, thin. Spire obtuse, whorls typically 5, slightly convex, the last about equal to the spire. Sculpture of faint, impressed lines. Aperture obliquely oval; peristome simple, thin, white, expanded, the right margin somewhat straightened, columellar margin dilated above, spreading above the umbilicus. Background color pale straw-colored with darker axial rays and brown lines. Adult length 13 to 18.5 mm, width 8 to 12 mm.

Range: *Partula radiolata* is a Guam endemic. It has been erroneously reported to occur on the island of New Ireland in the Bismarck Archipelago by Pfeiffer (1846), Hartman (1881), and Parkinson et al. (1987).

Partula salifana Crampton, 1925 (FIGURE 4)

Synonymy:

None.

Description: Shell dextral, ovate-conic, thick and heavy. Umbilicus open, slightly flattened. Spire somewhat protracted, whorls 5 to 5¼, slightly impressed below the suture. Sculpture of spiral striae on embryonic whorls becoming weaker on postembryonic whorls. Aperture elongate, interior purplish and shining, peristome expanded and flattened, gradually narrowing as



Figure 3. *Partula radiolata* on *Alocasia macrorrhiza* at Haputo, Guam.



Figure 4. *Partula salifana* (paratype, Bishop Museum, Honolulu).

it approaches contact with body whorl, color variable from white to yellowish brown or purple. Background color is a rich chestnut-brown or seal-brown to yellowish or olive; the apex color is often purple as a result of decortication. Adult length 17 to 19 mm, width 10.5 to 11.7 mm.

Range: *Partula salifana* is the most geographically restricted of the partulids in the Mariana Islands. It is known only from the summit of Mount Alifan and two adjacent peaks on the southwest coast of Guam.

Samoana fragilis (Férussac, 1821) (FIGURE 5)

Synonymy:

Partula quadrasi Möllendorff, 1894

Description: Shell dextral, ovate-conic, narrowly and half-covered perforate, fragile, pellucid. Spire conic, the apex somewhat obtuse; whorls typically 4, slightly convex, separated by adpressed, marginated suture; last whorl distinctly convex, nearly tumid. Sculpture of delicate spiral striae intersected by transverse growth striae. Aperture oblique, oval, a little excised; peristome simple, thin, well expanded, the columella dilated above, recurved, forming a distinct angle with the parietal wall. Background color buff-tinted, semi-transparent; narrow darker maculations and whitish banding due to colors of viscera visible through the shell. Adult length 12 to 16 mm, width 10 to 12 mm.

This species exhibits several reproductive characteristics that are unique among Mariana Islands partulids. The eggs are large (4.2 mm × 3.3 mm), and they are encapsulated by a tough, calcareous shell (Crampton, 1925). Further, *Samoana fragilis* reaches sexual maturity before it expands the varical lip that characterizes adults of terminal size (Crampton, 1925; Kondo, 1955). The latter trait has not been reported for any other partulid species.

Range: *Samoana fragilis* is the only member of the genus to occur outside southeastern Polynesia. In the Mariana Islands, *Samoana fragilis* has been reported from Guam and Rota.

METHODS

Forested areas of NCTS and the Guam Ordinance Annex were surveyed by visual census methods adapted from Hopper and Smith (1992). Mixed mesophytic forest predominated by native species identified by Hopper and Smith (1992) were the focus of this project. Survey sites were selected from satellite images after consultation with botanists acquainted with the areas. Special attention was given to sites where partulids were previously reported.

At survey sites, broad-leafed species were inspected for 30 min, and leaf litter was examined for 10 min in search of fresh ground shells; Hopper and Smith (1992) reported that, when present in an area, snails are generally found within the first 5 min of searching. Search



Figure 5. *Samoana fragilis* observed on *Annona reticulata* at NCTS, Guam.

area tracks were recorded by GPS when possible. If no live snails or fresh ground shells were found during the timed search, the site was recorded as not supporting tree snails. When live tree snails were located within the 30-min visual census period, four 25-m² quadrats were established under the densest understory, as determined by a spherical densiometer. All snails occurring within the quadrats were identified to species, and their shell length was measured to the nearest 0.1 mm with sliding vernier calipers. Host tree species were recorded for each snail observed.

Temperature, humidity, and air movement were measured with miniature probes in microhabitats inhabited by tree snails to quantify the “more ultimate ecological conditions which determine the distribution of suitable vegetation,” and presumably the distribution of tree snails, alluded to by Crampton (1925). Measurements were also taken in uninhabited areas to assess their suitability for supporting snail populations. These data from inhabited and uninhabited forest were compared to elucidate the minimum conditions for the survival of snail populations.

RESULTS

Four partulid colonies were located during the survey, two at NCTS (Figure 6) and two at the Ordinance Annex (Figure 7). Of the four colonies, only the Haputo colony was previously known.

Size-frequency distributions for partulids at the Pugua Point, Haputo Beach, and N. Kitts Road sampling stations are presented in Figures 8, 9, and 10, respectively. In the Pugua Point

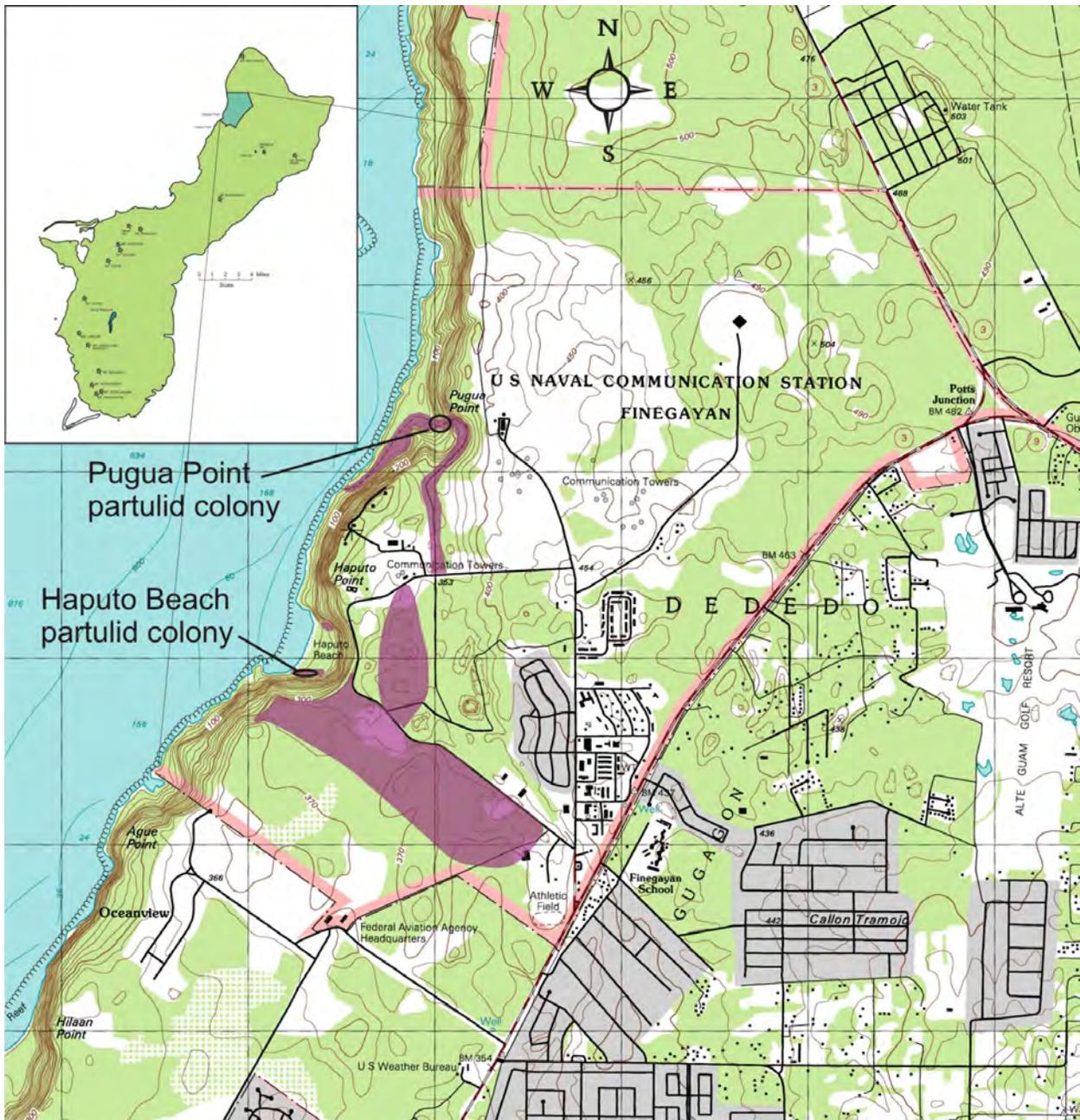


Figure 6. Map of Naval Computer and Telecommunications Station, Finegayan. Surveyed areas are shaded in purple, and locations of partiid colonies are indicated by ellipses.



Figure 7. Map of Naval Ordnance Annex. Surveyed areas are shaded in purple, and locations of partulid colonies are indicated by ellipses.

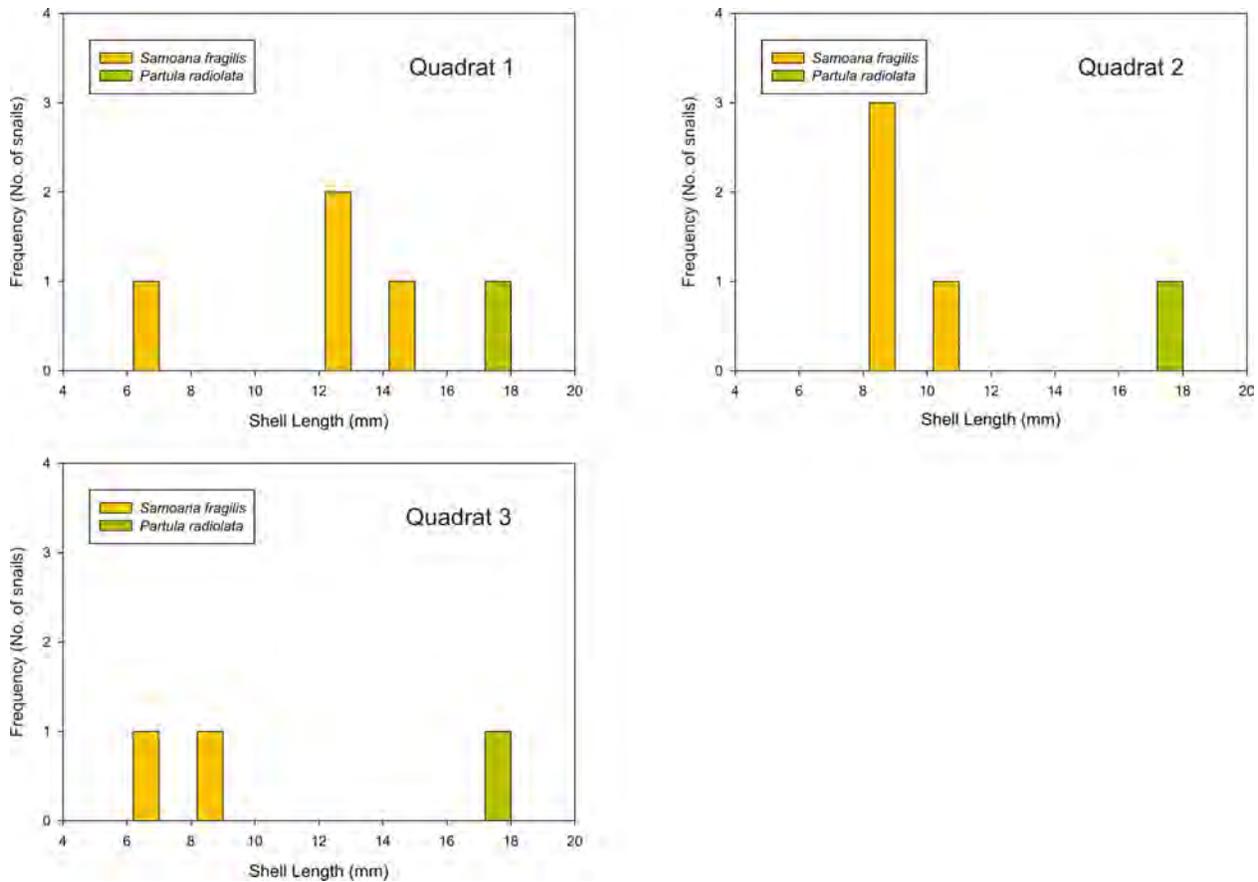


Figure 8. Size-frequency distributions of partulid species at the Pugua Point sampling station, NCTS, Guam. No tree snails were observed in Quadrat 4.

colony, all three *Partula radiolata* were reproductively mature, as indicated by the presence of a varical lip (see Crampton, 1925). It is not possible to determine the percentage of mature individuals in the *Samoana fragilis* colony because of the unique characteristic of this species to reach maturity before the formation of the varical lip. In the Haputo Beach colonies, some 43% of the *Partula gibba* were reproductively mature, while about 40% of the *Partula radiolata* were mature. Some 33% of the *Partula radiolata* in the N. Kitts Road colony were reproductively mature.

Box plots of the size data for partulid colonies are presented in Figures 11, 12, and 13. Box plots provide excellent visual summaries of the smallest observation, the lower quartile (Q1), the median, the upper quartile (Q3), the largest observation, and observations that are considered unusual, or outliers (Tukey, 1977). The box stretches from the lower hinge (defined as Q1, or the 25th percentile) to the upper hinge (Q3, or the 75th percentile) and therefore contains

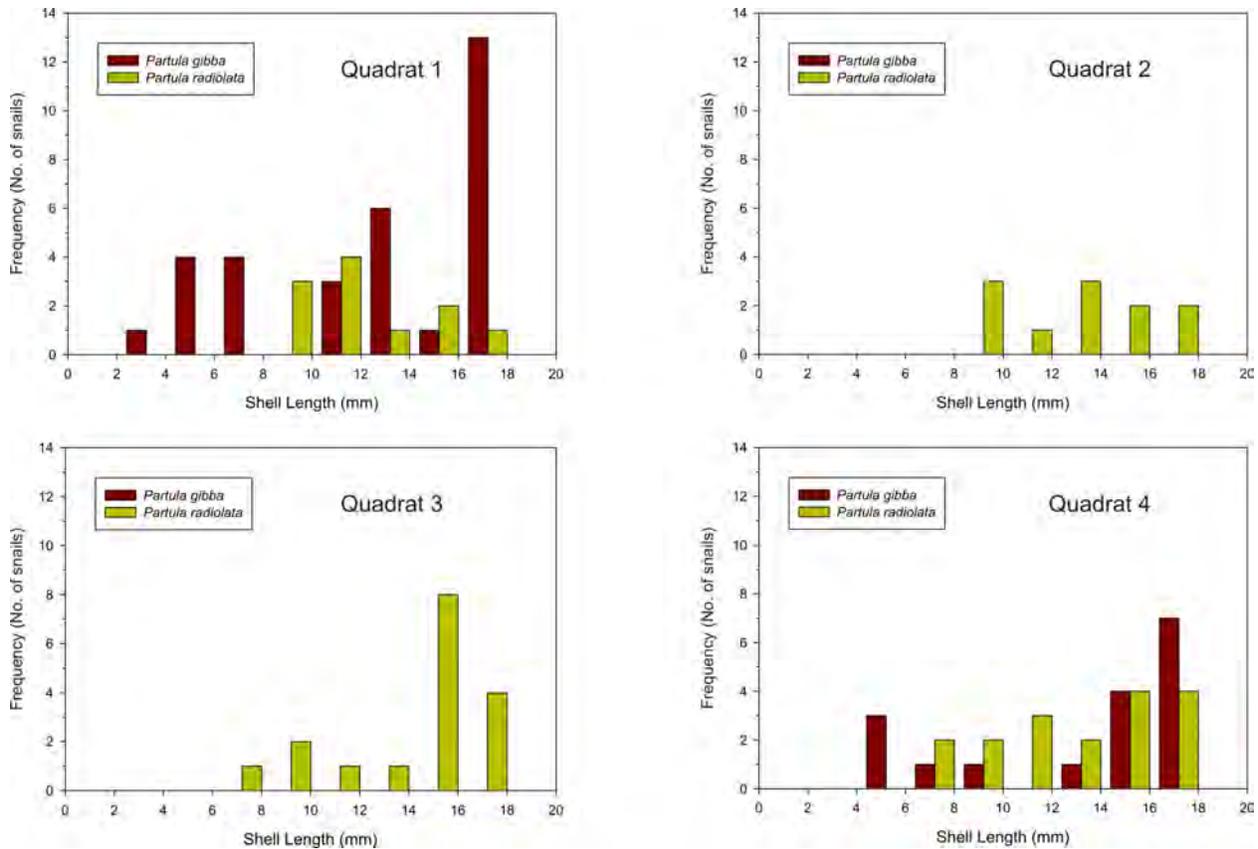


Figure 9. Size-frequency distributions of partulid species at the Haputo Beach sampling station, NCTS. *Partula gibba* was not observed in Quadrats 2 and 3.

the middle half of the scores in the distribution. The median is shown as a line across the box. Therefore, one-fourth of the distribution is between this line and the top of the box, and one-fourth of the distribution is between this line and the bottom of the box. Host plant species for the four colonies of tree snails are presented in Table 1. Of the host plants observed in this study, *Thelypteris* sp. is reported for the first time.

Environmental parameters of the microhabitat of the tree snails are given in Tables 2, 3, and 4, respectively, for Pugua Point, Haputo Beach, and Ordinance Annex. Average canopy cover at Pugua Point was 79% (n=15), and ranged from 56% to 97%. At Haputo Beach, average canopy cover was 80% (n=19), and ranged from 67% to 92%.

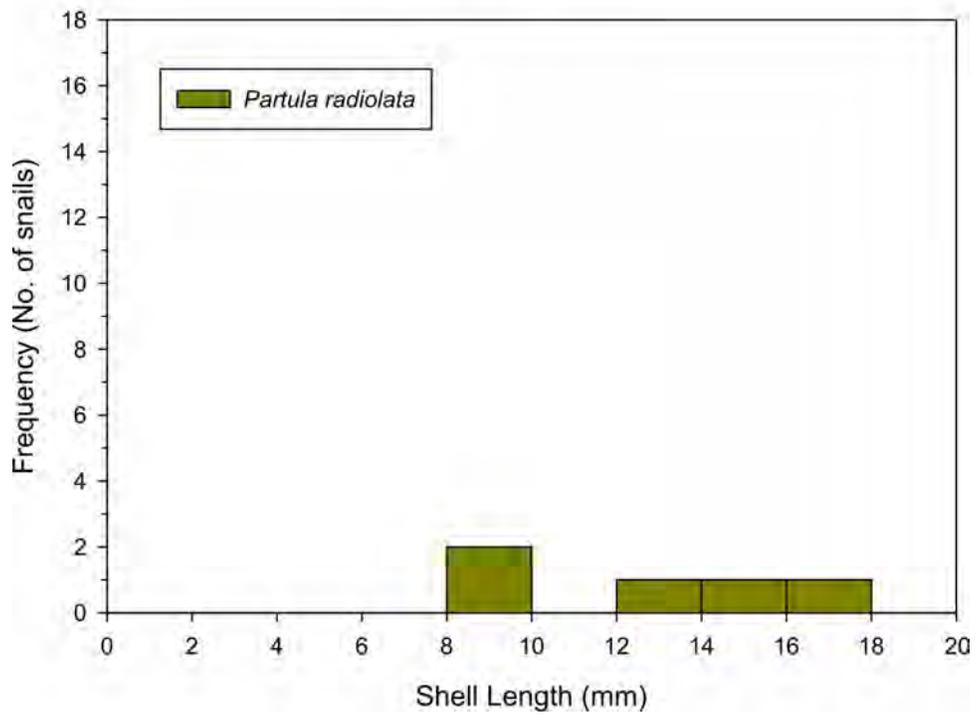
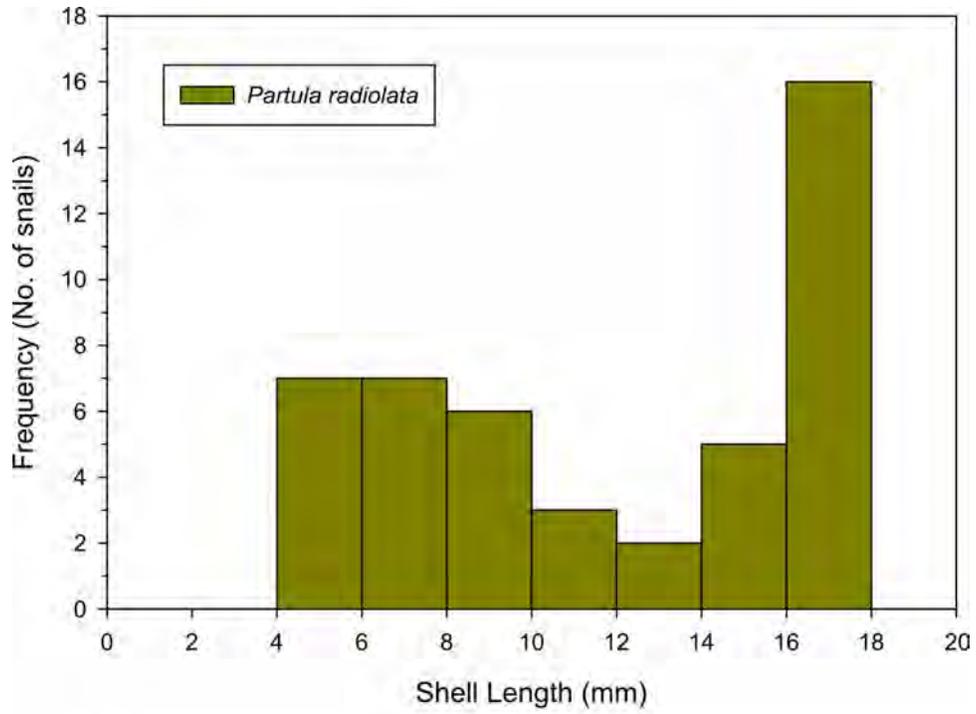


Figure 10. Size-frequency distributions of *Partula gibba* colonies at the N. Kitts Road sampling station, Naval Ordinance Annex.

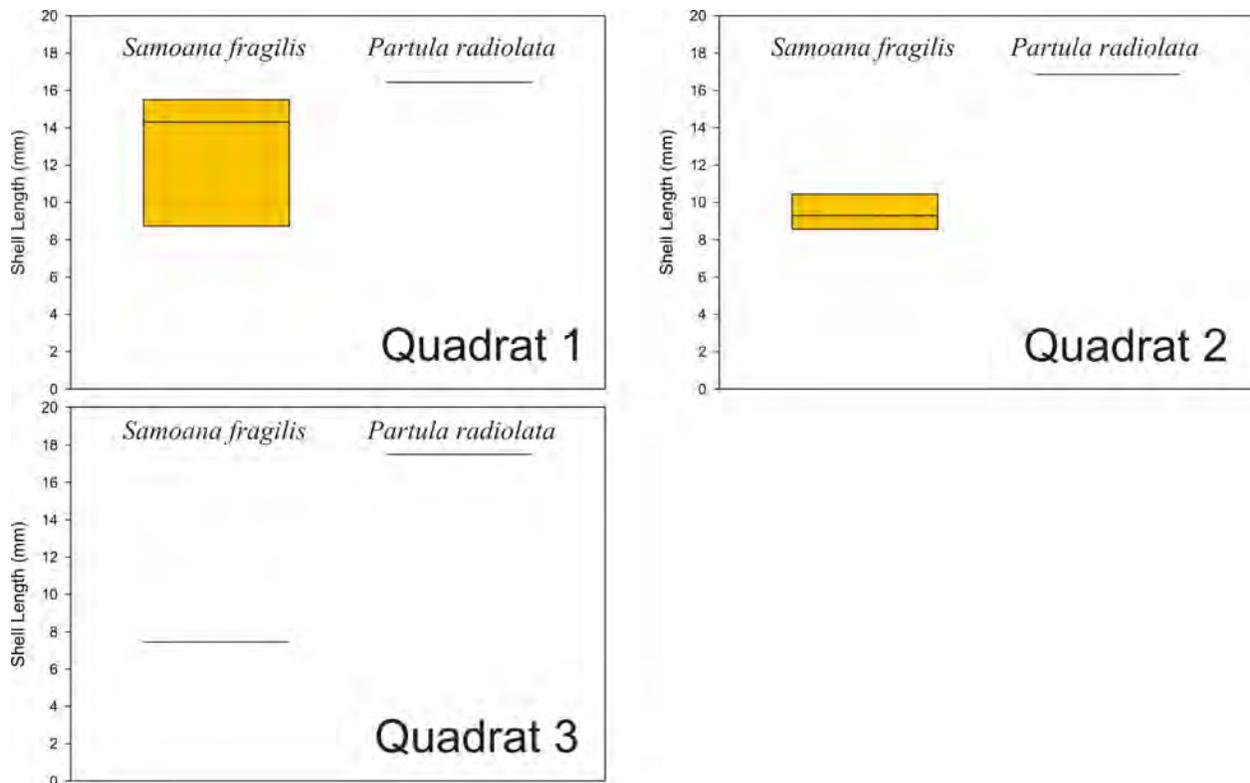


Figure 11. Box plots of shell length of partulid species at the Pugu Point, NCTS sampling station. Lines represent two few data to generate a box.

DISCUSSION

Four colonies of tree snails were observed during this study. The Pugu Point colony is distinct in being dominated by *Samoana fragilis*, a species that has not been observed in Guam since 1996 (A. Asqwith and S.E. Miller, personal communication, March 1996; Smith unpublished data). This is the only colony of *Samoana fragilis* presently known in Guam, and the status of only other reported colony, in Rota, remains to be determined.

Of the four colonies of tree snails found on Naval lands in this study, only the Haputo Beach colony was previously reported (see Hopper and Smith, 1992). None of the colonies were densely populated, and the Haputo Beach population has declined markedly since 1996. In three years of monthly population sampling at Haputo Beach from 1993 to 1995, Smith (unpublished data) found snail densities ranged from a minimum of 4.7 m⁻¹ to a maximum of 17.2 m⁻¹. We re-examined the same plot during this survey, and we found that snail density has declined to 2.2 m⁻¹, or fewer than half the minimum density previously observed. This decline has been accompanied, or possibly caused by, a change in forest structure from an understory dominated

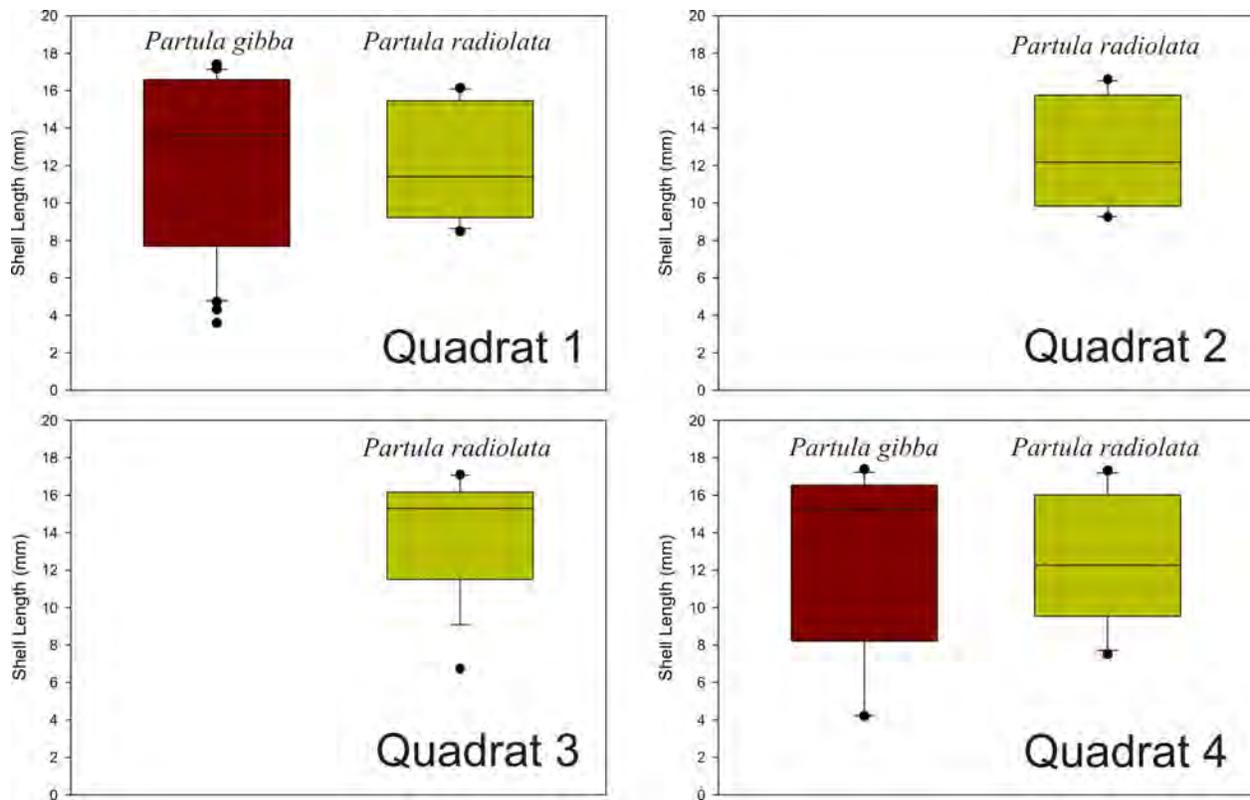


Figure 12. Box plots of shell length of partulids at the Haputo Beach, NCTS sampling station. No *Partula gibba* were observed in Quadrats 2 and 3.

by *Neisosperma oppositifolia*, a preferred host plant species (Hopper and Smith, 1992; Smith, 2007), to one dominated by the fern *Thelypteris* sp., which is here reported as a host plant for the first time. Although partulids were observed on *Thelypteris* sp., only a few snails inhabited them.

Partulids were found throughout the island when Crampton visited Guam in 1920. At sites from Merizo to Ritidian, and from coastal areas to highest elevations. Crampton found snails typically 1 to 3 m above the ground in cool, shaded forest habitats (Crampton 1925; Hopper and Smith, 1992) with high humidity and reduced air movement that might promote desiccation. Crampton (1925) described the habitat requirements of the partulid tree snails of the Mariana Islands as: “a sufficiently high and dense growth to provide shade, to conserve moisture, and to effect the production of a rich humus. Hence, the limits to the areas occupied by Partulae are set by the more ultimate ecological conditions which determine the distribution of suitable vegetation.” Crampton (1925) further described the intact structure of native Mariana forests as having four general levels: the high trees; the shrubs and *Pandanus*; the cycads and taller ferns; and the succulent herbs. He noted that the Mariana Islands partulid tree snails

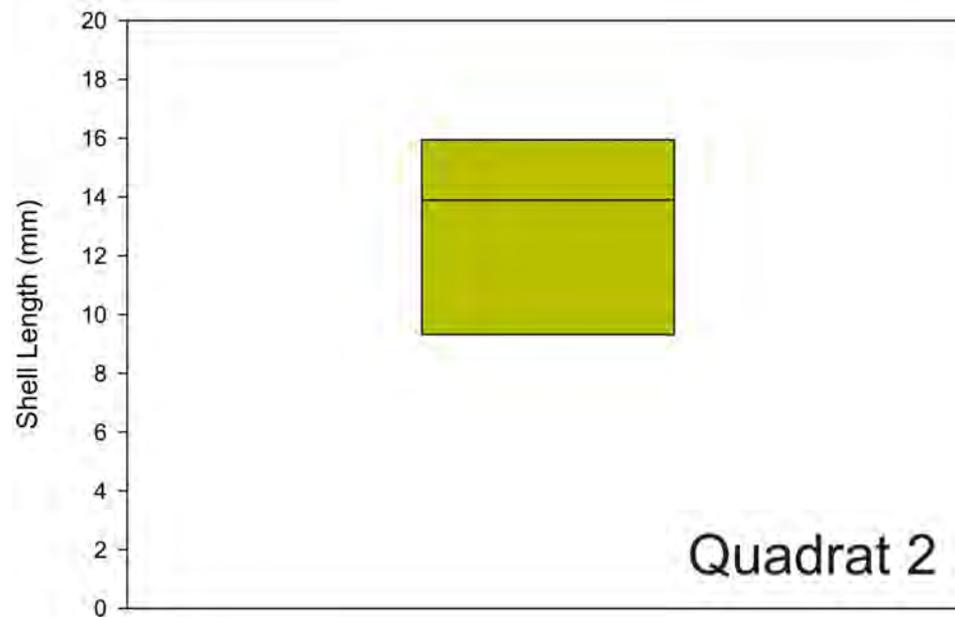
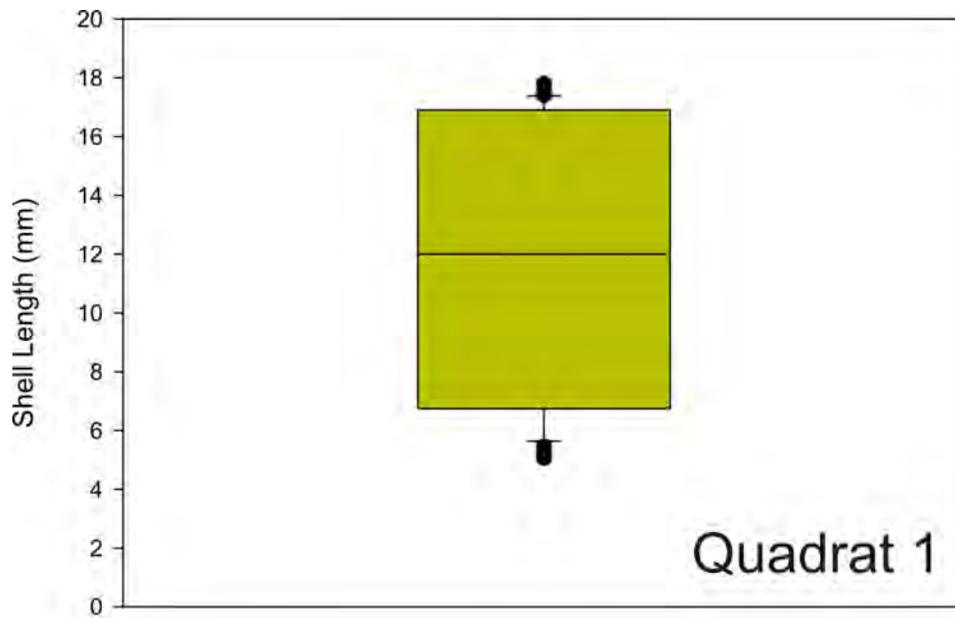


Figure 13. Box plots of *Partula radiolata* shell lengths at the N. Kitts Road, Ordinance Annex sampling station.

Table 1. Plant species hosting arboreal snails at Pugua Point, Haputo Beach, and N. Kitts Road . A filled circle (●) indicates that the snail species was observed on the host plant within one or more quadrats.

Plant taxa	<i>Partula gibba</i>	<i>Partula radiolata</i>	<i>Samoana fragilis</i>
<u>Pugua Point, NCTS</u>			
<i>Annona reticulata</i>		●	●
<u>Haputo Beach, NCTS</u>			
<i>Alocasia macrorrhiza</i>	●	●	
<i>Hernandia sonora</i>	●	●	
<i>Neisosperma oppositifolia</i>	●	●	
<i>Piper guahamense</i>	●	●	
<i>Thelypteris</i> sp.	●	●	
<u>N. Kitts Road, Ordinance Annex</u>			
<i>Hernandia sonora</i>		●	

preferentially live on understory vegetation and did not inhabit the high canopy trees. The habitat requirements for tree snails were numerous in the Mariana Islands prior to World War II, including coastal strand vegetation, forested river borders, and lowland and highland forests (Crampton 1925).

Tragically, we found no areas on NCTS or the Ordinance Annex that resemble Crampton’s descriptions. While the high trees remain in some areas, the understory has been severely damaged or removed altogether by feral ungulates. Ungulate scats were ubiquitous from the floors of ravines to the summit of Mt. Lamlam. Removal of the understory trees and shrubs has resulted in more xerophytic conditions by allowing greater air motion under the canopy. Air motion promotes desiccation, thereby making conditions unsuitable for the survival of land snails. Data in Tables 2–4 support this conclusion. Ambient temperatures and humidities at the sampling stations are very similar to microhabitat temperatures and humidities. However, ambient air velocities are markedly greater than air velocities in the snails’ microhabitat on the undersides of the leaves.

CONCLUSIONS AND RECOMMENDATIONS

Native tree snails in Guam have continued to decline in the last decade. Previously reported colonies at Mt. Alifan have been extirpated since the late 1980s. Elsewhere on Naval

Table 2. Ambient and microhabitat environmental parameters in quadrats at the Pugua Point, NCTS sampling station.

	Temperature (°C)	Relative Humidity (%)	Air Motion (m • sec ⁻¹)
<u>Quadrat #1</u>			
Ambient	34.7	73.5	0.0–1.1
<i>Annona reticulata</i>	30.5	70.3	0.02
<i>Annona reticulata</i>	30.1	75.5	0.24
<i>Annona reticulata</i>	30.2	75.1	0.06
<i>Annona reticulata</i>	30.3	77.0	0.03
<i>Annona reticulata</i>	31.9	71.2	0.41
<u>Quadrat #2</u>			
Ambient	35.5	77.6	0.0–0.9
<i>Annona reticulata</i>	32.3	61.0	0.25
<i>Annona reticulata</i>	32.3	65.7	0.14
<i>Annona reticulata</i>	31.5	66.2	0.22
<i>Annona reticulata</i>	31.5	66.2	0.62
<u>Quadrat #3</u>			
Ambient	35.9	70.7	0.1–1.0
<i>Annona reticulata</i>	34.1	56.6	0.42
<i>Annona reticulata</i>	33.1	61.6	0.79
<i>Annona reticulata</i>	31.8	69.1	0.34
<u>Quadrat #4</u>			
Ambient	38.0	65.6	0.3–0.8
<i>Annona reticulata</i>	33.9	61.5	0.46
<i>Annona reticulata</i>	33.5	61.9	0.62
<i>Annona reticulata</i>	32.8	60.5	0.23
<i>Annona reticulata</i>	32.4	64.6	0.29
<i>Annona reticulata</i>	32.2	63.4	0.32

Table 3. Ambient and microhabitat environmental parameters in quadrats at the Haputo Beach, NCTS sampling station.

	Temperature (°C)	Relative Humidity (%)	Air Motion (m • sec ⁻¹)	
<u>Quadrat #1</u>				
Ambient		30.9	81.5	0.7–1.0
<i>Alocasia macrorrhiza</i>		28.7	81.1	0.10
<i>Alocasia macrorrhiza</i>		28.4	81.1	0.32
<i>Piper guahamense</i>		28.6	84.2	0.32
<i>Piper guahamense</i>		28.7	84.7	0.03
<i>Thelypteris</i> sp.		28.7	83.7	0.18
<i>Thelypteris</i> sp.		28.7	82.8	0.09
<u>Quadrat #2</u>				
Ambient		31.3	82.1	1.2–1.8
<i>Alocasia macrorrhiza</i>		30.6	75.6	0.56
<i>Alocasia macrorrhiza</i>		30.5	76.0	0.03
<i>Piper guahamense</i>		31.3	74.6	0.21
<i>Piper guahamense</i>		30.9	74.8	0.50
<i>Hernandia nymphaeifolia</i>		30.5	76.3	1.22
<i>Hernandia nymphaeifolia</i>		30.7	75.7	0.44
<u>Quadrat #3</u>				
Ambient		32.4	76.8	0.8–1.4
<i>Neisosperma oppositifolia</i>		31.4	71.5	0.62
<i>Neisosperma oppositifolia</i>		30.9	73.1	0.42
<i>Piper guahamense</i>		30.6	73.5	0.28
<i>Piper guahamense</i>		30.6	74.0	0.21
<u>Quadrat #4</u>				
Ambient		32.5	82.2	0.5–0.8
<i>Alocasia macrorrhiza</i>		30.5	77.9	0.16
<i>Alocasia macrorrhiza</i>		30.4	77.9	0.09
<i>Piper guahamense</i>		30.6	78.5	0.12
<i>Piper guahamense</i>		30.6	77.3	0.29
<i>Thelypteris</i> sp.		30.4	76.9	0.15
<i>Thelypteris</i> sp.		30.6	77.2	0.22

Table 4. Ambient and microhabitat environmental parameters in quadrats at the N. Kitts Road, Ordinance Annex sampling station.

	Temperature (°C)	Relative Humidity (%)	Air Motion (m • sec ⁻¹)
<u>Quadrat #1</u>			
Ambient	28.1	69.5	0.6–2.9
<i>Hernandia sonora</i>	27.42	69.7	0.1–0.4
<i>Hernandia sonora</i>	26.32	69.7	0.36–0.7
<i>Hernandia sonora</i>	27.12	69.5	0.01–0.02
<i>Hernandia sonora</i>	26.82	69.1	0.01–0.17

lands, dead ground shells are all that remain of once-robust colonies studied by Crampton in 1920. These observations lead to the following recommendations for terrestrial gastropods on Naval lands in Guam.

1. Conservation management policies should be developed for colonies of endangered snails on Naval lands.

Although population declines and extinctions of native taxa are characteristic of the human-populated islands, tree snail colonies on Naval lands should be surveyed on a regular basis to monitor populations of these unique species. Management and conservation efforts should include protection and enhancement of the forest habitat that supports these species. This is especially important for the Pugua Point colony for two reasons: 1) this is the only colony of this species known to exist in Guam, and 2) between visits to the Pugua Point site during this survey, a large ifit log (*Intsia bijuga*) was removed from the forest floor in Quadrat 1, indicating that the habitat is at risk.

2. Protocols should be developed to manage populations of feral ungulates on Naval lands.

Environmental damage resulting from large populations of feral pigs, carabao, and deer at NCTS and Ordinance Annex is extensive. The forested areas of these lands are shrinking, and the structure of the remaining forests has been compromised by overgrazing. In Sarigan in the northern Mariana Islands, the eradication of feral goats was followed by recovery of tree snail populations along with the recovery of the forest in as little as six years (Smith, 2007).

3. Consideration should be given to construction of ungulate exclusion areas to restore tree snail populations to their former range and former abundance.

In the absence of ungulate removal, areas fenced to exclude ungulates have been shown to be very effective for restoration of native forests, and, therefore, snail habitat. As noted above, the eradication of feral goats in Sarigan resulted in the growth of dense *Partula gibba* populations, as well as other species of native snails.

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REFERENCES CITED

- Bauman, S. 1996. Diversity and decline of land snails on Rota, Mariana Islands. *American Malacological Bulletin* 12:13–27.
- Clarke, B., J. Murray, and M.S. Johnson. 1984. The extinction of endemic species by a program of biological control. *Pacific Science* 38:97–104.
- Crampton, H.E. 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.
- Cowie, R.H. 1992. Evolution and extinction of Partulidae, endemic Pacific island land snails. *Philosophical Transactions of the Royal Society, London B* 335:167–191.
- Cowie, R.H. 1996. Pacific island land snails: Relationships, origins, and determinants of diversity. Pages 347–372 in A. Keast and S.E. Miller, eds. *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes*. Amsterdam: SPB Academic.
- Cowie, R.H. 2000. Non-indigenous land and freshwater molluscs in the islands of the Pacific: Conservation impacts and threats.
- Cowie, R. H. 2001. Invertebrate invasions on Pacific Islands and the replacement of unique native faunas: A synthesis of the land and freshwater snails. *Biological Invasions* 3:119–136.
- Cowie, R.H., and R.P. Cook. 2001. Extinction or survival: Partulid tree snails in American Samoa. *Biodiversity and Conservation* 10:143–159.
- Diamond, J.M. 1984. “Normal” extinctions of isolated populations. Pages 191–246 in M.H. Nitecki (ed.). *Extinctions*. Chicago: University of Chicago Press.

- Federal Register. 1994. Endangered and Threatened Wildlife and Plants; Animal Candidate Review for Listing as Endangered or Threatened Species; Proposed Rule. Federal Register, Volume 59, November 15, 1994.
- Hartmann, W.D. 1881. Bulletin of the Museum of Comparative Zoology 9:172–196.
- Hopper, D.R., and B.D. Smith. 1992. The status of tree snails (Gastropoda: Partulidae) on Guam, with a resurvey of sites studied by H.E. Crampton in 1920. Pacific Science 46:77–85.
- Johnson, M.S., J. Murray, and B. Clarke. 1993. The ecological genetics and adaptive radiation of *Partula* on Moorea. Oxford Surveys in Evolutionary Biology 9:169–238.
- Kondo, Y. 1955. A revision of the family Partulidae. Ph.D. dissertation, Harvard University. 218 pages + 123 figures.
- Kondo, Y. 1968. Partulidae: Preview of anatomical revision. Nautilus 81:73–77.
- Kondo, Y. 1970. Some aspects of Mariana Islands Partulidae (Mollusca, Pulmonata). Occasional Papers of the Bernice P. Bishop Museum 24:73–90.
- Kurozumi, T. 1994. Land molluscs from the northern Mariana Islands, Micronesia. Natural History Research, Special Issue 1:113–119.
- Lydeard, C., R.H. Cowie, W.F. Ponder, A.E. Bogan, P. Bouchet, S.A. Clark, K.S. Cummings, T.J. Frest, O. Gargominy, D.G. Herbert, R. Hershler, K.E. Perez, B. Roth, M. Seddon, E.E. Strong, and F.G. Thompson. 2004. The global decline of nonmarine mollusks. Bioscience 54:321–330.
- Miller, S.E. 1993. Final report on surveys of the arboreal and terrestrial snail fauna of American Samoa. Unpublished report submitted to U.S. Fish and Wildlife Service, Pacific Region, Honolulu. 30 pages.
- Murray, J., E. Murray, M.S. Johnson, and B. Clarke. 1988. The extinction of *Partula* on Moorea. Pacific Science 42:150–153.
- Parkinson, B., J. Hemmen, and K. Groh. 1987. Tropical landshells of the world. Verlag Christa Hemmen, Wiesbaden, West Germany. 279 pages.
- Pfeiffer, L. 1846. Proceedings of the Zoological Society of London 14:38–39.
- Smith, B.D., and D.R. Hopper. 1994. The Partulidae of the Mariana Islands: Continued threats and declines. Hawaiian Shell News 42(2):10–11.
- Smith, B.D. 2007. Preliminary Assessment of Endemic Arboreal Snails in Three Forest Types in Sarigan, with Notes on Ground-dwelling Species. Report to Division of Fish and Wildlife, Commonwealth of the Northern Mariana Islands, Saipan. 23 pages.
- Smith, B.D. In Review. Seven Decades of Disruption, Decline, and Extinction of Land Snails in Aguiguan, Mariana Islands. Report to Division of Fish and Wildlife, Commonwealth of the Northern Mariana Islands, Saipan. 19 pages.

Tracy, C.R., and T.L. George. 1992. On the determinants of extinction. *American Naturalist* 139:102–122.

Tukey, J.W. 1977. *Exploratory Data Analysis*. Reading, Massachusetts: Addison-Wesley.