# How Many Hawaiian Land Snail Species Are Left? and What We Can Do for Them

# Alan Solem<sup>1</sup>

# ABSTRACT

Probably only 25–35% of the 1,461 species level taxa of endemic Hawaiian land snails that have been described are still extant. Unless immediate actions are taken, most of the 25% to 35% still left will vanish in a very few years. The extensive collections and research publications that resulted from the efforts of the late C. Montague Cooke, Jr. give us a good data base from which to start assessing what part of the fauna remains and where it lives. Extensive field surveys covering both previously collected and very remote areas will identify places that still shelter significant numbers of native land snails. Continued survival of the vegetation communities that contain land snails and other groups of native organisms will require careful management. We must encourage regeneration and expansion of the native plant communities, not just static preservation.

# INTRODUCTION

The Hawaiian Islands had the world's most extensive and spectacular radiation of land snails. The use of the past tense is deliberate, reflecting the extinction of probably more than half of this fauna since 1900. Much of this loss has occurred since the mid–1930s. Field surveys by d'Alte Welch and W. Meinecke in the early 1930s demonstrated the presence of many taxa that have not been found during field work from 1960 to 1988. These taxa are thus presumed to be "gone forever." Extinction is not spread equally, but appears to be concentrated within the most diverse taxa, which are endemic at the family or subfamily level. Use of the terms "probably" and "appears" is necessary when discussing the status of these snails, since we lack the data needed to establish what species still exist—and where they can be found today.

Evidence exists for a *minimum* of 1,461 recognizable endemic taxonomic units of Hawaiian land snails, comprising 931 species, 332 subspecies, and 198 unjudged "varieties" (Table 1). For comparison, the land snail fauna of North America north of Mexico (as of 1947) included 719 species and 416 subspecies (Pilsbry 1948: ix). The Hawaiian taxonomic statistics are based upon a combination of published monographs and preliminary reviews of unstudied materials in museum collections. There is no reason to assume that these figures represent anywhere near the actual land snail diversity that existed when the Polynesians first arrived in Hawai'i. Much lowland vegetation had been destroyed prior to initial sampling of the land snail fauna in the mid–1800s. Some record of the vanished lowland fauna can be retrieved from archaeological excavations (see references in Gagné & Christensen 1985; Christensen & Kirch 1986), but most

BISHOP MUSEUM OCCASIONAL PAPERS © BISHOP MUSEUM VOLUME 30

JUNE 1990 PAGES 27-40

<sup>1.</sup> Deceased (1931–1990). Department of Zoology, Field Museum of Natural History, Lake Shore Drive & Roosevelt Road, Chicago, IL 60605, USA. For reprints contact Division of Invertebrate Zoology, Field Museum of Natural History.

disappeared without a trace. An important remnant of this fauna recently has been found to exist on the isolated island of Nihoa (Conant et al. 1984). Many mountain tops and remote valleys still have not been sampled and can be expected to yield a number of additional endemic species.

Undoubtedly the pace of land snail extinction is continuing, although subtractions are now coming from a rapidly shrinking faunal base. The time left in which to seek out and protect remnant patches of Hawaiian land snail diversity is, at best, a *very* few years. It can certainly not be measured in decades.

The reasons for this loss are many and complex, involving human cupidity, stupidity, ignorance, incompetence and, finally, a long period of silence and inactivity by those of us who knew better (including myself). Good summaries of specific catastrophic changes wrought by man have been given by Gagné and Christensen (1985), Hadfield (1986), and Hadfield, Miller and Carwile (1988). Aspects of the factors that led to this drastic loss are mentioned below as a warning. My focus here is on why I consider that parts of this fauna still survive.

If we are to save what is left of the Hawaiian land snails, we must (1) find out what still exists, (2) identify areas retaining significant diversity, and (3) protect both the species themselves and the habitats in which they survive. The damage to native vegetation by feral pigs and other hoofed mammals must be stopped, halting the spread of alien plants into native forest, and protecting the remnant forests from both logging and wood-chipping are minimum initial steps that must be taken *now*.

Land snails do not live in an ecological vacuum. The places where they survive contain members of many other phyla that often are much more difficult to sample and whose taxonomy is poorly known. Snails can serve very effectively as indicator organisms. The extremely small geographic ranges of many land snail taxa (see below) also mean that areas of less than an acre, if protected against major disturbance, may be adequate to provide "thousand year" survival for some Hawaiian species.

#### SUMMARY OF HAWAIIAN LAND SNAILS

The native land snail fauna of Hawai'i is typically disharmonic and characteristic of "oceanic" islands, including only 10 of the more than 65 land snail families. Extensive diversity is restricted to only 7 family units (Table 1). Members of several other land snail families have been introduced accidentally (at least the Veronicellidae, some "pupilloids," Valloniidae, Ferussaciidae, Philomycidae, Arionidae, Limacidae, Zonitidae, Subulinidae, Bradybaenidae, Helicidae) or deliberately (Streptaxidae, Achatinidae, Oleacinidae). They are flourishing, often in both synanthropic habitats and native forests. Quite probably additional alien taxa are established, but not yet represented in collections or noticed by malacologists.

One aspect of the Hawaiian land snail fauna cannot be overemphasized. There is endemism at both the subfamily and family level, in contrast with other groups of native animals. There are no endemic subfamilies or families of terrestrial arthropods in Hawai'i. Even the justly famed radiation of Hawaiian honeycreepers is now judged to consist of somewhat aberrant finches, rather than a separate family of birds, the Drepanididae.

Although many Hawaiian publications have linked the amastrid land snails with the Holarctic family Cochlicopidae based on a parenthetical paragraph by Watson (1920:24), monographers have followed the judgement of Pilsbry and kept the Amastridae as a separate family (Zilch 1959; Solem 1978; Tillier 1989). The Cochlicopidae and Amastridae may be sister taxa, but their differentiation is at the family level. Both subfamilies of the Amastridae, the Amastrinae and Leptachatininae, are found only in Hawai'i. The family Achatinellidae consists of several Pacific Basin subfamilies: the Achatinellinae are restricted to Hawai'i and most other subfamilies to other parts of eastern Polynesia. These 3 Hawaiian family-level groups account for 753

#### SOLEM: OVERVIEW OF HAWAIIAN LAND SNAIL SPECIES

Family unit	Number of			
	Species	subspecies	Varieties*	
Prosobranchia	,			
Hydrocenidae	1			
Helicinidae	16		43	
Pulmonata				
Orthurethra				
Achatinellidae				
"Tornatellininae"	106	11		
Achatinellinae	103	106	6	
Amastridae				
Leptachatininae	129		113	
Amastrinae	202	94		
"Pupillacea"**	58	26	1	
Sigmurethra				
Endodontidae	195	85	35	
Punctidae	7			
Helicarionidae				
Euconulinae	6	2		
Microcystinae	54	8		
Zonitidae	10			
Succineidae	44			
Total	931	332	198	
Grand total = 1,461				

Table 1	Known	Hawaiian	endemic	land	enail	diversity	
Table L.	KIIOWII	1 14 W 411411	chachine	lanu	SHall	urversity.	

\* Some "varieties" may be polymorphisms within populations, but the status of most remains undetermined, reflecting the pre-1920 systematic literature.

**\*\*** Family limits within the "Pupillacea" are uncertain, and no attempt has been made to determine the affinities of the Hawaiian taxa.

(51.5%) of the 1,461 recognized Hawaiian land snails. The family Endodontidae (Solem 1976), restricted to Polynesia, Lau Archipelago, and Palau, had about 315 (21.6%) Hawaiian representatives. The achatinellid subfamily Tornatellininae is a Pacific Basin taxon with 117 (8.0%) Hawaiian taxa, and the helicarionid subfamily Microcystinae is another Pacific Basin group with 62 (4.2%) Hawaiian taxa described. These are the most speciose groups of the Hawaiian land snails (Table 1), accounting for 1,229 (84.1%) of the total fauna.

These families are not recently evolved or weakly differentiated. The Achatinellidae includes several of the earliest known land snails (Anthracopupinae) from the late Paleozoic of western Europe and eastern North America (Solem & Yochelson 1979), and the Endodontidae have a Miocene record in other parts of the Pacific (Solem 1976, 1983). They are best viewed as "island hopping relicts" that have been replaced on continental areas by more recently evolved taxa.

The family restricted endemicity for much of the Hawaiian land snail fauna has major practical consequences in terms of systematic and biological study. Specialists in other phyla may obtain their systematic training through overseas work on a particular group and then be attracted by the special problems presented by Hawaiian members of "their" family; in contrast, students of the Hawaiian-Polynesian land snail fauna must be developed locally, or "transfer their interest" from, at best, distantly related taxa residing in other parts of the world.

#### Soundness of Species Concepts

Especially where organisms are colorful, variable, and popular with collectors, there is a universal pattern of describing all variations as "species." The resulting inflated species numbers are dramatically (and often uncritically) reduced in a succeeding generation of workers. This is followed by later discovery of cryptic or sibling species, and the number of recognized species increases.

Where in this cycle does knowledge of the Hawaiian land snail fauna stand? There is a natural tendency, especially among vertebrate biologists, to view the number of described Hawaiian land snail species very sceptically (Diamond 1977). Particularly when they see the dates of the major monographic studies. I contend that the initial drastic reduction in "species numbers" has *already* taken place, and present 2 examples to support this argument.

Pilsbry and Cooke (1912–1914:xxxiii), in introducing their revision of the highly colorful and very popular tree snail genus *Achatinella*, stated that "While many conchologists may consider the treatment of *Achatinella* in this work an extreme example of 'lumping' (since we recognize but 43 species in place of 171 described), it really belongs to the splitting school. Both authors hold that a considerable further reduction would have to be made to make the species of equal value with most Hawaiian species of *Leptachatina* or *Amastra*." Christensen (1985) estimated that there might be as few as 12–16 "biological species" of *Achatinella*. Hadfield (1986) and Hadfield, Miller and Carwile (1989) implied recognition of 41 *Achatinella* species, although believing (pers. comm.) that adequate study might reduce this number significantly. No such study has been published. It is significant that the very people who published most of the systematic monographs on Hawaiian land snails held the above view of species in the most variable genus.

Only 1 genus has been revised subsequent to the early 1900's burst of study. Hyatt and Pilsbry (1911:100–18) monographed the amastrid genus *Carelia*. With very limited material available, they recognized 11 species and several varieties. By 1930, some 5,500 specimens had accumulated at the Bernice P. Bishop Museum. Cooke (1931), in an exhaustive study, recognized 20 species and 9 subspecies. Five of the latter (Cooke 1931:13) probably represent species. Cooke and Kondo (1952), in the only subsequent study, described another species, 2 new subspecies, and a "geographic race" of uncertain status. Species numbers thus have increased, not decreased.

I have pointed out elsewhere (Solem 1978:52–55) that Pilsbry had an extraordinary ability to recognize actual species from very limited material. It is very probably, on balance, that modern reviews of the Hawaiian land snails will result in increased, not decreased, species numbers.

#### Background

The obvious attractiveness and bewildering shell variation of the Oahu endemic genus *Achatinella* seized the interest of several generations. Collections by voyagers starting just after Captain James Cook's visit in 1778 resulted in descriptions of numerous species and varieties. In the 1820s, local collecting interest developed. The huge pre–1900 collections by J. T. Gulick and D. D. Baldwin, followed by later efforts of, among many, the Emersons, Irwin Spalding, W. D. Wilder, W. Meinecke, D. Thaanum, G. Arnemann, and d'Alte Welch, provided a massive data base for studies of not only this genus but also many others. J. T. Gulick (1905) produced a classic evolutionary study based upon his years of collecting and study in Hawai'i.

As is typical in early stages of biological inventorying, with the notable exception of Gulick's monograph, most synoptic and first analytical study was by overseas scientists. The early summary reports by a Frenchman (Ancey 1889, 1899, 1904) and an Englishman (Sykes 1900) set the stage for the classic revisionary studies, but a modest, locally produced checklist

(Baldwin 1893) probably had the most effect. Both local and overseas collectors could use this to document personal progress in "completing their collection" and as a challenge to collect or exchange for rare or newly named forms. How many collections this booklet inspired is unknown, but its effect was substantial.

In this century the influence of a most remarkable individual, Charles Montague Cooke, Jr., and his cooperation with the dean of terrestrial malacologists, Henry A. Pilsbry, from the Academy of Natural Sciences of Philadelphia, dominated. "Monte" Cooke died in 1948, leaving a still unfilled gap of interest and concern about Pacific land snails. The flavor of this very remarkable person is found in the highly readable bio-bibliography by Kondo and Clench (1952).

Pilsbry's publication career spanned 75 years. He started this century by publishing 2 of his most important contributions, which were based in large part on Hawaiian data. He established the basic ordinal units of land snails (Pilsbry 1900a) and made a major contribution to biogeographic theory and speculation concerning the Pacific Basin (Pilsbry 1900b). Following publication of 2 descriptive papers (Pilsbry and Vanatta 1905, 1906) based on very limited material, Pilsbry launched a period of intensive cooperation with Cooke. Major monographs of the endemic family Amastridae (Hyatt & Pilsbry 1911; Pilsbry & Cooke 1914–1916); native Helicinidae (Pilsbry & Cooke 1908); Achatinellidae and Tornatellinidae (Pilsbry & Cooke 1912–1914); and "pupilloid" taxa by Pilsbry and Cooke or Cooke and Pilsbry (Pilsbry 1918–1920, 1920–1921) covered several of the main groups. Pilsbry (1916, 1921) continued some Pacific biogeographic work, but then moved on to other projects.

Cooke, realizing that the Hawaiian fauna could not be fully understood without knowledge of taxa from the other Pacific islands, turned his attention to other parts of Polynesia and the Micronesian fauna. He promoted or participated in 3 major expeditions through Polynesia and Micronesia: the Mangarevan Expedition through eastern and southern Polynesia (15 April–28 October 1934); the Micronesian Expedition (8 December 1935–10 June 1936); and the Henry G. Lapham Expedition to Fiji (27 June–28 September 1936). Yoshio Kondo, who served first as an assistant, then collaborator, and finally as successor to Cooke as malacologist at the Bishop Museum, obtained his initial field training and malacological interests on these trips. Additionally, 2 generations of Bishop Museum staff and "mainland" scientists passing through on their way to the South Pacific, were cajoled, inspired, and persuaded by Cooke to collect land snails wherever they visited. Although Cooke continued to encourage active collecting throughout Hawai'i, little of the incoming Hawaiian material, except for specimens of *Achatinella*, were identified to species. They were cataloged and filed under a generic name.

The unparalleled collections at the Bishop Museum are a monument to Cooke's efforts and his inspiration of others. Like many "collection builders," Cooke published comparatively little, choosing instead to promote collaborative efforts or work by others. An important paper on the Succineidae (Cooke 1921); an excellent review of the largest Hawaiian land snails, members of the amastrid genus *Carelia* (Cooke 1931); a significant popular article on the land snails (Cooke 1941); and a posthumous collaborative monograph revising the genera and focussing on the anatomy of mostly non-Hawaiian Achatinellidae (Cooke & Kondo 1960), were his major publications, along with the monumental monographs published in cooperation with Pilsbry. Among the most significant publications that he promoted were an updated checklist of Hawaiian land snails (Caum 1928); a conchological revision of the Hawaiian Helicinidae (Neal 1934); and the landmark monographs of the Pacific Island Zonitidae and Helicarionidae (H. B. Baker 1938, 1940, 1941), which combined anatomical and shell data in an elegant fashion.

Under Cooke's guidance, a detailed program of collecting and analyzing variation in *Achatinella* on a colony by colony basis was started by d'Alte Welch. Welch's massive collection

	Number of Recognized Taxa				
Family	Caum (1928)	Current	•		
Helicinidae	22	59			
"Zonitoids"	35	80			
Endodontidae	27	ca. 300			
Succineidae	44	?			

Table 2. Changing species numbers, 1928–1988.

effort began in 1931. This effort was made possible by the publication of detailed maps (Welch 1938:4), which allowed the plotting of each colony with great accuracy. These maps and collections still exist and form the basis for future surveys of Oahu land snails. Welch left Hawai'i to spend the rest of his career as a college professor in Ohio. While he managed to produce studies on geographic and altitudinal variation in *Achatinella mustelina* (Welch 1938), *A. apexfulva* (Welch 1942), and *A. bulimoides* (Welch 1954, 1958), study of the remaining probable species of *Achatinella* was not completed. Parallel collecting and mapping efforts by William Meinecke from 1930 to 1941 and George Arnemann's collections of *Carelia* provide additional highly significant records.

Thus, Cooke was responsible for monographic work on 5 of the 7 diverse taxa—Helicinidae, Achatinellidae, Amastridae, "Pupillacea," and the Helicarionidae plus Zonitidae. Only the Succineidae and Endodontidae remained basically untouched at his passing.

Caum (1928:59–61) listed 44 taxa of Succineidae and 26 in the Endodontidae. While I used Cooke's collection legacy to monograph the 265 species level taxa of Polynesian and Micronesian endodontoid land snails (Solem 1976, 1983), time was not available to study the more than 300 Hawaiian taxa represented in the Bishop Museum collection by about 50,000 specimens in 5,197 lots (Solem 1976:3, Table II). Table 2 contrasts the number of taxa listed by Caum (1928) and those recorded in the few subsequent monographs. Known diversity in these taxa has significantly increased.

Despite all the monographic work accomplished, no overall summary of the Hawaiian land snail fauna was produced. It was left to an entomologist, Elwood C. Zimmerman, drawing upon the knowledge of Cooke and Kondo, to prepare what is still the best outline of the Hawaiian snail fauna that exists (Zimmerman 1948:97–104).

The periods of study can be roughly grouped into 3 eras: (1) the pre–1900 period of survey efforts by residents and description of the taxa, usually by overseas workers; (2) the 1905–1921 period of intensive cooperative work by Cooke and Pilsbry; and (3) the 1928–1948 period in which Cooke primarily promoted studies by others. The later publications by Welch (1954, 1958) belong intellectually to the latter period, and the monograph by Cooke and Kondo (1960) was essentially finished in 1948, although its publication was long delayed.

Except for the evolutionary study of Gulick (1905), published work through 1960 was almost exclusively systematic in content. Then began a period of malacological silence. Neither systematic nor biological work was accomplished for 2 decades. The popular article by Hart (1978) stimulated conservation of Hawaiian land snails and led to the listing by the Office of Endangered Species of all *Achatinella* species as endangered. Subsequently, the seminal report of Hadfield and Mountain (1981) on the life history of *Achatinella mustelina*, reviews on extinction in *Achatinella* by Christensen (1985) and Hadfield (1986) provided much useful data.

It is not that the Hawaiian land snails lack unusual biological features that make them "good organisms" for research studies. The fact that they have basically been ignored stems from other reasons. Perhaps it is simply that they did not have a spokesperson. Nobody proselytized

non-systematic biologists touting the opportunities that they present. There was no malacological equivalent to Elwood C. Zimmerman's challenge to *Drosophila* specialists (Zimmerman 1958) concerning the 300 Hawaiian species. The latter paper led directly to the current huge literature and the many evolutionary insights provided by study of the Hawaiian picture wing flies.

Time is very late, and much remains to be done.

#### Probable Status of Hawaiian Land Snail Families

The low-diversity families (Table 1) comprise the Hydrocenidae (an Indo-Polynesian group known from one collection on Kaua'i), the Punctidae (worldwide with perhaps 5 to 9 Hawaiian species in collections), and the Zonitidae (10 species of recent Holarctic origin). Probably both of the latter families are extant at higher elevations. Hydrocenids are easily overlooked because of their minute size. No comments can be offered on the basis of only 1 collection made many years ago.

Many of the Helicinidae were low elevation taxa and probably are extinct. Recent collections of living helicinids in Mākua Valley (1983) and several places in the Wai'anae Mts indicate that at least some helicinids persist (C. C. Christensen, pers. comm.). In other parts of the Pacific, helicinid taxa are still commonly found, often in mixed vegetation situations or even banana patches. As the only non-hermaphroditic land snails that diversified in Hawai'i, helicinids present many opportunities for biological studies. They are common in fossil deposits and adult shells are highly variable in size, which correlates with moisture differences. Thus, they can be good indicators of minor changes in climate.

The Succineidae are reported by Hadfield (1986:79–80) as "still abundant in many Hawaiian mountain locales." The little anatomical work on Hawaiian species (Odhner 1950; Patterson 1971; Solem unpubl.) shows that Hawaiian radiation is based on the subfamily Catinellinae. Species of Catinellinae have the lowest chromosome numbers (5–6) yet found in any land snail. Twenty years ago, I suggested that this low chromosome count was the result of a chromosome number reduction series, limiting variation in these inhabitants of often temporary habitats (Solem 1969). Unfortunately, no one has attempted to either test this hypothesis or to study the Hawaiian taxa, which represent the largest number of succineid species reported anywhere in the world. The several hundred lots in the Bishop Museum indicate 5 named species from Kaua'i, 7 named and 7 new from Oahu, 2 named and 17 unnamed from Hawai'i. Ranges of species on Kaua'i and Oahu appear extensive, with Hawaiian species very limited. The fact that *S. caduca* is listed from Kaua'i, Oahu, Moloka'i, and Hawai'i may indicate either an actual range (since it is a lowland "species") or that this is a generalized shell form, found in several anatomically distinct species.

The Helicarionidae often are arboreal. In many parts of the Pacific they remain abundant. Because of their uniform shell color and simple shell, they never have been popular with collectors. The latest systematic review of this complex (H. B. Baker 1938, 1940, 1941) was based on very limited material. Accurate species ranges cannot be delimited at present, and the actual diversity level remains to be determined.

The minute "pupilloids" are mostly extinct with only *Pronesopupa* common and persisting even in low elevation, non-native forest. Lowland *Lyropupa* (especially the subgenus *Lyropupa pilla*), *Pupoidopsis*, and *Nesopupa* have vanished, despite the recent record of *Lyropupa* from Barbers Point (Christensen & Kirch 1986). Some *Nesopupa* and sinistral *Lyropupa* still remain in upland native forests.

Catastrophic extinction has occurred in the remaining three families: Endodontidae, Amastridae, and Achatinellidae. Unfortunately, they were the most diverse families.

The Endodontidae were mostly ground dwellers. Many species laid their eggs in the um-

bilicus of the shell. Throughout Polynesia, wherever the ant *Pheidole* has become established, endodontids no longer exist. To my knowledge, no live material of *Endodonta* has been collected on the main islands since 1940 (both it and *Cookeconcha* survive on Nihoa). In 1962 I did find a few *Cookeconcha* alive on Wai'anae Mts high ridges on 2 occasions, and M. Hadfield (pers. comm.) once saw two "*Cookeconcha* chasing each other on a leaf" in the 1980s. Low and mid-elevation species, accounting for nearly all of the described taxa, were extinct by 1960. I would guess that less than 5% of the endodontid species may still exist, and these only at high elevations.

Within the Amastridae, the genus *Carelia*, which included the largest native Hawaiian land snail species, is restricted to Kaua'i and 1 species on Ni'ihau. A few living colonies of *Carelia* may exist on the isolated small valleys of the Na Pali coast, but no live specimens have been seen since George Arnemann's collections in 1950. Cooke, in a note on his copy of the *Carelia* monograph, stated in April 1946 that only 10 forms had been taken alive "in the last thirty years." We do not know the current status of most other genera, but since many were ground dwellers, we can predict that considerable extinction has occurred.

Hadfield (1986:80) reported that minute tornatellinids and "a few hardy Auriculella species persist in areas from which the achatinellines have disappeared." The status of the species belonging to Achatinella was summarized as "22 species of Achatinella as extinct, with the remaining 19 species endangered" (Hadfield 1986:67). Subsequently, Hadfield, Miller and Carwile (1988) revised this to "16 species extinct (no living specimens have been observed over 25 years); another 5 species have not been seen for over 15 years." Most of the rest are restricted to a tiny fragment of their historic ranges. The status of most tornatellinids remains unknown, but the degree of extinction must be large. The long life span and low fecundity of Achatinella (Hadfield & Mountain 1981; Hadfield 1986) present many interesting opportunities for developmental and ecological studies. Some taxa still exist, but the spread of the introduced carnivorous land snail Euglandina rosea quite possibly will do to both the larger Amastridae and Achatinellidae of Hawai'i what it has already done to the Partula of Moorea, Society Islands (Clarke, Murray & Johnson 1984; Murray et al. 1988)-eat them unto extinction, except for a few experimental laboratory and zoo colonies. Another temporary option is to establish captive breeding colonies in Hawai'i (see Hadfield, Miller & Carwile 1988), with future hopes of reintroduction into natural areas that are (by then) Euglandina-free.

Given the above notes, my earlier statement that 50% of the Hawaiian land snail fauna is extinct probably is wildly optimistic. It may be much higher, since no comprehensive surveys have been made since the late 1930s. But the critical point is that many species still exist, although precariously. Even if only 25% of the documented forms are still extant, these 365 land snail taxa from such a small area represent extraordinary high diversity compared with any other area of the world. They merit study and strenuous efforts toward their preservation.

The fact that many represent families or subfamilies that are *restricted* to Hawai'i, without living representatives elsewhere in the world, increases the urgency. Their loss will be the equivalent of the dodo and elephant bird extinctions, the only island restricted families of vertebrates to become extinct in historic times. This must not be permitted to happen to the Hawaiian land snails.

## CAUSES OF LAND SNAIL EXTINCTIONS

"Human interference," be it habitat alteration to complete destruction; chance and deliberate introduction of predators or competitors; or exploitation by collecting activities, is the summary reason for the crisis of 20th century extinctions in all groups of organisms. What had been the gradual pattern of change through geological time (= evolution), of which extinction was a natural part, has become a "momentary" and immediate crisis, which will strip from

34

Earth many of its species. The fragile and wonderfully diverse biota of oceanic islands lead the list of the vanished.

Much of the damage no longer can be remedied. The process of rapid extinction began when people first arrived on islands. In Hawai'i, the cutting of lowland forests and introduction of foreign land snails started when the initial Polynesian settlers landed (Christensen & Kirch 1986). Habitat destruction and the number of exotic introductions accelerated after 1778. While the Polynesians had carried with them Polynesian and probably a few Indonesian species, Caucasian commerce added taxa from Africa, the West Indies, and India. Such introductions have reached jet speeds today (see Gagné & Christensen 1985; Christensen 1985; Hadfield, Miller & Carwile 1988).

Hadfield (1986) presented a superb summary of the probable causes for the apparent 50% extinction of *Achatinella* species and endangerment of the remainder. His paper should be required reading for Hawaiian biologists.

Unless an island area is clear-cut and burned, total and immediate land snail extinction does not occur. A clear distinction must be made between ground dwelling and arboreal species. Species that forage or shelter in the litter die out first. A change in the ground plant cover, scratching by chickens, trampling by cattle, pigs or goats, the presence of alien ground snails, predation by introduced ants, other arthropods, or predatory flatworms—any or all of these catastrophies can lead to almost immediate extinction of the ground taxa. The arboreal species will have a short reprieve. If the native bushes and trees form a near natural canopy, the tree snails seem to survive. But this may be very short term. Invasive alien plants can choke out the seedlings of the native plants, preventing replacement as the older plants succumb, and trampling by ungulates also can kill off the seedlings. Either of these factors limits the patch as suitable snail habitat to the remaining lifetime of the mature trees.

Until very recently, vegetational changes probably have been the primary causes of tree snail extinction (Gagné & Christensen 1985). Introduced rats also are implicated in the decline of the arboreal snails. Hadfield (1986) has demonstrated how overcollecting could and almost certainly did result in local extinction. Hopefully this no longer will be a factor. But the most immediate and serious threat resulted from State of Hawai'i agricultural officials who introduced a Floridian carnivorous snail, *Euglandina rosea* (Férussac) in an attempt to control the results from the equally stupid introduction of the Giant African Snail, *Achatina fulica*. The introduction of *Euglandina* was against the unanimous protests of malacologists, whose advice obviously was ignored.

Clarke, Murray and Johnson (1984) documented the spread of *Euglandina* on the island of Moorea in the Society Islands. They could thus predict the rate of extinction for the endemic tree snails of the genus *Partula*. Their prediction unfortunately was fulfilled (Murray et al. 1988). *Partula* is the ecological equivalent of *Achatinella*, although independently derived and belonging to a different family. Hadfield (1986:74) noted the extinction of specific *Achatinella* colonies through predation by *Euglandina*.

The above picture is gloomy. If *Euglandina rosea* can be exterminated in Hawai'i, then the salvage of many larger land snails would be relatively simple. A very high conservation priority should be given to the study of ways to exterminate *Euglandina*, 1st in Hawai'i, then from the other islands of Polynesia, and Micronesia, where it is exterminating many other native land snails. If this project fails, we may have to resign ourselves to the inevitable loss of at least the larger native land snails. There are suggestive observations that *Euglandina* may have some altitudinal limitations that could spare the comparatively few higher elevation endemic taxa.

#### HOPE STILL EXISTS

Despite the above, I think it is possible to save and protect a significant portion of the native Hawaiian land snail fauna. A small portion, perhaps less than 5% of the species, will be found to have adjusted to introduced plant cover or mixed vegetation. So long as any combined forest remains, they will survive. But we do not know currently which species they are or what their minimum requirements may be.

Neither vertebrate biologists nor botanists, who have been much more active in conservation matters than malacologists, appreciate how small an area is adequate to maintain a viable colony of many land snail species.

They must be educated. The view of Diamond (1977) that only Madagascar, New Guinea, and possibly New Zealand, of all Pacific islands, were large enough for *in situ* speciation of land birds, stands in sharp contrast to the situation found in land snails.

Unfortunately, the Hawaiian examples of exceedingly small ranges are based upon the memory of formerly active collectors and involve areas now stripped of trees. But several situations were known in which "father and son," over much more than half a century, repeatedly visited a grove of trees to collect a special form of *Achatinella*. They found that the colony continued to be restricted to 1 or 2 trees only, even though their branches interdigitated extensively with many neighboring trees of the same species, and the whole grove contained 50–100 trees. While this is an extreme situation, the diversity of Hawaiian land snails was not based upon many species living in the same place. It was based upon many species having small, mainly allopatric ranges. Altitudinal zonation, rain shadow changes in moisture and vegetation, plus single ridge effects, combined to provide the opportunity for many local speciation events.

This contrasts, for example, with the situation in wetter parts of the mid North Island of New Zealand, where up to 72 relatively small land snail species can be microsympatric (Solem, Climo & Roscoe 1981). The Hawaiian pattern parallels the situation found in the monsoon fringe habitat of the Ningbing Ranges in the northeast corner of Western Australia (Solem 1988). An endemic radiation of camaenid land snails has resulted in over 28 relatively large species (shell diameter 15–25 mm), which are mainly allopatric, and have area ranges of only 0.01–7.45 km<sup>2</sup> (median 0.825 km<sup>2</sup>). In fact, most areas of the world have only 5 to 10 sympatric land snail species (Solem 1984).

The contemporary Hawaiian pattern of low sympatric land snail diversity, perhaps 5 to 10 species present in 1 patch of bush only 10 meters<sup>2</sup> in size, may complicate initial conservation efforts. Hopefully there still will be large numbers of such bush or tree clusters found to contain snail colonies. The plant or vertebrate-oriented conservationist, raised in the "species/area" dogma, will view such patches as inconsequential and incapable of sustaining populations. This is not true for land snails!

In the emergency situation that exists, we must think initially of "hundred year survival." If two trees can hold a colony for over a half century, then 10–20 trees should be good for at least 1 century, buying time for longer range solutions to be implemented. And this is where our view must start.

## ACTIONS TO TAKE

The following statement, taken from Pilsbry and Cooke (1915–1916:68) is nearly 75 years old, but remains as true today as when first penned to paper. "The higher mountain slopes of the Hawaiian Islands offer an almost unlimited field of study to the painstaking collector of small or minute species of land Mollusca. This region, especially on Oahu, Molokai and Lanai, has been pretty well covered for the larger arboreal species (*Achatinellidae*), but in what is known

to the average collector as "small trash" (such as *Tornatellina* [used as a general descriptive term for small, brownish, conical or globular land snails]), it is practically an unexplored country."

The collections of land snails in the Bishop Museum and private collectors provide a wonderful data base. They demonstrate where species were from the 1900s through 1930s and what the species look like. They can be used immediately to demonstrate where collections have not yet been made—usually because of remoteness and difficulty of access. It is in these remote and upland areas of Hawai'i that we are most apt to discover healthy colonies of land snails and then focus our efforts on salvage and preservation.

Collecting and study of the Hawaiian land snails followed the typical pattern of coast 1st, low level forest next, midlevel forest later, and high forest only after the rest became extinct. For altitudinally zoned taxa, such as the endodontid genus *Libera* in the Society Islands (Solem 1976:385–86), species collected by early explorers were not found after 1840, and similar situations will be documented for Hawai'i.

Our 1st priority must be extensive survey work, not only reinvestigating areas sampled in the early 1930s (the last period of rigorous sampling), but also working the "areas out of reach." Because of the existing collection and monographic data base, it will be relatively simple to identify places that contain land snail colonies and differentiate those places containing only widespread taxa from those with mainly local endemics. Considerable mapping of ranges will be required and the data for major systematic revisions will accumulate. It is hoped that this initial phase will gain the enthusiastic cooperation of local biologists, and that work on many aspects of snail biology and evolution can be started. At the very least, establishing "Baseline 1990s," where native land snails still persist, will permit intelligent attempts at preservation and recovery for those taxa remaining.

Perhaps 3–5 years of primary field survey and identification work can accumulate the data needed to carry out the 2nd phase of work. If such survey work is done on an island by island basis, it will be possible very early in the survey to begin targeting areas of snail and biotic diversity worth saving, identify immediate threats to these areas, and start the difficult process of managing them back to a healthy state.

Identification and legal protection of colonies is only the 1st step. Perhaps 15–20 small clusters of trees in an upper valley may have snail colonies, but they will be surrounded and isolated by dense stands of alien vegetation. The snails may enable targeting such areas, but the patches will contain many other organisms. Regeneration and expansion of the native plant stands must be encouraged over a period of decades, allowing the now isolated patches to coalesce and thus turn these remnants into an approximation of the native stands of yesteryear. This is the only way that longer term survival of the biota can be achieved.

Innumerable systematic and biogeographic problems will be encountered, especially as the field surveys of remote areas are completed. If we are fortunate, the successors and intellectual equals to Pilsbry and Cooke will rise to these new challenges and opportunities for study. The lengthy process of major monographic work must be emphasized. The monograph on the anatomy and classification of the Achatinellidae by Cooke and Kondo (1960:3) was in progress nearly full-time from late 1941 through most of 1948, required additional time for polishing, and did not appear in print until 19 years after its inception. My own studies on the Pacific Island Endodontidae and Charopidae (Solem 1976, 1983) were initiated in 1961. The time needed for completion of writing was extended by three and four-year "in press" periods, respectively.

#### SUMMARY AND CONCLUSIONS

Protection for and possible recuperation of the Hawaiian land snail fauna thus requires: (1) surveys to identify where native land snails persist; (2) identification of immediate threats to

these colonies; (3) legal and managerial protection for selected areas; (4) work to permit regeneration of the native vegetation to provide expanded habitat; and (5) systematic and biogeographic studies of the material collected and the colonies protected.

These objectives cannot be carried out during occasional visits of overseas specialists. It must be the responsibility of the people of Hawai'i to provide the energy, efforts, dedication, and funding needed to save important natural elements of their wonderful land that they are in immediate danger of losing.

Only because of the lifetime dedication by a single person, C. Montague Cooke, Jr., do we have the knowledge and collections that will permit salvaging an important portion of the natural heritage of Hawai'i. Committees may come and recommend, but they will go. So often in human affairs, it is the action of a single person, or at most a few people, who provide real progress.

Who will be the next "Monte Cooke?"

## ACKNOWLEDGMENTS

The many suggestions made by Carl C. Christensen, Allen Allison, and Mike Hadfield have greatly improved this report.

# LITERATURE CITED

- Ancey, C. F. 1889. Étude sur la Fauna malacologique des Îles Sandwich. Bull. Soc. Malacol. France 6:171–258.
- . 1899. Some notes on the non-marine molluscan fauna of the Hawaiian Islands, with diagnoses of new species. Proc. Malacol. Soc. London 3:268–74.
- -----. 1904. Report on semi-fossil land shells found in the Hamakua District, Hawaii. J. Malacol. 11:65-71.
- Baker, H. B. 1938. Zonitid snails from Pacific Islands. Part 1. Southern genera of Microcystinae. Bernice P. Bishop Mus. Bull. 158:1–102.
- ------. 1940. Zonitid snails from Pacific Islands. Part 2. Hawaiian genera of Microcystinae. Bernice P. Bishop Mus. Bull. 165:103-202.
- . 1941. Zonitid snails from Pacific Islands. Part 3. Genera other than Microcystinae. Part 4. Distribution and indexes. Bernice P. Bishop Mus. Bull. 166:203–370.
- Baldwin, D. D. 1893. Catalogue, land and fresh water shells of the Hawaiian Islands. Press Publishing Company, Honolulu, 25 p.
- **Caum, E. L.** 1928. Check list of Hawaiian land and fresh water Mollusca. Bernice P. Bishop Mus. Bull. 56:1–79.
- Christensen, C. C. 1985. Oahu Tree Snail, Genus Achatinella Swainson, 1828. Endangered Species Information System Species Workbook. Part I—Species Distribution. Part II—Species Biology, p. 1–79. Office of Endangered Species, Fish and Wildlife Service, U.S. Department of the Interior.
- Christensen, C. C. & P. V. Kirch. 1986. Nonmarine mollusks and ecological change at Barbers Point, O'ahu, Hawai'i. Bernice P. Bishop Mus. Occas. Pap. 26:52–80.
- Clarke, B., J. Murray & M. S. Johnson. 1984. The extinction of endemic species by a program of biological control. Pac. Sci. 38:97-104.
- Conant, S., C. C. Christensen, P. Conant, W. C. Gagné & M. L. Goff. 1984. The unique terrestrial biota of the northwestern Hawaiian Islands. Proc. 2nd Symposium on Resource Investigations in the northwestern Hawaiian Islands 1:77–94.
- Cooke, C. M., Jr. 1921. Notes on Hawaiian Zonitidae and Succineidae. Bernice P. Bishop Mus. Occas. Pap. 7: 263–77.
  - . 1931. The land snail genus Carelia. Bernice P. Bishop Mus. Bull. 85: 1-85.
- . 1941. Hawaiian Land Shells. Paradise of the Pacific 53 (12): 20-25.
- Cooke, C. M., Jr. & Y. Kondo. 1952. New fossil forms of *Carelia* and *Partulina* (Pulmonata) from the Hawaiian Islands. Bernice P. Bishop Mus. Occas. Pap. 20:329–46.

38

- —. 1960. Revision of the Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata). Bernice P. Bishop Mus. Bull. 221:1–303.
- Diamond, J. M. 1977. Continental and insular speciation in Pacific land birds. Syst. Zool. 26:263-680.
- Gagné, W. C. & C. C. Christensen. 1985. Conservation status of native terrestrial invertebrates in Hawai'i, p. 105–26. Hawai'i's terrestrial ecosystems: Preservation and management. Univ. of Hawaii Press, Honolulu.
- Gulick, J. T. 1905. Evolution, racial and habitudinal. Carnegie Inst. Washington, Publ. 25: i-xii + 1-169.
- Hadfield, M. G. 1986. Extinction in Hawaiian achatinelline snails. Malacologia 27: 67-81.
- Hadfield, M. G. & B. S. Mountain. 1981. A field study of a vanishing species, *Achatinella mustellina* (Gastropoda, Pulmonata), in Waianae Mountains of Oahu. Pac. Sci. 34: 345–58.
- Hadfield, M. G., S. E. Miller & A. H. Carwile. 1988. Recovery Plan for the O'ahu tree snails of the genus *Achatinella*. Draft submitted to USDA, Fish and Wildlife Service, Pacific Islands Office. 55 p.
- Hart, A. 1978. The onslaught against Hawaii's tree snails. Natur. Hist. 87: 46-57.
- Hyatt, A. & H. A. Pilsbry. 1911. Manual of Conchology. 2nd Series. 21: i-xxii + 1-387.
- Kondo, Y. & W. J. Clench. 1952. Charles Montague Cooke, Jr., a bio-bibliography. Bernice P. Bishop Mus. Bull. 42: 1–56.
- Murray, J., E. Murray, M. S. Johnson & B. Clarke. 1988. The extinction of *Partula* on Moorea. Pac. Sci. 42: 150–53.

Neal, M. C. 1934. Hawaiian Helicinidae. Bernice P. Bishop Mus. Bull. 125: 1-102.

- Odhner, N. H. 1950. Succineid studies: Genera and species of subfamily Catinellinae nov. Proc. Malacol. Soc. London 28: 200–10.
- Patterson, C. M. 1971. Taxonomic studies of the land snail family Succineidae. Malacol. Rev. 4: 131-202.
- Pilsbry, H. A. 1900a. On the zoological position of *Partula* and *Achatinella*. Proc. Acad. Natur. Sci. Philadelphia 1900: 561–67.
- . 1900b. The genesis of the mid-Pacific faunas. Proc. Acad. Natur. Sci. Philadelphia 1900: 568-81.
- . 1916. Mid-Pacific land snail faunas. Proc. National Acad. Sci. 2: 429-33.
- ------. 1918–1920. Manual of Conchology. 2nd Series. 25: i-ix + 1-401.
- ------. 1920-1921. Manual of Conchology. 2nd Series. 26: i-iv + 1-254.
- -----. 1921. The dispersal and affinities of Polynesian land snail faunas. Proc. 1st Pan-Pac. Sci. Congr., p. 147–52.
- ——. 1948. Land Mollusca of North America (north of Mexico). Acad. Natur. Sci. Philadelphia, Monogr. 3 2(2): i–xlvii + 521–1113.
- Pilsbry, H. A. & C. M. Cooke, Jr. 1908. Hawaiian species of *Helicina*. Bernice P. Bishop Mus. Occas. Pap. 3: 197–210.

------. 1912–1914. Manual of Conchology. 2nd Series. 22: i-lviii + 1–428.

------. 1914–1916. Manual of Conchology. 2nd Series. 23: i-xi + 1–302.

Pilsbry, H. A. & E. G. Vanatta. 1905. Notes on some Hawaiian Achatinellidae and Endodontidae. Proc. Acad. Natur. Sci. Philadelphia 1905: 570–75.

- ——. 1906. Hew Hawaiian Species of *Endodonta* and *Opeas*. Proc. Acad. Natur. Sci. Philadelphia 1905: 783–86.
- Solem, A. 1969. Phylogenetic position of the Succineidae. Third Europ. Malacol. Congress, Malacologia 9: 289.
- -----. 1978. Classification of the land Mollusca. In: Fretter, V. & J. Peake, Pulmonates, Volume 2A, Systematics, evolution, and ecology, p. 49–97. Academic Press, London.
- ——. 1983. Endodontoid land snails from Pacific islands (Mollusca: Pulmonata: Sigmurethra). Part II. Families Punctidae amd Charopidae, zoogeography. Field Museum Press, Chicago. ix + 336 p.
- -----. 1984. A world model of land snail diversity and abundance. In: Solem, A. & A. C. van Bruggen, Worldwide Snails. Biogeographical studies on non-marine Mollusca, p. 6–22. E. J. Brill, Leiden.

<sup>—. 1988.</sup> Maximum in the minimum: Biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, northeast Kimberley, Western Australia. J. Malacol. Soc. Aust. 9: 59–113.

- **Solem, A. & E. Yochelson.** 1979. North American Paleozoic land snails, with a summary of other Paleozoic Nonmarine snails. U.S. Geol. Surv. Prof. Pap. 1072: i–iii + 1–42.
- Solem, A., F. M. Climo & E. J. Roscoe. 1981. Sympatric species diversity of New Zealand land snails. N. Z. J. Zool. 8: 453–85.
- Sykes, E. R. 1900. Mollusca. Fauna Hawaiiensis 2(4): 271-412.
- Tillier, S. 1989. Comparative morphology, phylogeny and classification of land snails and slugs (Gastropoda: Pulmonata: Stylommatophora). Malacologia 30: 1–303.
- Watson, H. 1920. The affinities of *Pyramidula*, *Patulastra*, *Acanthinula*, and *Vallonia*. Proc. Malacol. Soc. London 14: 6–30.
- Welch, d'A. 1938. Distribution and variation of the Hawaiian tree snail *Achatinella mustelina* Mighels in the Waianae Mountains, Oahu. Bernice P. Bishop Mus. Bull. 152: 1–164.
- -----. 1942. Distribution and variation of the Hawaiian tree snail Achatinella apexfulva Dixon in the Koolau Range, Oahu. Smithson. Misc. Coll. 103(1): 1–236.
- . 1954. Distribution and variation of the Hawaiian tree snail Achatinella bulimoides Swainson on the leeward and northern slopes of the Koolau Range, Oahu. Proc. Acad. Natur. Sci. Philadelphia 106: 63–107.
- -----. 1958. Distribution and variation of the Hawaiian tree snail *Achatinella bulimoides* Swainson on the windward slope of the Koolau Range, Oahu. Proc. Acad. Natur. Sci. Philadelphia 110: 123–212.

Zilch, A. 1959. Gastropoda. Teil 2. Euthyneura. Handbuch der Paläozoologie. 6, Lfg. 1: 1-200.

- Zimmerman, E. C. 1948. Insects of Hawaii. Volume 1. Introduction. Univ. of Hawaii Press, Honolulu. 206 p.