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Conservation Status of Tree Snail Species in the Genus *Partulina* (Achatinellinae) on the Island of Hawai'i: A Modern and Historical Perspective[1]

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ABSTRACT: The Hawaiian tree snail genus *Partulina*, from Maui, Moloka'i, Lāna'i, O'ahu, and the island of Hawai'i, is the sister-genus of the endangered *Achatinella*, found only on the island of O'ahu. Life histories of species in the two genera are similar, and undoubtedly the *Partulina* species have been as severely impacted by the collective effects of habitat destruction and introduced predators as have those of the genus *Achatinella*. Three species of *Partulina* have been described from the island of Hawai'i: *Partulina physa*, *P. confusa*, and *P. horneri*. Until 1992, there were no recorded sightings of these species for more than 46 yr. Historically, *Partulina* spp. were recorded at various locations in almost all districts of the island of Hawai'i, including North and South Kona, North and South Kohala, Hāmākua, North and South Hilo, and Puna. *Partulina physa* was found nearly islandwide, whereas *P. confusa* and *P. horneri* were mostly located in the Hāmākua and Kohala Districts. *Partulina confusa* and *P. horneri* were not found in the current surveys. Extensive field surveys on the island of Hawai'i between May 1995 and December 1997 resulted in the location of only one population of *Partulina physa*, inhabiting a narrow range in the Kohala Mountains. The shell length and reproductive state were recorded for 82 individuals of *P. physa* from that population. Mean adult shell length was 15.08 mm. Habitat loss, much of which occurred between 200 and 100 yr ago, has likely been the greatest factor contributing to the decline of the *Partulina* spp. of the island of Hawai'i. Predation and shell collecting, and possibly climatic changes and pathogens, have also contributed to the decline of the *Partulina* species on Hawai'i Island. A small captive population of *P. physa* at the University of Hawai'i at Mānoa has suffered high juvenile mortality (78%).

THE ISOLATION OF THE Hawaiian Archipelago has been the setting for the evolution of a unique suite of native land snails. More than 750 species, representing 10 families, are known from the Islands (Cowie et al. 1995*a*). Since the arrival of the Polynesians, and later the Europeans, this unique fauna has declined dramatically as a result of human activities, including introduction of predators, habitat destruction, and overcollecting (Hadfield and Mountain 1981, Hadfield 1986, Hadfield and Miller 1989, Hadfield et al. 1993). The decline of the O'ahu tree snails in the genus *Achatinella* is well documented, and the entire genus is classified by the U.S. Fish and Wildlife Service (USFWS) as Endangered (Hadfield 1986). Other genera, such as *Carelia* from Kaua'i, are thought to be entirely extinct (IUCN 1996). There are many other taxa, including the Succineidae, Pupillidae,

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Zonitidae, and Helicarionidae, for which very little is known. Worse yet, there is only one documented study that examined an entire assemblage of Hawaiian land snails (Cowie et al. 1995*b*). It is critical that the status of the remaining land snails be determined so that management practices may be implemented to limit further loss of this unique fauna.

The Hawaiian tree snail genus *Partulina*, found on Maui, Moloka'i, Lāna'i, O'ahu, and the island of Hawai'i, is the sister-genus of *Achatinella*, found only on the island of O'ahu. *Achatinella* spp. are live bearing, slow growing, late maturing, and low in fecundity. They reach sexual maturity in 4 to 6 yr and bear five to seven offspring per year. Longevity exceeds 10 yr. Life histories of species in the two genera are similar (Hadfield 1986, Hadfield and Miller 1989, Kobayashi and Hadfield 1996), and undoubtedly the *Partulina* species have been as severely impacted by the collective effects of habitat destruction and introduced predators as have those in the genus *Achatinella*. Three species of *Partulina* have been described from the island of Hawai'i: *Partulina physa*, *P. confusa*, and *P. horneri*. The last recorded sighting of these species was in 1946 by Y. Kondo (D. J. Chung and R. H. Cowie, 1991, An archival inventory of the land snails of the State of Hawaii Natural Area Reserves system, unpubl. report, Bishop Museum, Honolulu). A brief survey in 1992 on private land in the Kohala Mountains revealed a small population of *Partulina physa* (M.G.H., pers. obs.). Historically, dense populations of *Partulina* spp. were recorded at various locations in almost all districts of the island of Hawai'i, including North and South Kona, North and South Kohala, Hāmākua, North and South Hilo, and Puna. Loss of habitat, resulting from forest removal for agriculture and the destructive activities of nonnative ungulates, is considered to be the major factor contributing to the decline of these snails. Other factors such as predation and recreational shell collecting are implicated in the decline of *Partulina* species on the island of Hawai'i. Climatic changes and pathogens may also have contributed to the loss of these species.

The disappearance of species of *Partulina* and *Achatinella* on O'ahu, Maui, Moloka'i, and Lāna'i has been well documented. Research has included demographic studies in the field (Hadfield and Mountain 1981, Hadfield and Miller 1989, Hadfield et al. 1993) and in the laboratory (Kobayashi and Hadfield 1996). Comparative efforts are needed for *Partulina* species from the island of Hawai'i to set the base for future conservation efforts. This study was designed to document the status of the *Partulina* spp. on the island of Hawai'i by surveying the areas in which they were historically found, recording their current distributions, and determining, as far as possible, the causative agents in the snails' local extinctions. The condition of the habitat and the status of extant populations were also assessed. General location information on other species of land snails was also collected. It is hoped that the information gained in this study will contribute to the conservation of the only remaining species, *Partulina physa*, over its current, very restricted range.

MATERIALS AND METHODS

Historical Distribution

Data from the malacological collections at the Bishop Museum were used to map the historical distributions of the *Partulina* species on the island of Hawai'i. Based on catalog and label information, the general locations for every collection lot of *Partulina confusa*, *P. horneri*, and *P. physa* were recorded and mapped. In many cases there were numerous collection lots from a single location. For example, 49 lots, representing hundreds of individual shells, were recorded from a single locale for *P. confusa* in the Kohala Mountains. The map served as a guide for areas to search to determine the current distribution of *Partulina* spp.

Field Surveys

Field surveys were conducted on the island of Hawai'i between May 1995 and

December 1997. For some areas, such as the Hāmākua District, historical records were vague in detailing where the *Partulina* species were found. State forest reserves of the Hāmākua District were assessed for the presence of native vegetation by examining infrared aerial photos taken in 1992 and 1993, in which it was easy to distinguish between areas planted in nonnative trees and those with native vegetation by the colors and patterns of the trees. Only reserves containing areas of native vegetation were considered useful to survey. Where appropriate, permission to survey private land was obtained from the landowner, but most of the surveys were concentrated in public lands including Natural Area Reserves (NARs) and state forest reserves.

Many surveys conducted in Natural Area Reserves were made along preestablished, numbered transect lines. In these areas, stations every 250 m along the transect line were searched intensively for land snails for approximately 20 min, both in the trees and on the ground. If areas between the 250-m stations contained suitable habitat, they too were searched for a shorter time period (5 min). In other reserves and private land, surveys were conducted mostly along roadways and trails, although in some areas, such as Ponoholo Ranch, more comprehensive searches were conducted including areas off of trails.

When snails were found, locality, host vegetation, and the number of individuals was recorded. Snails were arbitrarily considered rare if fewer than 10 individuals were found and common when 10 or more snails were found in an area. When the snails could not be identified in the field, a few individuals were collected to be used for identification at the Bishop Museum. All materials collected will be deposited in the malacology collection at the Bishop Museum. No individuals of *Partulina* spp. were collected. To avoid destructive sampling, pictures were taken when individuals were not collected, although certain identification from photographs is difficult.

For each individual of *Partulina physa* found in the field, shell chirality (direction of coiling), presence or absence of an apertural callus or "lip" (indicative of terminal growth and sexual maturity), and shell length were measured and recorded. A number of the snails were also photographed to record shell banding patterns. The Global Positioning System (GPS) was used to accurately map the sites where *Partulina physa* was found on Ponoholo Ranch.

The tree with the greatest number of *Partulina physa* found at one time was selected for a mark-recapture study. The snails were removed from the tree and individually marked with a paint pen, and shell length, presence of an apertural callus, and chirality were recorded. This technique has been employed by Hadfield et al. (1993) for many years with no apparent detrimental effects to the snails. The site was revisited approximately 6 months later, the same tree was again searched, and both the total number of snails found and the number with marks were recorded. Mark-recapture analysis was used in an attempt to estimate the population size.

Captive Propagation

In January 1995, two adults of *Partulina physa* were collected alive from Ponoholo Ranch by John Giffin of the State Division of Forestry and Wildlife. The snails were first taken to Hilo, where they were photographed, and subsequently were cool shipped via air cargo and housed at the captive propagation facilities in the laboratory of M. G. Hadfield at the University of Hawai'i on O'ahu. Other snails in the genera *Partulina* and *Achatinella* have been reared successfully at this facility since 1986. Detailed captive rearing methods are outlined in Kobayashi and Hadfield (1996). Briefly, the snails are housed in environmental chambers that emulate field conditions in their natural habitats (i.e., temperature and light cycle, and precipitation). Leaves of the native tree 'ōhi'a lehua (*Metrosideros polymorpha*), a common host for the snails, and a laboratory-cultured fungus, which the snails eat, are replaced biweekly in the chambers. Number

TABLE 1

LOCATIONS OF COLLECTION LOTS OF *Partulina* SPP. FROM THE ISLAND OF HAWAI'I

LOCATION	*Partulina physa*	*Partulina horneri*	*Partulina confusa*	*Partulina confusa* FOSSIL	TOTAL	DATE
Kohala	—	—	43	—	43	Historical
Kohala Mountains	—	2	—	—	2	Historical
Pu'u Pili	1	—	—	—	1	1992
Ponoholo Ranch	1	—	—	—	1	1992
Waimea Plains	2	—	11	—	13	Historical
Mānā	—	1	8	3	12	Historical
Hāmākua	27	13	25	—	65	Historical
Kukuihaele	4	9	—	—	13	Historical
Pā'auhau	—	—	—	4	4	Historical
Pa'auilo	—	1	2	—	3	Historical
Kaiwiki	2	—	—	—	2	Historical
'Ōla'a	2	—	—	—	2	Historical
Pāhoa	1	—	—	—	1	Historical
Puna	2	—	—	—	2	Historical
Pāpā	3	3	—	—	6	Historical
Pāpā ('Ōhi'a Mill)	1	—	—	—	1	Historical
Kīpāhoehoe	1	—	—	—	1	Historical
Kapu'a	—	1	—	—	1	Historical
Kahalu'u	1	—	—	—	1	Historical
Hōlualoa (tract 1–2)	2	1	—	—	3	Historical
Hōlualoa (tract 3)	3	—	—	—	3	Historical
Honua'ula	6	3	—	—	9	Historical
Hualālai	1	1	—	—	2	Historical
Hu'ehu'e	—	—	—	1	1	Historical
Pu'u Wa'awa'a	—	—	—	14	14	Historical
Waiki'i Paddock	—	—	—	1	1	Historical
Total	60	35	89	23	207	Historical

Data were obtained from collection labels in the Bishop Museum except the modern location information from 1992. Diacritics have been added. Numbers are the number of collection lots from any one location, not number of snails. The lots contain variable numbers of specimens, from one snail to hundreds.

of births and deaths is recorded, along with shell length for each snail.

RESULTS

Historical Distribution

Data, compiled principally from the collections of the Bishop Museum, are shown in Table 1. Also included in Table 1 are two recent reports of *Partulina physa*. Figure 1 illustrates the historical distribution of *Partulina* species on the island of Hawai'i and survey locations for the current study (refer to Table 3). Some collection labels provided additional information on habitat and more specific location information. For example, *Partulina physa* historically was recorded at elevations between 914 and 2134 m on the slopes of Hualālai. In addition, *P. physa* was often found on the trunks of trees and sometimes dead tree stumps. *Partulina confusa* was recorded at elevations as high as 1828 m near the Waiki'i area on the leaves of māmane (*Sophora chrysophylla*), a tree often associated with drier upper-elevation forests. Fossil shells of *P. confusa* were found in the Pu'u Wa'awa'a area 2 m below the surface. The highest recorded elevation for *Partulina horneri* on the museum labels was 914 m. Label information also provided descriptions of some host plants for this species, including 'ōhi'a (*Metrosideros polymorpha*), kōlea

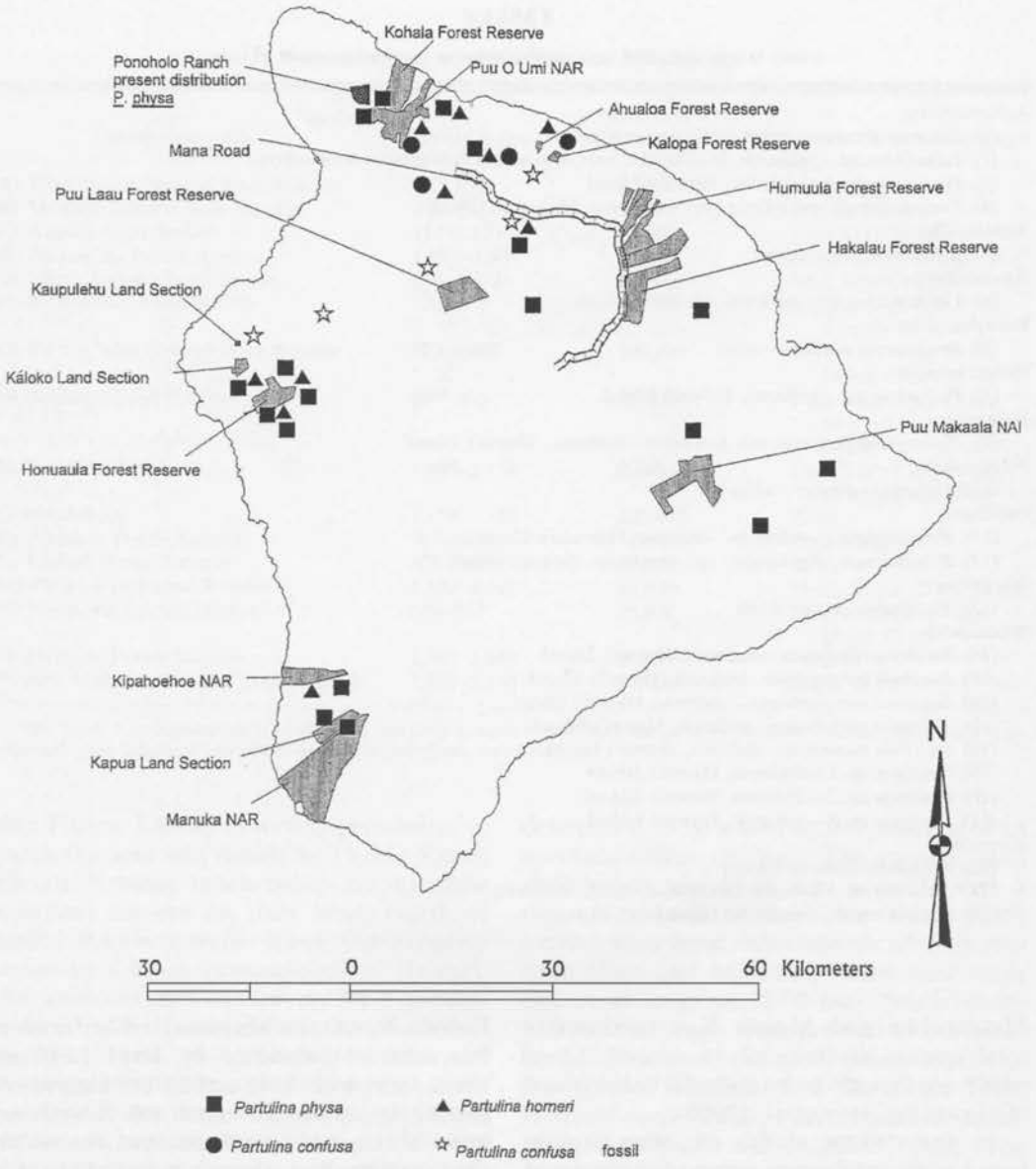

FIGURE 1. Historical distribution of *Partulina* spp. on the island of Hawai'i. Areas surveyed in 1995–1997 are shaded.

(*Myrsine* spp.), olopua (*Nestegis sandwicensis*), kōpiko (*Psychotria* spp.), and the introduced guava (*Psidium guajava*). There are a total of 2827 shells of *Partulina* spp. from the island of Hawai'i in the Bishop Museum collection. Over half of these, 1655, are from *Partulina confusa*.

Field Surveys

One of the least-known assemblages of native land snails is that of Hawai'i Island, from which 126 species have been described (Cowie 1995, Cowie et al. 1995*a*). A study in 1992–1993 in the "saddle" area between

TABLE 2

LAND SNAIL TAXA FOUND DURING SURVEYS OF THE ISLAND OF HAWAI'I

Achatinellidae
(1) *Elasmias fuscum*—endemic, Hawaiian Chain
(2) *Lamellidea* sp.—endemic, Hawaiian Chain or possible Polynesian introduction
(3) *Partulina physa*—endemic, Hawai'i Island
(4) *Tornatellides/Tornatellaria* spp.—endemic, Hawaiian Chain
Achatinidae
(5) *Achatina fulica*—alien
Amastridae
(6) *Leptachatina* sp.—endemic, Hawai'i Island
Bradybaenidae
(7) *Bradybaena similaris*—alien
Helicarionidae
(8) *Philonesia* sp.—endemic, Hawai'i Island
Helicinidae
(9) *Pleuropoma laciniosa* var. *konaensis*—endemic, Hawai'i Island
Polygyridae
(10) *Polygyra cereolus*—alien
Pupillidae
(11) *Pronesopupa acanthinula*—endemic, Hawaiian Chain
(12) *Pronesopupa (Sericipupa)* sp.—endemic, Hawai'i Island
Spiraxidae
(13) *Euglandina rosea*—alien
Succineidae
(14) *Succinea bicolorata*—endemic, Hawai'i Island
(15) *Succinea inconspicua*—endemic, Hawai'i Island
(16) *Succinea newcombiana*—endemic, Hawai'i Island
(17) *Succinea garrettiana*—endemic, Hawai'i Island
(18) *Succinea konaensis*—endemic, Hawai'i Island
(19) *Succinea* sp. 1—endemic, Hawai'i Island
(20) *Succinea* sp. 2—endemic, Hawai'i Island
(21) *Succinea* sp. 3—endemic, Hawai'i Island
Zonitidae
(22) *Oxychilus alliarius*—alien
(23) *Striatura* sp.—possibly introduced, status unknown
(24) *Vitrina tenella*—endemic, Hawaiian Chain

Mauna Loa and Mauna Kea produced a total species diversity of 16 species, 15 of which are thought to be endemic to the island of Hawai'i (Cowie et al. 1995*b*).

In the current study, all other species found while conducting surveys for species of *Partulina* on the island of Hawai'i were also recorded. In all, 24 species were identified, at least five of which are alien introductions to the Hawaiian Islands (Table 2). More detailed location information is given in Table 3.

A Field Population of Partulina physa

Living *Partulina physa* were located in only one area, on Ponoholo Ranch in the Kohala Mountains (Figure 1). The forest in this area is dominated by large (>10 m) 'ōhi'a trees with little understory because of grazing by cattle. The area was fenced and most of the cattle were removed for watershed conservation, though a few wild cattle remain in the forested area. Ponoholo Ranch is flanked by Parker Ranch to the north and Kahuā Ranch to the south. In 1992, 16 individuals of *P. physa* were found on the ranch by M.G.H., S. Miller, and J. Giffin. In the more-extensive surveys of 1996–1997, 82 individuals of *P. physa* were found between 1000 and 1158 m elevation. Snail locations were recorded by GPS when possible. It is likely that the habitat for *P. physa* extends

TABLE 3

RESULTS OF LOCATIONS SURVEYED FOR *Partulina* SPP.

SURVEY LOCATION	ELEVATION (m)	APPROXIMATE AREA SURVEYED (m^2)	LAND SNAIL SPECIES FOUND[a]
(A) Kīpāhoehoe Natural Area Reserve	402–872	23,000	4 (c); 5 (r); 8 (r); 22 (c)
(B) Manukā Natural Area Reserve	548–762	15,000	7 (r; d); 13 (r; d)
(C) Kapu'a Land Section	914–1,439	25,000	1 (r); 4 (r); 12 (r)
(D) Honua'ula Forest Reserve	1,890–2,439	25,000	18 (r); 22 (c); 24 (r)
(E) Upper Kaloko Land Section	610–1,414	22,500	4 (c); 12 (r); 13 (c)
(F) Ka'ūpūlehu Land Section	530–671	12,000	4 (r; d); 6 (r; d); 7 (r; d); 9 (r; d); 23 (r; d)
(G) Pu'u o 'Umi Natural Area Reserve	975–1,603	190,000	1 (c); 4 (c); 8 (r); 11 (r); 14 (c); 15 (c); 22 (c)
(H) Kohala Forest Reserve	597–866	25,000	1 (c); 4 (c); 7 (r); 13 (r); 14 (c); 15 (c); 16 (c); 22 (c)
(I) Ponoholo Ranch	1,000–1,158	2,400,000	1 (c); 3 (c); 4 (c); 14 (c); 15 (r); 16 (c); 19 (r)
(J) Mānā Road	1,158–2,195	325,000	22 (r)
(K) Āhualoa Forest Reserve	567–805	30,000	1 (r); 22 (r)
(L) Kalōpā Forest Reserve	610–769	25,000	22 (r)
(M) Pu'u Lā'au Forest Reserve	1,890–2,621	35,000	18 (r); 22 (c); 23 (r); 24 (r)
(N) Humu'ula Forest Reserve	610–927	25,000	2 (r); 4(c); 8(c); 17 (c); 19 (c); 22 (c)
(O) Hakalau Forest Reserve	1,585–1,890	30,000	4 (r); 22 (c)
(P) Pu'u Maka'ala Natural Area Reserve	1,036–1,158	10,000	21 (c); 22 (c)

[a] See Table 2 for explanation of numbers. C, common; d, dead; r, rare. Snail species were considered common when 10 or more individuals were found and rare when less than 10 individuals were found.

onto Parker Ranch; however, permission to search the area was denied by Parker Ranch officials, it being ranch policy not to allow biological surveys on their land. North of Parker Ranch toward Hāwī lies property owned by Chalon International of Hawai'i. This area was used extensively for sugar cultivation in the past, and no suitable forest remains. Hence, the probable boundary of this population of *P. physa* lies at the northern edge of the Parker Ranch parcel. There are two records of *P. physa* from Pu'u Pili in Kahuā Ranch to the south of Ponoholo Ranch, one historical and one modern (M. Severns, pers. comm.). Permission to search Pu'u Pili was also denied. An area southeast of Pu'u Pili, transect 10 in the Pu'u o 'Umi Reserve, was also surveyed, but no *Partulina* spp. were found there despite the presence of suitable habitat.

The 82 *P. physa* found on Ponoholo Ranch included 11 adults, 64 juveniles, and 7 newborn snails (<5.01 mm). Snails were determined to be adults by the presence of an apertural callus, or "lip." The average adult shell length was 15.08 mm ($n = 11$) with a range from 14.01 to 16.13 mm. This is much smaller than most other species of *Partulina* from Maui and Moloka'i, where adult sizes can be as large as 25.00 mm. Snails under 5.01 mm in length were deemed to be "newborn," based on studies of other achatinelline species (Hadfield and Mountain 1981, Hadfield and Miller 1989, Hadfield et al. 1993, Kobayashi and Hadfield 1996). The average newborn size was 4.56 mm. The smallest snail found, 2.95 mm, was dead. All of these snails had sinistral shell coiling.

The size distribution of the 82 snails found on Ponoholo Ranch is shown in Figure 2. Most of the snails were in the intermediate size classes, with few adults and newborns. Many of the trees were very large (>10 m), making a thorough search nearly impossible for most. Searching was also difficult because many of the trees were limbless up to 2 m

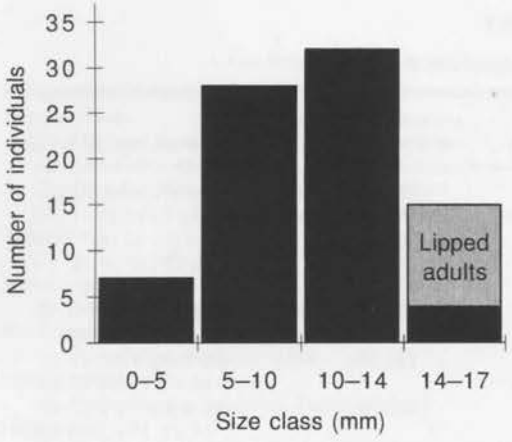

FIGURE 2. Size distribution of *Partulina physa* in the field.

from the ground because of cattle grazing: our inability to search the tops of the trees may have skewed the results. The very smallest snails are the most difficult to see, which may also be reflected in the low number of snails less than 5 mm.

On the first visit to Ponoholo Ranch in the current study (March 1997), few trees were found with more than two individuals. A search of an *Ilex anomala* located under a large 'ōhi'a tree (>10 m) revealed six small *P. physa* ranging in size from 4.87 to 6.90 mm. These snails were marked individually with a paint pen to conduct a mark-recapture study. On the return to this site in September 1997, none of the snails initially marked was located, although 12 new individuals, ranging in size from 2.95 to 16.13 mm, were found. Three of these snails were adults. It was evident from this study that the snails were moving between the *Ilex anomala* and the adjoining 'ōhi'a trees. In fact, one of the new individuals located on the return visit was found 2 m above the ground on the bark of the 'ōhi'a tree. The results of this mark-recapture study cannot be used to estimate population size because none of the originally marked snails was found, but the observations make it evident that the population on Ponoholo Ranch is much larger than the 82 snails seen.

Captive Population of Partulina physa

The two snails collected alive in 1995 were adults, but between the time of their collection and their arrival on O'ahu, one snail was born. One of the adults and the newborn arrived in good condition, but the other adult had a crack through its shell and the tip of its aperture was broken off. As of August 1997, eight snails had been born in the laboratory, but seven of these and one adult died. It is surprising that the adult that came to the laboratory with a damaged shell is still alive. The current population consists of three individuals, one adult and two juveniles. Average adult length is 15.26 mm. For snails born in the laboratory, birth size averaged 4.35 mm.

The population size of the *P. physa* housed at the laboratory over a 31-month period is shown in Figure 3. More than three-fourths (78%) of the juveniles born in the laboratory have died from unknown causes. In addition, one of the adults died within 7 months of arriving in the laboratory. The surviving adult gave birth to five young in the 24-month period (2.5 births per year) after the death of the other adult (see Figure 3).

DISCUSSION

Of the 16 areas surveyed for *Partulina* spp. on the island of Hawai'i only one, Ponoholo Ranch, harbors a living population of *P. physa*. Some of the other areas surveyed contained habitats deemed suitable to sustain populations of these snails, and it is difficult to ascertain why snails persist in some areas and not others.

Factors that are thought to have caused the decline of *Partulina* spp. on the island of Hawai'i since the arrival of humans include (1) habitat destruction and alteration; (2) predation; and (3) recreational collecting. In addition, (4) climatic changes and (5) the effects of pathogens may perhaps be having some impact. Each of these factors is discussed in greater detail below. It is important to note that *Partulina* species were frequently cited as rare in many areas on the island of

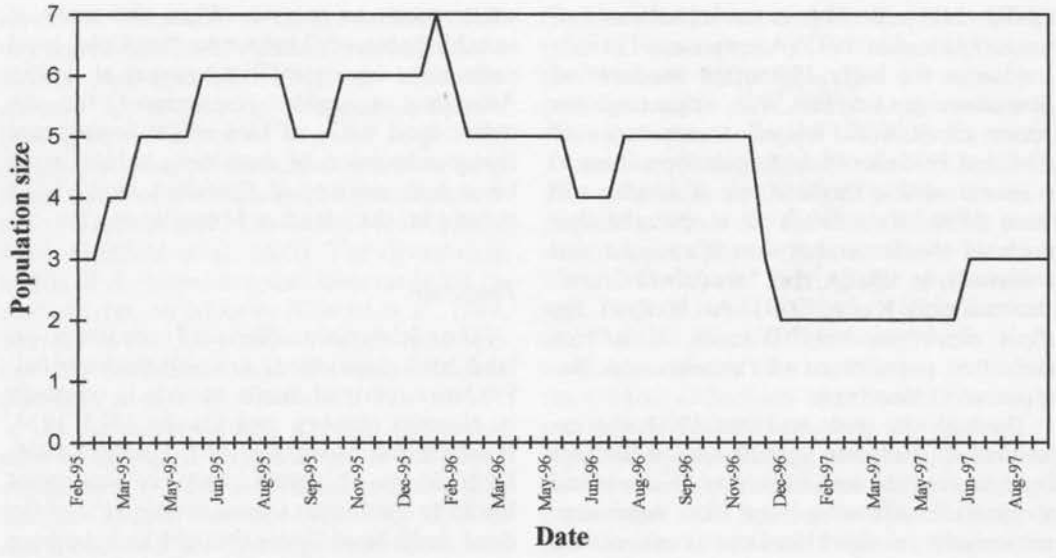

FIGURE 3. Captive population of *Partulina physa*.

Hawai'i in the historical literature, and in some of the historical collections only fossil shells of *P. confusa* were found (Figure 1).

Habitat Destruction

Pressures from expanding human populations in both agricultural and urban areas have lead to concern over declining land-snail populations in Hawai'i and in other parts of the world: Moorea, Murray et al. (1988); Guam, Hopper and Smith (1992); Nigeria, Osemeobo (1992); New Zealand, Triggs and Sherley (1993); Gulf of Guinea, Gascoigne (1994); Rodrigues Island, Griffiths (1994); Sweden, Bengtsson et al. (1995); Madagascar, Emberton (1995). Decline of snail populations on the island of Hawai'i because of habitat destruction was noted as early as the 1890s (H. W. Henshaw, 1903, unpublished letters in the Museum of Natural History Archives, London), although the history of forest removal dates back to the arrival of the Polynesians some 1500 yr ago. The early Hawaiians used slash-and-burn techniques to clear vegetation for agriculture, and shells of numerous snail species have been found in the ash deposits that resulted from these prehistoric fires (Kirch 1982). Many of these fires occurred in the Kohala region of Hawai'i Island, where historical records for *Partulina* spp. exist.

The arrival of Europeans and the resulting introduction of ungulates to the island of Hawai'i had another direct and negative impact on populations of *Partulina* spp. Captain Vancouver introduced cattle (*Bos taurus*) to Hawai'i in 1793, and King Kamehameha immediately placed a kapu (prohibition) on the cattle so that they would increase. By 1823 there were an estimated 12,000 head of wild cattle on the island (Cuddihy and Stone 1990). By the mid-1800s the destructive force of cattle was realized, as it was noted that the forests of Waimea had turned to "open plains" (Cuddihy and Stone 1990). Cattle damage was also recorded for the upper elevations of Kona. Both of these areas historically harbored populations of *Partulina* spp. Goats (*Capra hurcus*) were also a major factor in habitat destruction in the early 1800s (Cuddihy and Stone 1990). The deleterious effects of these animals were also realized early on, and huge drives were held to "get the destructive goats" (Anonymous 1915); nearly 2400 goats were slaugh-

tered on one such drive in the Kohala area of Hawai'i Island in 1915 (Anonymous 1915).

Also in the early 1800s, the sandalwood (*Santalum* spp.) trade was impacting the forests of Hawai'i Island. Large areas of low- and mid-elevation forests were burned in search of this fragrant tree (Cuddihy and Stone 1990, Kay 1997). It is thought that much of the forest between Kawaihae and Waimea was lost in the "sandalwood era" (Barrera and Kelly 1974). At least at the upper elevations near Waimea, it is very likely that populations of *Partulina* spp. disappeared at that time.

Through the mid- and late 1800s the expansion of plantation agriculture was another force causing the loss of forests on the island of Hawai'i. Clearing land for sugarcane, particularly on the Hāmākua coast, caused the destruction of a great deal of snail habitat. *Partulina confusa* was known from the area above Kukuihaele, which became a vast field of sugarcane (Pilsbry and Cooke 1912–1914). A large accidental fire that burned 12,600 ha of forest in the Hāmākua region in 1912 was also attributed to the sugar plantations (Anonymous 1912). Ranching activities also expanded in that period, reducing and degrading the forests even more.

In 1933, Bryan recognized that the native land snails of Hawai'i were disappearing "due to the ravages of cattle, goats, cultivation, . . . and the spread of 'civilization'" (Bryan 1933). Many of the same causes of habitat destruction 100 to 200 yr ago continue today on the island of Hawai'i. The human population is growing and pushing farther into the remaining areas of native forest. Developments such as the subdivision of Kaloko in North Kona, which reaches elevations of 1370 m on the slopes of Hualālai, exemplify this. Feral and domestic ungulates remain a threat to snail habitat. In particular, feral pigs are responsible for destroying large areas of understory in the wet forests (Cuddihy and Stone 1990), including many plant species that typically support native snail populations.

A study conducted on forested islands of Sweden found that there was a minimum forested area required for threatened land snail species to survive. When the areas of suitable habitat fell below the threshold, local extinctions occurred (Bengtsson et al. 1995). Assuming a similar requirement for the native land snails of Hawai'i, it is apparent that preservation of remaining habitat must be a high priority if *Partulina physa* is to survive on the island of Hawai'i.

Predation

The deleterious effects of predators on land snail populations are well documented. Predation of land snails by rats is common in Hawai'i (Pilsbry and Cooke 1912–1914, Hadfield and Mountain 1981, Hadfield 1986, Hadfield et al. 1993), and on Rodrigues Island in the Indian Ocean, where 81% of the dead shells found were thought to have been eaten by rats (Griffiths 1994). The Polynesian rat (*Rattus exulans*) accompanied the pioneering Polynesians to Hawai'i (Kirch 1982). With the arrival of the Europeans, the black rat (*Rattus rattus*) and the Norway rat (*Rattus norvegicus*) became established in the Islands. In 1903, Henshaw transplanted a colony of *Partulina physa* snails from the forest to his backyard in Hāmākua only to have it quickly "discovered by rats and exterminated" (Pilsbry and Cooke 1912–1914). It was also noted in the early 1900s that populations of *Succinea* were being "destroyed in their natural habitats by rats and mice" (Pilsbry and Cooke 1912–1914).

No evidence of rat predation on the populations of *Partulina physa* on Ponoholo Ranch was detected in the current study. However, a Polynesian rat was recently captured at the summit cabin in the Pu'u o 'Umi Reserve, and rat activity was also noted in the Kohala Forest Reserve near the Kaukini Cabin (L.J.H., pers. obs.). Rats were also present in the Kīpāhoehoe Natural Area Reserve as evidenced by typical destruction of 'ie'ie (*Freycinetia arborea*) inflorescences. Certainly rats have played a role in past destruction of land snail populations on the island of Hawai'i (Pilsbry and Cooke 1912–1914) and will most likely continue to be a threat.

In 1955 the carnivorous snail *Euglandina*

rosea was introduced to the Hawaiian Islands to control the Giant African Snail (*Achatina fulica*). However, *E. rosea* was soon discovered to be another biocontrol failure, having little effect on its intended target, and it quickly invaded the native forest to prey upon snails of the endangered genus *Achatinella* (Hadfield and Mountain 1981, Hadfield 1986, Hadfield et al. 1993). The devastating effects of *E. rosea* have also been recorded on *Partula* spp. on Moorea (Clarke et al. 1984, Murray et al. 1988) and on native snail species on Rodrigues and Mauritius Islands (Griffiths et al. 1993, Griffiths 1994).

In the current study, *E. rosea* was found alive in the forest in two areas on the island of Hawai'i: (1) five individuals were seen in Kaloko Mauka between 610 and 1219 m elevation; and (2) one live individual was found on the Kohala Ditch Trail at 610 m elevation. Dead shells of *E. rosea* were found in the Manukā Natural Area Reserve, at sea level in Pololū Valley, and in urban Hilo. Although *E. rosea* was not located live in the Hāmākua District in the current survey, it is nevertheless abundant there (P. Q. Tomich, pers. comm.). The location of live *E. rosea* in native forest areas indicates that this species has likely played a role in the decline of *Partulina* spp. on the island of Hawai'i.

Hopper and Smith (1992) reported predation on *Partula* spp. on Guam by the New Guinea flatworm *Platydemus manokwari*. Concern was raised that this flatworm could be a threat to *Achatinella* spp. on the island of O'ahu, where it was found in 1992 (M.G.H., pers. obs.), but there is no evidence as yet that it has reached forest habitats and is feeding on the endangered snails. A survey in 1995 near Hilo (elevation 70 m) revealed the presence of *P. manokwari*, the first record for the island of Hawai'i (A. Asquith, pers. comm.). *Platydemus manokwari* may be limited to the warmer, lower elevations in the Islands, but this has yet to be demonstrated.

Recreational Shell Collecting

In the late 1800s and early 1900s, land-snail collecting was a popular pastime on the Hawaiian Islands (Hadfield 1986, Kay 1997). Henshaw (*in* Pilsbry and Cooke [1912–1914]) referred to a colony of *Partulina confusa* on the Waimea Plains that had an estimated population size of 75,000 and where he and other collectors collected 10,000 shells in just 3 months (Pilsbry and Cooke 1912–1914). The collections at the Bishop Museum also provide evidence for the shell-collecting pressure that was put on these snails on Hawai'i Island. There are 2827 shells of *Partulina* spp. from Hawai'i Island in the collection, over half of them (1655) being shells of *P. confusa*, a species that now seems to be extinct. Most collections were made by private individuals and subsequently donated to or acquired by the Bishop Museum. Collecting has been an important factor in the decline of other land snail species in Guam (Hopper and Smith 1992) and Nigeria (Osemeobo 1992). Today, specimens of *Partulina* spp. are so rare that few, if any, people ever see them alive.

Climatic Changes

A review of the historical literature makes it evident that the *Partulina* spp. were already in decline in the late 1800s. *Partulina horneri* was described as "extremely rare" in the early 1900s (Gouveia and Gouveia 1920), and Henshaw described large numbers of dead shells of *P. horneri* along the ridges of Waipi'o and Waimanu ". . . that had been found live in abundance ten years earlier" (*in* Pilsbry and Cooke [1912–1914]). Those areas were apparently still forested with native trees when the mass snail deaths occurred, and the shells were without evidence of rat predation (Pilsbry and Cooke 1912–1914). It is possible that part of this early decline of the *Partulina* spp. was caused by climatic changes, both on the microclimatic and macroclimatic levels.

Land snail decline has been correlated with climatic change in a few instances. For example, Baur and Baur (1993) speculated that increased thermal radiation caused by urban development led to the extinction of 16 populations of the land snail *Arianta arbustorum* in Switzerland. The manner in which changing heat and water regimes can

have negative effects on land snails was also evident in a forest on Puerto Rico, where tree-fall gaps caused microclimate shifts that resulted in the decline of the snail *Caracolus carocollus* (Alvarez and Willig 1993). It is possible that forest degradation and destruction on the island of Hawai'i have caused these types of microclimatic changes and led to the decline of *Partulina* spp. in many, but not all, areas surveyed.

On a larger scale, there is evidence that there has been a marked decrease in the rainfall between 1900 and 1977 at Kamuela (Doty 1982), an area where *Partulina* spp. once occurred. Doty (1982) surmised that the reduction in rainfall was due to a shift in the direction of the prevailing trade winds, a factor that has not been proven. A drought on the island of Hawai'i in 1992 had a detrimental effect on the survival of certain plants (Lohse et al. 1995), and it is possible that drying climatic trends have played a role in the decline of *Partulina* spp. on some parts of Hawai'i Island. It must be noted, however, that across the Hawaiian Chain, achatinelline snails have vanished unevenly, and we lack a unifying theory to tie climate change to these snail extinctions.

Pathogens

Land snail diseases are not well understood. However, Hadfield and Miller (1989) mentioned the possibility that pathogens have played a role in the decline of the native land snails of the Hawaiian Islands. Such a factor could help explain the scores of dead snails found by Henshaw in the late 1800s in the Kohala District. Evidence of pathogens has been found in captive snails of the genus *Partula* from French Polynesia; two types of flagellate protozoans were found associated with dead snails (Cunningham et al. 1996). This topic warrants more investigation.

Captive Propagation

No strong conclusions can be drawn from the captive-propagation study of *Partulina physa* because the sample size was very small. However, this study did reveal differences between *P. physa* and other achatinelline snails held in the laboratory. In laboratory studies of *Partulina redfieldi*, the juvenile mortality rate was lower, with 42% (Kobayashi and Hadfield 1996) compared with 78% for *P. physa*. The birth rate of 2.5 births per year for *P. physa* is lower than that for the other species of *Partulina* reared in the laboratory, which can be as high as five to seven births per year (Kobayashi and Hadfield 1996). Dissections by Thaanum (1903, unpubl. notes on dissections of snails collected, Bishop Museum Archives) revealed that *P. physa* tended to brood fewer embyros at one time than other species of *Partulina* and *Achatinella*. The majority of *Achatinella* and *Partulina* species tend to have two to three embryos at one time, whereas Thaanum (1903, unpubl. notes) usually found only one in *P. physa*.

The endemic terrestrial biotas of oceanic islands are some of the most disturbance sensitive and extinction prone on earth. The species making up many of these biotas evolved in the absence of pathogens, predators, or competitors, making them highly vulnerable to anthropogenic changes. The results of this study reveal yet another example of the crisis of extinction on oceanic islands. Surveys on the island of Hawai'i between May 1995 and December 1997 resulted in the location of only one population of *Partulina physa*. Historically, *P. physa* was found islandwide, and *P. confusa* and *P. horneri* were mostly found in the Hāmākua and Kohala Districts. *Partulina confusa* and *P. horneri* were not found in the survey reported here and may very well be extinct. Twenty-three other species of land snails were located during the course of the surveys, five of which were alien species.

Habitat loss, most of which occurred 200 to 100 yr ago, has likely been the greatest factor contributing to the decline of the *Partulina* spp. of the island of Hawai'i. Predation and shell collecting, plus possibly climatic changes and pathogens, have also contributed to the decline.

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Bean and Wilcove (1997) noted that without effective strategies to conserve en-

dangered species on private land many conservation plans cannot succeed. Because the only remaining population of *Partulina physa* occurs on private land, it will be necessary to have cooperation with the landowners if the snails are to survive. Ponoholo Ranch has already removed most of the cattle from the areas where the snails exist in attempts to conserve the watershed. There was no evidence of predation on the snails at the time the cattle were removed, and thus prospects for the persistence of this population are good. However, a species that was once distributed across a landmass as large as Hawai'i Island and is now reduced to a single population in one restricted area is highly vulnerable to local extinction events. The status of *P. physa* can only be characterized as highly endangered, and *P. confusa* and *P. horneri* are probably extinct.

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