

EFFECTS OF COMPETITION AND FOREST TYPE ON SIZE AND ABUNDANCE
OF AN ARBOREAL SNAIL ALONG AN ELEVATIONAL GRADIENT

THESIS

Presented to the Graduate Council of
Texas State University-San Marcos
in Partial Fulfillment
of the Requirements

for the Degree

Master of SCIENCE

by

Susan K. Uthappuru, B.A.

San Marcos, Texas
August 2013

EFFECTS OF COMPETITION AND FOREST TYPE ON SIZE AND ABUNDANCE
OF AN ARBOREAL SNAIL ALONG AN ELEVATIONAL GRADIENT

Committee Members Approved:

Ivan Castro-Arellano, Chair

Floyd W. Weckerly

Joseph A. Veech

Approved:

J. Michael Willoughby
Dean of the Graduate College

COPYRIGHT

by

Susan K. Uthappuru

2013

FAIR USE AND AUTHOR'S PERMISSION STATEMENT

Fair Use

This work is protected by the Copyright Laws of the United States (Public Law 94-553, section 107). Consistent with fair use as defined in the Copyright Laws, brief quotations from this material are allowed with proper acknowledgement. Use of this material for financial gain without the author's express written permission is not allowed.

Duplication Permission

As the copyright holder of this work I, Susan K. Uthappuru, authorize duplication of this work, in whole or in part, for educational or scholarly purposes only.

ACKNOWLEDGEMENTS

I would first like to thank Dr. Ivan Castro-Arellano for taking me on as his graduate student and providing me the opportunity to take on this project. His patience and confidence in me as a student gave me the much-needed encouragement to carry on and keep improving upon myself. I would like to thank him, along with my other committee members, Dr. Joseph A. Veech and Dr. Floyd W. Weckerly for their countless hours of guidance and advice. Dr. Christopher P. Bloch was irreplaceable in providing me insight into the system, comments on my manuscript, and for allowing me to accompany him in the field in Puerto Rico. Lastly, I would like to thank my parents, William N. Kane, and my fellow classmates Desirae M. Weyland and Claire A. Parra for their continual support and assistance throughout my graduate school career.

This manuscript was submitted on July 5th, 2013.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	v
LIST OF TABLES	vii
LIST OF FIGURES	viii
ABSTRACT	ix
CHAPTER	
I. THESIS	1
Materials and Methods	4
Results	9
Discussion	11
APPENDIX A	31
APPENDIX B	32
APPENDIX C	38
APPENDIX D	39
LITERATURE CITED	43

LIST OF TABLES

Table	Page
1. Summary of AIC _c Model selection table showing variables influencing <i>P. caracolla</i> maximum shell size within the mixed forest transect.....	17
2. Coefficient estimates for intercept and predictors of <i>P. caracolla</i> maximum shell size in the mixed forest transect	18
3. Summary of AIC _c Model selection table showing variables influencing <i>P. caracolla</i> maximum shell size within the palm forest transect.....	19
4. Coefficient estimates for intercept and predictors of <i>P. caracolla</i> maximum shell size in the palm forest transect	20
5. Coefficient estimates for intercept and predictors of <i>P. caracolla</i> density in the mixed forest transect.....	21
6. Coefficient estimates for intercept and predictors of <i>P. caracolla</i> density in the palm forest transect.....	22

LIST OF FIGURES

Figure	Page
1. Topographic map of the location of sites for the elevational transects in mixed forest along the Sonadora creek.....	23
2. Diagram of the rectangular strata and internal plot arrangement used for sampling along the elevational transects at the LEF.....	24
3. <i>P. caracolla</i> maximum shell sizes (mm) per plot graphed against elevation (m).....	25
4. <i>P. caracolla</i> maximum shell size (mm) per plot graphed against elevation (m).....	26
5. <i>P. caracolla</i> maximum shell size (mm) per plot graphed against total snail density.....	27
6. Graph of <i>P. caracolla</i> average densities per plot in the mixed forest transect against elevation (m).....	28
7. Graph of <i>P. caracolla</i> average densities per plot in the palm forest transect against elevation (m).....	29
8. Distribution of <i>P. caracolla</i> shell sizes collected from the LFDP.....	30

ABSTRACT

EFFECTS OF COMPETITION AND FOREST TYPE ON SIZE AND ABUNDANCE OF AN ARBOREAL SNAIL ALONG AN ELEVATIONAL GRADIENT

by

Susan K. Uthappuru, B.A.

Texas State University-San Marcos

August 2013

SUPERVISING PROFESSOR: IVAN CASTRO-ARELLANO

Intra- and interspecific competition has been shown through numerous studies to negatively affect individual size and population densities of organisms. Along an elevational gradient, these competitive effects may intensify due to differences in environmental conditions. Elevational clines are known to give rise to changes in soils, vegetation, insolation and temperature, which can directly affect availability of resources, or even the organisms themselves. For terrestrial gastropods, which are at high risk of desiccation, increases in altitude pose a greater threat to survival in temperate systems,

but this relationship has not been studied in tropical mountains. I analyzed maximum size and mean densities of the Puerto Rican land snail, *Pleurodonte caracolla*, among two different groups of forest types along an elevational gradient to evaluate possible effects of intra- or interspecific competition. Maximum shell size was weakly correlated with total snail density and elevation in both forest types, and *P. caracolla* density was negatively correlated with elevation in both forest types. The high productivity of the study site likely reduces competition by providing an abundance of resources for all snails present. Low population densities are hypothesized to be due to temperature fluctuations, lower egg hatching success, and higher predation rates on juveniles. More studies are needed on gastropod populations in other tropical montane systems.

CHAPTER I

THESIS

An inverse relationship between individual body size and population density due to resource competition has become a widely documented pattern in biological sciences. As body size increases, so do resource requirements for space and food, thereby decreasing the number of individuals that can be supported in a given location. This association has been demonstrated for a number of different organisms across a wide array of habitats, from trout in California to brown bears in Sweden (Skogland 1983; Jenkins et al. 1999; Zedrosser et al. 2006; Drago et al. 2010). Literature on invertebrates is scarce, but several studies have investigated these patterns among groups of terrestrial gastropods.

Snail shell size variation has long been studied throughout the world, and is commonly used as a proxy of total body size of terrestrial gastropods (Goodfriend 1986). Studies have shown a decrease in shell size with increases in population densities, both in laboratory and field conditions (Williamson et al. 1976; Cameron and Carter 1979; Burla 1984; Baur and Baur 1990). Even under conditions where resources are abundant, interference competition through chemical cues in the mucous trails of some land snails have been shown to reduce activity of syntopic species, resulting in decreased growth rates (Oosterhoff 1977; Cameron and Carter 1979; Baur and Baur 1990). However, a variety of biotic and abiotic factors (e.g., vegetation, temperature, rainfall) play an important part in the shaping of these patterns, directly affecting resource

availability or even the organisms themselves (Goertz 1964; Mathis 1990; Hilderbrand et al. 1999; Pettorelli et al. 2001). Ectothermic invertebrates with low vagility like terrestrial snails, may be more susceptible to such environmental changes.

A recent study found that a Puerto Rican species, *Pleurodonte caracolla*, achieved largest adult shell sizes at highest population densities of conspecifics, as well as other snail species (Bloch and Willig 2009). *P. caracolla* is a generalist feeder, it is both detritivorous and herbivorous, capable of consuming a wide variety of foods and able to live on almost any tree species throughout the Luquillo Experimental Forest (LEF) (Heatwole and Heatwole 1978; Willig et al. 2011). This flexibility in diet combined with the high productivity of the area may likely decrease any limitations in resources, thereby eliminating any effects of competition (Bloch and Willig 2009). However, Bloch and Willig (2009) only examined size and abundance of *P. caracolla* within the lower elevation tabonuco forest. In the Luquillo Mountains of Puerto Rico there are four different forest types distributed along an elevational gradient. The tabonuco forest occurs at the lowest elevation and the dwarf, or elfin, forest at the highest. The palo colorado forest occurs between these two, and the fourth forest type, the palm forest, can be found throughout the elevational gradient, emerging in areas affected by severe disturbances (e.g., hurricanes; Presley et al. 2011; Willig et al. 2011). Within the LEF elevational gradient, forest type has been shown to affect abundances of various invertebrates. Many species, including *P. caracolla*, are found in greater densities in palm forests than in corresponding elevational mixed forests (Richardson et al. 2005; Willig et al. 2011). Palm litter has higher amounts of P, N, Ca, and other nutrients, than mixed litter, and palm fruits can provide phosphorus rich food for litter-dwelling

invertebrates. Additionally, palm fronds are heavy and form layers as they decay, which may provide greater stability and humidity for organisms at risk of desiccation (Richardson et al. 2005).

Along with different plant communities, increases in elevation bring about changes in temperature, rainfall and humidity in the LEF that also create different gastropod communities along the gradient (Willig et al. 2011). These environmental factors likely have a direct impact on snail sizes and population densities as well. Other studies have indeed shown an inverse relationship between shell size and elevation, but these have been restricted to temperate environments (e.g., the Swiss Alps; Burla and Stahel 1983; Baur and Raboud 1988). At the highest elevations of a temperate site “the light of the sun is up to twice brighter, the proportion of UV four times larger, the yearly average temperature ten degrees lower, the air is half as humid and the summer lasts less than half as long” (Burla and Stahel 1983, p. 105) as the lower elevations. However, in Puerto Rico, humidity is nearly constant throughout the elevational gradient, and average temperatures are lower by only 5° C at highest elevations (Presley et al. 2011; Willig et al. 2011).

In addition to environmental differences, snail species assemblages have also been shown to change with elevation, as in the Luquillo Mountains of Puerto Rico (Willig et al. 2011). While some species, like *P. caracolla*, occur at all elevations, others were found only at either low or high elevations. One species in particular, *Polydortes luquillensis*, produces a presumably defensive secretion (i.e. interference competition) that is detrimental to other snails, including *P. caracolla* (Heatwole and Heatwole 1978). *P. luquillensis* is not known to occur at the lower elevation of LEF, therefore effects of

interference competition may become more evident with increasing elevation (Willig et al. 2011).

The present study compares the relationship between snail densities on shell size of *P. caracolla* along dual elevational gradients in both mixed forest and exclusively palm forest transects. Within the LEF, overall gastropod abundance has been shown to decrease with increasing elevation (Presley et al. 2011; Willig et al. 2011). Therefore, it seems reasonable then to surmise that *P. caracolla* density, too, should decrease with increasing altitude in both mixed and palm forest transects. If *P. caracolla* does indeed show a positive correlation with shell size and population density, then size is also expected to decrease with elevation. Because densities are known to be significantly higher in palm forests, it is hypothesized that *P. caracolla* size should decrease in mixed forest types as elevation increases but remain constant in palm forests.

Materials and Methods

Study Area.—The Luquillo Experimental Forest (LEF) covers 11,300 ha in northeastern Puerto Rico. It is a Man and the Biosphere Reserve and a site in the National Science Foundation's Long-Term Ecological Research network. The LEF can be separated into three different elevational zones, each coupled with a different forest type (see Appendix A). The tabonuco forest occurs at lowest elevations, between 200-600 m a.s.l., and is the most widespread region of the LEF. It is dominated by a hardwood species, *Dacryodes excelsa*, with trees reaching 35 m tall and a canopy height of 20-39 m (Brown et al. 1983; Weaver and Murphy 1990; Reagan and Waide 1996). Rainfall averages 3.52 m annually, humidity is between 84-90%, and temperatures range between 21-25°C (Brown et al.

1983; García-Martínó et al. 1996). Cloud condensation begins at 600 m a.s.l., where the palo colorado forest begins, ending at around 900 m a.s.l. The dominant tree here is the colorado tree (*Cyrilla racemiflora*), with a dense branching canopy of 20 m (Brown et al. 1983; Weaver and Murphy 1990; Reagan and Waide 1996). Rainfall is estimated at 4.19 m annually, and temperatures fall between 19-23°C (García-Martínó et al. 1996). The elfin forest occurs above 900 m a.s.l. It averages 4.44 m of rainfall annually, a humidity >95%, with temperatures between 16-20°C (García-Martínó et al. 1996). The increased moisture results in nutrient leached, anoxic soils, yielding short shrubs and trees and an abundance of surface roots. Canopy height is 3-5 m, with *Calycogonium squamulosum*, occurring as the most abundant woody tree (Weaver and Murphy 1990). Elfin forest averages 4.44 m of rainfall annually, a humidity >95%, with temperatures between 16-20°C (García-Martínó et al. 1996). Palm forests are found throughout the elevational gradient in LEF. They grow on wet soils and steep slopes, and patches of regenerating forest that were created by treefalls or landslides associated with hurricanes (Brown et al. 1983). The forest is predominantly sierra palm (*Prestoea acuminata*) with a canopy of 17 m and little other tree or herbaceous species (Weaver and Murphy 1990). At mid-elevations, palm forests are the most productive forest type in this region (Richardson et al. 2005).

Study Organism.—*P. caracolla* is an arboreal land snail, with a maximum recorded shell diameter of 65.9 mm (Bloch and Willig 2009). It is a nocturnal, long-lived species (over 10 years; Heatwole and Heatwole 1978) found throughout all forest types and elevations of the LEF (Heatwole and Heatwole 1978; Presley et al. 2011; Willig et al. 2011). *P. caracolla* is hermaphroditic, and copulating individuals have been noted during all

months except September and November. Mating occurs more than once between more than one individual, and snails remain in breeding condition for at least two months per season. No information is known about clutch numbers or number of eggs per clutch (Heatwole and Heatwole 1978). During wet seasons, adults commonly occur on the trunks of trees with smooth bark, typically not exceeding heights of approximately 3 m in order to reduce risk of desiccation higher up in the canopy (Heatwole and Heatwole 1978; Alvarez and Willig 1993; Willig et al. 1998). Similarly, they appear to select for habitats with high ground cover and foliar density in closed canopy forest, and against habitats with higher insolation, such as treefall gaps with open canopies (Heatwole and Heatwole 1978; Cary 1992; Willig et al. 1998). Juveniles, due to their smaller size, have a higher surface area-to-volume ratio and, along with adults during the dry season, can be found more often under leaf litter or under rocks and logs (Heatwole and Heatwole 1978; Willig et al. 1998). *P. caracolla* is a generalist feeder, consuming a wide range of foods from dead and live leaves, flowers, fruits, fungi and diatoms (Heatwole and Heatwole 1978). Within the LEF, it shares its range with 44 other species of terrestrial snails, 5 of which are carnivorous (*Austroselenites alticola*, *A. concolor*, and genus *Oleacina*), and 26 of which forage above ground level, (Garrison and Willig 1996; Bloch and Willig 2009). In addition to carnivorous snails, other possible predators of *P. caracolla* include several species of birds, frogs and lizards, and the introduced black rat, *Rattus rattus* (Reagan and Waide 1996).

Data Collection.—Two transects were established along opposite banks of the Sonadora Creek watershed at the LEF. One transect included tabonuco, colorado, and elfin forest types (hereafter referred to as mixed forest), and the other was restricted to sites with only

palm forest. Each elevational transect consisted of 15 strata spaced at 50-m elevational increments, from 300-1000 m a.s.l. (Fig. 1), with one exception: due to a lack of sufficient contiguous palm stands, a 750 m elevational strata in palm stands could not be established. Each stratum was arranged parallel to the Sonadora Creek as a 0.1-ha rectangle (20 x 50 m). Palm forest strata were located within 1 km of corresponding mixed forest strata so as to minimize effects of other environmental factors. Each of these strata comprised 10 circular plots, each with a radius of 3 m. Circular plots were aligned in two parallel rows with 10 m between plot centers (Fig. 2).

Since *P. caracolla* is a nocturnal species, surveys were carried out between 20:00–4:00 hours and performed in the same manner as Bloch and Willig (2009). All surfaces (e.g. leaf litter, rocks, vegetation) of each sampling plot, from the forest floor up to a height of 3m, were surveyed by two to three individuals. Plots were surveyed for 15 minutes using headlamps (Petzl DUO LED 14 ACCU, Crollas, France). Substrate was disturbed as little as possible to reduce modification of long-term study plots. Every *P. caracolla* snail found was measured to the nearest 0.1 mm with dial calipers from the lip of the aperture to the most distal part of the shell, then released within the same plot as close as possible to the site of capture. All other species of snails were counted and recorded, but not measured. Plots were surveyed 3 times during the wet season (summer) in 2008, and sampling of plots was repeated only after completion of the full gradient (one run) in order to diminish effects of survey sequence on elevational patterns (Presley et al. 2011).

Maturation size assessment.—After data were collected for the elevational gradients, it was noted that information about the maturity of snails had been omitted. *P. caracolla*

growth ceases when snails reach sexual maturity, and size of juvenile snails that are still growing may not be relevant in the assessment of size and density relationships. In order to differentiate between juveniles and adults, I collected additional data in an attempt to determine mean size of maturity. Data for maturation size were collected separately from elevational data, and not on the elevational gradient. Snail data were gathered from the Luquillo Forest Dynamics Plot (LFDP) in the northwest region of the LEF, which is situated in tabonuco forest below 600 m a.s.l. (Bloch and Willig 2009). The LFDP is located within 1 km of the elevational transects sampled for the present study. Forty circular plots were spaced evenly within a rectilinear grid. Each plot was 3 m in radius, and plot centers were 60 m apart from all other adjacent plots. Using the same survey techniques described in the previous section, all *P. caracolla* snails found were measured to the nearest 0.1 mm with dial calipers and noted if they were juvenile or adult. Adults were easily distinguishable from juveniles by a closed umbilicus and thickened lip (Heatwole and Heatwole 1978).

Statistical Analysis.—Due to lack of substantial variance in snail densities between runs, repeated measures analysis was not attained. For each run, *P. caracolla* density, heterospecific density, and total snail densities were averaged for each plot. Then, densities were averaged again for each plot across all runs. Initially, I used average *P. caracolla* shell size per plot in the analyses. However, it was later noted that this created an artifact of average shell size due to uneven sample sizes at each plot/strata. Therefore, average shell sizes were discarded and maximum *P. caracolla* shell size for each plot was calculated and used instead for the analyses. Plots where no *P. caracolla* were found were not included in the analysis. I used least squares regressions to analyze the

following predictors for both transects: conspecific density, heterospecific density, total snail density, elevation, additive effects of elevation with each density group, and the interaction between elevation and each density group. After all models were fitted to the data, I used Akaike's Information Criterion corrected for bias (AIC_c) to select the model that best predicted the response variable, *P. caracolla* maximum shell size for each transect. Models with the lowest AIC_c values and highest r^2 values were considered for best fit.

A separate least squares regression was used to analyze the interaction between forest type (mixed versus palm transects) and elevation on *P. caracolla* densities. For the maturation size assessment, Welch's t-test was used to determine if there is a true difference in means of juvenile and adult shell sizes. All statistical analyses were performed using the program R version 2.11.1.

Results

A total of 3,963 *P. caracolla* shell sizes were recorded for the three runs from both LEF elevational transects. Slightly less (1,561) came from mixed forests (565, 494 and 502 for runs one, two and three, respectively) than from palm forests (total of 2,402; 933, 776 and 693 for runs one, two and three, respectively). Shell size ranged from 15.3 to 68.3 mm, with a mean shell size of 41.1 mm. Sixteen other snail species were identified throughout the gradient. In the mixed forest transect, average density (number of individuals per plot sampling event) was 5 for *P. caracolla* (range: 1-31), 7 for the rest of the gastropod species (range: 0-20), and 11 for total snail density (range: 1-40). In the palm forest transect, average density was 7 for *P. caracolla* (range: 1-40), 9 for all other

gastropod species (range: 1-27), and 18 for total snail density (range: 2-49). Maximum shell size of *P. caracolla* and average snail densities were first calculated for every plot for each run. Snail densities were then averaged together again across all three runs for each plot, resulting in a final sample size of 108 values from mixed forest and 129 values from palm forest that were used in the regression analysis. For the maturation size assessment a total of 58 *P. caracolla* adults and 157 juveniles were measured and recorded at the LFDP.

The AIC_c model selection analysis for the mixed forest transect resulted in 7 possible suitable models ($\Delta AIC_c < 4$; Table 1), but all models had low adjusted R^2 values (< 0.2). All suitable models included the variable elevation, and since the model with elevation alone had the second lowest ΔAIC_c value (0.1) and the least number of parameters this was selected as the best model for the mixed forest transect (Table 2). Figure 3 illustrates the quadratic relationship found between shell size and elevation, however the adjusted R^2 value indicates that this model explains only 15.9% of the variation in the data. The AIC_c model selection analysis for the palm forest transect resulted in only 2 suitable models, both with the same number of parameters and very close in ΔAIC_c and adjusted R^2 values (Table 3). I selected the model with the interaction between total snail density and elevation as the best predictor of *P. caracolla* shell size in palm forests since it had the lowest ΔAIC_c (0) and highest R^2 (0.207) value (Table 4). Since the interaction between elevation and total snail density is significant, two separate graphs were used to show the relationship with *P. caracolla* shell size. Figure 4 illustrates shell size relationship with elevation, using the mean total snail density (16) to calculate the regression line. Figure 5 illustrates shell size as determined

by total snail density, using mean elevation (612 m) to calculate the regression line. As with the mixed forest transect, the best fit model still does not account for more than 20.7% of the variation seen in the data.

Least squares regression results for elevational effects on *P. caracolla* density in both forest transects indicate a significant quadratic association with increasing elevation (Table 5 and 6). Average densities are highest at 300 m a.s.l., lowest between 750-850 m a.s.l., and increase slightly at the summit (Fig. 6 and 7). The rate of change in density is less in the palm forest transect than in mixed.

Results of the paired t-test comparing shell sizes of juvenile and adult *P. caracolla* for the maturation size assessment confirm a true difference in the means ($t = 23.4146$, $df = 199.493$, $P < 0.001$). Average shell size for adults was 53.21 mm ($sd = 2.41$). Average shell size for sub-adults was 34.24 mm ($sd = 9.35$). Figure 8 illustrates the frequency distribution of *P. caracolla* juvenile and adult shell sizes.

Discussion

Results of this study suggest that the association between maximum *P. caracolla* shell size and elevation and density is weak, and that maximum shell size is similar throughout all elevations and snail densities. Combined with previous findings, this suggests that there is no apparent limiting resource affecting *P. caracolla* maximum shell size within this study area (Bloch and Willig 2009). The LEF, indeed, is highly productive, even when compared to other tropical forest systems (Wang et al. 2003). Frequent storms and hurricanes bringing organic debris to the forest floor likely provide an abundant flow of food sources for a generalist species such as *P. caracolla*, thereby

likely reducing any observable effects of competition (Secrest et al. 1996; Bloch and Willig 2006, 2009). Large areas cleared by hurricanes allow for the establishment of palm forests, which are more resource rich than other forest types, providing ideal habitat for a detritivore like *P. caracolla*. Indeed, palm forests have been shown to harbor larger densities of snails and other invertebrates, including *P. caracolla* (Richardson et al. 2005; Willig et al. 2011).

The AIC_c model selection table for the palm forest transect indicated that two models, the interaction between conspecific density with elevation and the interaction between total snail density with elevation, were the best fit for the data. This result corresponds with the fact that *P. caracolla* is the most abundant snail within the LEF, so total snail densities are likely very similar to *P. caracolla* densities. Since palm forests are higher in nutrients than their corresponding mixed forests, they are likely better habitat for all snails, which would account for this slightly better fit of the model with total snail density and elevation.

Inhibition of shell sizes at increased densities due to interference competition is likely not applicable with regards to *P. caracolla* within the LEF. As stated previously, only one species of gastropod in Puerto Rico, *P. luquillensis*, is suspected to have defensive secretions in its mucous that affects *P. caracolla* survival (Heatwole and Heatwole 1978). However, *P. luquillensis* was only found at 6 plots within 3 strata in the mixed forest, and 9 plots within 3 strata in palm forests during the course of this study. And at a maximum abundance of 2 snails, it is unlikely that they would have a detrimental effect on *P. caracolla* snails to reduce overall shell sizes.

The overall decrease in *P. caracolla* densities with increasing elevation supports previous studies of terrestrial gastropods along elevational gradients. However, these studies took place in temperate environments, and they attributed this trend to yearly climatic variation, which can increase risk of desiccation due to greater amounts of insolation at peak elevations, or drastically reduce available forage (Burla and Stahel 1983; Baur and Raboud 1988). At the LEF, the upper elevations of the palo colorado and dwarf forests are more stable in regards to humidity. At the highest elevations, the forest is wet year round and frequently enveloped by fog or clouds, thereby negating any risk of desiccation. At the LEF, the structure of the vegetation at the highest elevations is different than the middle and lower elevations. Epiphytic growth at the summit is extensive, with mosses covering a majority of tree trunks in the dwarf forests and bromeliads occurring throughout the area of both dwarf and upper elevational palm forests (Weaver et al. 1986; Richardson et al. 2000). Tree density itself has also been shown to increase with elevation in mixed forests, reducing insolation, and should therefore provide ample habitat and forage for the arboreal snail, *P. caracolla*, and allow for greater population densities (Weaver and Murphy 1990). Temperature, then, remains the only other possible significant climatic variable at this study site. Although only 5°C lower at the highest elevations in the LEF compared to the lowest elevations, it is possible that this is enough of a difference to affect development of *P. caracolla*. Similar studies on land snails and other invertebrates along an elevational gradient revealed that organisms living at higher altitudes exhibit slower growth rates and produced fewer and larger eggs per clutch than populations of the same species at the lower elevations (Baur and Raboud 1988; Blanckenhorn 1997; Smith et al. 2000). Likewise, *P. caracolla* may

exhibit different reproductive strategies at higher elevations, but currently, little data exists on this subject matter.

Another possibility is a decline in egg hatching success or juvenile survival at higher elevations. Like other terrestrial snails, it is assumed *P. caracolla* lays egg clutches in or hidden on top of the soil (Heatwole and Heatwole 1978; Cowie 1984; Baur 1988; Baur and Raboud 1988). It is possible that their eggs are more susceptible to the temperature fluctuations found in the upper elevations. Additionally, soil type itself may impact egg viability. A study on marine sand snails found that eggs laid in the middle of clutches were more susceptible to hypoxia, which either delayed or prevented embryonic development (Booth 1995). The anoxic soils at top elevations at the LEF may therefore have a deleterious effect on egg hatching success (Weaver et al. 1986).

For eggs that lay hidden on top of the soil and for juvenile snails whose shells are softer than those of adults, increased predation may also be causing the loss of smaller snails among these upper elevational strata. Both tree species diversity and net aboveground primary production (NPP) decrease with increasing elevation in the LEF (Weaver and Murphy 1990). This in turn reduces the amount of available food sources for forest floor foragers. The dwarf forest also has the least amount of loose litter on the soil surface, owing to smaller average leaf sizes and poor productivity, which could not only limit available food supplies for litter-dwelling snails, but also increase chances of detection by predators (Weaver and Murphy 1990). Above the forest floor, while bromeliads may provide accessible habitat for snails, they are also ideal resources for birds. Birds in other tropical forests frequently utilize bromeliads for water, nesting material, and foraging for invertebrates hidden within (Nadkarni and Matelson 1989;

Nadkarni 1994). This includes snails, which can provide a much-needed source of calcium in a nutrient deficient system like the dwarf forest and thus used heavily as a resource (Graveland and van der Wal 1996).

It is also possible that the dense cover of epiphytic growth throughout the dwarf forest may simply make it harder to locate smaller snails. Due to saturated, anoxic soils, available root space is restricted, creating a thick cover of surface roots (Weaver et al. 1986). Bromeliad proliferation above ground level has shown to provide ample habitat for other litter invertebrates, so it is possible that juvenile snails may also take advantage of this resource, which would provide shelter, food, and moisture (Richardson et al. 2005). In order to disturb the plots as little as possible, snail searching was confined only to visible surfaces. In an environment as dense as the dwarf forest, snails hiding under surface roots or within arboreal bromeliads may have easily been overlooked.

The ecological implications of this study suggest that changes in microhabitat environmental conditions (temperature, humidity) may play a strong role in shaping the size versus density relationships of gastropod communities. For species with low vagility and high risk of desiccation, like terrestrial snails, this can be especially important due to the fact that dispersal ability is low and costly. The high productivity of the LEF likely allows snails here to allocate less energy towards resource acquisition and more towards growth, thereby reducing effects of competition seen in other resource limited temperate systems. Elevational gradients also lead to changes in microclimate, and these changes become more extreme in temperate regions. There, organisms at high altitudes are already nearing their physiological limits, where even minute changes in microclimate

can have a strong impact on these populations when compared to those in tropical regions.

The higher productivity, stable climates, and low predator densities of tropical island systems likely dampen the effects of competition seen in other temperate mainland regions, but more studies are needed to determine whether or not the results of this study are unique to the LEF. Firstly, more research is needed on gastropod species on other tropical montane islands in order to compare results from a similar ecological setting. Secondly, *P. caracolla* is found throughout the island of Puerto Rico, but little information is available on coastal populations. Climate there is hotter and drier, and vegetation composition is likely very different from the upper montane forests, and studies on these coastal populations may yield different results for shell size and density relationships than these found here in the LEF.

Table 1. Summary of AIC_c model selection table showing variables influencing *P. caracolla* maximum shell size within the mixed forest transect. Parameters estimated were conspecific density (D), heterospecific density (ID), total snail density (TD), elevation linear (E), and elevation quadratic (E²).

Model	nPar	ΔAIC _c	Adjusted R ²
Null	2	16.6	-
D	3	12.8	0.044
D, E, E ²	5	2.2	0.152
D, E, E ² , D x E	6	0.7	0.173
ID	3	17.1	0.005
ID, E, E ²	5	-	0.169
ID, E, E ² , ID x E	6	2.2	0.161
TD	3	12.9	0.043
TD, E, E ²	5	1.6	0.156
TD, E, E ² , TD x E	6	2.3	0.16
E, E²	4	0.1	0.159

Table 2. Coefficient estimates for intercept and predictors of *P. caracolla* maximum shell size in the mixed forest transect. Adjusted R^2 value is 0.159 with 105 degrees of freedom for error.

Parameter	Estimate	SE	t	P
Intercept	83.71	6.38	13.118	< 0.001
Elevation	-0.10	0.022	-4.677	< 0.001
Elevation ²	0.00008	0.00002	4.543	< 0.001

Table 3. Summary of AIC_c model selection table showing variables influencing \mathcal{P} .

caracolla maximum shell size within the palm forest transect. Parameters estimated were conspecific density (D), heterospecific density (ID), total snail density (TD), elevation linear (E), and elevation quadratic (E²).

Model	nPar	ΔAIC_c	Adjusted R ²
Null	2	25.4	-
D	3	21.1	0.041
D, E, E ²	5	16.4	0.091
D, E, E ² , D x E	6	0.7	0.203
ID	3	25.0	0.011
ID, E, E ²	5	11.0	0.129
ID, E, E ² , ID x E	6	10.9	0.137
TD	3	20.4	0.046
TD, E, E ²	5	6.8	0.156
TD, E, E², TD x E	6	-	0.207
E, E ²	4	21.0	0.050

Table 4. Coefficient estimates for intercept and predictors of *P. caracolla* maximum shell size in the palm forest transect. Adjusted R^2 value is 0.207 with 124 degrees of freedom for error.

Parameter	Estimate	SE	t	P
Intercept	78.63	8.51	9.240	< 0.001
Total Density	-0.33	0.21	-1.492	0.14
Elevation	-0.09	0.024	-3.798	< 0.001
Elevation ²	0.00007	0.00002	4.261	< 0.001
Total Density x Elevation	0.001	0.0004	2.987	0.003

Table 5. Coefficient estimates for intercept and predictors of *P. caracolla* density in the mixed forest transect. Adjusted R^2 value is 0.588 with 105 degrees of freedom for error.

Parameter	Estimate	SE	t	P
Intercept	36.63	3.209	11.415	< 0.001
Elevation	-0.10	0.011	-8.643	< 0.001
Elevation ²	0.00006	0.000009	7.240	< 0.001

Table 6. Coefficient estimates for intercept and predictors of *P. caracolla* density in the palm forest transect. Adjusted R^2 value is 0.477 with 126 degrees of freedom for error.

Parameter	Estimate	SE	t	P
Intercept	37.43	4.000	9.359	< 0.001
Elevation	-0.086	0.013	-6.452	< 0.001
Elevation ²	0.00005	0.00001	5.112	< 0.001

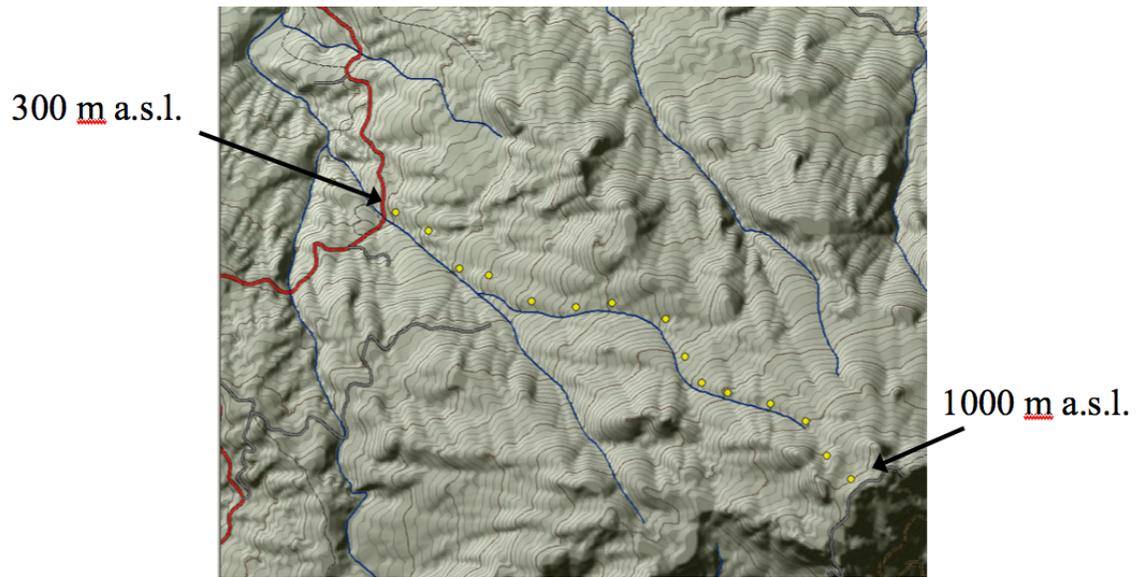


Figure 1. Topographic map of the location of sites for the elevational transects in mixed forest along the Sonadora creek. Corresponding palm transects were located within 1 km of mixed transects on the opposite bank of the creek. Elevation increases from upper left to lower right.

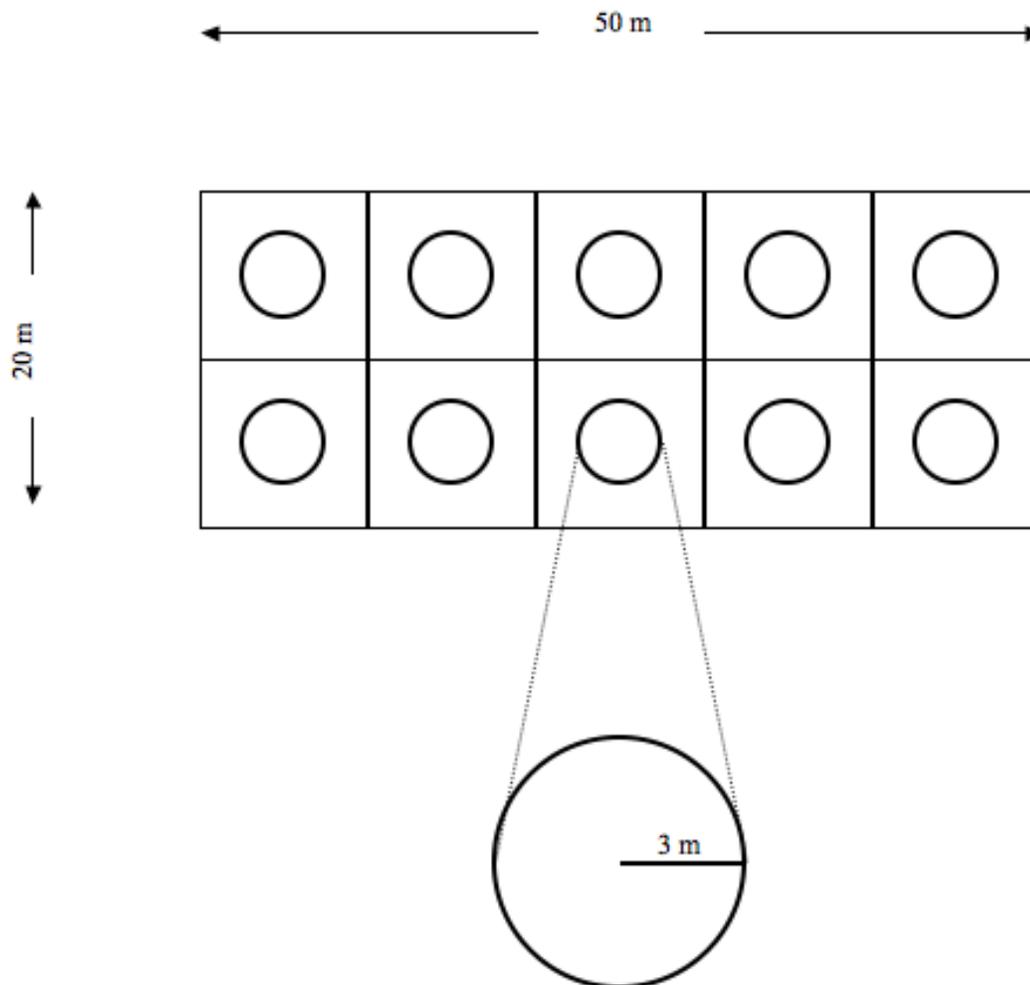
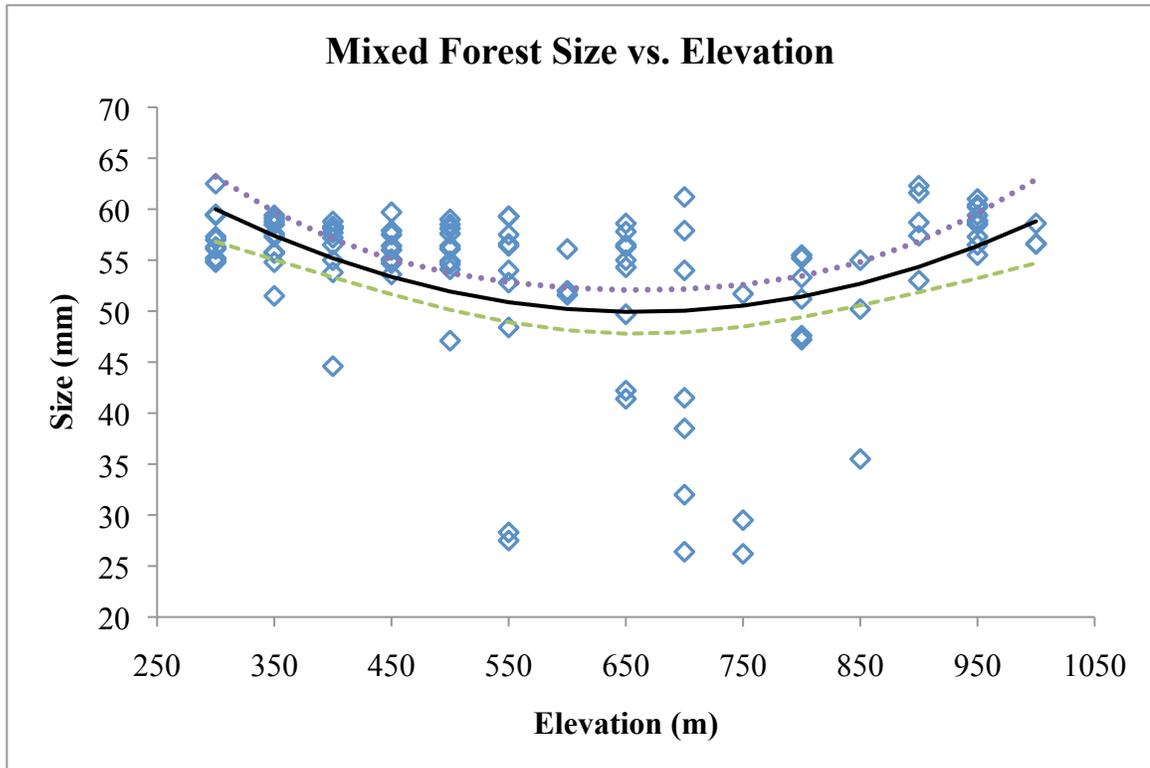


Figure 2. Diagram of the rectangular strata and internal plot arrangement used for sampling along the elevational transects at the LEF.



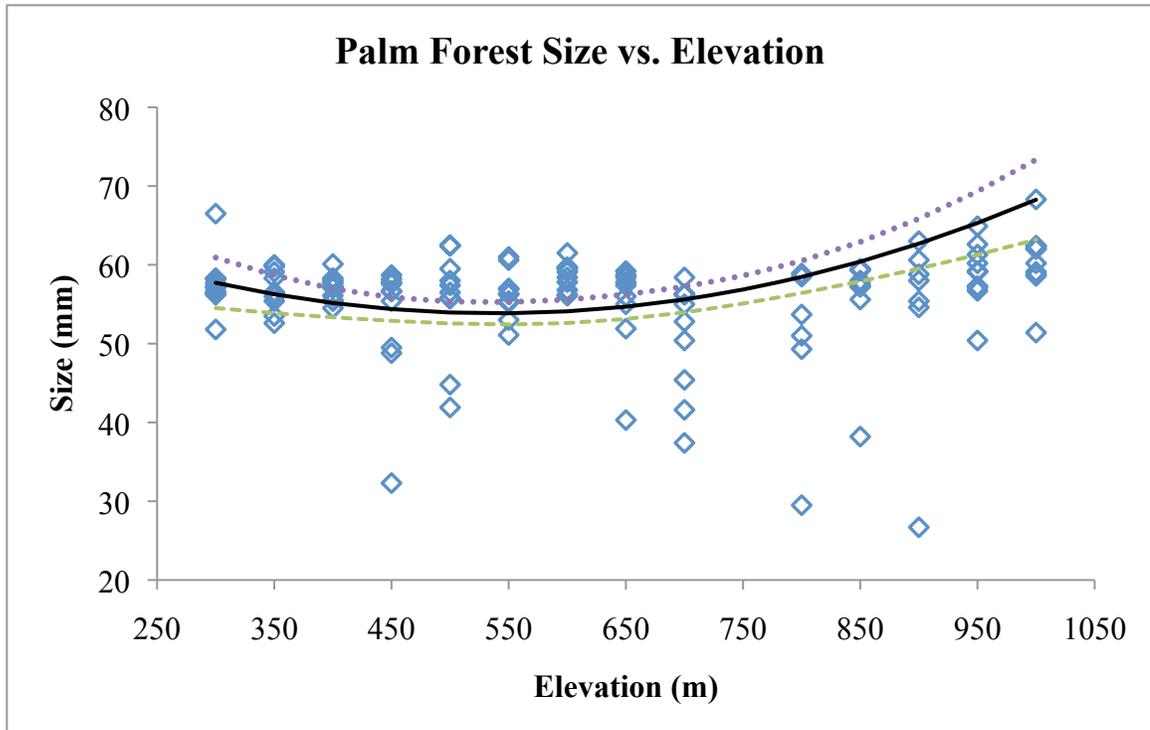


Figure 4. *P. caracolla* maximum shell size (mm) per plot graphed against elevation (m).

The solid black line represents the regression line with upper (purple dotted line) and lower (green dashed line) 95% confidence intervals. Due to the interaction between elevation and total snail density, the mean total snail density (16) was used to calculate the regression line.

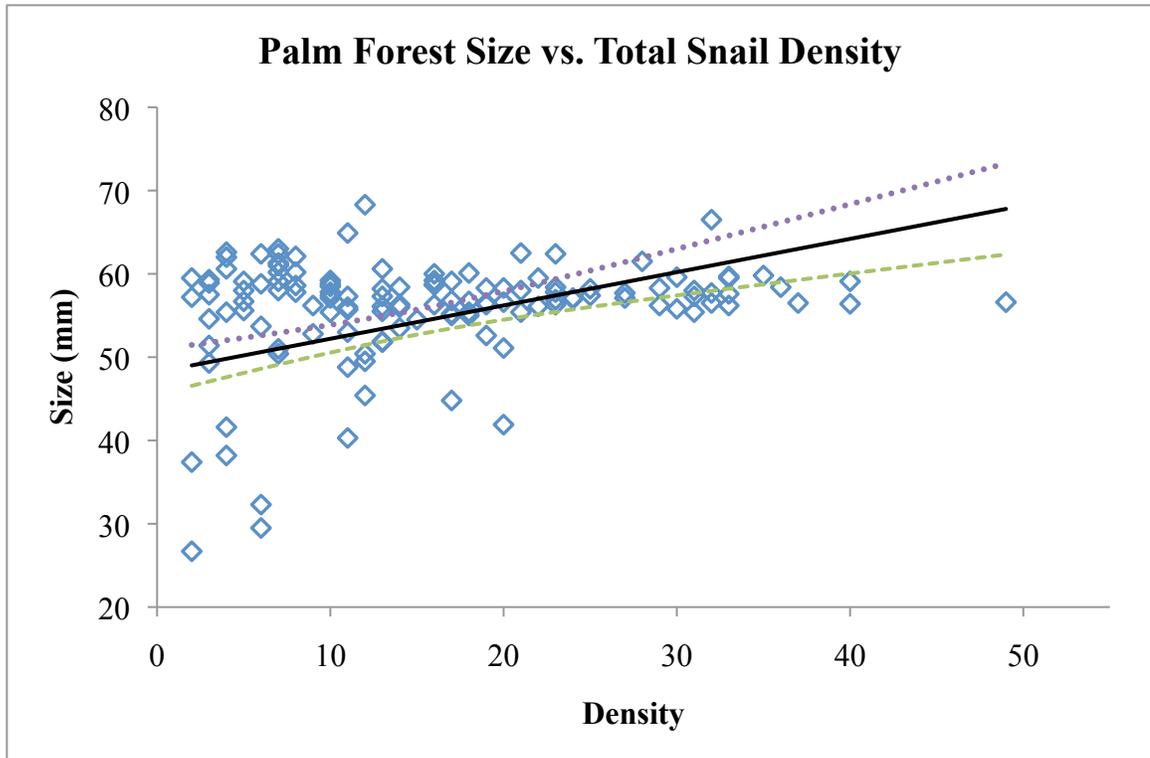


Figure 5. *P. caracolla* maximum shell size (mm) per plot graphed against total snail density. The solid black line represents the regression line with upper (purple dotted line) and lower (green dashed line) 95% confidence intervals. Due to the interaction between total snail density and elevation, the mean elevation (612 m) was used to calculate the regression line.

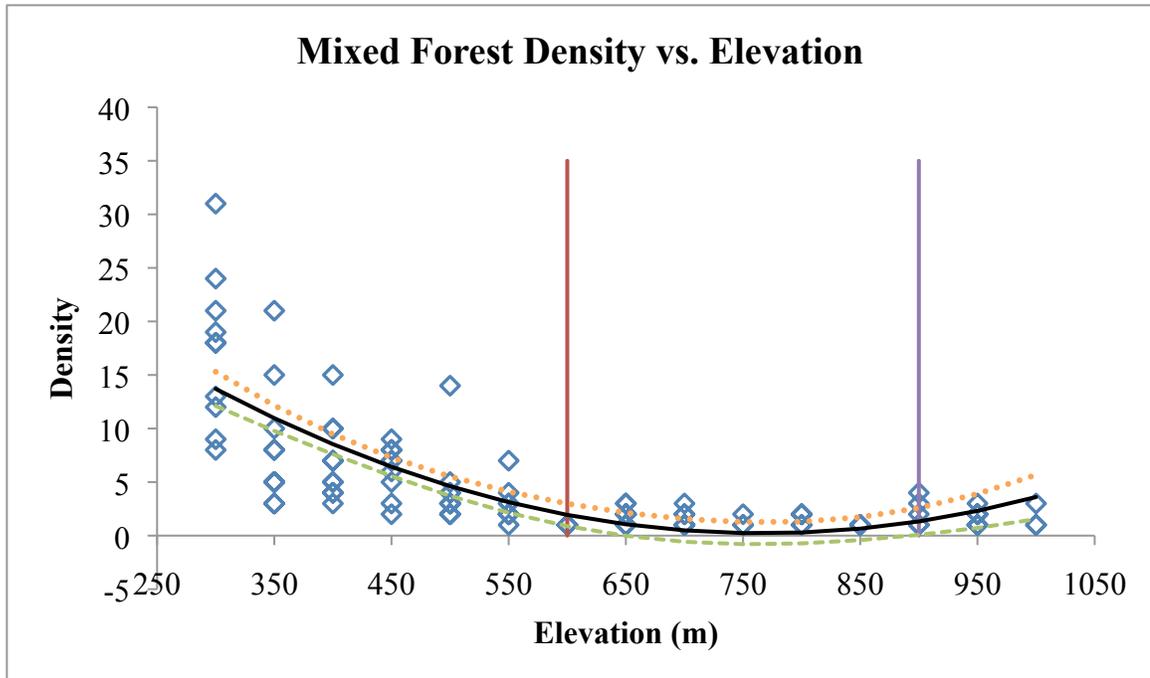


Figure 6. Graph of *P. caracolla* average densities per plot in the mixed forest transect against elevation (m). The regression line is indicated by the solid black line, with upper (orange dotted) and lower (green dashed) 95% confidence intervals. The vertical red line represents the division between tabonuco and palo colorado forests, and the vertical purple line represents the division between palo colorado and dwarf forests.

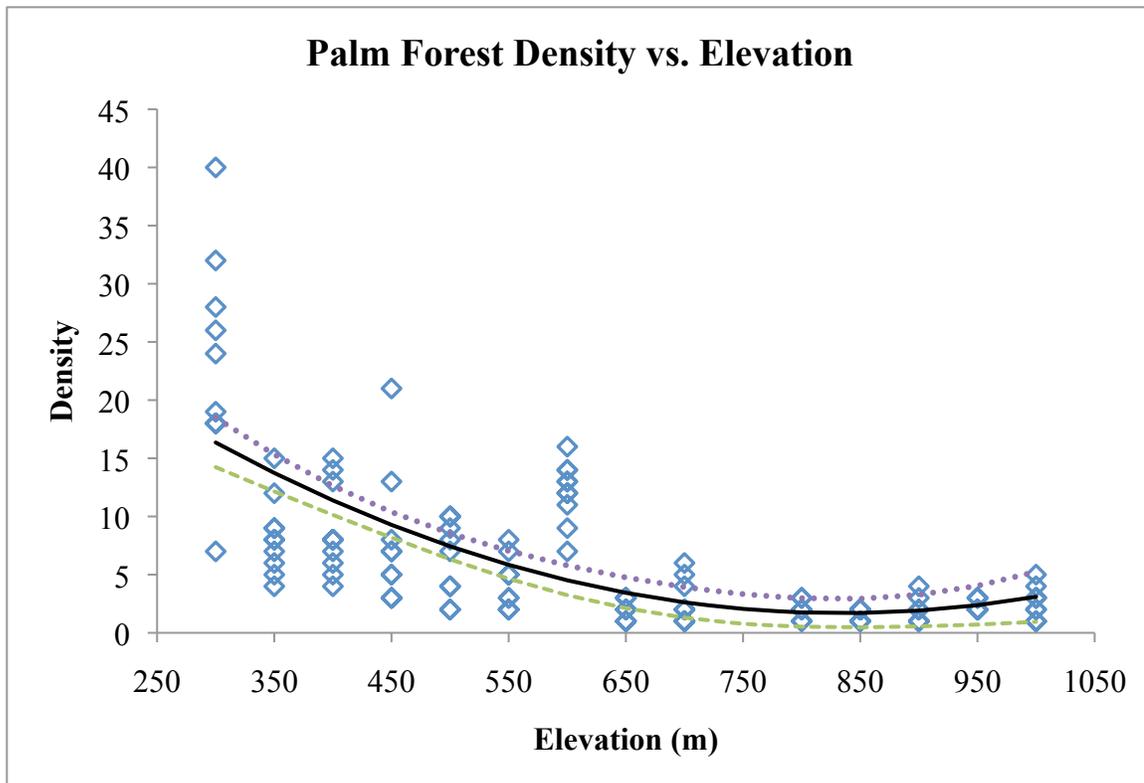


Figure 7. Graph of *P. caracolla* average densities per plot in the palm forest transect against elevation (m). Regression line is indicated by the solid black line, with upper (purple dotted) and lower (green dashed) 95% confidence intervals.

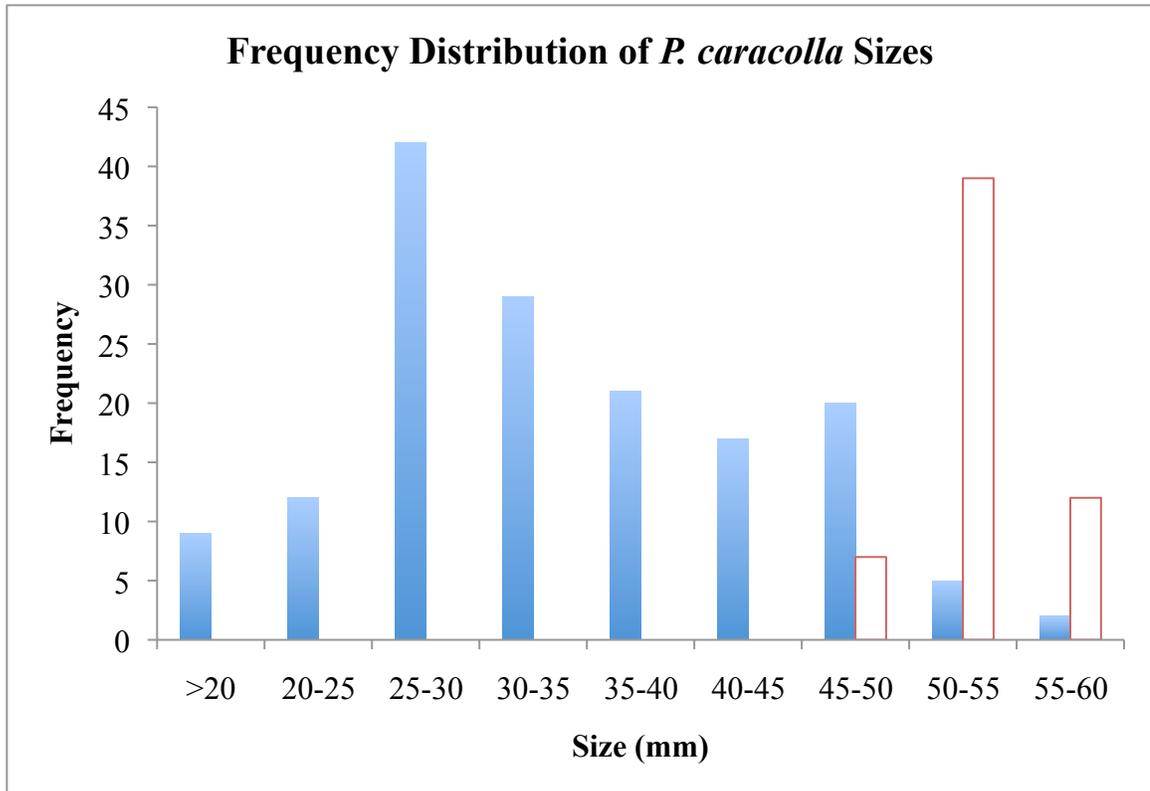
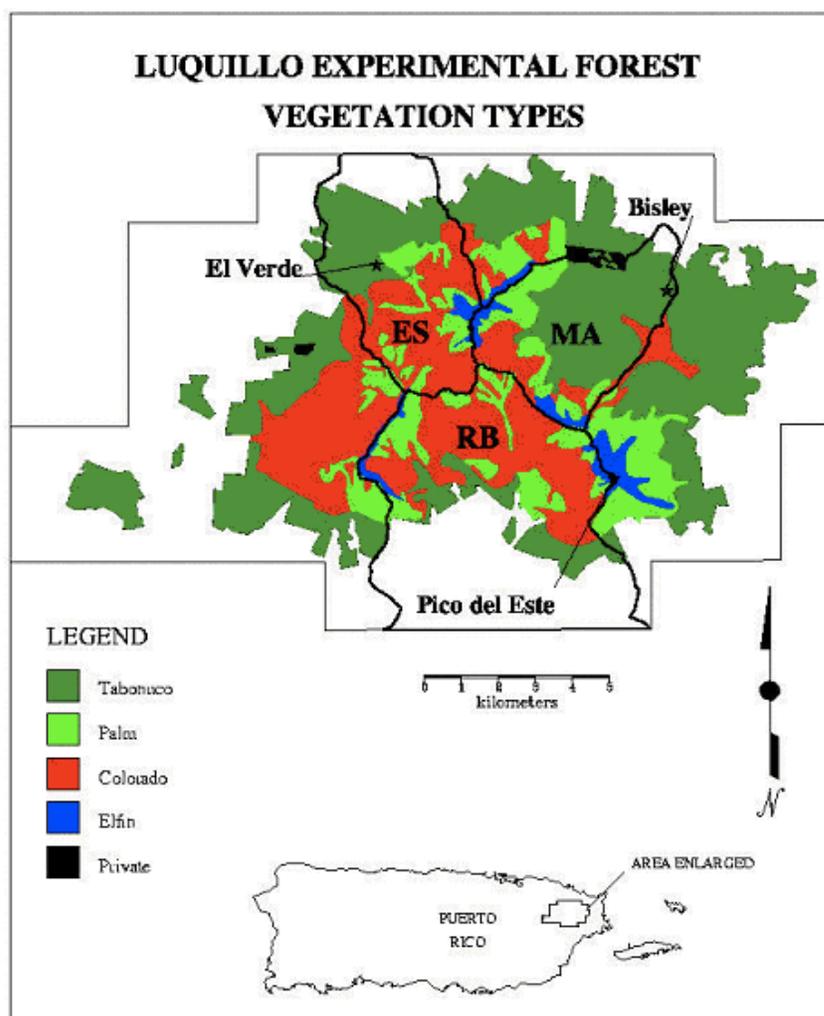


Figure 8. Distribution of *P. caracolla* shell sizes collected from the LFDP. Mean size of juveniles was $34.24 \text{ mm} \pm 9.35 \text{ mm}$. Mean size of adults was $53.21 \text{ mm} \pm 2.41 \text{ mm}$.

Juveniles are represented by shaded blue bars, and adults are represented by unshaded red bars.

APPENDIX A

Figure of Luquillo Experimental Forest in relation to Puerto Rico, taken from <http://luq.lternet.edu/research/history/programs/environmentalsettings> (Copyright © 2012 Long Term Ecological Research Network). Research for the present study was conducted within the Espíritu Santo (ES) watershed, which is bordered by the Mameyes (MA) and Río Blanco (RB) watersheds.



APPENDIX B

Data used for linear regression. Max Size = maximum size (mm) of *P. caracolla* per plot; Density = average density of *P. caracolla* per plot; Hetero Dens = average density of heterospecific competitors per plot; Total Dens = average density of all gastropods per plot.

Elevation	Max Size	Density	Hetero Dens	Total Dens	Forest Type
300	55	8	1	9	MIX
300	57	9	4	13	MIX
300	59.5	12	4	15	MIX
300	56.1	13	2	15	MIX
300	55.2	18	10	28	MIX
300	59.4	18	3	21	MIX
300	54.8	19	4	23	MIX
300	62.5	21	10	31	MIX
300	57.3	24	8	32	MIX
300	56.3	31	9	40	MIX
350	51.5	3	5	8	MIX
350	59.1	3	9	13	MIX
350	54.8	5	5	10	MIX
350	55.8	5	6	11	MIX
350	57.3	5	4	8	MIX
350	58.8	8	8	16	MIX
350	59.4	8	16	24	MIX
350	55.7	10	9	19	MIX
350	58.5	15	11	26	MIX
350	57.6	21	6	16	MIX
400	44.6	3	12	15	MIX
400	58.2	4	5	9	MIX
400	58.8	4	10	14	MIX
400	56.5	5	9	14	MIX
400	58.1	5	10	15	MIX
400	55	7	18	25	MIX
400	57.2	7	9	17	MIX
400	53.8	10	7	18	MIX
400	58.3	10	20	29	MIX
400	57.7	15	20	35	MIX
450	56	2	6	8	MIX

450	53.6	3	6	9	MIX
450	54.7	5	7	11	MIX
450	57.5	6	2	8	MIX
450	55.1	7	15	22	MIX
450	57.9	7	5	12	MIX
450	55	8	8	16	MIX
450	59.7	8	2	10	MIX
450	56.4	9	8	17	MIX
500	54.1	2	16	18	MIX
500	54.6	2	4	6	MIX
500	58.1	2	8	10	MIX
500	54.9	3	9	12	MIX
500	57.6	3	17	19	MIX
500	59	3	10	13	MIX
500	47.1	4	7	11	MIX
500	56.4	4	9	12	MIX
500	56.1	5	14	18	MIX
500	58.5	14	10	25	MIX
550	59.3	1	3	4	MIX
550	28.3	2	6	8	MIX
550	52.8	2	6	8	MIX
550	54	2	2	4	MIX
550	56.4	2	6	8	MIX
550	56.6	2	8	10	MIX
550	57.5	3	6	10	MIX
550	59.3	3	17	20	MIX
550	27.5	4	8	12	MIX
550	48.4	7	12	19	MIX
600	51.6	1	1	2	MIX
600	52	1	5	6	MIX
600	56.1	1	11	12	MIX
650	41.4	1	8	9	MIX
650	55	1	6	7	MIX
650	56.5	1	6	7	MIX
650	49.7	2	4	5	MIX
650	54.3	2	6	7	MIX
650	57.8	2	4	5	MIX
650	58.6	2	9	11	MIX
650	42.2	3	7	10	MIX
650	56.3	3	11	13	MIX
700	26.4	1	8	9	MIX
700	54	1	8	9	MIX
700	57.9	1	5	6	MIX
700	61.2	1	7	8	MIX
700	38.5	2	1	3	MIX
700	41.5	2	13	15	MIX
700	32	3	5	7	MIX
750	26.2	1	0	1	MIX
750	29.5	1	6	7	MIX

750	51.7	2	4	6	MIX
800	47.2	1	3	4	MIX
800	55.2	1	0	1	MIX
800	47.6	2	2	3	MIX
800	51.2	2	2	3	MIX
800	53.3	2	4	6	MIX
800	55.5	2	9	11	MIX
850	35.5	1	0	1	MIX
850	50.2	1	1	2	MIX
850	55	1	1	2	MIX
900	53	1	6	7	MIX
900	58.7	1	5	6	MIX
900	57.4	2	2	4	MIX
900	62.3	3	4	7	MIX
900	61.6	4	2	6	MIX
950	55.5	1	3	4	MIX
950	58.5	1	3	4	MIX
950	59.4	1	5	6	MIX
950	60.4	1	2	3	MIX
950	61	1	7	8	MIX
950	57.3	2	3	5	MIX
950	58.7	2	4	6	MIX
950	58.9	2	2	4	MIX
950	60.2	2	2	3	MIX
950	56.5	3	3	6	MIX
1000	56.6	1	5	6	MIX
1000	58.6	1	6	7	MIX
1000	56.6	3	14	17	MIX
300	51.8	7	6	13	PALM
300	58.2	18	7	25	PALM
300	57.1	18	9	27	PALM
300	58.3	19	10	29	PALM
300	57.3	18	13	31	PALM
300	66.5	24	8	32	PALM
300	57.7	28	4	32	PALM
300	56.2	26	8	33	PALM
300	56.4	32	8	40	PALM
300	56.6	40	10	49	PALM
350	55.4	6	4	10	PALM
350	53.5	4	10	14	PALM
350	56	5	8	14	PALM
350	60	9	7	16	PALM
350	59.1	8	9	17	PALM
350	52.6	7	12	19	PALM
350	58.3	8	11	19	PALM
350	56.5	9	23	32	PALM
350	59.8	12	22	35	PALM
350	56.5	15	22	37	PALM
400	57.3	4	6	11	PALM

400	56.1	5	9	13	PALM
400	55.5	8	6	13	PALM
400	54.5	7	8	15	PALM
400	60.1	6	11	18	PALM
400	55.4	8	10	18	PALM
400	58.3	8	12	20	PALM
400	58	14	8	21	PALM
400	57.1	13	12	24	PALM
400	57.7	15	12	27	PALM
450	32.3	3	4	6	PALM
450	57.8	3	5	8	PALM
450	48.8	3	9	11	PALM
450	49.5	5	7	12	PALM
450	58.2	8	5	13	PALM
450	58.7	5	10	16	PALM
450	56.7	7	10	18	PALM
450	56.6	7	12	20	PALM
450	55.4	13	18	31	PALM
450	57.6	21	13	33	PALM
500	55.7	2	9	11	PALM
500	44.8	2	15	17	PALM
500	56.5	4	15	19	PALM
500	41.9	4	16	20	PALM
500	62.5	8	13	21	PALM
500	62.4	7	16	23	PALM
500	57.4	10	15	25	PALM
500	55.8	9	21	30	PALM
500	58	10	21	31	PALM
500	59.5	10	23	33	PALM
550	61	2	5	7	PALM
550	53	2	9	11	PALM
550	60.6	2	11	13	PALM
550	55.2	5	12	17	PALM
550	56.3	3	15	19	PALM
550	51.1	5	15	20	PALM
550	55.4	3	18	21	PALM
550	56.3	7	16	23	PALM
550	56.9	8	16	23	PALM
550	57	5	19	24	PALM
600	56.8	9	8	17	PALM
600	59.5	7	15	22	PALM
600	56.1	12	10	22	PALM
600	57.8	11	12	23	PALM
600	61.5	16	12	28	PALM
600	56.2	14	15	29	PALM
600	59.6	13	17	30	PALM
600	59.7	13	20	33	PALM
600	58.4	14	22	36	PALM
600	59.1	12	27	40	PALM

650	57.8	1	9	10	PALM
650	57.4	3	7	10	PALM
650	40.3	1	10	11	PALM
650	56	1	10	11	PALM
650	51.9	2	11	13	PALM
650	58.4	3	10	14	PALM
650	58.7	2	14	16	PALM
650	59.2	3	12	16	PALM
650	55	2	17	18	PALM
700	37.4	1	1	2	PALM
700	41.6	2	3	4	PALM
700	56.2	1	8	9	PALM
700	52.8	2	6	9	PALM
700	45.4	1	11	12	PALM
700	50.4	2	10	12	PALM
700	56.3	1	13	14	PALM
700	56.3	5	11	16	PALM
700	55	4	14	17	PALM
700	58.4	6	17	23	PALM
800	49.3	1	2	3	PALM
800	58.9	2	1	3	PALM
800	29.5	1	5	6	PALM
800	53.7	3	4	6	PALM
800	51	2	5	7	PALM
800	58.5	3	7	10	PALM
850	59.5	1	1	2	PALM
850	57.2	2	1	2	PALM
850	59.3	1	2	3	PALM
850	57.5	2	1	3	PALM
850	38.2	1	3	4	PALM
850	55.6	2	3	5	PALM
850	58	2	3	5	PALM
900	26.7	1	1	2	PALM
900	54.6	1	2	3	PALM
900	55.4	1	3	4	PALM
900	60.6	3	1	4	PALM
900	58	2	5	7	PALM
900	63	2	5	7	PALM
900	58.8	4	6	10	PALM
950	62.6	2	2	4	PALM
950	56.7	2	4	5	PALM
950	50.4	2	5	7	PALM
950	59.1	2	5	7	PALM
950	60.2	3	4	7	PALM
950	61.3	3	4	7	PALM
950	57.1	2	8	10	PALM
950	59.2	2	8	10	PALM
950	64.9	3	8	11	PALM
950	57.3	2	12	13	PALM

1000	51.4	1	2	3	PALM
1000	62	1	3	4	PALM
1000	59.1	3	2	5	PALM
1000	58.8	1	4	6	PALM
1000	62.4	4	3	6	PALM
1000	62.4	3	4	7	PALM
1000	58.6	2	6	8	PALM
1000	60.2	2	6	8	PALM
1000	62.1	3	5	8	PALM
1000	68.3	5	7	12	PALM

APPENDIX C

List of species other than *P. caracolla* found throughout each of the two elevational gradients.

Mixed Forest

Alcadia striata
Austroselenites alticola
Caracolus marginella
Cepolis musicola
Cepolis squamosa
Gaeotis nigrolineata
Megalomastoma croceum
Nenia tridens
Oleacina glabra
Oleacina playa
Platysuccinea portoricensis
Polydontes acutangula
Polydontes luquillensis
Vaginulus occidentalis

Palm Forest

Alcadia striata
Austroselenites alticola
Caracolus marginella
Cepolis squamosa
Gaeotis nigrolineata
Megalomastoma croceum
Nenia tridens
Obeliscus terebraster
Oleacina glabra
Oleacina playa
Platysuccinea portoricensis
Polydontes acutangula
Polydontes luquillensis
Vaginulus occidentalis

APPENDIX D

Data used for *P. caracolla* maturation size assessment (adult vs. juvenile sizes). Point = location of plot within LFDP; J = juvenile; A = adult; Size = diameter (mm) of shell.

Point	Age	Size
40	J	40.3
40	J	34.9
49	J	41.3
49	J	39
49	J	21.5
91	J	26.4
97	J	56.6
139	J	53
139	J	39.5
139	J	37
139	J	36.9
139	J	35.1
139	J	31.8
139	J	29.3
139	J	28.7
139	J	27.5
139	J	24.4
142	J	53.8
142	J	42.3
142	J	40
142	J	39.5
142	J	36.7
142	J	34.9
142	J	34.8
142	J	33.1
142	J	30.7
142	J	28.2
142	J	28.1
142	J	27.8
142	J	27.2

142	J	25.1
142	J	20
145	J	34.2
145	J	25.4
145	J	24.1
148	J	43.8
148	J	37.5
148	J	26.8
151	J	41.9
151	J	36.6
151	J	31.4
190	J	48.3
190	J	20.3
193	J	45.7
193	J	45.2
193	J	43
193	J	39
193	J	38.7
193	J	33.3
193	J	31.4
193	J	29.8
193	J	29
193	J	28.8
193	J	27.3
193	J	22.2
196	J	39.4
202	J	32.1
202	J	24.5
202	J	20.6
202	J	18.7
202	J	18.5
202	J	18.4
244	J	43.5
250	J	43.2
250	J	30.7
250	J	29.4
250	J	26.6
250	J	23.6
250	J	19.2
253	J	53.8
253	J	48
253	J	45.7
253	J	35.2

253	J	32.3
253	J	30.7
253	J	30.1
253	J	29.9
253	J	29.1
253	J	28.1
253	J	27.8
253	J	26
253	J	20.5
253	J	20
253	J	17.4
292	J	44.8
292	J	39.4
292	J	39
292	J	34.3
292	J	30.8
292	J	28.6
292	J	26.7
295	J	49.9
295	J	46.2
295	J	45.8
295	J	39.4
295	J	38.7
295	J	37.6
295	J	30.5
295	J	26.2
295	J	25
298	J	30.2
298	J	27.4
298	J	26.4
301	J	55.3
301	J	39.6
301	J	27.3
304	J	49.5
304	J	47.4
304	J	40.4
304	J	26
304	J	20.9
343	J	49.3
343	J	47.6
343	J	40.2
343	J	34.5
343	J	33.4

343	J	29.6
343	J	27.1
343	J	26.3
343	J	19.1
346	J	44.9
346	J	41.6
346	J	37.8
346	J	33.4
349	J	46.7
349	J	40.6
352	J	52.5
352	J	47.7
352	J	45.2
352	J	33.1
352	J	29.4
352	J	27.2
352	J	26.6
352	J	16.6
355	J	50
355	J	40.9
355	J	33.9
394	J	54
394	J	46.3
394	J	46
394	J	41.4
394	J	31.6
394	J	29.1
394	J	25.3
394	J	24.5
397	J	46.1
397	J	44.5
397	J	33.4
397	J	26
400	J	45.4
400	J	30.6
400	J	30.2
400	J	28
400	J	27
403	J	27.6
403	J	25.5
406	J	32.3

LITERATURE CITED

- ALVAREZ, J., AND M. R. WILLIG. 1993. Effects of treefall gaps on the density of land snails in the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 25: 100-110.
- BAUR, B. 1988. Population regulation in the land snail *Arianta arubstorum*: density effects on adult size, clutch size and incidence of egg cannibalism. *Oecologia* 77: 390-394.
- BAUR, B., AND A. BAUR. 1990. Experimental evidence for intra- and interspecific competition in two species of rock-dwelling land snails. *Journal of Animal Ecology* 59: 301-315.
- BAUR, B., AND C. RABOUD. 1988. Life history of the land snail *Arianta arbustorum* along an altitudinal gradient. *Journal of Animal Ecology* 57: 71-87.
- BLANCKENHORN, W. U. Altitudinal life history variation in the dung flies *Scathophaga stercoraria* and *Sepsis cynipsea*. *Oecologia* 109: 342-352.
- BLOCH, C. P., AND M. R. WILLIG. 2006. Context-dependence of long-term responses of terrestrial gastropod populations to large-scale disturbance. *Journal of Tropical Ecology* 22: 111-122.
- BLOCH, C. P., AND M. R. WILLIG. 2009. Effects of competition on size and growth rates of *Caracolus caracolla* (L.) in Puerto Rico. *Journal of Molluscan Studies* 75: 133-138.

- BOOTH, D. T. 1995. Oxygen availability and embryonic development in sand snail (*Polinices sordidus*) egg masses. *The Journal of Experimental Biology* 198: 241-247.
- BROWN, S., A. E. LUGO, S. SILANDER, AND L. LIEGEL. 1983. Research history and opportunities in the Luquillo Experimental Forest. General Technical Report SO-44, U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, 132 pp.
- BURLA, H. 1984. Induced environmental variation in *Arianta arbustorum* (L.). *Genetica* 64: 65-67.
- BURLA, H., AND W. STAHEL. Altitudinal variation in *Arianta arbustorum* (Mollusca, Pulmonata) in the Swiss Alps. 1983. *Genetica* 62: 95-108.
- CAMERON, R. A. D., AND M. A. CARTER. 1979. Intra- and inter-specific effects of population density on growth and activity in some helicid land snails (Gastropoda: Pulmonata). *Journal of Animal Ecology* 48: 237-246.
- CARY, J. F. JR. 1992. Habitat selection, home range, and population dynamics of *Caracollus caracolla* in the Luquillo Experimental Forest of Puerto Rico. Unpublished MS thesis, Texas Tech University, Lubbock, Texas.
- COWIE, R. H. 1984. The life-cycle and productivity of the land snail *Theba pisana* (Mollusca: Helicidae). *Journal of Animal Ecology* 53: 311-325.
- DRAGO, M., L. CARDONA, E. A. CRESPO, M. F. GRANDI, AND A. AGUILAR. 2010. Reduction of skull size in South American sea lions reveals density-dependent growth during population recovery. *Marine Ecology Progress Series* 420: 253-261.

- GARCÍA-MARTINÓ, A. R., G. S. WARNER, F. N. SCATENA, AND D. L. CIVCO. 1996. Rainfall, runoff and elevation relationships in the Luquillo Mountains of Puerto Rico. *Caribbean Journal of Science* 32: 413-424.
- GARRISON, R. W., AND M. R. WILLIG. 1996. Arboreal invertebrates. Pp. 183-245 in *The food web of a tropical rain forest* (D. P. Reagan and R. B. Waide, eds.). University of Chicago Press, Chicago, Illinois.
- GOERTZ, J. W. 1964. The influence of habitat quality on density of cotton rat populations. *Ecological Monographs* 34: 359-381.
- GOODFRIEND, G. 1986. Variation in land-snail shell form and size and its causes: a review. *Systematic Biology* 35: 204-223.
- GRAVELAND, J., AND R. VAN DER WAL. 1996. Decline in snail abundance due to soil acidification causes eggshell defects in forest passerines. *Oecologia* 105: 351-360.
- HEATWOLE, H., AND A. HEATWOLE. 1978. Ecology of the Puerto Rican camaenid tree snails. *Malacologia* 17: 241-315.
- HILDERBRAND, G. V., C. C. SCHWARTZ, C. T. ROBBINS, M. E. JACOBY, T. A. HANLEY, S. M. ARTHUR, AND C. SERVHEEN. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77: 132-138.
- JENKINS, T. M., JR., S. DIEHL, K. W. KRATZ, AND S. D. COOPER. 1999. Effects of population density on individual growth of brown trout in streams. *Ecology* 80: 941-956.

- MATHIS, A. 1990. Territoriality in a terrestrial salamander: the influence of resource quality and body size. *Behaviour* 112: 162-175.
- NADKARNI, N. M. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *American Zoologist* 34: 70-78.
- NADKARNI, N. M., AND T. J. MATELSON. 1989. Bird use of epiphyte resources in Neotropical trees. *The Condor* 91: 891-907.
- OOSTERHOFF, L. M. 1977. Variation in growth rate as an ecological factor in the landsnail *Cepaea nemoralis* (L.). *Netherlands Journal of Zoology* 27: 1-132.
- PERRY, R., AND W. ARTHUR. 1991. Shell size and population density in large helioid land snails. *Journal of Animal Ecology* 60: 409-421.
- PETTORELLI, N., J. GAILLARD, P. DUNCAN, J. OUELLET, AND G. VAN LAERE. 2001. Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. *Oecologia* 128: 400-405.
- PRESLEY, S. J., M. R. WILLIG, C. R. BLOCH, I. CASTRO-ARELLANO, C. L. HIGGINS, AND B. T. KLINGBEIL. 2011. A complex metacommunity structure for gastropods along an elevational gradient. *Biotropica* 43: 480-488.
- REAGAN, D. P., AND R. B. WAIDE (EDS). 1996. *The food web of a tropical rainforest*. University of Chicago Press, Chicago.
- RICHARDSON, B. A., M. J. RICHARDSON, F. N. SCATENA, AND W. H. MCDOWELL. 2000. Effects of nutrient availability and other elevational changes on bromeliad populations and their invertebrate communities in a humid tropical forest in Puerto Rico. *Journal of Tropical Ecology* 16: 167-188.

- RICHARDSON, B. A., M. J. RICHARDSON, AND F. N. SOTO-ADAMES. 2005. Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico. *Journal of Animal Ecology* 74: 926-936.
- SCHEFFER, V. B. 1955. Body size with relation to population density in mammals. *Journal of Mammalogy* 36: 493-515.
- SECRET, M. F., M. R. WILLIG, AND L. L. PEPPERS. 1996. The legacy of disturbance on habitat associations of terrestrial snails in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 28: 502-514.
- SKOGLAND, T. 1983. The effects of density-dependent resource limitation on size of wild reindeer. *Oecologia* 60: 156-168.
- SMITH, R. J., A. HINES, S. RICHMOND, M. MERRICK, A. DREW, AND R. FARGO. 2000. Altitudinal variation in body size and population density of *Nicrophorus investigator* (Coleoptera: Silphidae). *Environmental Entomology* 29: 290-298.
- WANG, H., C. A. S. HALL, F. N. SCATENA, N. FETCHER, AND W. WU. 2003. Modeling the spatial and temporal variability in climate and primary productivity across the Luquillo Mountains, Puerto Rico. *Forest Ecology and Management* 179: 69-94.
- WEAVER, P. L., E. MEDINA, D. POOL, K. DUGGER, J. GONZALES-LIBOY, AND E. CUEVAS. 1986. Ecological observations in the dwarf cloud forest of the Luquillo Mountains in Puerto Rico. *Biotropica* 18: 79-85.
- WEAVER, P. L., AND P. G. MURPHY. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* 22: 69-82.

- WILLIAMSON, P., R. A. D. CAMERON, AND M. A. CARTER. 1976. Population density affecting adult shell size of *Cepaea nemoralis* L. *Nature* 263: 496-497.
- WILLIG, M. R., E. A. SANDLIN, AND M. R. GANNON. 1998. Structural and taxonomic correlates of habitat selection by a Puerto Rican land snail. *The Southwest Naturalist* 43: 70-79.
- WILLIG, M. R., S. J. PRESLEY, C. P. BLOCH, I. CASTRO-ARELLANO, L. M. CISNEROS, C. L. HIGGINS, AND B. T. KLINGBEIL. 2011. Tropical metacommunities along elevational gradients: effects of forest type and other environmental factors. *Oikos* 120: 1497-1508.
- ZEDROSSER, A., B. DAHLE, AND J. E. SWENSON. 2006. Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy* 87: 510-518.

VITA

Susan Kina Uthuppuru was born in Bloomington, Indiana, on March 13, 1978, the daughter of Cheruvathoor Zachariah Uthuppuru and Masako Kina Uthuppuru. She received her B.A. in Biology from Indiana University in December 2002. After spending several years working as a veterinary technician in Texas, her interest in wildlife brought her to the Wildlife Ecology program at Texas State University in San Marcos, Texas. She looks forward to applying her skills and expanding her knowledge in this field upon graduation.

Permanent E-mail Address: zoozan313@gmail.com

This thesis was typed by Susan K. Uthuppuru.