

Demographic Studies on Hawaii's Endangered Tree Snails: *Partulina proxima*¹

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ABSTRACT: Populations of the tree snail *Partulina proxima*, endemic to higher elevations of Molokai, Hawaiian Islands, were studied for 3 years. Analyses of the data derived from 17 bimonthly mark-recapture events determined that each tree harbors a small, mostly nonmigratory population of 8–26 snails of which 2–4 are adults; the snails average 4.2 mm long at birth and 21.3 mm long when growth stops; growth is slow, with maturity reached in 5–7 years; annual fecundity averages 6.2 offspring per adult; and mortality is about 98% over the first 4 years of life. Given the high rate of juvenile mortality, adult snails must reproduce for at least 12 years to replace themselves. From this we calculate a minimum maximal life-span of 18–19 years. We conclude that the current high rate of unexplained juvenile mortality, combined with late age at first reproduction and low fecundity, place this species at very high risk to any sort of perturbation, particularly any selective predation on adults.

AMONG THE MOST RAVAGED BIOTAS in the world is that of the Hawaiian Islands (Zimmerman 1970). Hawaii's unique, insular fauna and flora, once a showcase of diversification through evolution, are now better known as ledgers of extinction. Recorded extinctions include 40% of endemic birds (Berger 1970), uncounted numbers of endemic insects (e.g., Gagne 1982, Gagne and Howarth 1982), and probably 50% of the nearly 1000 species of terrestrial gastropods (Kondo 1970) that once inhabited these islands. Fosberg and Herbst (1975) estimated that 66% of Hawaii's native plants are rare, endangered, or extinct. Agents of annihilation are known to include the following: habitat destruction (clearing for farming, logging, and housing; grazing by introduced mammals); introduction of exotic grasses, shrubs, weeds, and trees, which out-compete native plants and prove inhospitable to native animals; introduction of competitor

and predatory animals; probably introduced pathogens (though essentially unstudied); and, for a number of groups of plants and animals, selective harvesting (e.g., hardwood trees, the nene goose).

The endemic achatinelline tree snails of Hawaii have long been known for their beauty, variety, and great local evolutionary radiation (Gulick 1905). On the island of Oahu, more than 170 varieties of the endemic genus *Achatinella* have been described. The 30–40 species represented by these forms are now more than 50% extinct (Kondo 1970), and the remainder are rare and found only in high-elevation residues of once widespread native forest. Members of the closely related genus *Partulina* of Molokai, Maui, and Lanai are probably equally devastated, but they have not been systematically surveyed in many years. The *Partulina* species of the island of Hawaii have not been recorded for 20–30 years, and are probably extinct. The entire genus *Achatinella* is on the U.S. endangered species list, and was cited in 1985 as one of the 12 most critically endangered species in the world by the International Union for the Conservation of Nature and Natural Resources (Anonymous 1985).

Until recently, scientific knowledge of the achatinelline snails was virtually confined to

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taxonomic descriptions of shells and, to a small extent, radulae. Although a number of workers described soft-part anatomy, they did so mainly with taxonomic questions in mind (e.g., Cooke and Kondo 1960). The types of trees inhabited by the snails and the epiphytic fungal diet of the snails were briefly described in older works, but only recently have major life history characteristics become known. Only three papers, all completed in this decade, discuss growth, fecundity, or other demographic characteristics of any achatinelline species (Hadfield 1986, Hadfield and Mountain 1980, Severns 1981).

Extinction, as an observable process, has two major facets: causal agents (i.e., what is killing the organisms?) and specific vulnerability factors (i.e., why do some organisms die out while others survive?). For the achatinelline snails, much has been written about the destructive factors (summarized by Hadfield 1986), but the basis of their vulnerability is less clear. Certainly, they share the sensitivity known to characterize many insular biotas evolved in the absence of predators and herbivores (Carlquist 1970). The data for the pres-

ent analyses were obtained by field mark-recapture techniques on members of the achatinelline species *Partulina proxima* (Figure 1) on the island of Molokai. These data provide insights into the species' life history pattern, the possible evolutionary history of this pattern, and the role of the pattern in the decline of local populations. Such information is essential to an understanding of extinction in this fascinating molluscan group and for devising means to protect (or even replenish) remaining species. Similar preliminary data have been presented for two other species (Hadfield 1986, Hadfield and Mountain 1980).

MATERIALS AND METHODS

Partulina proxima populations were studied in three small o'hia trees (*Metrosideros polymorpha*) in a wet forest at an elevation of about 1200 m. The site lies in The Nature Conservancy's Kamakou Preserve, near the ridgeline of the island of Molokai. Each of the study trees, labeled X-I, X-II, and S (Figure 2), is about 2 m tall and 2–3 m in diameter.

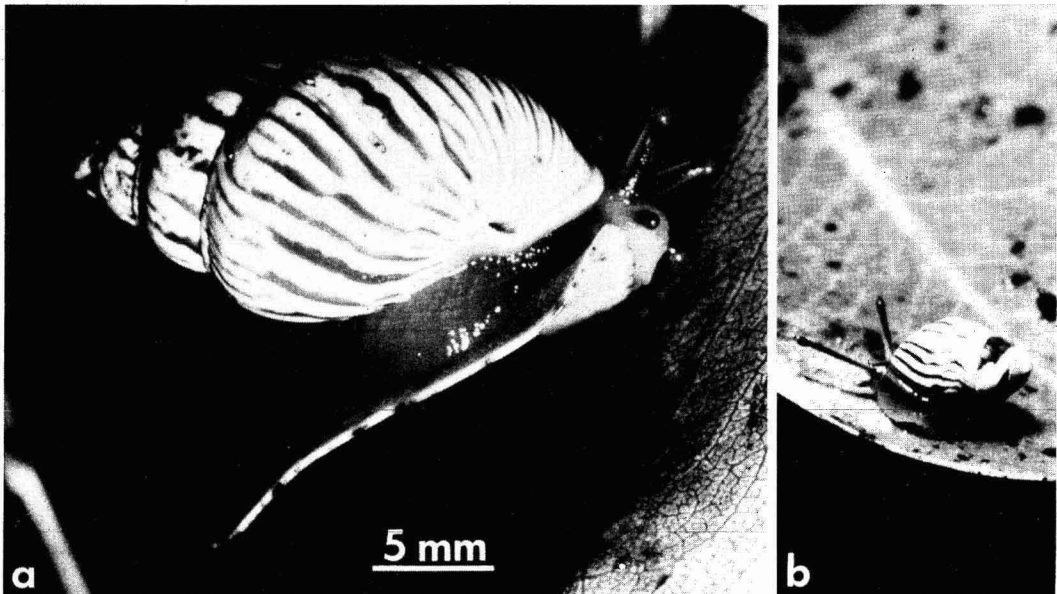


FIGURE 1. *Partulina proxima*. a, adult; b, juvenile, about 10 months old. Scale is the same for both photographs. (Photographs courtesy of Peter C. Galloway.)

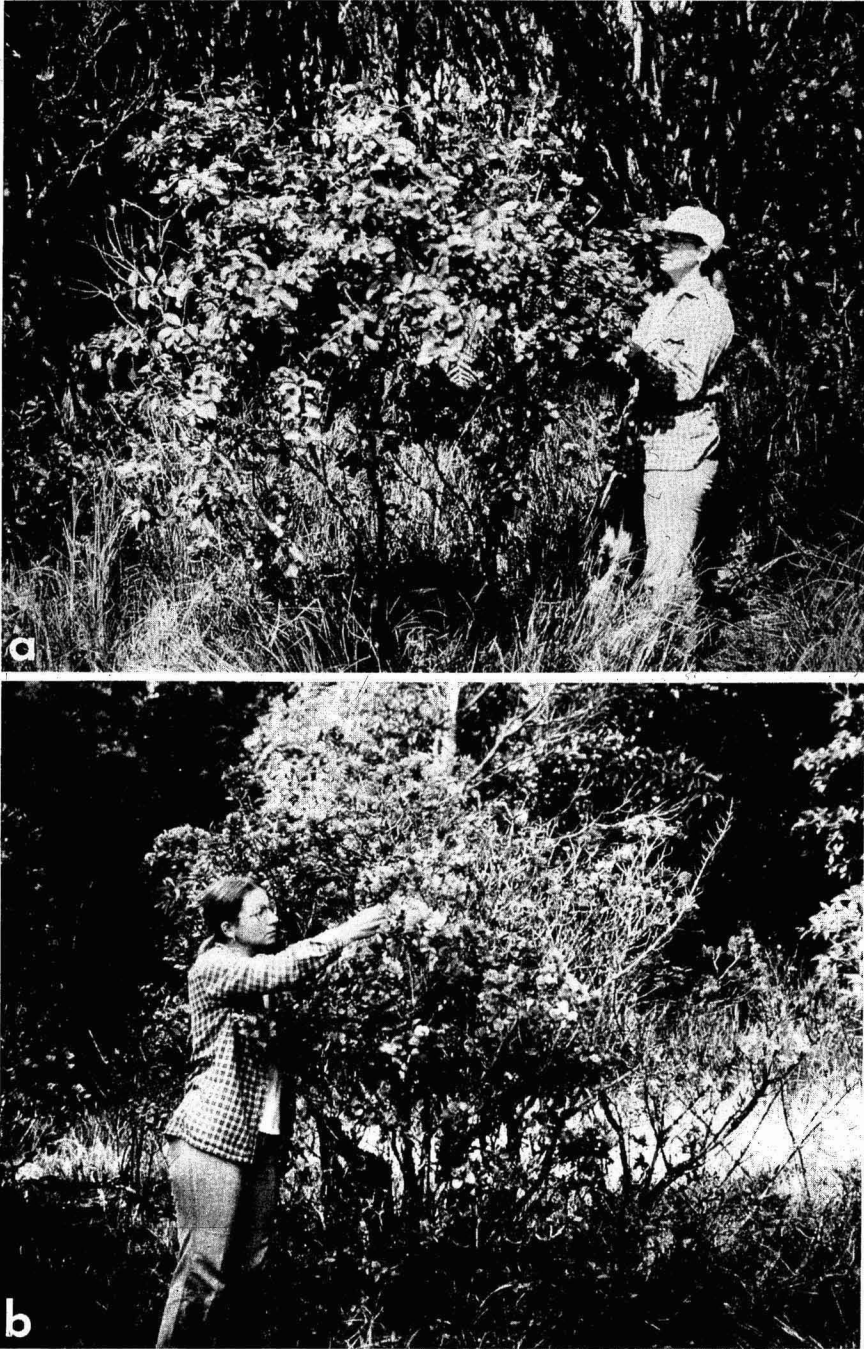


FIGURE 2. Study trees (*Metrosideros polymorpha*). a, tree X-I; b, tree S. Person in photographs is about 160 cm tall. (Photographs courtesy of E. Jane Albert.)

Trees X-I and X-II are about 2 m apart; tree S is about 800 m away. While the forest in this area is dominated by native trees, with *M. polymorpha* and *Cheirodendron* sp. the most common, there is an added component of introduced species, including Monterey cypress and New Zealand flax. The native snails have never been encountered on either of the latter, although they are seen on other native shrubs in the area, including species of *Coprosma* and *Wikstroemia*.

The study site was visited 17 times at approximately 2-month intervals between November 1983 and July 1986. On each visit, each of the study trees was visually searched by four workers for at least 1 hr, and all snails were carefully removed and placed in screened, lidded boxes containing moistened filter paper. Each snail was then examined to determine whether it had been marked previously, and if not, an individual code number was assigned to the snail. Numbers were written on the snails' shells with india ink and coated with a fast-drying, waterproof lacquer. For very small shells, where applying a number would have been nearly impossible, codes were applied with small dots of fast-drying paint (Uni-Paint Markers, manufactured by FaberCastell®). After marking, lengths and widths of all animals were measured with precision calipers to 0.01 mm. Subsequently, the snails were returned to the trees from which they were collected. Small snails crawl readily and were replaced directly on moistened leaves or limbs. Larger snails that were crawling were also put onto the trees, but deeply retracted snails were placed, together with moistened leaves, in screen-bottomed, plastic cups that were tacked directly to a trunk. All such snails returned to the tree during the first night following collection.

The mark-recapture data were analyzed to determine population size and survivorship in each tree; sizes at birth and maturity; snail growth rate; size-age relationships and age-frequency distributions in the populations; and fecundity. The methods used for each of these analyses were as follows: (1) Population densities were determined for each tree using the Manly-Parr and Jolly methods for multiple-recapture data (Begon 1979). (2) Size

at birth was determined by taking the average size of all snails whose length was less than 4.6 mm when first observed. Size at maturity was taken as the average length of shells with a thickened apertural lip or callus. (3) Growth rate was analyzed by a variety of techniques including the von Bertalanffy model and a series of regression analyses including linear, logarithmic, exponential, and allometric models and curvilinear regressions up to the fourth power (Sokal and Rohlf 1981). None of these resulted in predictions consistent with empirical knowledge of the snails. This is undoubtedly due both to the parameter measured (shell length is probably not a good indicator of growth in animal mass) and to the extremely high variance in growth rate in all size categories (see Figure 4). The most satisfactory growth curve (rate versus size) was obtained by first calculating growth rate (mm/day) and midsize for all intervals available for all growing snails. Then the growth rate data were averaged over various size intervals until a pattern emerged (based on large enough samples to be reliable) that showed a rate-size relationship consistent with the distribution of all data in a scatter diagram. The animal size data were then converted to ages, and age-frequency histograms were constructed. (4) Fecundities were determined for the two trees X-I and X-II together and for tree S. These were calculated by assuming that only snails with a thickened shell lip were reproductively mature (Neal 1928). All snails with shells of less than 7 mm when first observed were assumed to have been born into the population within the year under consideration. This number divided by the average number of mature snails in the tree is the annual individual fecundity. The fecundity numbers were then averaged over all possible successive 12-month intervals (16 total) of the study.

Finally, survivorships were analyzed by dividing the populations into two groups: snails less than 18.1 mm long and snails 18.1 mm and longer. Because mortality is very low in adult *Partulina proxima*, it was analyzed both by the Manly-Parr and Jolly methods and by empirical examination of the data. In the empirical analysis, all large snails that disappeared from the study trees for 6 months or

longer were considered to be dead. While such disappearances are "mortalities" in terms of the population, they may represent emigration. Snails seen only once or twice during the study were considered to be "transients" and not counted as part of the populations. Juvenile mortality rates were calculated from the age-frequency distributions and by the Manly-Parr and Jolly methods applied only to recapture data from snails less than 18.01 mm long.

RESULTS

A total of 160 snails was labeled in the study trees between November 1983 and July 1986; 36 were seen in tree X-I, 28 in X-II, and 96 in S. These snails accounted for 296 recapture events on one or more of the last 16 visits to the site. However, 68 snails, constituting 43% of the snails observed, were seen on only one occasion and thus do not contribute to extrapolations such as growth rate. Forty snails (25%) were observed on only two occasions. Thus, 86% [(296 - 40) ÷ 296] of the recapture events were based on three or more observations of 52 snails. These data provide the basis for all the life history parameters determined below.

1. Population Densities

The number of snails observed in each tree varied among visits from 3 to 11 for tree X-I, 2 to 7 for tree X-II, and 10 to 22 for tree S, with averages of 5.6, 4.8, and 16.8, respectively. Using the Manly-Parr method for estimating population numbers from multiple mark-recapture data, we determined the average number of snails per tree to be 7.8 (± 3.8) for tree X-I, 9.1 (± 3.8) for tree X-II, and 26.5 (± 5.6) for tree S. Estimates by the Jolly method were 7.1 (± 3.8), 8.5 (± 3.0), and 27.1 (± 6.0), respectively.

All the trees were characterized by constant numbers of reproductive adults (2 in each of trees X-I and X-II, and 4 in tree S), and the same adult snails were seen repeatedly in each tree for many successive visits. For example, snail X7 was seen in tree X-II on every visit to

the site; snail S2 was seen on all but one occasion; and snails X1 and X17 were seen on all but two visits. A few large snails were seen once, or perhaps twice, and then never again. We assume that such snails were "transient" animals living in a much broader area than most large snails, which tend to remain loyal to a single tree. Because all three study trees are isolated by surrounding grassy areas and do not have branches that touch any other tree, the transient snails must cross ground covered with deep grass when moving from tree to tree. When a snail had been present in one of the study trees for long periods of time and then vanished, we considered it to be a result of mortality. However, on only two occasions did we find dead shells on the ground, although a careful search was made for such shells on each visit. Their thinness, perhaps coupled with wet and acid soil conditions, may lead to rapid disintegration of the shells. It is also possible that wild pigs, which are very abundant in the study area, eat snails or empty shells when encountered on the ground. (Calcium may be at a premium in these high forested areas.)

Undoubtedly, the number of snails fluctuates in each of the trees. The major cause of the fluctuation is the birth and disappearance of juvenile snails. While large numbers of new small snails were observed on some occasions and none on others, no seasonal or annual periodicity was detected in the birth of young snails, and birth clearly occurs throughout the year.

2. Sizes at Birth and Maturity

Birth size in *Partulina proxima*, calculated as the mean size of all snails (from all trees) under 4.6 mm long at first capture, is 4.2 ± 0.2 mm ($n = 25$). The smallest shells seen were 3.8 mm long. It is possible that some snails are born at sizes larger than 4.5 mm, but captive culture will be necessary to determine this. Mean birth size was slightly different when the two groups of trees were considered separately: for the X trees, it was 4.1 ± 0.2 mm ($n = 14$) and for the S tree, 4.4 ± 0.1 mm ($n = 11$). These differences are significant at the level of $P > 0.05$, but not at $P > 0.01$ (t test).

The combined average birth size was utilized to calculate year groups (below), because of the extremely small sample sizes for some size classes that would have resulted from treating the two groups of trees separately.

Average size at maturity was taken to be the mean length of all shells with a thickened shell lip. The formation of this distinctive feature signals the end of shell growth and has been previously noted to be a necessary characteristic of reproducing snails (Neal 1928). Due to the endangered status of all achatinellines, our studies have been entirely nonsacrificial, and we have not performed the numerous dissections that would be necessary to verify the relationships among shell size, shell lip, and reproductive state. The average size of all lipped shells we observed was 21.3 ± 1.3 mm ($n = 17$). As was the case for size at birth, the average sizes of lipped shells differed between the two tree groups: for the X trees, it was 20.9 ± 0.8 mm ($n = 10$) and for the S tree, 21.9 ± 1.6 mm ($n = 7$). The difference between these means is not significant (t test;

$P < 0.05$). Sizes of lipped shells varied widely, ranging from 19.7 to 24.4 mm in length.

3. Size-Frequency Distributions

Size distributions of the snails in the X trees and the S tree were determined for 2-mm size classes by averaging the numbers of snails found on each of the 17 visits to the study area. The resultant histograms (Figure 3) aptly demonstrate the preponderance of small young snails, the paucity of snails in the midsize (12–18 mm), and the larger numbers of large snails. The patterns are similar for the two sites, as can be seen in Figures 3a and 3b. Most of the snails in the smallest size class were newly observed on each visit, and most were seen only once, indicating the frequency of addition of small snails to the populations. Large lipped shells were found in more than three 2-mm size classes (Figure 3), indicating a significant variance in the size at which maturity (and the cessation of shell growth) occurs.

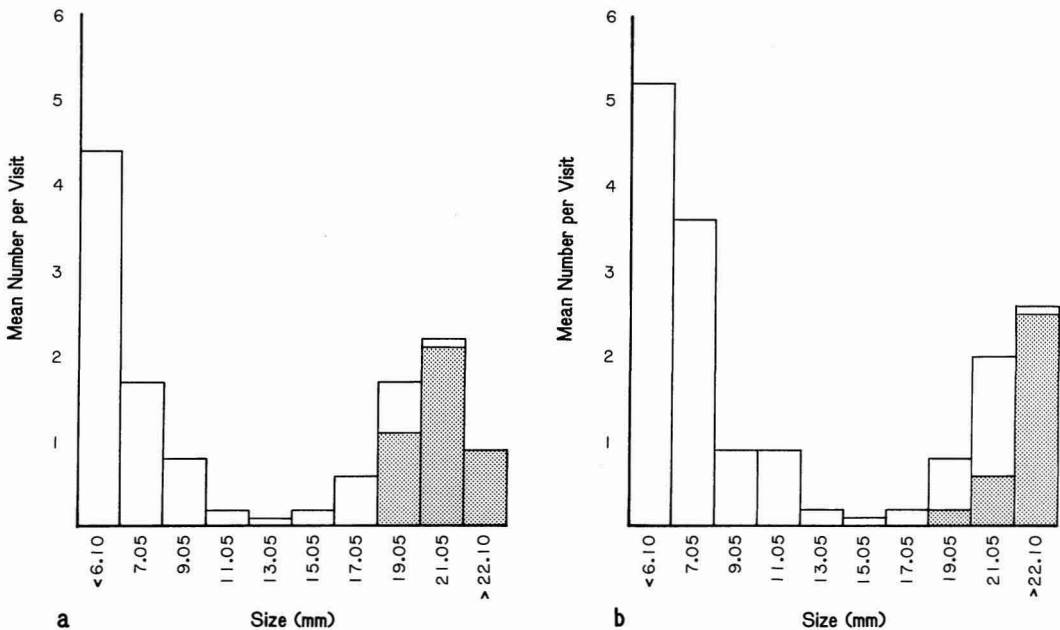


FIGURE 3. Size-frequency distribution of *Partulina proxima*. a, trees X-I and X-II combined; b, tree S. Sizes are expressed as class marks for 2-mm size classes; bar lengths represent the mean number of snails captured in each size class during 17 visits to the study site. Stippled bars represent mature, nongrowing snails (those with lipped shells).

Needless to say, this currently presents an insurmountable problem for determining the age of snails with lipped shells.

4. Growth Rate

All repeat measurements for all snails were translated into growth rates by determining the amount grown by each snail during each interval and dividing it by the number of days that had elapsed between measurements. These rates ($\text{mm} \times 10^{-3} \text{ day}^{-1}$) were then plotted against the midsizes of the snails during the intervals for which rate was determined. The resulting scatter diagram (Figure 4) presents a rough picture of the pattern of change in growth rate as snails grow. Variance in growth rate is extremely high across all size classes, but is greatest in the smaller classes (4–12 mm).

As rate decreases, so does variance, and largest shells, as previously stated, do not grow.

The high growth rate variance, coupled with the low number of measurements for the much more rarely occurring midsize snails, presented considerable difficulty in devising a growth curve for the *Partulina proxima* populations studied. Simple examination of mean growth rates across all 2-mm size classes suggested that snails mature after reaching 6 years of age (Table 1, Figure 3). Entering all the growth data into the calculations for the von Bertalanffy growth model resulted in a prediction of maturity (i.e., the attainment of asymptotic shell length) at 33 years—clearly a false prediction. The series of regression models tested on all data for growing shells (omitting lipped shells) produced equations with a best fit of $r^2 = 0.26$.

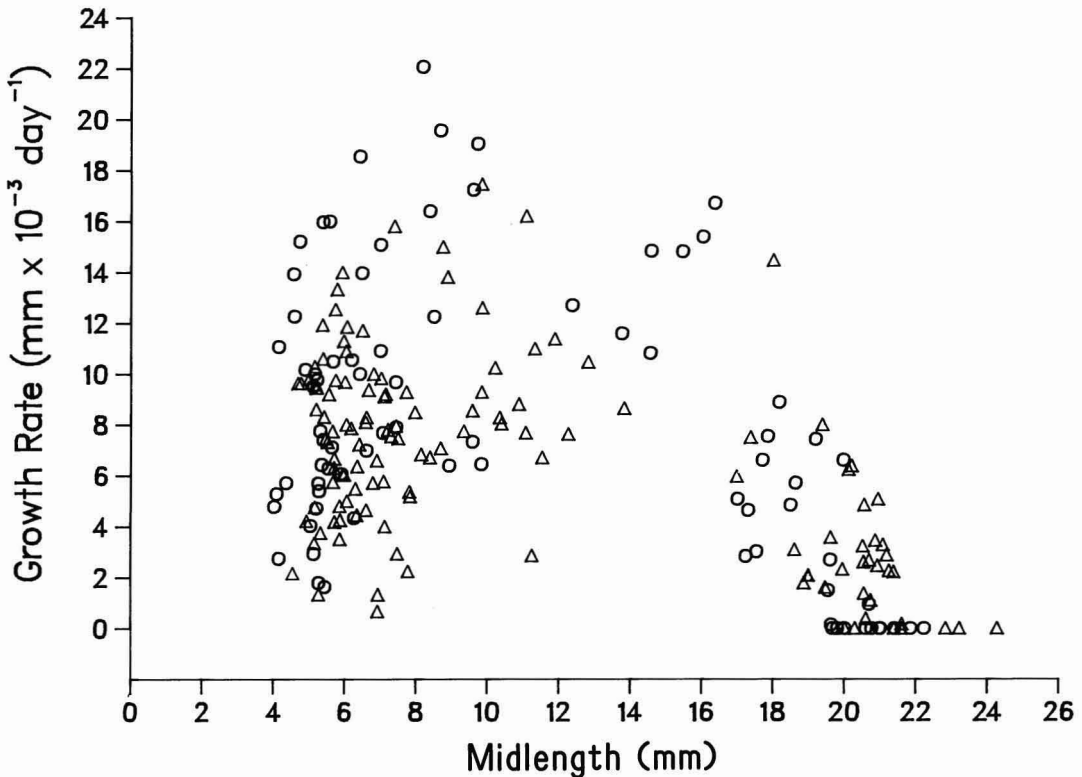


FIGURE 4. Growth rate as a function of animal size in *Partulina proxima*. Growth rates for all recapture intervals of growing snails were calculated and plotted against midlength of the snail during the interval (O, X trees, $n = 80$; Δ , S tree, $n = 128$).

TABLE 1
 SIZE-GROWTH RATE RELATIONSHIPS IN *Partulina proxima*

1-mm SIZE CLASSES				2-mm SIZE CLASSES				ADJUSTED SIZE CLASSES*			
SIZE (mm)	n	\bar{x} -RATE	SD	SIZE (mm)	n	\bar{x} -RATE	SD	SIZE (mm)	n	\bar{x} -RATE	SD
<5.0	12	7.59	4.46	<6.0	65	7.41	3.69	<6.0	65	7.41	3.69
5.0- 5.9	53	7.37	3.54	6.0- 7.9	54	8.09	3.43	6.0- 7.9	54	8.09	3.43
6.0- 6.9	31	8.05	3.56	8.0- 9.9	22	10.41	5.22	8.0- 9.9	22	10.41	5.22
7.0- 7.9	23	8.20	3.32	10.0-11.9	11	9.07	3.31	10.0-16.9	21	10.33	3.37
8.0- 8.9	11	11.48	5.47	12.0-13.9	5	10.21	2.08	17.0-18.9	13	6.17	4.01
9.0- 9.9	11	9.31	4.97	14.0-15.9	3	13.47	2.31	19.0-19.9	12	3.23	2.67
10.0-10.9	4	8.83	0.97	16.0-17.9	9	6.83	4.22	20.0-20.9	18	2.68	2.23
11.0-11.9	7	9.21	4.21	18.0-19.9	18	4.46	3.73	21.0-21.9	9	1.44	1.34
12.0-12.9	3	10.28	2.54	20.0-21.9	27	2.27	2.04				
13.0-13.9	2	10.12	2.09								
14.0-14.9	2	12.80	2.83								
15.0-15.9	1	14.80	—								
16.0-16.9	2	12.90	5.37								
17.0-17.9	7	5.09	1.76								
18.0-18.9	6	6.92	4.57								
19.0-19.9	12	3.23	2.67								
20.0-20.9	18	2.68	2.23								
21.0-21.9	9	1.44	1.34								

NOTE: n = number of animals examined; \bar{x} rate = mean growth rate of animals with midsizes in the corresponding size range, measured as $\text{mm} \times 10^{-3} \text{ day}^{-1}$; SD = standard deviation.

*See text for explanation.

Because of the poor fit of the models described above, a more empirical approach was taken. Data were first tabulated as average growth rate per 1-mm size class (Table 1). Sample sizes were as low as $n = 1$ for one of these (15.0-15.9 mm) and $n = 2$ for three others in the midsize range, and rates were highly variable between the 9- and 15-mm size classes. Data were then tabulated as rate per 2-mm size class and reexamined (Table 1). While trends began to emerge, sample sizes were still quite low for some groups and consistent trends were still unclear. From the first tabulation, it was deduced that growth rate dropped significantly between sizes of 16 and 18 mm and that snails in the midrange of approximately 10-17 mm were growing at about the same rate. Thus, a final tabulation was carried out by combining size classes with similar growth rates and splitting the 16-18-mm class to reflect the significant change in rate that occurred within this class. These new size categories were large enough to provide reliable means and variances. This final tabulation is shown in Table 1 under "Adjusted

Size Classes". These size-rate relationships were then used to calculate size limits for year classes, assuming a birth size of 4.2 mm. The resulting year class-size data are presented in Table 2. When converted to a rate curve, the data take the form presented in Figure 5, a curve that appears to agree well with the distribution of data shown in Figure 4.

Another empirical test of the conclusions drawn above comes from examining the growth curves for individual snails that have

TABLE 2
 SIZE-YEAR CLASS RELATIONSHIPS IN *Partulina proxima*

AGE (yr)	YEAR CLASS	SIZE RANGE (mm)
0-1	0	4.2- 7.0
1-2	1	7.1- 9.6
2-3	2	9.7-13.1
3-4	3	13.2-16.9
4-5	4	17.0-19.0
5-6	5	19.1-20.1
6-7	6	20.2-21.0
7-8	7	21.1-21.5
>8	—	>21.5

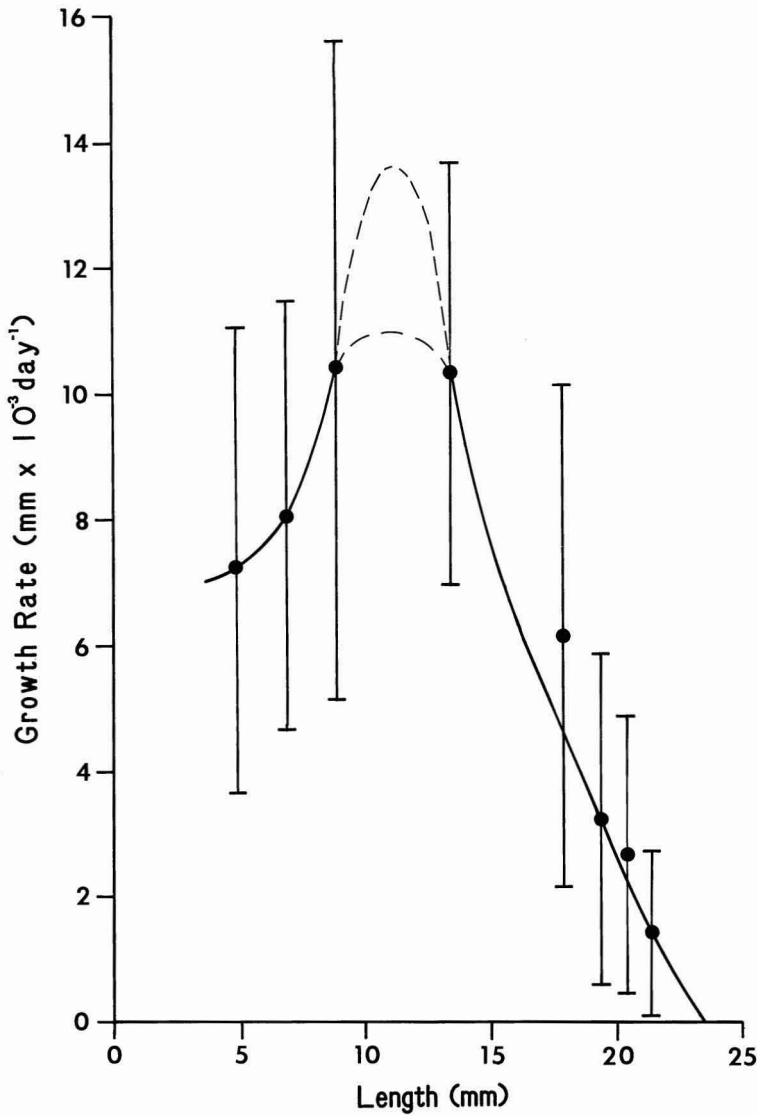


FIGURE 5. Hypothetical growth rate curve for *Partulina proxima*. Rates are taken from Table 1. "Adjusted Size Classes." Too few growth rates were available for animals between 10 and 16 mm long to be certain of the shape of the curve in this range.

been remeasured a sufficient number of times to show basic growth trends. A series of such curves is presented in Figure 6. The increase in slope of the curves from small to midsize is apparent (note particularly snail X29), as is the decrease in slope as larger size is achieved (e.g., snail X19). The curve for snail S48 clearly demonstrates the confounding variance in

growth rate that even individual snails demonstrate over time, regardless of size.

5. Age-Frequency Distribution and Survivorship

Age-frequency histograms (Figure 7) were made by sorting the capture data into the size

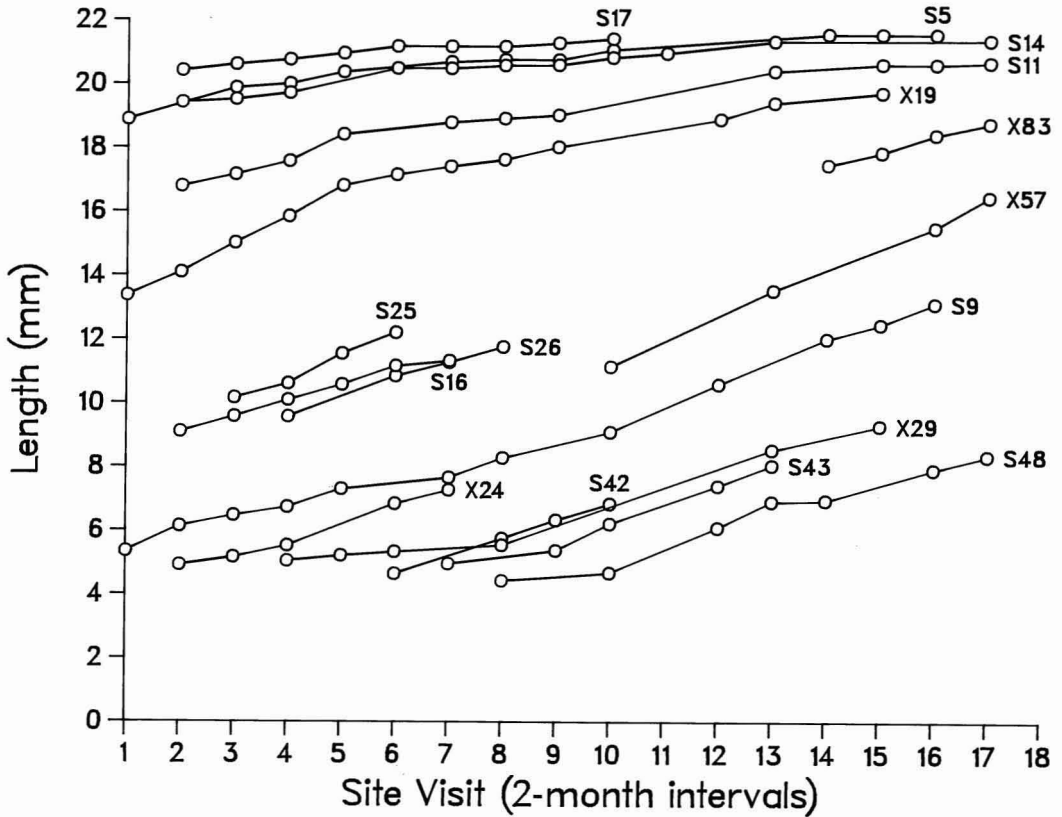


FIGURE 6. Growth curves for 16 marked snails. Code numbers on each line are those used in the marking studies. The first visit occurred in November 1983 and the last (number 17) in July 1986.

categories presented in Table 2. While these histograms show the same trends as the size-frequency analyses (Figure 3), they also indicate the age at which snails probably mature—some after reaching 5 years of age, but most after reaching 7 years of age!

The age-frequency histograms also demonstrate the great loss of small snails from each of the study sites. In tree S (Figure 7b), the average number of snails observed in year class 3 (0.18) is less than 2% of that in year class 0 (7.65), indicating a mortality of 98% between birth and 4 years of age. Similar calculations from the age-frequency data for the X trees indicate a mortality of about 92% between birth and the beginning of the 4th year. When annual survivorship of all snails under 18.1 mm was calculated, results by the Manly-Parr method were 0.32 for the X trees

and 0.19 for the S tree; and results by the Jolly method were 0.34 and 0.19, respectively. As snails enter the largest size classes, mortality drops off sharply, resulting in a "pile-up" of animals in the larger size classes, particularly among mature lipped snails.

Annual survivorship of snails larger than 17.1 mm was determined by several techniques. Empirical examination of the 2.8 years of recapture data showed a total of 14 adults observed in all the study trees combined (4 additional snails were considered transients and were not counted). Of the 14 adults, 4 (28.6%) disappeared for periods long enough to be considered dead. Survivorship of 0.714 over 2.8 years equals an annual survivorship of 0.887. Annual survivorship of snails larger than 18 mm was an unrealistic 1.163 when calculated by the Manly-Parr multiple recap-

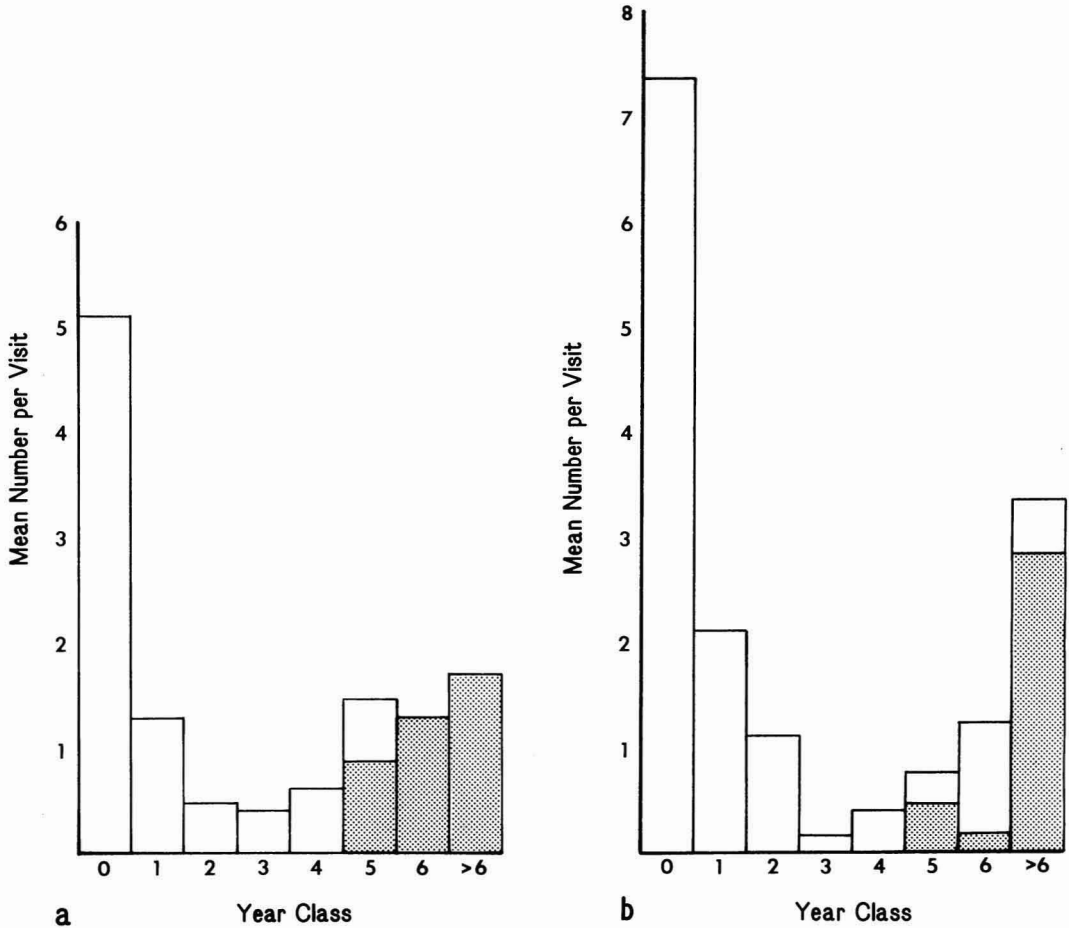


FIGURE 7. Age-frequency distribution for populations of *Partulina proxima*. *a*, trees X-I and X-II combined; *b*, tree S. Average numbers per visit were tabulated by age according to size classes shown in Table 2. Stippled bars represent mature, nongrowing snails (those with lipped shells).

ture analysis and 0.854 by the Jolly method. The average of all three estimates is 0.968, a figure not inconsistent with our numerous repeat observations of most large *Partulina proxima*. Thus, juvenile mortality is very high, a trend that breaks abruptly when snails achieve a size of about 18 mm. At this point the annual probability of survivorship becomes very high.

6. Fecundity

All newly found snails less than 7.0 mm long belong to the first year class (determined

from the age-size relationships described above) and were assumed to be the offspring of co-occurring adults. As mentioned previously, the average number of mature snails (those with lipped shells) was 4 in tree S and 4 in trees X-I and X-II combined. The number of newborn snails recorded per year in the study trees varied between 16 and 25 in the X trees and from 23 to 33 in the S tree. Annual fecundities per adult snail, calculated by averaging the mean number of offspring per adult from all possible successive 12-month intervals (i.e., 1-6, 2-7, 3-8, etc.), were 5.20 (± 0.6) in the X trees and 7.14 (± 0.8) in the S tree

TABLE 3
ANNUAL FECUNDITY OF *Partulina proxima*

SITE VISIT INTERVAL	X TREES			S TREE			ALL
	MEAN NO. OF ADULTS	TOTAL NO. NEWBORN	MEAN BIRTHS/ADULT/YR	MEAN NO. OF ADULTS	TOTAL NO. NEWBORN	MEAN BIRTHS/ADULT/YR	MEAN BIRTHS/ADULT/YR
1-6	4.17	24	5.76	3.83	23	6.00	5.87
2-7	4.17	24	5.76	4.17	24	5.76	5.75
3-8	4.17	24	5.76	4.17	26	6.24	5.99
4-9	4.17	25	6.00	4.00	26	6.50	6.24
5-10	4.00	22	5.50	4.00	27	6.75	6.13
6-11	4.00	19	4.75	4.00	28	7.00	5.87
7-12	4.00	19	4.75	4.00	28	7.00	5.87
8-13	3.83	20	5.22	4.00	33	8.25	6.77
9-14	3.67	20	5.45	4.00	32	8.00	6.78
10-15	4.64	17	4.64	4.17	33	7.92	6.38
11-16	3.67	17	4.64	4.33	33	7.61	6.25
12-17	3.83	16	4.17	4.17	32	7.92	6.00
Mean (\pm SD)			5.20 \pm 0.6			7.14 \pm 0.8	6.16 \pm 0.3

(Table 3). Average annual fecundity among all adult snails was 6.16 (\pm 0.3).

7. Adult Longevity

We have, as yet, no adequate means for directly estimating adult longevity from the mark-recapture data. However, if we assume that the populations we observed are stable, we can calculate how long the average adult must live to replace itself in the population. In the X trees, juvenile survivorship for 4 years (i.e., to achieve about 17 mm length) is 2.1% (i.e., annual survivorship of 0.33, the mean of the Jolly and Manly-Parr estimates, to the 3.5th power). The inverse of 0.021, 47.6, is the number of offspring that must be produced for 1 to survive through the fourth year and reach 17 mm. This snail must then live more than 3 years to achieve reproductive maturity (i.e., the average size at lip formation, 21.3 mm). At 5.2 offspring per year, it will then have to reproduce for 9 years (i.e., $47.6 \div 5.2$) to replace itself. Life-span after achieving 17 mm should thus be 12 years, and total life-span should be over 16 years!

For the S tree, using the Manly-Parr and Jolly estimates for annual survivorship up to age 4 of 0.19 and a calculated adult fecundity of 7.1, reproductive life-span should be 47 years, a figure difficult to believe. A juvenile

survivorship rate of 0.27, extrapolated from the age-frequency data for the S tree, yields a prediction for reproductive life of 13.8 years. Using means of all possible estimates (six means; three for each tree group) of juvenile survivorship (0.29) and adult fecundity (6.2 offspring per year) for all trees, we obtain a prediction of 12 years of reproductive life to successful replacement and a total life-span of 19 years. This figure will increase or decrease by about 2 years for the earliest and latest reproducers. The number of extrapolations of raw field data necessary to achieve these figures is great, and the resultant predictions cannot be considered highly accurate. However, they do indicate that adult survivorship must be close to that predicted by the various methods (i.e., in the high 90's) for these small populations to persist.

DISCUSSION

The populations of *Partulina proxima* studied between 1983 and 1986 are small, but, based on other observations we have made in the woodlands of upper Molokai, are typical for this species. Survey observations of the species have included sightings in five different locations across a linear distance greater than 3 km, and nowhere have we seen snails scattered evenly across the full size

TABLE 4
LIFE HISTORIES OF THREE ACHATINELLINE SNAILS

CHARACTER	<i>Achatinella mustelina</i> *	<i>Partulina redfieldii</i> *	<i>Partulina proxima</i>
Birth size (length, mm)	4.5	5.1	4.2
Mean maximum size (mm)	18.4	23.0	21.3
Range (mm)	16.7–20.4	21–24	19.7–24.4
Age at first reproduction (yr)	7	4	7
Fecundity (annual)	1	1–4	6
Longevity (yr)	11	11	19

*Data from Hadfield (1986).

range, nor in great abundance. Thus, our observations, while deficient in many aspects (e.g., number of snails seen, number of recaptures, growth rate measurements in midsize animals), are not likely to be improved upon, and are at least representative of the current status of the species. Past population sizes and densities of *P. proxima* are impossible to estimate from recent data, and nowhere in the literature have we found reference to the biology or abundance of this species.

The low densities of adults of *Partulina proxima* are not typical of most other achatinelline species we have studied (Hadfield 1986, Hadfield and Mountain 1980). However, we have unpublished observations of *Achatinella sowerbyana* on Oahu that suggest a similar fragility of populations. For populations of *P. redfieldii* on Molokai and *A. mustelina* on Oahu, preliminary data showed a much greater density of adults, greater numbers of snails in midsize classes, and higher juvenile survivorship (Hadfield 1986). *Partulina proxima* is unique among these species in its higher juvenile mortality, longer estimated life-span, and higher fecundity (see Table 4). At 6 offspring per year per adult, this species is at least 2–6 times more fecund than other species for which we have estimates (Hadfield 1986, Hadfield and Mountain 1980). Low numbers of adults can colonize new trees successfully only if they retain a fecundity of this magnitude for more than 12 years! Population stability, if indeed that is the current status, is accomplished by two major facets of the life history of this species: great adult longevity and relatively high fecundity.

We have no adequate explanation for the high mortality rates observed in juvenile *Partulina proxima*, and we lack evidence for why these juveniles should be more vulnerable than those of the other species studied. A number of possibilities exist, including the following: (1) They may suffer more quickly from desiccation and may lack behavioral traits that keep them in moist, shaded parts of the trees during periods of intense solar exposure. (2) They may be more readily dislodged by winds and become “lost” in the grassy areas surrounding the study trees, where they may fall prey to rats, the predatory gastropod *Oxychilus* sp., and perhaps other unrecognized predators. (3) They may be less efficient in finding sufficient food among the scattered patches of fungus on the leaves of the o’hia trees. (4) Or, they may suffer from an unidentified pathogen, perhaps an introduced virus or bacterium. Captive studies, only recently begun, may shed light on these possibilities.

Migration does occur in *Partulina proxima*, as demonstrated by occasional and brief appearance in our study trees of large snails that we have labeled “transients.” On one occasion, we moved two large snails from one tree to another, only to find them eventually back in the tree from which they were removed. Follow-up studies on the homing abilities of *P. proxima* have not been done. However, while large snails are known to be able to move from tree to tree, small snails appear to stand less chance of such migration. We have attempted to detect such activity by carefully examining bushes and trees near the study trees for the presence of labeled juveniles.

None have been found. Additionally, if the "mortality" of young snails was to be explained by out-migration, one would expect that, due to chance alone, equal numbers of small snails would in-migrate. Among very small snails, this could be occurring and remain undetected. However, migration cannot explain the virtual absence of snails in midsize classes (10–16 mm); they appear to be no more abundant in trees near the study trees than in the S and X trees themselves. The intense loyalty we have observed of most snails to single trees is in agreement with earlier natural history observations on other *Partulina* species (e.g., H. W. Henshaw in Pilsbry and Cooke 1912–1914).

Other families include threatened tree snails, but for none of them do we have data comparable to those presented here and earlier for the Hawaiian achatinellines (Hadfield 1986, Hadfield and Mountain 1980). In the higher-elevation forests of Oahu and Molokai, Hawaii, many other arboreal gastropods co-exist with the achatinellines, including species of *Auriculella*, *Tornatellides*, *Philonesia*, and *Succinea*. In many areas, species in some of these genera persist where achatinellines long ago disappeared. Comparisons of these hardier survivors with the achatinellines would be useful. They may show great differences in reproductive mode (several are oviparous and more fecund), growth rate, and age at maturation.

Other well-studied tree snails show interesting contrasts with achatinellines like *Partulina proxima*. What we know of the life histories of groups such as the *Liguus* species of Florida and the Caribbean (Davidson 1965, Tuskes 1981, Voss 1976) and the camaenids of Puerto Rico (Heatwole and Heatwole 1978) shows them to be oviparous animals with annual—not continuous—reproduction. Both *Liguus* and the camaenids lay their eggs in the ground in relatively large clutches. However, these snails resemble the achatinellines in maturing late [about 4 years for *L. fasciatus* (Tuskes 1981, Voss 1976), 3–6 years for the camaenids (Heatwole and Heatwole 1978)]. *Liguus fasciatus* may live 6 years or longer (Tuskes 1981), and some of the Puerto Rican camaenids live up to 10 years (Heatwole and Heatwole 1978).

Neither the camaenids of Puerto Rico nor *L. fasciatus* from Florida appear to be in immediate danger of extinction (Heatwole and Heatwole 1978, Voss 1976).

The Partulidae of tropical islands stretching across the Pacific from the Marianas in the west to the Society Islands in the east were monographed by Crampton (1916, 1925, 1932), and some Moorean partulid species have become models for laboratory study of patterns of inheritance in gastropods (e.g., Murray and Clarke 1966). Members of the Partulidae resemble the achatinelline snails in many aspects, including habitat (some even live on the same genera of trees), viviparity, and, at least in some species, food habits (Crampton 1916, 1932). However, the partulas are distinctly different in their much higher growth rates, earlier ages at first reproduction (10 months–1.5 years), and higher annual fecundities (16–19 offspring per year) (Murray and Clarke 1966). Life-spans of the *Partula* species have not been determined.

We can now return to the major question posed at the beginning of this paper: What makes the achatinelline snails particularly vulnerable to the agents of extinction (habitat destruction, predators, collectors)? It appears that great loss of juvenile snails is typical of the species studied here, and predation may be a partial cause. In light of this high early mortality, populations survive only by the relatively high fecundity (compared to other achatinellines) and great longevity of adults. It is clear that any agent that selectively destroys the adults (such as visual predators that do not detect the more numerous juveniles) would quickly annihilate the populations. If a population of adults is only 4 snails (such as in tree S), and they are producing, altogether, only 28 juveniles a year, then at a survivorship rate of 0.29 (the average for all trees by all methods) at least 3 years of offspring production are required for a single adult "replacement." If a rat or a human collector took all 4 adults from such a tree on one occasion, the population would essentially be dead. We have found piles of exclusively large, rat-killed shells among nearby, dense populations of the congener *Partulina redfieldii*. Furthermore, well-documented collections in museums could

easily represent the type of harvesting by collectors that would be destructive (see also Hadfield 1986).

As previously noted (Hadfield and Mountain 1980), the achatinelline snails appear to have evolved in the absence of predators. We may thus assume that these snails, like other fragile island species, owe their imminent extinction to their lack of protective structures or behaviors, their currently maladaptive life history characteristics, and the abundant and varied destructive agents now existing over their greatly restricted habitat ranges. Preservation of remaining habitats, eradication of introduced predators, and, most importantly, a more exact understanding of the causes of juvenile mortality are central issues in the preservation of species such as *Partulina proxima*. The Moorean *Partula* species vanished at a great rate, and this was due to at least one of the same factors that is destroying the *Achatinella* species of Oahu—the introduced predatory gastropod *Euglandina rosea* (Clarke et al. 1984, Murray et al. 1988). The achatinellines have been vanishing for a long period of time, longer than the occupancy of the Hawaiian Islands by *E. rosea*. However, this latter-day predator may be destined to destroy the high-elevation, isolated populations that survived long-term habitat destruction and the collectors. The destruction of the Moorean *Partula* species shows that even early reproduction and a 200–300% greater fecundity were not sufficient to offset the depredations of a predator like *E. rosea*. Introduction of nonnative plants and animals (often for the best of humanitarian reasons) for which there are no adequate means of regulating population growth, is the critical factor that has sealed the fate of the Moorean partulas and possibly the Hawaiian achatinelline snails as well.

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