THE EFFECTS OF HABITAT FRAGMENTATION ON THE ENDANGERED LAND SNAIL *PARTULA TAENIATA* IN MOOREA, FRENCH POLYNESIA

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Abstract. Endemic island species create unique opportunities to study morphologic and genetic patterns found only in that specific region of the world. However, these species often live in isolation and thus exhibit elevated vulnerability to introduced predation and human interference to their habitat. The Partulidae land snail genus has faced one of the most rapid instances of extirpation because of high levels of predation by the introduced predatory land snail *Euglandina rosea,* leaving most of the genus extinct or extremely endangered. To make matters worse, the last native Partula habitat on the island of Moorea has been impacted by habitat clearing and fragmentation that nearly destroyed their entire microhabitat. This study sought to examine the effects of this habitat fragmentation on the *Partula taeniata* population while also increasing knowledge of the population's demographics and behavior in their surviving habitat. To do this, extensive surveys were conducted in situ testing the hypothesis that the loss of foliage and canopy cover would cause negative effects on the snails' viability. The survey completed in this study showed more *P. taeniata* than ever recorded at this site by previous studies. However, they are also located in the smallest microhabitat out of all surviving Partulid populations. The population was most active under wet conditions and during the morning period under dry conditions. The *Partula taeniata* population is small but seemingly stable and increasingly at risk for extinction if permanent conservation efforts and habitat protection are not put into effect.

Key words: island ecosystems; endemic species; Partula*; Moorea; French Polynesia; predation; habitat fragmentation*

INTRODUCTION

Island ecosystems have provided centuries of vital research opportunities for scientists to observe unique lineages, evolutionary patterns, and instances of adaptive radiations (Darwin 1859, Crampton 1916, Emerson 2002, Gerlach 2016). Increased geographic isolation as well as low diversity and competition rates are characteristic to the small surface area of the island. These factors coupled with empty niches create the ideal circumstances for certain species to thrive and diversify in conditions not often available on the mainland (Clarke *et al*. 1969, Clarke *et al*. 1986). From the well-known reports on the Galapagos finches to more recent studies on Polynesian *Tetragnatha* spiders, such extensive instances of adaptive radiation and species differentiation make oceanic islands attractive models for evolution studies. (Darwin 1859, Gillespie 2002) High levels of isolation allow for specific morphological differentiation, genetic variations, and DNA studies to be explored through population genetics to increase what is known about evolutionary biology and ecology (Powell 1997). The high percentage of endemic species found on islands prompt an elevated need for increased conservation efforts.

Endemic island species in particular are at an increased risk for extinction as a result of population bottlenecks and inbreeding depression (Mayr 1942, Frankham 1998). The lack of large herbivores and predators leave organisms and fauna vulnerable to introduced species (Atkinson 1989, Paulay 1994). Human threats have been proven to result in significantly greater, negative impacts on islands than continental landmasses when the same amount of habitat has been compromised (Paulay 1994, Kier *et al*. 2009). Due to the minimal amount of land available for habitation, high levels of endemic richness, and increased risks for disruption, oceanic islands require an increased emphasis on conservation efforts in order to preserve as much global biodiversity as possible (World Conservation Monitoring Centre 1992, Kier *et al*. 2009).

Over the past century, many studies have been completed on Partulidae found on the Pacific islands, turning them into a model organism for evolutionary biology and origin studies (Lipton and Murray 1979, Gerlach 2016). Limited gene flow characteristic to isolated volcanic islands result in distinct lineages (Gouveia 2012). The native *Partula* land snails were first recorded in Capt. Cook's voyage and have since provided excellent opportunities for studies on adaptive radiation and differentiation of species within the Society islands (Clark *et al*. 1984, Gouveia 2012). Unfortunately, over the last half-century high levels of predation have led to the extirpation of many species of *Partula* (Hardesty-Moore 2014).

Introduction of a new invasive species to an area can change the dynamics of an entire ecosystem (Bayshtok *et al*. 2017). *Euglandina rosea* was introduced to the Society Islands in an effort to reduce the population of a pest species, the giant African land snail, *Lissachatina fulica*. Tragically, this biocontrol method failed as *E. rosea* preferred instead to prey on *Partula*, leading to the extinction of the majority of the Partulid genus (Clark *et al*. 1984). The partulids show one of the most extreme rates of extinction ever recorded in scientific history (Gerlach 2016). By 1987, all populations of *Partula* in were believed to be extinct in the wild, with efforts being made by the International Union for the Conservation of Nature to preserve the last five species in zoo habitats (Murray *et al*. 1987, Lee *et al*. 2009). However, more recent studies found residual populations of *Partula* enduring the effects of the invasion on a few of the Society islands (Cunningham *et al*. 1996). Scientist Carol Hickman discovered a single population of *Partula taeniata* in 2001 persisting in a microhabitat in Opunohu Bay on the island of Moorea (Lee *et al*. 2009). This single population of *P. taeniata* is suspected to be the only surviving native *Partula* population on the entire island of Moorea. In a recent survey effort of the Society Islands, this population was found to be one of the healthiest populations out of all species observed (Gerlach 2017).

The health of this population in a mangrove fern (*Achrostichum aureum*) estuarine microhabitat is believed to be an effect of the substantial land crab population and high salinity from the nearby river estuary. This combination of factors keeps the *Euglandina* from encroaching, and thus the Opunohu Bay habitat acts a unique refuge for *Partula* (Gerlach 2017). The *P. taeniata* population was last studied in August of 2017; the population was found to be existing at a higher density than any other recorded Partulidae with a high proportion of juveniles (Gerlach 2017). However, this population also exists in one of the smallest habitats out of all recorded *Partula* species (Gerlach 2017).

In the last two years this microhabitat has been extensively cleared and burned, causing habitat fragmentation and edge effects to increase for this endangered snail population. The overhead shade of the canopy cover has been shown to be a necessary variable for *Partula;* by keeping the microhabitat cool and humid *Partula* are significantly more likely to thrive (Hardesty-Moore 2014). Additionally, the leaf litter from the canopy cover is necessary for providing food for the land crab population. Past studies have found that temperature, relative humidity, and light all significantly affect the viability of the Partulidae (Gouveia 2012). *Partula* are extremely vulnerable to changes in their environment. Even when bred in captivity entire populations have gone extinct due to minimal disturbances within the habitat (Gouveia 2012). With the intensive clearing and burning of the microhabitat over the past few years, much of the canopy cover has been lost. In recent months the destruction has been halted due to concerns voiced by scientists about the *P. taeniata* population. The effects of this habitat fragmentation are suspected to have negative consequences on the *Partula* population, but have not yet been tested.

To make matters worse, the overhead canopy cover and foliage that has been cleared away has also taken away the factors necessary for the viability of the tree snails' main food source, microorganisms growing on leaf biofilm (O'Rorke *et all*. 2015). Humidity and shade are vital for providing the necessary damp surface for the colonization of microorganisms on biofilm (Gaylarde and Morton 2009). By reducing the overhead canopy, it is very possible that the microorganism communities growing on the ferns' biofilm have also been affected. Without a proper diet, snail populations in captivity have experienced detrimental impacts to their survival and reproductive success (Gouveia 2012).

The present study sought to examine the effects of this habitat destruction. This was done by exhaustively surveying the current population distribution, density, and health in comparison to previous surveys. In addition, samples were taken of the *Partula*'s suspected food source -microorganisms located on the mangrove ferns' biofilm layer- from across the in-tact and destroyed habitat. Behavioral assessments were then completed and compared to previous studies from before the habitat clearing occurred. I expected to find a small, dense population of *Partula taeniata* rebuilding in size compared to surveys completed during recent years. Three specific questions were addressed: (1) What are the effects of habitat fragmentation on the health, density, and distribution of the *Partula* taeniata (2) Does the behavior of *P. taeniata* change at different times of the day under varying weather and conditions? (3) Which microorganisms are fed on by *Partula* and how are these communities of microorganisms influenced by the loss of canopy cover?

METHODS

Study Site

The main study site was located at the head of Opunohu Bay, on the island of Moorea in French Polynesia (Figure 1).

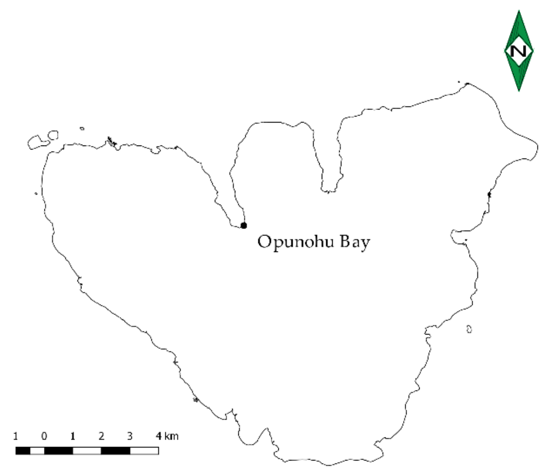

FIG. 1. The site surveyed in this study

The site approximately encompassed 20x30 m² and was surrounded by the main road on the north side, shrimp farm on the south side, the Opunohu river estuary to the east and the Belvedere side road to the west. The primary habitat for the *Partula taeniata* are the mangrove ferns, *Achrostichum aureum (*Appendix A, Fig. 8). These large herbaceous ferns are found in wet estuarine zones in high intertidal regions. This species often colonizes disturbed or open areas and is both fast growing and difficult to remove once it has overtaken the system (Ellison et all. 2010). This site underwent two periods of habitat clearing, first in 2010 and then again in 2015 leading to the majority of the original site's foliage being cleared away (See Appendix B, Fig. 9). This reduced the area of the Opunohu Bay site from an estimated 100x60m² to the current 20x30m². The habitat destruction has recently been halted for environmental concerns.

Animal Subjects

The primary organism I studied was the native Pacific snail, *Partula taeniata (*Appendix A, Fig. 6 & Fig. 7). The common name for this terrestrial gastropod is the Moorean viviparous tree snail (Mollusc Specialist Group 1996). Identification of *P. taeniata* was first completed using photos from previous studies and were then confirmed by an expert (Trevor Coote, pers. com.) (Coote 1999, Coote 2004, Coote 2007, Maher 2010, Gerlach 2017). I observed the organisms in situ without collection, while attempting to minimize disturbance as much as possible.

(1) Snail density and distribution survey

I surveyed the site for *Partula taeniata* density and distribution surveys. The most recent survey of this population was conducted in August of 2017, during which the population was estimated to be ~40 individuals (Gerlach 2017). Because of the small expected sample size, I surveyed all ferns and counted all individuals present. In short, I attempted to conduct an exhaustive survey of the entire *P. taeniata* population. Past studies have shown that *Partula* mobility is so low that there are genetic differences between natural populations only short distances apart (20m or less) so movement beyond the survey area was not predicted to be an issue (Clarke 1969).

Every fern was given a letter identity and each snail located on a given fern was given a numbered identity. In the field, I attached a flag to the base of each fern upon which *P. taeniata* were located, and marked the flag with the corresponding fern letter and *Partula* number(s). For each fern, I collected information on the height which a *P. taeniata* individual was found, what percentage of canopy cover each fern was located under, which side of the leaf the individual was found. I also took GPS points, recording the longitude and latitude for each fern upon which a *Partula* snail was found (Appendix A, Table 1). To estimate canopy cover four readings were taken and averaged using a spherical densiometer. I grouped *Partula taeniata* into one of three age categories based on the shell length and development. Juveniles were categorized as being less than ¾ of the average shell length of the adults. Subadults consisted of snails who were greater than ¾ of the average shell length of the adult *Partula* but do not yet exhibit a developed ridge on the front of the shell. Adults possessed the developed ridge on their shells.

To test for the relationship between canopy cover, number of *P. taeniata* found and snail age I ran an ANOVA -analysis of variance-followed by a Tukey posthoc pairwise analysis. To test for the relationship between snail height on the fern, number of snails found, and snail age I again ran an ANOVA followed by a Tukey posthoc test. This information was compared to population densities and distributions found in past years in order to estimate how the current population compares and if the recent habitat fragmentation was having effects on the *Partula*.

(2) Relationship between activity and time of day and/or wetness

Trips were made to the site on various sunny and rainy occasions at three different times of the day: morning (0700-1000), afternoon (1200-1500), and evening (1900-2200). Observations were made on the snails' activity based on methods and results from previous studies and preliminary observations: active (body visible outside of the shell) or inactive (body retracted inside of the shell.) To test if there was a significant difference in activity among the three times of day as well as between wet and day days and among the three age groups I completed an ANOVA followed by a Tukey posthoc test.

(3) Identification and locations of microorganisms on the biofilm of the mangrove ferns

To collect microorganism samples from the fern fronds, I used a knife to scrape the biofilm off mangrove fern leaves onto a microscope slide. This task required the fern leaves to be wet; as a result, I sampled after a recent session of rain. Biofilm samples were taken from five ferns on which a *Partula* snail was found as well as randomly from five ferns located in two different percentage groups of canopy cover. In order to ensure random sampling, the non- *Partula* ferns were placed in two groups corresponding to percentage of canopy cover at 0-65% and 85-100%. Within each group the ferns were given a specific number and a random number generator was used to determine which ferns to sample for microorganisms. Samples were transported by hand back to the lab and observed under a microscope to determine which microorganisms were present.

The relationship between the percentage of canopy cover and community composition of microorganisms was hypothesized to vary with different microorganisms being found in low percentages of canopy cover versus at higher percentages of canopy cover.

Statistical Analyses

All analyses for this study were performed in R Studio with an alpha value set equal to 0.05.

RESULTS

Population Surveys

85 *Partula taeniata* were found in total while surveying the population in Opunohu Bay; 58 were juveniles, 10 were subadults, and 17 were adults. The site's total area has been measured to be 4000m^2 with an estimated coverage of 200 mangrove ferns. The *Partula* were found in a smaller area of 703m^2 with 150 to 200 densely packed ferns. See Table 1 in Appendix E for a list of detailed coordinates for each occupied fern's location.

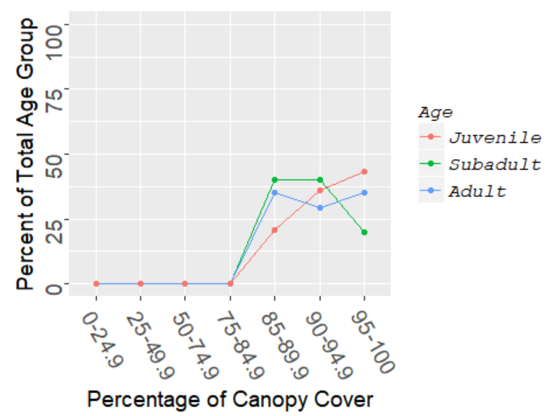

FIG. 2. A survey of the population distribution within the canopy cover.

All *Partula* were found under canopy cover greater than 85%. There were no significant differences (ANOVA, $p>.05$) among any *P. taeniata* age groups for where they preferred to live under canopy cover greater than 85%.

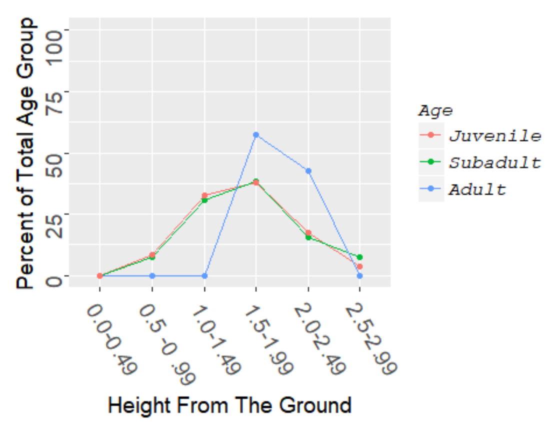

FIG. 3. A survey of the population distribution among the height of the ferns.

Within the population survey the heights where the *Partula* were found on the fern were observed. All individuals were found less than 3.0m high. The adult P. taeniata were found at a significantly more restricted height preference than the juveniles and subadults. (ANOVA, p-value≤.001)

To view all surveyed variables and findings reference Table 2 in Appendix D.

Behavioral Observations

Results show that significantly fewer adults are active during the afternoon compared to the morning and night (ANOVA, p-values≤ .01 and .001) as well as compared to juveniles and subadults during the afternoon under wet conditions (ANOVA, p-values≤ .001 and .05).

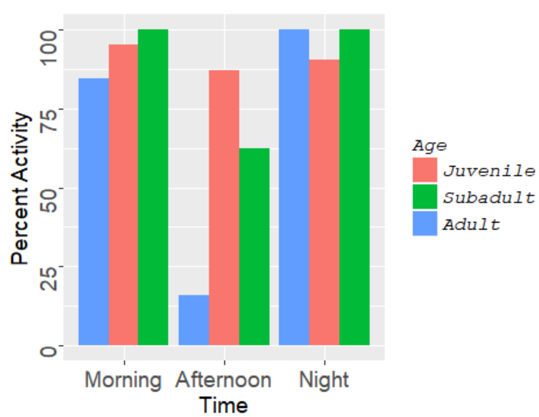

FIG. 4. A survey of Partula activity during different times of day under wet conditions.

Additionally, significantly more snails are active under wet conditions compared to dry conditions among all age groups (ANOVA, p-value≤ .001). All age groups are significantly more active in the morning compared to the afternoon and night under dry conditions ANOVA, p-values≤ .001 and .001). Adults are significantly less active than juveniles and subadults in the morning (ANOVA, p-values≤ .01 and .05).

All behavioral results are listed under the tables titled "Wet Activity Results" and "Dry Activity Results" (Appendix E, Table 3 & Table 4).

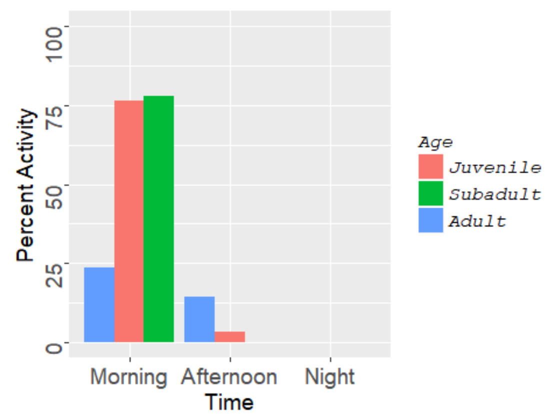

FIG. 5. A survey of Partula activity during different times of day under dry conditions.

Microorganism Surveys

The microorganisms found on the fern biofilm samples were few and inconsistent overall. Little data could be collected on the biofilm samples besides for the unidentifiable photos taken of the microorganisms found on each microscope slide. Not enough microorganisms were recognized to allow for running statistical analyses.

DISCUSSION

Field Surveys

The results of the population survey indicate that the *Partula* population in Opunohu Bay is one of the healthiest and largest populations in the Society Islands. However, it also is contained in the smallest microhabitat out of all surviving populations.

Canopy cover has been observed to have a significant effect on the *Partula*'s habitat preference (Fig. 2), with the land snails only being found under canopy cover of 85% or higher. The ferns located at this site also show this preference for increased canopy cover with only five ferns found within a canopy cover less than 85%. The Opunohu habitat shows signs of ferns having been located in a larger area previously that were either destroyed by the habitat clearing or died due to drying out from the increased heat and sunlight shining from the lack of overhead canopy (See Appendix B, Fig. 9).

Only the adult *Partula* differ from the bell curve within the preferred height on the fern (Fig. 3). Adults may show such a limited height preference due to their larger size and increased vulnerability to drying out. The adult *P. taeniata* were only found between 1.5-2.5m of height on the mangrove ferns surveyed. Given that finding, they may prefer a more specific wetness and humidity level only available at that height range.

Behavioral Observations

The results of the activity observations indicate that the *Partula*'s activity is significantly increased during wet weather conditions compared to dry weather conditions (Fig. 4 & Fig. 5). This could reflect the land snails' preference for conditions wet enough to allow for movement without the risk of drying out. The adult *P. taeniata* showed a significant decrease in activity during the afternoon under wet conditions. This could be reflective of the adult *Partula* snails being more sensitive to increased temperatures and sunlight exposure that often occur during the latter part of the day.

Contrary to previous surveys, under dry conditions the *Partula* seemed to be most active in the morning (Fig. 5). This is most likely attributed to the low temperatures and high levels of moisture expected to occur around sunrise. More data would need to be taken to confirm this. On sight, moisture on the ferns was still present around sunrise but dried up by afternoon and stayed dry into the evening. The adults were significantly less active than the juveniles and subadults during the morning under dry conditions (Fig. 5). This is most likely due to the same factors as previously mentioned with the adult *Partula* snails being more sensitive to higher temperatures, sunlight, and dryness.

Microorganism Samples

The microorganisms collected from the ferns showed no visible differences between sample groups or relationship with percentage of canopy cover present. This could reflect that the canopy cover has no effect on the microorganism communities that grow there. However, this result could be that the samples were taken under conditions which were too dry for scraping the biofilm or that the samples weren't comprehensive enough for the communities present on the fern. The status of the microorganisms is extremely important as they act as food for the *Partula.* If the microorganisms are lost with the lack of canopy cover then the surviving *P. taeniata* are likely to die out as well.

Broader Implications

This study demonstrates the importance in preserving the remaining *Partula* species. The *Partula taeniata* population at the head of Opunohu Bay is the last native *Partula* population on the entire island of Moorea and one of a small fraction of species of Partulidae living in French Polynesia. Their population is seemingly stable now, but unlikely to continue holding on without preservation of the increasingly reduced area of foliage containing their population's preferred living conditions. Opunohu Bay is the smallest surviving microhabitat (20x30m^2) in all of French Polynesia. The high salinity from the nearby river estuary coupled with the large coconut land crab population occupying the ground and leaf litter makes the Opunohu Bay site a natural refuge habitat in an otherwise unviable island for Partula snails. Reintroduction efforts are being made elsewhere on Moorea, but none are in an area free from predation like the *Partula taeniata* species' habitat and thus have not been largely successful.

We have seen through the Partulid genus how human interference and species introductions can have devastating chain-reaction effects if not planned well-enough beforehand. The extirpation of the Partulidae genus is one of the most extreme and rapid examples of extinction to have ever been recorded in scientific history.

The most important aspect to consider for increasing this species' chances for survival is human action. By making this site a permanently conserved area and increasing awareness surrounding *Partula* in French Polynesia they stand a better chance of surviving for years to come. We can make a worthwhile difference for the future conservation of endemic island species if more people understand the risks of habitat fragmentation and possible environmental effects. If permanent conservation efforts are not upheld at this site, we stand to lose the last of the native *Partula* species on Moorea, an incredible loss of research opportunities and even more so for the biodiversity on the Polynesian islands.

Future Studies

In the future, much more research needs to be completed within all *Partula* species to expand our knowledge of the current conditions and stability of the Partulid genus. It would be beneficial to look further into how the microorganism communities depend on the canopy cover. If given more time I would like to take more extensive samples from multiple fronds from every fern found at this site to obtain a comprehensive understanding of which microorganisms are living there. I would like to compare these samples along a canopy cover gradient to see if there is a relationship between the cover percentage and the number of microorganisms that are found on that frond. It is important to know if the microorganisms are affected by the loss of canopy cover as they are the suspected food source for *P. taeniata*.

In addition, if given the time I would like to take samples from the fern in front of active *Partula* and then of their slime to see if some microorganisms are not found in the slime, indicating they were eaten by the *Partula taeniata* individual. Although assumptions have been made and artificial diets have been developed in locations where captive *Partula* populations are raised, there have been no published studies examining what any species of the snails are eating.

It would also be interesting and beneficial to look further into the behavior of the *Partula* as little is currently known about any of the species' behavioral preferences in the wild. Some examples of this include examining their preferred humidity, light, and temperature conditions more closely. Further studies could also be taken to look more closely at the weather and daytime preferences of the adult *P. taeniata* to narrow down the exact reason why they exhibit a narrower preference range compared to juveniles and subadults.

If the stability of this population is to be prioritized, further surveys and observation must be continued over the years. Conservation efforts must be made and permanently upheld if we ever hope to bring these species off the critically endangered species list.

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Literature Cited

Atkinson, I. 1989. Introduced animals and extinctions. in D. Western and M.C. Pearl, editors. Conservation for the Twenty-first Century. Oxford University Press, New York and Oxford.

Bayshtok, G., S. Bayshtok, and K. Prior. 2017. Restoring invaded ecosystems: Do native communities recover from invasive species management? Research Days Student Posters. 1

Clarke B., and J. Murray. 1969. Ecological Genetics and Speciation in Land Snails of the Genus Partula. Biological Journal of the Linnean Society. 1: 31–42.

Clarke B., J. Murray, and M.S. Johnson. 1984. The extinction of endemic species by a program of biological control. Pac Sci. 38: 97-104.

Clarke B., J. Murray, E. Murray, and M.S. Johnson. 1987. The Extinction of Partula on Moorea. Pac Sci. 42: 3-4

Collen B., L. McRae, S. Deinet, A. De Palma, and T. Carranza. 2011. Predicting how populations decline to extinction. Philosophical Transactions of the Royal Society B: Biological Sciences 366: 2577–2586.

Coote, T., E. Loeve, J-Y Meyer, and D. Clarke. 1999. Extant populations of endemic partulids on Tahiti, French Polynesia. Oryx 33:215-222

Coote, T., D. Clarke, and C.J. Hickman. 2004. Experimental release of endemic Partula species, extinct in the wild, into a protected area of natural habitat on Moorea. Pacific Science 58:429-434.

Coote, T. 2007. Partulids on Tahiti: Differential persistence of a minority endemic taxa among relict populations. American Malacological Bulletin 22:83-87.

Cunningham, A. A., P. Daszak,, S.K. MacGregor, I. Foster, D. Clarke, P. Pearce-Kelly. 1996. Mortality of endangered snails of the genus Partula: Preliminary results of pathologic investigations. J. Zoo Wild. Med. 27(1): 19- 27.

Crampton, H. E. 1916. Studies on the variation, distribution, and evolution of the genus Partula. The species inhabiting Tahiti. Carnegie Institution Washington Publishing 228: 131

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. D. Appleton and Company. 1: 1-466

Ellison, J., N.E. Koedam, Y. Wang, J. Primavera, O. Jin Eong, J. Wan-Hong Yong, and V. Ngoc Nam. 2010. Acrostichum aureum. The IUCN Red List of Threatened Species 2010

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.

Gaylarde, C., and G. Morton. 2009. Deteriogenic biofilms on buildings and their control: A review. The Journal of Bioadhesion and Biofilm Research. 14(1)

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

Gerlach J. 2001. Predator, prey and pathogen interactions in introduced snail populations. Anim Conserv. 4: 203-209.

Gerlach, J. 2016. Icons of Evolution: Pacific Island tree-snails of the family Partulidae. Phelsuma Press.

Gerlach, J. 2017. Partula survival in 2017, a survey of the Society islands. Unpublished.

Gouveia, A. 2012. Investigation of the Factors Affecting the Populations Dynamics of Captive Partula Snails. Thesis for PhD Advisor: Quicke DLJ, Leather SR.

Hardesty-Moore, M. 2014. On the edge of extinction: distribution and behavior of the endangered Partulid snails of Moorea, French Polynesia. "Biology and Geomorphology of Tropical Islands" class, University of California, Berkeley: Student Papers. [http://ib.berkeley.edu/moorea/uploads/6/6/8/3/6683664/molly_hardesty-moore_moorea_final_paper.pdf]

Johnson MS., J. Murray, B. Clarke. 1986. Allozymic similarities amng species of Partula on Moorea. Heredity. 56: 319-327.

Kier G., H. Kreft, T. Ming Lee, W. Jetz, P.L. Ibisch, C. Nowicki, J. Mutke, W. Barthlott. 2009 A global assessment of endemism and species richness across island and mainland regions. National Academy of Sciences. 106(23): 9322-9327

Lee T., T. Coote, J. Bayward Burch, and D. Foighil 2009. Moorean Tree Snail Survival Revisited: A Multi-Island Genealogical Perspective. PubMed.

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" class, University of California, Berkeley: Student Papers. [http://ib.berkeley.edu/moorea/uploads/6/6/8/3/6683664/maher.final.paper.pdf]

Mayr, Ernst. 1942. Systematics and the origin of species, from the viewpoint of a zoologist. Harvard University Press, Cambridge.

Mollusc Specialist Group. 1996. *Partula taeniata ssp. nucleola*. The IUCN Red List of Threatened Species 1996

O'Rourke, R., B. Holland, G. Cobian, K. Gaughen, and A. Amend. 2016. Dietary preferences of Hawaiian tree snails to inform culture for conservation. Biological Conservation.198: 117-182

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.

QGIS Development Team 2015. QGIS Geographic Information System. Open Source Geospatial Foundation Project. [http://qgis.osgeo.org]

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna Austria. [http://www.R-project.org]

Wagner-Porter, K. 1999. The distribution and predation of tree snails on Moorea, French Polynesia. "Biology and Geomorphology of Tropical Islands" class, University of California, Berkeley: Student Papers. [http://ib.berkeley.edu/moorea/uploads/6/6/8/3/6683664/1999_final_papers.pdf]

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

APPENDIX A

Photos representing the *Partula taeniata* snails and *Achrostichum aureum* ferns observed at this site.

FIG. 6. Inactive adult P. taeniata.

FIG.7. Active subadult P. taeniata.

FIG. 8. Achrostichum aureum ferns.

APPENDIX B

Photos illustrating the habitat destruction at Opunohu Bay.

FIG. 9. Six photos exemplifying the extent of the most recent habitat destruction at the Opunohu Bay site.

APPENDIX C

Table recording the latitude and longitude for every fern upon which a Partula taeniata snail was found.

TABLE 1. GPS Coordinates

Fern ID	Latitude (W)	Longitude (S)
A	149◦50'57.6"	17◦31'00.9"
B	149◦50'57.6"	17◦31'01.0"
C	149◦50'57.4"	17◦31'00.6"
D	149◦50'57.3"	17◦31'00.4"
E	149◦50'57.2"	17◦31'00.4"
F	149◦50'57.4"	17◦31'00.4"
G	149◦50'57.5"	17◦31'00.5"
H	149◦50'57.2"	17◦31'00.3"
I	149◦50'57.2"	17◦31'00.3"
J	149◦50'57.2"	17◦31'00.2"
K	149◦50'57.1"	17◦30'59.9"
L	149◦50'57.0"	17◦31'00.0"
M	149◦50'57.1"	17◦30'59.8"
N	149◦50'56.9"	17◦30'59.9"
O	149◦50'57.0"	17◦31'00.6"
P	149◦50'56.7"	17◦31'00.3"
Q	149◦50'56.8"	17◦31'00.2"
R	149◦50'56.7"	17◦31'00.3"
S	149◦50'56.7"	17◦31'00.2"
T	149◦50'56.7"	17◦31'00.2"
U	149◦50'56.8"	17◦31'00.1"
V	149◦50'56.7"	17◦30'59.8"
W	149◦50'57.1"	17◦31'00.1"
X	149◦50'56.8"	17◦31'00.1"
Y	149◦50'56.8"	17◦31'00.1"
Z	149◦50'57.2"	17◦31'00.2"
AA	149◦50'57.3"	17◦31'00.0"
BB	149◦50'57.4"	17◦31'00.2"
CC	149◦50'57.1"	17◦31'00.1"
DD	149◦50'57.2"	17◦31'00.2"
EE	149◦50'57.1"	17◦31'00.1"
FF	149◦50'57.2"	17◦31'00.0"
GG	149◦50'57.1"	17◦31'00.1"
HH	149◦50'57.0"	17◦30'59.9"
II	149◦50'57.1"	17◦31'00.2"

APPENDIX D

Table recording the date, fern ID, snail ID, location on the fern leaf, height the snail was found on the fern from the ground, length of the shell, age, time the snail was found, and percent canopy cover above the fern the snail was found on.

TABLE 2. *P. taeniata's* population density and distribution across the Opunohu Bay site.

Date	Fern ID	Snail ID	Location On Leaf	Height From Ground	Length of Shell (mm)	Age	Time	Percent Cover
10/19/2017	A	1	Bottom	1.45	8	Juvenile	13:56	89.34
10/19/2017	A	2	Top	2.2	6	Juvenile	13:58	89.34
10/19/2017	A	3	Bottom	1.65	10	Subadult	14:33	89.34
10/19/2017	A	4	Bottom	1.5	14	Subadult	14:35	89.34
10/19/2017	A	5	Bottom	1.8	18	Adult	14:41	89.34
10/19/2017	A	6	Bottom	1.8	16	Subadult	14:41	89.34
10/19/2017	A	7	Bottom	1.9	18	Adult	14:42	89.34
10/19/2017	A	8	Bottom	2.3	16	Subadult	14:45	89.34
10/19/2017	B	9	Bottom	0.75	8	Juvenile	14:58	87.78
10/20/2017	C	10	Top	1.25	8	Juvenile	13:01	93.5
10/20/2017	C	11	Top	1.1	5	Juvenile	13:03	93.5
10/20/2017	C	12	Bottom	0.8	15	Subadult	13:05	93.5
10/20/2017	C	13	Bottom	0.55	6	Juvenile	13:21	93.5
10/20/2017	C	14	Top	0.7	5	Juvenile	13:36	93.5
10/20/2017	D	15	Bottom	1.8	7	Juvenile	14:47	96.62
10/20/2017	D	16	Bottom	1.25	5	Juvenile	14:48	96.62
10/20/2017	D	17	Bottom	1.25	6	Juvenile	14:58	96.62
10/20/2017	E	18	Bottom	1.4	17	Adult	15:05	97.14
10/20/2017	E	19	Bottom	1.35	9	Juvenile	15:08	97.14
10/21/2017	F	20	Bottom	1.2	8	Juvenile	13:02	93.76
10/21/2017	F	21	Bottom	1.15	5	Juvenile	13:02	93.76
10/21/2017	F	22	Bottom	1.4	6	Juvenile	13:05	93.76
10/21/2017	F	23	Bottom	1.45	8	Juvenile	13:05	93.76
10/21/2017	F	24	Bottom	1.65	6	Juvenile	13:08	93.76
10/21/2017	F	25	Bottom	2	7	Juvenile	13:09	93.76
10/21/2017	G	26	Bottom	1.3	7	Juvenile	13:15	97.44
10/21/2017	G	27	Bottom	1.5	8	Juvenile	13:18	97.44
10/21/2017	H	28	Bottom	1.3	8	Juvenile	13:20	97.44
10/21/2017	H	29	Bottom	1.9	9	Juvenile	13:21	97.44
10/21/2017	I	30	Bottom	1.3	18	Adult	13:28	96.1
10/21/2017	I	31	Bottom	1.8	11	Juvenile	13:30	96.1
10/21/2017	I	32	Bottom	1.45	10	Juvenile	13:30	96.1
10/21/2017	I	33	Bottom	1.65	18	Adult	13:31	96.1

10/21/2017	J	34	Bottom	1.95	10	Juvenile	13:43	94.8
10/21/2017	J	35	Bottom	2.15	8	Juvenile	13:43	94.8
10/21/2017	K	36	Bottom	1.6	13	Subadult	13:45	97.71
10/21/2017	L	37	Bottom	2.5	15	Subadult	13:59	95.92
10/21/2017	M	38	Bottom	1.7	12	Juvenile	14:04	95.58
10/21/2017	M	39	Bottom	1.45	12	Juvenile	14:06	95.58
10/21/2017	M	40	Bottom	1.45	11	Juvenile	14:06	95.58
10/21/2017	M	41	Bottom	1.25	10	Juvenile	14:06	95.58
10/21/2017	M	42	Bottom	1.4	5	Juvenile	14:10	95.58
10/21/2017	L	43	Bottom	2	7	Juvenile	14:12	95.92
10/21/2017	N	44	Bottom	1.8	11	Juvenile	14:15	97.62
10/21/2017	O	45	Bottom	1.7	6	Juvenile	15:00	88.3
10/21/2017	O	46	Bottom	1.6	16	Adult	15:02	88.3
10/21/2017	O	47	Bottom	2.3	16	Adult	15:02	88.3
10/21/2017	O	48	Bottom	1.95	5	Juvenile	15:04	88.3
10/21/2017	P	49	Bottom	1.1	12	Juvenile	15:10	92.46
10/21/2017	P	50	Bottom	0.65	11	Juvenile	15:16	92.46
10/21/2017	Q	51	Bottom	1.65	7	Juvenile	15:18	93.24
10/21/2017	Q	52	Bottom	1.2	9	Juvenile	15:18	93.24
10/21/2017	Q	53	Bottom	1.2	15	Subadult	15:18	93.24
10/21/2017	Q	54	Bottom	1.25	6	Juvenile	15:20	93.24
10/21/2017	Q	55	Bottom	1.8	10	Juvenile	15:23	93.24
10/21/2017	Q	56	Bottom	1.85	10	Juvenile	15:23	93.24
10/21/2017	R	57	Bottom	1.4	17	Adult	15:30	86.48
10/21/2017	S	58	Bottom	1.75	6	Juvenile	15:33	94.28
10/21/2017	T	59	Bottom	1.65	8	Juvenile	15:38	94.02
10/21/2017	U	60	Bottom	1.7	6	Juvenile	15:45	97.92
10/21/2017	U	61	Bottom	1.8	11	Juvenile	15:50	97.92
10/21/2017	U	62	Bottom	2	7	Juvenile	15:50	97.92
10/24/2017	V	63	Bottom	1.7	8	Juvenile	14:27	93.5
10/24/2017	V	64	Bottom	2.25	14	Subadult	14:27	93.5
10/24/2017	V	65	Bottom	2.2	16	Adult	14:28	93.5
10/24/2017	W	66	Bottom	2.15	18	Adult	14:30	94.02
10/24/2017	W	67	Bottom	2.15	16	Adult	14:30	94.02
10/24/2017	X	68	Bottom	1.95	18	Adult	14:39	88.89
10/24/2017	Y	69	Bottom	1.9	17	Adult	14:39	94.64
10/24/2017	Y	70	Bottom	2.15	6	Juvenile	14:53	94.64
10/24/2017	Z	71	Bottom	2.05	9	Juvenile	15:02	98.44
10/24/2017	AA	72	Bottom	1.55	6	Juvenile	15:09	88.5
10/28/2017	CC	73	Bottom	1.7	13	Subadult	6:34	92
10/28/2017	BB	74	Bottom	1.8	18	Adult	7:00	95.5

10/28/2017	CC	75	Bottom	1.5	8	Juvenile	6:37	92
10/28/2017	DD	76	Bottom	1.75	12	Juvenile	6:45	92
10/28/2017	EE	77	Bottom	2.6	10	Juvenile	6:45	95.5
10/28/2017	DD	78	Bottom	2.05	8	Juvenile	6:53	92
10/28/2017	FF	79	Top	2.3	12	Juvenile	7:07	98
10/28/2017	GG	80	Bottom	1.8	9	Juvenile	7:18	97.25
10/28/2017	HH	81	Bottom	2.05	12	Juvenile	7:27	93
10/28/2017	HH	82	Bottom	1.5	18	Adult	7:27	93
10/28/2017	II	83	Bottom	2.3	17	Adult	7:35	97.5
10/28/2017	II	84	Bottom	2.7	6	Juvenile	7:35	97.5
10/28/2017	II	85	Top	2.2	17	Adult	7:43	97.5

APPENDIX E

Tables recording the behavioral status and age of the *Partula taeniata* observed during the morning, afternoon, and night under wet and dry conditions.

TABLE 3. Wet Activity Results.

Time	Age	Percent Active	Sample Size
Morning	Juvenile	95.2	21
Morning	Subadult	100	7
Morning	Adult	84.6	13
Afternoon	Juvenile	87. 1	31
Afternoon	Subadult	62.5	8
Afternoon	Adult	15.8	22
Night	Juvenile	90.5	21
Night	Subadult	100	11
Night	Adult	100	10

TABLE 4. Dry Activity Results.

Time	Age	Percent Active	Sample Size
Morning	Juvenile	76.5	34
Morning	Subadult	77.8	9
Morning	Adult	23.5	16
Afternoon	Juvenile	3.2	31
Afternoon	Subadult	0	4
Afternoon	Adult	14.3	7
Night	Juvenile	0	26
Night	Subadult	0	4
Night	Adult	0	0