ON THE EDGE OF EXTINCTION: DISTRIBUTION AND BEHAVIOR OF THE ENDANGERED PARTULID SNAILS OF MOOREA, FRENCH POLYNESIA

MOLLY HARDESTY-MOORE

Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. Due to restricted gene flow, remote islands often contain unique lineages that do not exist elsewhere in the world; unfortunately, human-mediated introductions of foreign species have caused extirpations and extinctions of many endemic island species. Snails of the family *Partulidae* have experienced mass extirpations because of high levels of predation by the introduced predatory snail, *Euglandina rosea*. This study aimed to document the current status of Moorean partulid snails by surveying four populations that were documented in 2010. Eleven additional sites were surveyed within the Three Pines and Three Coconuts regions to determine if there were any partulid populations in this area. This study also aimed to increase knowledge about partulid behavior in the wild by observing *Partula taeniata* during the morning, afternoon, and night. It was hypothesized that the snails would be more active at night, when the temperatures were low and there was no direct sunlight. Three of the four *Partula* populations that had been documented four years prior could not be found. The fourth population, in Opunohu Bay, was documented and observed for the behavioral portion of the study. No other populations of the genus *Partula* were found in this study. Six individuals of the genus *Samoana* were documented. From the behavioral observations, it was found that the *P. taeniata* individuals were significantly more active at night. Based on the findings of this study, the partulid snails still teeter on the edge of extinction, and their conservation continues to be an issue of great importance.

Key words: conservation; predation; Partulidae; *extinction;* Euglandina rosea; *distribution;* Partula taeniata*; behavior; Moorea, French Polynesia*

INTRODUCTION

Island systems have been key contributors to our understanding of evolution, biogeography, and ecology for centuries (Darwin 1859; Carlquist 1974; Powell 1997). Isolated islands provide examples of unique speciation events and thus house species and ecosystems that are exceedingly rare; species that have evolved on islands are typically endemic to a very small area and do not exist elsewhere in the world (Pauley 1994). The classic example of distinctive island lineages is the Galapagos finch radiation, but there are many more: for example, Hawaiian honeycreepers are thought to be one of the most diverse groups that have undergone an adaptive radiation (Pratt 2005). Such unique species and distinct evolutionary processes make islands critical systems to study.

Unfortunately, many species endemic to islands have already been lost, and many more are threatened (Sax 2002). Since 1600, 75% of all animal extinctions have been of island species, even though island species comprise a minority of animal species (World Conservation Monitoring Centre 1992). Habitat destruction, invasive species, and other anthropogenic impacts have made the conservation of endangered species a global concern, and the conservation of endemic island lineages is especially critical because of the rarity of these species and the sensitivity of island systems to environmental changes. The extinction risk for island populations is much higher than mainland populations (World Monitoring Centre 1992; Frankham 1998). Oceanic islands have never been attached to a continent and are often isolated from sources of life (Emerson 2002). Few species are able to reach the most remote islands, and those that do successfully colonize the island will often evolve to fill the empty niche space (Gillespie 2002; Pauley 1994). Species that evolve on isolated islands often do not have robust defensive or competitive abilities, and they are vulnerable to introductions of organisms from diverse continental ecosystems that are better competitors or predators (Pauley 1994). Humans often act as ecosystem engineers and bring such harmful foreign species to islands. Many species that humans have introduced to

islands have become invasive, such as rats, cats, and rabbits, and frequently these invasive species have caused extinctions or extirpations of native populations (Zavaleta *et al.* 2001).

In recent years, the extinction and extirpation of many species from the *Partulidae* family of tree snails has been one of the most notable human-mediated extinctions. Partulid tree snails are endemic to the Society Islands of French Polynesia, and before their decline there were 61 documented species: four *Samoana* and 57 *Partula* species (Lee *et al.* 2009). The partulid species were quite prominent in studies of evolution and genetics for much of the twentieth century, and their loss was significant to the scientific community (Crampton 1916; Lipton and Murray 1979; Johnson 1982; Lee *et al.* 2009). Many of the partulid species are extinct or extremely endangered due to the introduction of a biological control agent, the predatory snail *Euglandina rosea* (Clarke *et al.* 1984). *Euglandina rosea*, or the rosy wolfsnail, was introduced to the Society Islands to help rid the islands of *Achatina fulica*, the introduced giant African land snail, which had become an agricultural pest (Murray *et al.* 1988). This introduction and the unfortunate events that followed were best documented for the island of Moorea; *Euglandina rosea* was released in Moorea in 1977, and as a result, the partulid populations of Moorea declined to an undetectable level and were declared extinct in 1987 (Murray *et al.* 1988). If these populations had indeed gone extinct, many unique species of snail would have been lost; fortunately, relict populations survived and remain today. Carole Hickman (pers. com.) has monitored a relict population of *Samoana* since 1996, and relict populations of six of the seven Moorean species of the genus *Partula* have been discovered since 2000 (Lee *et al.* 2009). It is critical to monitor these relict populations and ensure their survival.

This study aimed to document the current status of partulid populations on Moorea and to increase knowledge about their behavior in the wild. Lani Maher (2010) surveyed sites around Moorea and found partulids at eight of the 24 sites (Appendix A). The first component of my study was a resurvey of the four key sites from Maher's study to determine the current status of these partulid populations and a survey of eleven sites from the surrounding area. Maher documented a total of 187 partulid individuals from her surveys and two live *E. rosea*. Given the low occurrence of *E. rosea*, I expected that the partulid populations of Moorea would have increased in range or density over the past four years. The second component was a behavioral study of the *Partula taeniata* population inhabiting the Opunohu Bay site. It is important to understand the behavior of the partulid snails in order to assess their survival ability and aid in their conservation. I examined the activity of *P. taeniata* at three different times of the day: morning, afternoon, and night. Previous observations indicated that the partulid snails may be less active in the middle of the day and in the morning than at night, and snails are typically sensitive to high temperatures and dry weather. Thus, I hypothesized that the partulids would display significantly more activity at night.

METHODS

Organism

The study organisms were individuals from the *Partulidae* snail family in Moorea, French Polynesia. These snails are endangered and protected, and this study was designed to have the least impact on the snails as possible. Consequently, there was no touching, handling, marking, or moving of the partulid snails at any time.

The individuals were identified first using pictures from previous studies (Maher 2010; Lee *et al.* 2009), and then an expert (Carole Hickman, pers. com.) confirmed the identifications (Appendix D).

Study sites

This study was conducted on the island of Moorea, French Polynesia. Sites were selected from Maher (2010) to resurvey. Only sites at which Maher documented partulid individuals were chosen. Maher found a total of 187 partulid snails at eight sites: B, P, R, N, K, V, W, and X (Appendix A). GPS coordinates from Maher provided site locations. Partulid snails are known to prefer certain host plant species, including *Angiopteris evecta, Acrostichum aureum, Cyclophyllum barbatum, Freycinetia demissa*, and *Syzygium malaccense* (Maher 2010). Areas in which there was a high abundance of preferred host plants were most likely to contain partulid populations, and the resurvey sites were established in areas of high host plant abundance within 30 meters of the GPS points, as the GPS devices have a wide range

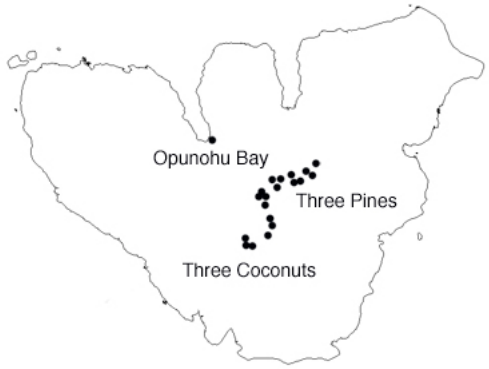


FIG. 1. Sites surveyed in this study.

of error. Of Maher's eight sites, B, X, N, and K were resurveyed in this study. The remaining sites, P, R, W, and V, were either unreachable or not selected for this study due to difficult conditions. It was most important to resurvey sites B, X, N, and K because these sites had been noted to contain large populations of partulids. Additionally, 11 new sites were added to the four previously established sites (Fig.1). The new sites were in the same region as Maher's sites, specifically the Three Pines and Three Coconuts trails, and were chosen by walking the trail and searching for ideal partulid habitat. Each site, besides the Opunohu Bay site, had a high density of *Angiopteris evecta*. The Opunohu Bay site is the lowest elevation site, and had a high density of *Acrostichum aureum*, the mangrove fern. The four resurvey sites, as well as Three Coconuts sites 3, 4, and 5, were near a stream. The Three Pines Trail sites were along a steep slope, and are counted as one site due to the very small area searched at each GPS point. Site names and GPS points are given in the table provided in Appendix B.

Survey procedure

Surveying took place in 2014 between October 15 and November 11. Following the methods of Maher (2010), each site was marked with a handheld GPS and each habitat was characterized by recording air temperature, canopy cover density, weather, and approximate site size and elevation. Additionally, observations were recorded about the presence of local flora and fauna.

As the sites had differing accessibility (for example, some were dense forest, while others were relatively cleared), each site was searched until the entire area of suitable habitat had been searched, until 45 minutes had passed without finding a partulid or *E. rosea* individual, or until a physical boundary prevented further searching. If no partulid or *E. rosea* individuals were found, the GPS point was recorded and the search for a new site began. When partulid individuals were discovered, the search was extended at the site in order to locate other individuals to allow determination of population size, density, and species composition. When an individual was detected, the host plant species and position of the snail on the plant (under the leaf, on top of the leaf, or on the stalk) were recorded, as well as shell length and width, which gave an idea of the life stage of the individual. Only the individuals large enough to be conclusively identified as partulid were recorded (greater than about 4 mm long). When multiple adults were found, individuals too small to be definitively identified as partulids were tallied and recorded as juveniles. All empty partulid shells encountered during surveys were collected and recorded. When a live *E. rosea* individual was found, its life stage and substrate on which it was found were recorded. When *E. rosea* shells were discovered they were collected and recorded.

Beyond counting the partulids and *E. rosea*, the presence of *A. fulica* and other terrestrial snails was also recorded.

A diagram was created that visually represents the Opunohu Bay population survey findings (Fig. 2). This was done to examine the distributional pattern of this population.

Behavioral study

The Opunohu Bay site was selected for the behavioral study because it was the only site with a substantial population of *Partula* snails. The only species known to live at this site is *P. taeniata*; thus, this species was observed for the behavioral study. The behavioral study took place in 2014 between October 23 and November 20.

To categorize each snail's behavior, possible behaviors were determined. As terrestrial snails typically display very little activity, I settled on two key behaviors to observe, which were chosen based on information from previous literature and preliminary observations: inactive (the body is retracted inside the shell), and active (the body is visible outside of the shell). These categories were titled "Behavioral Status" (Appendix C).

Observations took place in the morning (7:00-9:00 am), in the afternoon (12:00-2:00 pm), and at night (7:00-9:30 pm). There were three observation periods for each time of day.

A 20 meter transect was laid along an accessible area of suitable *Partula* habitat. Along the transect, the positions of 10 individuals were marked by flagging the frond on which they were observed. Only individuals that were large enough to be conclusively identified as partulid were included in this study (greater than about 4 mm in length). The individuals chosen for observation were distributed as evenly along the transect as possible; however, in certain areas individuals were very difficult to find, and if no individuals could be found, the area was not marked along the transect, causing some clumping of marked individuals.

The behavior of each individual was observed for one minute and recorded. The shell length and width, position of the individual on the plant (underneath the leaf, on top of the leaf, or on the stalk), host plant species, meters along the transect, and presence of other gastropods (*E. rosea*, *A. fulica*, and other partulids in particular) were recorded. A picture was taken of each individual to help determine if the same individuals were found more than once and to keep a record of the snails observed in the study. An identification number was assigned to each individual.

In the subsequent observation periods, there was an attempt to find the same ten individuals. If the same individuals could not be found, each unfound individual was replaced with the *Partula* individual closest to the original marker, and the new individual was noted as different by assigning it a new number and taking a picture. The same data as above were recorded for each observation period. Notes on movement and other miscellaneous observations were also taken.

Statistical tests

For the behavioral study, there was one independent variable, time of day, and one dependent variable, count of active individuals. Using log transformation, the data was able to meet the assumptions of an ANOVA. In order to determine whether there was a significant difference between the observed activity at different times of the day, an ANOVA (alpha value 0.05) was performed on the data. Next, a Tukey posthoc test was performed to determine which time(s) of day had levels of activity that were significantly different from the other times of the day.

RESULTS

Field surveys

A total of 30 partulids were documented during the field surveys: 24 of the 30 were of the genus *Partula*, and of these, all were *Partula taeniata*. The other six partulids were of the genus *Samoana*; both species of *Samoana*, *Samoana attenuata* and *Samoana diaphana*, were observed during the surveys. In addition, 17 partulid shells were collected. As the shells were bleached and in some cases damaged, it was difficult to identify them past the family level. For a more detailed list of the findings, see Appendix B.

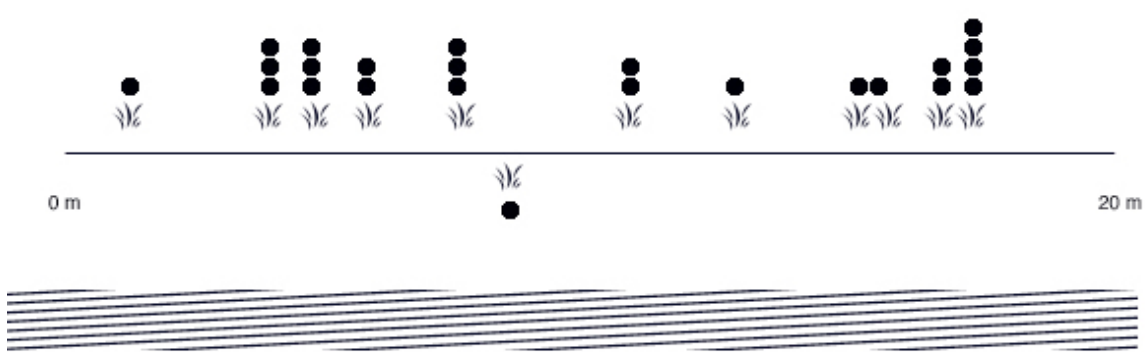


FIG. 2. Diagram of the survey findings in Opunohu Bay. The black dots represent individual *P. taeniata*, the plant symbols represent individual host plants, and the striped pattern represents the canal.

TABLE 1. Table representing site, species, status, shell length and width, and host plant of documented *Samoana* individuals.

Location	Species	Behavioral Status	Shell Length/Width	Host Plant
Three Pines Site 3	*Samoana attenuata*	Inactive	18 x 6 mm	*Angiopteris evecta*
Three Coconuts Site 2	*Samoana diaphana*	Inactive	16 x 6 mm	*Angiopteris evecta*
Three Coconuts Site 2	*Samoana* sp.	Active	6 x 3 mm	*Angiopteris evecta*
Three Coconuts Site 2	*Samoana* sp.	Active	6 x 3 mm	*Miconia* sp.
Three Coconuts Site 3	*Samoana* sp.	Active	5 x 2 mm	*Angiopteris evecta*
Three Coconuts Site 3	*Samoana diaphana*	Active	11 x 6 mm	*Angiopteris evecta*

Snails of the genus *Partula* were only found at the Opunohu Bay site. All 24 documented individuals were from this site. The area surveyed was an estimated 200 square meters, which amounts to a population density of one individual per 8.33 square meters. The individuals were not evenly spaced throughout the 200 square meters; many individuals were observed on the same plant, while other plants contained zero partulids. The areas closer to the canal were observed to have very few individuals (Fig. 2). Of the sites resurveyed from Maher (2010), the Opunohu Bay site was the only site at which *Partula* individuals were rediscovered.

Samoana individuals were documented at three sites in this study: Three Pines Site 3, Three Coconuts Site 2, and Three Coconuts Site 3 (Fig. 3). Only one *Samoana* individual was documented in the Three Pines locality, and it was identified as *S. attenuata*. The other five individuals were found in the Three Coconuts locality, and two were identified as *S. diaphana*; however, three individuals were at such an early growth stage that they could not be conclusively identified (Table 1).

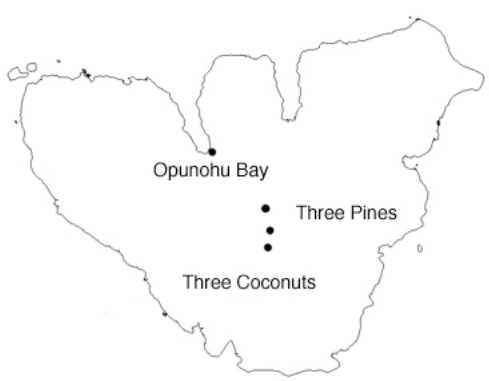


FIG. 3. Map showing sites where partulids were documented.

Only one of the six partulids documented in the field surveys, outside of the Opunohu Bay population, was found in the Three Pines locality; however, 15 of the 17 partulid shells were found in the Three Pines locality. No partulid shells were found in areas where live partulids were documented in this study.

Although scarce traces of partulids could be found at Three Pines and Three Coconuts, there was an abundance of data regarding the presence of *E. rosea*. During the surveys, 15 live *E. rosea* were documented. All of the live *E. rosea* were discovered in the Three Pines locality, and none of them were found in an area that contained live partulids. The substrate on which the live *E. rosea* were found was highly variable: they were found on dirt; dead leaves; the trunk of an *Inocarpus* tree; small, fern-like plants; and twice on *A. evecta*. A total of 113 *E. rosea* shells were collected. About 63% of the shells were found in the Three Pines area, and 69% of these were from Three Pines sites 4, 5, and 6. No *E. rosea* shells were found in areas that contained partulids. There were no signs of *E. rosea* at the Opunohu Bay site.

Behavioral observations

An average of 1.7 individuals were active during the morning observations, an average of 0.7 individuals were active during the

afternoon observations, and an average of 8.3 individuals were active during the night observations (Appendix C). The standard deviation of all active individuals was 3.97.

It was found that there was a significant difference between the three times of the day (p-value= 0.00876, ANOVA). Using a pairwise statistical test, it was determined that the amount of activity at night was significantly different from the amount of activity recorded in the morning (p-value= 0.0396, Tukey) and the afternoon (p-value= 0.0080, Tukey). As seen in the boxplot below (Fig. 4), the amount of activity was much higher at night than during either of the other times of day.

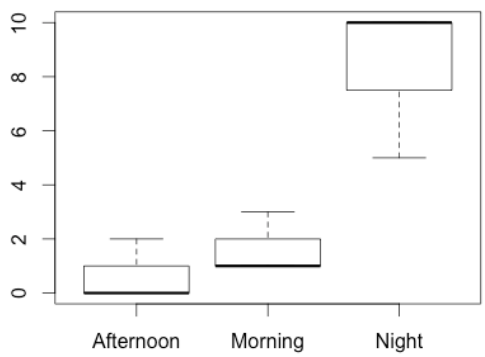


FIG. 4. Boxplot showing the amount of activity observed at each time of the day.

DISCUSSION

Field surveys

The results of the survey indicate that there has been a change in the partulid populations in the past four years. The area in which Maher (2010) found 75 out of 123 live subadult or adult partulids (Three Pines sites 4, 5, and 6) did not yield any live partulids in this survey. Thus, the populations in this area have either been extirpated, decreased significantly in size, or moved to another area. The latter is very unlikely, due to the low amount of movement partulids tend to display in a lifetime (Murray and Clarke 1984). Given the evidence of live *E. rosea* in the area, the most likely scenario, as in many previous cases, is that *E. rosea* found the partulid populations and preyed upon them until none remained. It is possible partulid individuals survived at a level that was difficult to detect and that the populations in this area will return once the *E. rosea* populations have subsided. As *E. rosea* was found at several Three Pines sites, it would seem that they are currently a dominant force; however, the one *Samoana* documented at Three Pines is an indicator that there are partulids who have survived in this area.

By comparing the amount of live *E. rosea* found in this study to the amount of live *E. rosea* found four years ago, it seems that there has been a resurgence in their populations in the Three Pines locality. Out of the 15 documented *E. rosea* from this study, 11 were found in the Three Pines resurvey sites. Maher found only two live *E. rosea* during all of her surveys, 24 sites in total. Neither of these two *E. rosea* were found in an area that contained live partulids, which means that there were either no *E. rosea* in the Three Pines area four years ago, or there were very few. It is likely that *E. rosea* now resides in this area because they were drawn to a source of prey, the partulid populations. Feeding on the partulid populations allowed them to increase in abundance and inhabit much of the Three Pines locality. Several of the documented *E. rosea* were juvenile or subadult, and these young individuals are evidence of turnover in their populations.

Over one hundred *E. rosea* shells were documented at the sites in the Three Pines and Three Coconuts areas, which indicates the existence of widespread populations of *E. rosea* at some point in the past. This follows with the history of *E. rosea*, which expanded throughout the island and decimated the partulid populations within ten years. However, it is interesting to note that Maher documented 43 *E. rosea* shells in total, while this study documented 113. Of these, 49 were from the Three Pines resurvey area. As more *E. rosea* shells were found from the three resurvey sites in Three Pines than in the entirety of Maher's 24 sites, there is a strong indication that there has been an increase in the number of *E. rosea* in the Three Pines area. Based on observations from the past several years (Brent Mishler, pers. com.) that indicate almost no sightings of *E. rosea*, this could be extrapolated to signify a general increase of *E. rosea* throughout the island. More study is needed to conclusively determine the state of *E. rosea*.

The evidence of live *E. rosea* and empty *E. rosea* shells from the Three Pines resurvey sites suggests the occurrence of a predator-prey cycle between *Partulidae* snails and *E. rosea*. Predator-prey cycles are characterized by regular intervals of increasing population size

followed by decreasing population size of the predators and the prey, with the fluctuations in predator population size following the fluctuations in the prey population size (Hoagstrom 2014). The theory is that when a prey population increases, there is a subsequent increase in the predator population due to the higher availability of nutrients, which, as more of the prey are being consumed, will cause a decrease in the prey population, followed by a decrease in the predator population. After some time, the prey population will be able to increase again, and the cycle will start over. There is evidence of at least part of one such cycle occurring at Three Pines. In 1987 partulids were so rare that experts were unable to detect them, but recently, partulid populations have been able to reestablish themselves in certain areas. Four years ago there was a sizeable population of partulids inhabiting Three Pines, and at some point in the past four years, *E. rosea* discovered this population. As they began to consume the partulids, their population increased, which is indicated by the 49 *E. rosea* shells found in this area. When the prey source ran out, *E. rosea* decreased in population size. To determine if there is a predator-prey cycle that is occurring, the fluctuations in partulid and *E. rosea* populations would need to be documented for an extended period of time. If there were such a cycle, in order for the partulid populations to subsist, they likely would have a refuge from *E. rosea* (Chivers *et al.* 2014). This would be beneficial for the partulids, as it would help them to survive, but it would allow the *E. rosea* populations to persist as well.

It is of interest that there were no live *E. rosea* found at Three Coconuts, as it is geographically close and visually similar to Three Pines. Very similar vegetation can be found in both places, and it seems that *E. rosea* should be able to live there. One possible explanation for their absence is rather obvious: the preferred food source of *E. rosea,* partulids, does not exist there in high enough abundance. Five *Samoana* were found in the Three Coconuts area, but no large populations were documented. As there were no empty *E. rosea* shells at the highest elevation of Three Coconuts, and further down the trail at lower elevations there were 42 shells, another potential explanation is that there is an elevational limit to *E. rosea*. There could be many other limiting factors as well.

The most optimistic findings from this study for the future of *Partula* came from the Opunohu Bay, which, although the only large population of partulids documented, has sustained itself in the four years since the last survey. The population had a diverse mixture of ages, from the still-translucent young, to the subadults, to the lipped adults. The population density was estimated at one snail per 8.33 square meters, and Maher estimated the population density at one snail per 13 square meters in the previous survey. It is difficult to conclusively compare the densities, however, due to the difference in sample size, but it does not appear that the population has decreased much, if at all, since the previous survey. There were no signs of *E. rosea* at the Opunohu Bay.

Behavioral observations

The results indicate that there was a significant difference between the amounts of individual activity observed at the three times of day. As the *P. taeniata* individuals display significantly more activity at night, it follows that there is a factor related to the night that encourages their activity. Potential factors include the lower temperature, lack of direct sunlight, and increased moisture. Moisture was apparent on the ferns more often during the night observations than during the day, although it is important to note that many of the day observations took place during a period of very dry weather. Even so, there were observations that occurred while it was raining during the day (not included in this study), and there were no visibly active individuals. It would be interesting to learn more about how temperature, humidity, and sunlight affect *Partula* individuals, and under what conditions are they most likely to be active.

Broader implications

It is clear from this study that *E. rosea* are still a dominant presence on Moorea. They are impacting partulid populations that are beginning to reemerge. If there is a predator-prey cycle occurring, the *E. rosea* will most likely feed on partulid populations for many years to come, and will not disappear on their own unless the partulids disappear as well.

However, it is possible that partulids may have certain refuges from *E. rosea*. The Opunohu Bay may function as a refuge, as it seems that *E. rosea* has not yet impacted that area. The mangrove fern forest in Opunohu Bay is very close to the ocean, and the soil is likely more saline than in the higher elevation

areas. There are also many physical boundaries, such as the canal and the stream, that surround the Opunohu Bay population. Another factor, as mentioned by Maher, that may play a role in protecting this area are the coconut crabs, which remove leaf litter from the ground. *Euglandina rosea* travel mostly in leaf litter and may lay their eggs there as well.

The most critical influence on the future of partulid snails is human action. By protecting important refuges, such as the Opunohu Bay mangrove forest; increasing awareness of areas that may house partulids; finding ways to rid the island of *E. rosea*; and continuing to study the distribution and biology of the endangered partulid snails, humans can help ensure their survival. The mangrove forest in Opunohu Bay is next to a shrimp farm, and Maher noted that there had been development in areas that housed *P. taeniata*. It was also observed, on my final visit to Three Coconuts, that three of the five *Angiopteris* fronds on which a *Samoana* had been documented were chopped off, presumably during trail pruning, and I could no longer find the *Samoana* individuals. This most likely would not kill the individuals, but as they are an extremely endangered taxon, it is important to be wary of the areas in which they are typically found. A systematic method for removing *E. rosea* would greatly improve the chances of partulid survival, but it may be difficult, given that the partulids live in many of the same areas as *E. rosea*; although, I would recommend against introducing another predatory species. Increasing the public awareness of and knowledge surrounding partulid snails would contribute greatly to their future. Their history and biology is fascinating, and there is much more research that needs to be done.

Future research

Future research will be necessary in order to further our understanding of these endangered snails. As my survey was limited to a relatively small area, many future surveys in different areas of the island and in later years will prove useful to understanding the distribution and subsistence of partulid snails. Such surveys could be around the coast in areas similar to the mangrove fern area or on the other side of the island, and could be based on Maher's original survey. There are other types of behavioral observations that would be worthwhile to look into, as there is very little knowledge currently about partulid behavior. Some examples include: examining whether the snails are more responsive to temperature or humidity, comparing behavior between species, conducting a more extensive study of night versus day to determine the factors that cause the difference in activity, and examining their behavior while it is raining.

As it is increasingly difficult to locate partulids to observe, it may be interesting to instead study *E. rosea*. Studies of *E. rosea* will also lend information to the history and future of partulids. With fewer partulids around, the exact diet of *E. rosea* is not clear, and a study could be done on *E. rosea* feeding preference. Dissecting *E. rosea*, as they can swallow their prey whole, could yield some evidence on what they are eating by identifying shells from within their stomach. *Euglandina rosea* often finds its prey by tasting and following their slime trails. Swabbing different snails' slime trails and watching which trail *E. rosea* follows could help determine feeding preference. There could also be studies of *E. rosea* habitat preference on Moorea and surveys of their existing populations.

ACKNOWLEDGMENTS

I would like to acknowledge the considerable amount of work that goes into running a course such as this: thank you Brent Mishler, Stephanie Carlson, Vince Resh, and Jonathon Stillman for all of your time and support. I would like to acknowledge all of the GSIs – Jenna Judge, Seth Kauppinen, and Jason Hwan – who each contributed a significant amount of knowledge to this project and to this course. I would like to acknowledge all of the outside support I had: Lani Maher, Patrick Kirch, and Carl Christensen. I would like to especially thank Carole Hickman for all of her invaluable advice and expertise, and for giving me the idea to do the project in the first place. I would like to thank my parents for making this experience possible and for providing endless encouragement. Finally, I would like to thank Christopher Everett, who was always by my side, rain or shine, looking for snails.

LITERATURE CITED

Carlquist, S. 1974. Island Biology. New York, Columbia University Press.

Chivers, W. J., W. Gladstone, R. D. Herbert, and M. M. Fuller. 2014. Predator-prey systems depend on a prey refuge. Journal of Theoretical Biology **360**: 271-278.

Clarke, B., J. Murray, and M. S. Johnson. 1984. The Extinction of Endemic Species by a Program of Biological Control.

Crampton, H. E. 1916. Studies on the variation, distribution, and evolution of the genus *Partula*. The species inhabiting Tahiti. Carnegie Institution Washington Publishing **228**: 1311.

Darwin, C. R. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London. [1st edition].

Emerson, B. C. 2002. Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. Molecular Ecology **11**: 951-966.

Frankham, R. 1998. Inbreeding and Extinction: Island Populations. Conservation Biology **12**: 665-675.

Gillespie, R. G. 2002. Biogeography of spiders on remote oceanic islands of the Pacific: archipelagoes as stepping stones? Journal of Biogeography **29**: 655-662.

Hoagstrom, C. 2014. Predator-prey cycles. Retrieved from http://www.eoearth.org/view/article/155342.

Johnson, M. S. 1982. Polymorphism for direction of coil in *Partula suturalis*: Behavioural isolation and positive frequency dependent selection. Heredity **49**: 145-151.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. N. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of Food and Predation on the Snowshoe Hare Cycle. Science **269**: 1112-1115.

Lee, T., J. B. Burch, T. Coote, P. Pearce-Kelly, C. Hickman, J. Meyer, and D. O. Foighil. 2009. Moorean tree snail survival revisited: a multi-island genealogical perspective. BMC Evolutionary Biology **9**: 204-220.

Lipton, C. S., and J. Murray. 1979. Courtship of land snails of the genus *Partula*. Malacologia **19**: 129-146.

Maher, L. 2010. The Distribution and Demography of Relict *Partulidae* on Mo'orea, French Polynesia: Back from the Brink of Extinction? Biology and Geomorphology of Tropical Islands. UC Berkeley.

Murray, J. and B. Clarke. 1984. Movement and Gene Flow in *Partula taeniata*. Malacologia **25**: 343-348.

Murray, J., E. Murray, M. S. Johnson, and B. Clarke. 1988. The Extinction of *Partula* on Mo'orea. Pacific Science **38**: 97-103.

Paulay, G. 1994. Biodiversity on oceanic islands – its origin and extinction. American Zoology **34**: 134-144.

Powell, J. R. 1997. Progress and Prospects in Evolutionary Biology: The *Drosophila* Model. Oxford University Press, New York.

Pratt, H. W. 2005. The Hawaiian Honeycreepers: *Drepanidinae*. Oxford University Press, Oxford.

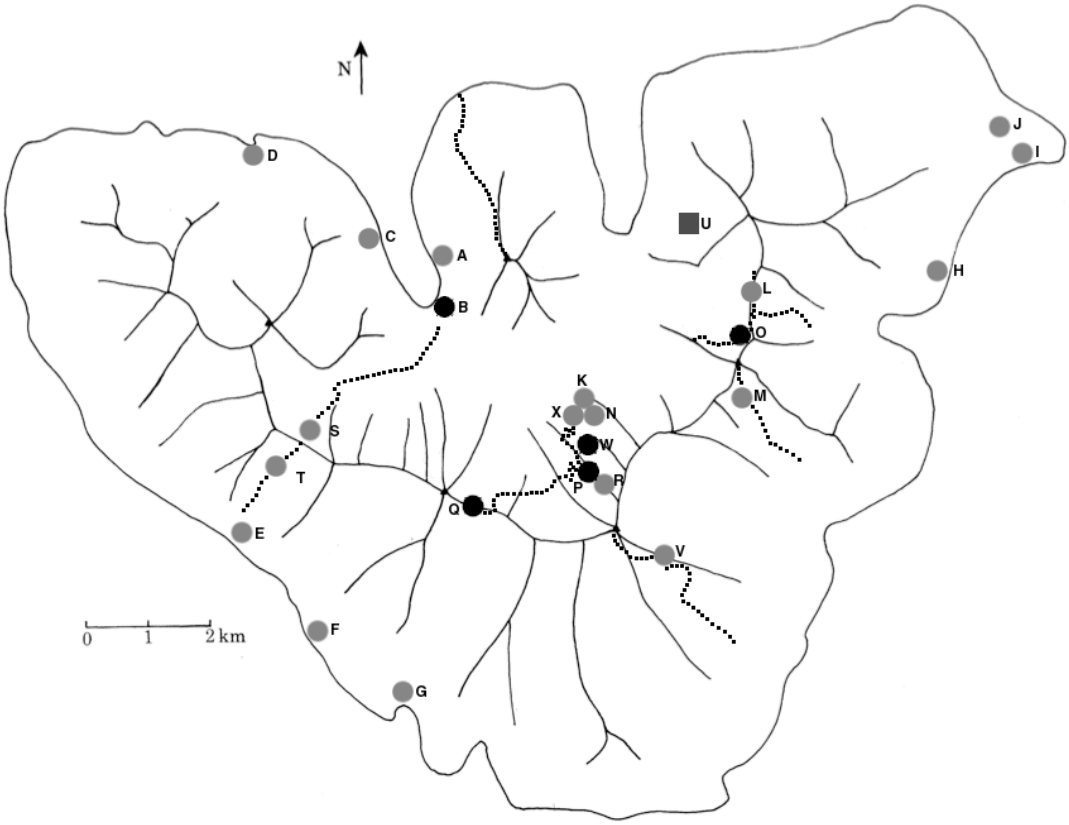
Sax, D. F., S. D. Gaines, and J. H. Brown. 2002. Species Invasions Exceed Extinctions on Islands Worldwide: A Comparative Study of Plants and Birds. The American Naturalist **160**: 766-783.

World Conservation Monitoring Centre. 1992. Global Biodiversity: the status of the Earth's living resources. Chapman and Hall, London.

Zavaleta, E. S., R. J. Hobbes, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution **16**: 454-459.

APPENDIX A

Map taken from Maher (2010). Sites surveyed in that study are represented by dots, the dotted lines indicate search paths, black dots indicate previously documented relict populations, and the square indicates the site where Euglanina rosea was released in 1977. Partulids were found in Maher's study at sites B, P, R, N, K, V, W, and X. In the present study, however, partulids were only found at site B, and at three new sites (described in Fig. 3 and Appendix B).



APPENDIX B

Table containing site name, GPS data, site area, number of live *Euglandina rosea*, *E. rosea* shells, live *Partula*, live *Samoana*, and partulid shells.

Site	GPS point	Est. Site Area (m^2)	Live *E. rosea*	*E. rosea* shells	Live *Partula*	Live *Samoana*	Partulid shells
3 Pines Site 1 (P1)	S 17.5367 W 149.8277	900	4	1	0	0	0
P2	S 17.5369 W 149.8275	500	0	1	0	0	0
P3	S 17.5386 W 149.8259	450	0	0	0	1	0
P4	S 17.5350 W 149.8247	500	5	38	0	0	5
P5	S 17.5354 W 149.8248	400	5	7	0	0	2
P6	S 17.5390 W 149.8259	400	1	4	0	0	0
P7	S 17.5377 W 149.8268	400	0	5	0	0	8
3P Trail 1	S 17.5359 W 149.8206	N/A	0	2	0	0	0
3P Trail 2	S 17.5363 W 149.8204	N/A	0	1	0	0	0
3P Trail 3	S 17.5363 W 149.8204	N/A	0	1	0	0	0
3P Trail 4	S 17.5357 W 149.8188	N/A	0	3	0	0	0
3P Trail 5	S 17.5357 W 149.8188	N/A	0	7	0	0	0
3P Trail 6	S 17.5328 W 149.8117	N/A	0	1	0	0	0
3 Coconuts Site 1 (C1)	S 17.6792 W 149.8275	250	0	0	0	0	0
C2	S 17.5413 W 149.8269	200	0	0	0	3	2
C3	S 17.5436 W 149.8280	400	0	0	0	2	0
C4	S 17.5450 W 149.8349	200	0	15	0	0	0
C5	S 17.5444 W 149.8349	100	0	18	0	0	0
C6	S 17.5357 W 149.8188	50	0	9	0	0	0
Opunohu Bay	S 17.5169 W 149.8493	400	0	0	24	0	0
Total			15	113	24	6	17

APPENDIX C

Tables showing the date, individual number, behavioral status, and shell length and width for the morning, afternoon, and night observations.

Morning

Date	Individual	Behavioral Status	Shell Length/ Width (mm)
10/25/14	MHM001	Inactive	15 x 6
10/25/14	MHM002	Active	16 x 6
10/25/14	MHM003	Inactive	16 x 7
10/25/14	MHM004	Active	17 x 6
10/25/14	MHM005	Inactive	12 x 7
10/25/14	MHM006	Inactive	---
10/25/14	MHM007	Inactive	20 x 7
10/25/14	MHM008	Inactive	---
10/25/14	MHM009	Inactive	17 x 7
10/25/14	MHM010	Active	17 x 7
10/30/14	MHM016	Inactive	17 x 8
10/30/14	MHM002	Inactive	15 x 7
10/30/14	MHM012	Inactive	15 x 6
10/30/14	MHM013	Active	13 x 6
10/30/14	MHM005	Inactive	15 x 7
10/30/14	MHM014	Inactive	12 x 5
10/30/14	MHM015	Inactive	15 x 8
10/30/14	MHM008	Inactive	16 x 7
10/30/14	MHM009	Inactive	15 x 7
10/30/14	MHM011	Inactive	16 x 8
11/3/14	MHM017	Inactive	7 x 4
11/3/14	MHM002	Inactive	16 x 7
11/3/14	MHM012	Inactive	---
11/3/14	MHM018	Inactive	16 x 6
11/3/14	MHM020	Inactive	11 x 6
11/3/14	MHM021	Inactive	15 x 7
11/3/14	MHM015	Active	16 x 8
11/3/14	MHM022	Inactive	15 x 7
11/3/14	MHM019	Inactive	15 x 6
11/3/14	MHM023	Inactive	15 x 6

Afternoon

Date	Individual	Behavioral Status	Shell Length/ Width (mm)
10/23/14	MHM001	Inactive	13 x 6
10/23/14	MHM002	Inactive	15 x 7
10/23/14	MHM003	Inactive	15 x 7
10/23/14	MHM004	Active	16 x 6
10/23/14	MHM005	Inactive	12 x 5
10/23/14	MHM006	Inactive	10 x 5
10/23/14	MHM007	Inactive	20 x 8
10/23/14	MHM008	Inactive	14 x 6
10/23/14	MHM009	Inactive	20 x 8
10/23/14	MHM010	Active	16 x 7
10/29/14	MHM001	Inactive	13 x 6
10/29/14	MHM002	Inactive	15 x 7
10/29/14	MHM012	Inactive	13 x 8
10/29/14	MHM004	Inactive	15 x 7
10/29/14	MHM005	Inactive	13 x 7
10/29/14	MHM006	Inactive	11 x 6
10/29/14	MHM007	Inactive	15 x 6
10/29/14	MHM008	Inactive	---
10/29/14	MHM009	Inactive	15 x 7
10/29/14	MHM011	Inactive	15 x 8
11/5/14	MHM017	Inactive	17 x 4
11/5/14	MHM002	Inactive	16 x 7
11/5/14	MHM026	Inactive	16 x 8
11/5/14	MHM025	Inactive	10 x 5
11/5/14	MHM029	Inactive	18 x 7
11/5/14	MHM021	Inactive	16 x 8
11/5/14	MHM015	Inactive	16 x 6
11/5/14	MHM030	Inactive	21 x 9
11/5/14	MHM028	Inactive	7 x 4
11/5/14	MHM027	Inactive	9 x 5

Night

Date	Individual	Behavioral Status	Shell Length/ Width (mm)
11/15/14	MHM036	Active	11 x 6
11/15/14	MHM037	Inactive	---
11/15/14	MHM038	Inactive	---
11/15/14	MHM045	Inactive	---
11/15/14	MHM041	Active	---
11/15/14	MHM043	Inactive	17 x 6
11/15/14	MHM042	Active	---
11/15/14	MHM044	Active	---
11/15/14	MHM040	Inactive	12 x 6
11/15/14	MHM039	Active	---
11/19/14	MHM036	Active	11 x 6
11/19/14	MHM002	Active	16 x 7
11/19/14	MHM026	Active	16 x 7
11/19/14	MHM048	Active	13 x 6
11/19/14	MHM029	Active	15 x 7
11/19/14	MHM043	Active	17 x 6
11/19/14	MHM007	Active	18 x 7
11/19/14	MHM047	Active	---
11/19/14	MHM040	Active	12 x 6
11/19/14	MHM039	Active	---
11/20/14	MHM001	Active	15 x 6
11/20/14	MHM002	Active	16 x 7
11/20/14	MHM026	Active	16 x 8
11/20/14	MHM048	Active	13 x 7
11/20/14	MHM051	Active	13 x 6
11/20/14	MHM052	Active	12 x 6
11/20/14	MHM015	Active	17 x 6
11/20/14	MHM008	Active	16 x 7
11/20/14	MHM050	Active	11 x 7
11/20/14	MHM049	Active	13 x 6

APPENDIX D

Representative pictures of the three *Partulidae* species and *Euglandina rosea* observed in this study.

Samoana attenuata

Samoana diaphana

Partula taeniata

Partula taeniata

Euglandina rosea