

## **Herbivory Defense of Island Plants and their Mainland Relatives**

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### **ABSTRACT**

It is generally hypothesized that over evolutionary time island plant communities develop reduced herbivory defense traits in the absence of herbivores. However, few studies have actually measured differences in herbivory traits between island and mainland plant communities, and no studies have been done in the southern Channel Islands, California. I compared the herbivory defense traits (spinescence, leaf toughness, and cyanogenic glycosides) of plant communities on Santa Catalina Island with those in the Santa Ana Mountains. Additionally, I did a feeding preference test using goats to measure the palatability of plants from the two locations. I found that plants on Santa Catalina Island had lower levels of spinescence than the plants in the Santa Ana Mountains. Leaf puncture strength was also lower on Santa Catalina Island, while leaf mass per area was similar between the two sites. I observed no difference in cyanogenic glycoside concentrations between the two locations. During the feeding preference tests, goats preferred the plants from Santa Catalina Island over plants from the Santa Ana Mountains. Overall, the island plants had reduced herbivory defense traits, and were more preferred by goats. This phenomenon may be explained by a long historical absence of native mammalian herbivores, as well as several other factors associated with island climate.

### **KEYWORDS**

cyanogenesis, feeding preference, spinescence, leaf toughness, chaparral

## INTRODUCTION

Conservation of island ecosystems is important because they are typically rich in endemic species and support unique communities (Mueller-Dombois 1981). Endemic species on islands disproportionately contribute to worldwide biodiversity. However, there has been a major increase in the extinction rate of endemic plant species on islands since the 1600's (Atkinson 1989). A large contributor to this is exotic herbivore species introduced to islands by humans (Vitousek 1988).

The Mediterranean-type climate region of southern California is dominated by a diverse native plant community of evergreen sclerophyllous shrubs, the chaparral (Cooper 1922). Large mammalian herbivores, such as mule deer, are native to chaparral communities and browse on the woody shrubs. Santa Catalina Island, off the coast of southern California, shares much of the same vegetation as the mainland mountain ranges in the same latitude (Minnich 1980), but for most of its history it has been without large mammalian herbivores. It was only 150 years ago that such herbivores, including goats, hogs, mule deer, and bison were introduced to Santa Catalina Island (Minnich 1982). Because of the difference in natural history between Santa Catalina Island and the nearby mainland, plants in these environments may have evolved under different selective pressures. One suite of traits that may have been affected is herbivory defense, the ability of plants to fend off herbivores using morphological and chemical means.

Two morphological traits that influence herbivory defense are spinescence (Belovsky et al. 1991) and leaf toughness (Lowman and Box 1983). Spinescence protects the plant in several ways. The spines deter the herbivore from the plant, as well as make it uncomfortable to chew. Additionally, herbivores bite smaller chunks of plants with greater spinescence, resulting in less plant biomass loss (Belovsky et al. 1991). Leaf toughness is determined by the strength of the leaf material and the leaf thickness (Read et al. 2009). Leaves that are tougher limit the chewing capacity of herbivores (Lowman and Box 1983). Digestion is also more difficult as leaf toughness increases (Hanley et al. 2007).

Bowen and Van Vuren (1997) conducted an experiment to examine differences in herbivory defense between the plants on Santa Cruz Island, a neighbor of Santa Catalina Island, and plants on the southern California mainland. Their results showed that plants on Santa Cruz Island displayed fewer morphological traits associated with herbivory defense than did plants on

the mainland. Additionally, their experiments showed that sheep had a preference for the island plants as measured by feeding preference trials. Since the work of Bowen and Van Vuren (1997), there has been little done to follow up on their findings and test the generality of their conclusions on other islands. I studied the plants of Santa Catalina Island to test for further evidence of the lack of herbivory defenses in island plants.

## **Questions and Hypotheses**

A variety of closely related chaparral species occur on Santa Catalina Island and the Santa Ana Mountains in southern California. I compared those plants to answer the following questions: (1) How do the physical defenses of plants differ between the two sites? and (2) Do herbivores have a higher preference for plants on the island than for those on the mainland? My hypotheses are: (1) Plants on Santa Catalina Island will exhibit fewer physical defenses than will those from the mainland, and (2) Herbivores will prefer vegetation from Santa Catalina Island over those from the mainland.

## **METHODS**

### **Study Sites and Species**

Santa Catalina Island (33°21'N; 118°21'W) is located approximately 25 miles off the coast of southern California. The mainland site in the Santa Ana Mountains is located in Cleveland National Forest (33°38'N; 117°23'W). Both sites have similar characteristics, in that they are located at roughly the same latitude (33°N), and have the same altitude (600m), slope, aspect (north-facing), mean annual temperature (17°C) and precipitation (300mm). In addition, they are both covered in chaparral vegetation with similar plant community composition. To compare herbivory traits between sites, ten island-mainland species pairs were sampled from the two sites (Table 1). The species pairs were either congeneric pairs (two species from the same genus) or conspecific pairs (the same species from both sites). Pairing closely related species for analysis allows for more informative trait analyses. Species were chosen because they are abundant and are a good representation of the chaparral communities in the two field sites.

**Table 1.** Selected species for Santa Catalina Island and the Santa Ana Mountains. Each of the species is common in chaparral communities. Each species pair is closely related between the two sites, and is either congeneric or conspecific.

<b>Genus</b>	<b>Island Species</b>	<b>Mainland Species</b>
<i>Rhus</i>	<i>integrifolia</i>	<i>ovata</i>
<i>Arctostaphylos</i>	<i>catalinae</i>	<i>glauca</i>
<i>Quercus</i>	<i>pacifica</i>	<i>berberidifolia</i>
<i>Ceanothus (Cerastes)</i>	<i>megacarpus insularis</i>	<i>crassifolius</i>
<i>Ceanothus (Ceanothus)</i>	<i>arboreus</i>	<i>oliganthus</i>
<i>Rhamnus</i>	<i>pirifolia</i>	<i>ilicifolia</i>
<i>Prunus</i>	<i>ilicifolia lyonii</i>	<i>ilicifolia</i>
<i>Heteromeles</i>	<i>arbutifolia</i>	<i>arbutifolia</i>
<i>Cercocarpus</i>	<i>betuloides traskiae</i>	<i>betuloides</i>

## Sampling Methods

I selected ten individuals from each species at each of the two sites. I selected individuals that were close to the central location, and were fully mature and healthy. To measure each of the morphological and chemical traits (described below), mature, healthy leaves were clipped, immediately sealed in zip lock bags, and stored in an ice chest to keep them fresh until they could be returned to the lab. I took all measurements no longer than one week after collecting the samples.

## Morphological Traits

The morphological traits I tested were spinescence and leaf toughness. I measured spinescence for the three pairs of plants that exhibit spines: *Heteromeles*, *Prunus*, and *Rhamnus*. For each location and species I measured 18 leaves, three from each of six individuals. Spinescence was quantified following Bowen and Van Vuren (1997) in two ways: (1) counting the number of spines per leaf area, and (2) measuring spine length per leaf area. I used ImageJ 1.46 (U.S. National Institutes of Health, Bethesda, Maryland) to calculate spine length and leaf area for each of the spinescence measurements.

For my first measure of leaf toughness, I measured ten leaves from each of ten individuals from each location and species. I measured leaf mass per area, as a measure of leaf thickness. I calculated leaf area using a leaf area meter. I then dried the leaves in a 60°C drying oven for 24 hours and measured the dry leaf mass. Another measurement of leaf toughness I used was leaf puncture strength, using a leaf penetrometer as described by Lowman and Box (1983) using three fresh leaves from each of six individuals from each location and species. The leaf penetrometer is a device that records the maximum force required to puncture a hole through a leaf.

### **Chemical Traits**

I measured leaf cyanogenic glycoside concentration to quantify chemical defenses against herbivores. I collected leaves from both locations in the month of February to be sure of sufficient cyanogenic glycoside levels. The leaves were stored in a -80°C freezer for two months prior to analysis. I used the Pyridine-Pyrazalone method to test for cyanogenic glycosides in *Heteromeles*.

I sliced each leaf along the midvein using a razorblade. One half of the leaf was used to determine the dry weight. They were put in a 60°C drying oven and the dry weights were recorded. I ground the remaining half of the leaf in liquid nitrogen. In an Erlenmeyer flask I added 15 ml of 0.1M phosphate buffer at pH 6.2 to 35-45 mg of the Santa Catalina Island leaf or 10-15 mg of the Santa Ana Mountains leaf. I placed a small plastic tube containing 0.4 ml 1M sodium hydroxide inside the Erlenmeyer flask. I sealed the flask with parafilm and incubated it at 30°C for 48 hours, allowing the cyanide to distill into the plastic tube. After incubation I removed the plastic tube and lowered the pH by adding a few drops of 3M acetic acid. I diluted the solution to 100 ml using deionized water. I prepared a blank solution, as well as six standard cyanide solutions ranging from 0.01 mg/L to 0.2 mg/L using a potassium cyanide stock solution.

For each sample, blank, and standard I transferred 25 ml of the solution to a 50 ml plastic tube. I used the Hach Cyanide Reagent Set, CyaniVer, 10 ml and added the kit to the solution as directed. I measured the absorbance at 614 nm using a diode array spectrophotometer. I plotted the absorbance of the cyanide standard versus the known concentration. The calibration equation

was determined using Beer's Law. I used the calibration equation to determine the concentration of each sample solution. Finally, I calculated percent cyanogenic glycoside per dry leaf mass.

### **Feeding Trials**

I conducted a feeding preference test using methods modified from Bowen and Van Vuren (1997) to determine if there is a natural preference for island plants or mainland plants. All ten pairs of species were used in the feeding trials, with one trial for each species pair. I collected 18 branches 50 cm long from each species and stored them in an ice chest. All branches were used within one week after harvesting. For each species, three bouquets of branches were made, with each bouquet representing one branch from each of six individuals. I used domesticated goats provided by a company called Goats R Us (Orinda, CA). The same group of ten goats was used in each of the trials. The goats were left without food in a corral for four hours to ensure sufficient hunger. After four hours, 3 island bouquets and 3 mainland bouquets were provided, all at a uniform height of 75 cm. The bouquets were placed 60 cm apart from each other and were arranged in a random order. The bouquets were secured along both sides of the feeding station and the goats were allowed to browse for 10 minutes. The branches were weighed before and after the feeding trial to determine the mass consumed during the feeding time. Only five trials were completed each day to maintain sufficient hunger.

### **Data Analysis**

For the morphological traits, I compared the mean values for spinescence and leaf toughness between the two sites using two-tailed paired t-tests. I included both a community level comparison between island and mainland, as well as individual comparisons for each pair of related species. For the feeding trials, I used two-tailed paired t-tests to compare the difference in herbivory rates for each pair of related plants. For each group of paired t-tests, I used the Holm's Bonferroni p-value correction to correct for the family-wise error rate.

## RESULTS

### Morphological Traits

#### *Comparison of all island plants and all mainland plants*

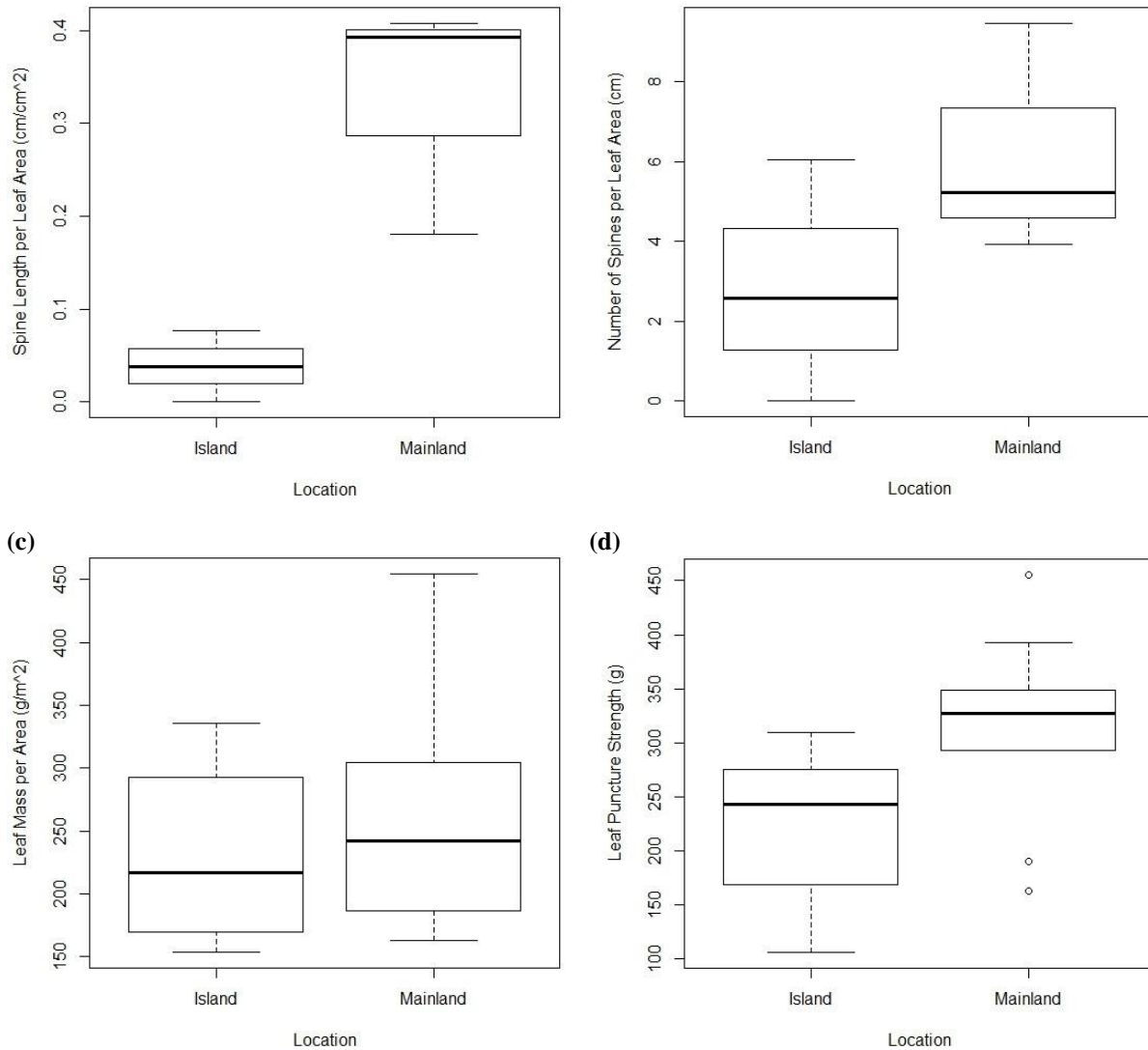
When comparing all island plants with all mainland plants, I found that leaf puncture strength was significantly higher in the mainland plants than in the island plants (Table 2; Figure 1d). Both measures of spinescence were nearly significantly higher in mainland plants compared to in island plants (Table 2; Figures 1a and 1b). I found a higher leaf mass per area for mainland plants than for island plants, though this difference was not statistically significant (Table 2; Figure 1c).

**Table 2. Summary of the paired t-tests comparing the island site to the mainland site.** The difference in means is calculated by island - mainland.

<b>Trait</b>	<b>t value</b>	<b>p value</b>	<b>Difference in means</b>
Total spine length per leaf area	-3.71	0.098	-0.29
Number of spines per leaf area	-2.99	0.098	-3.34
Leaf mass per area	-1.30	0.112	-22.0
Leaf puncture strength	-4.76	0.003	-89.6

(a)

(b)



**Figure 1.** The above boxplots compare herbivory defense traits between the two sites. The bolded line is the median, and the box represents the interquartile range. **(a)** Total spine length per leaf area compared between island and mainland plants ( $n=3$ ). Mainland plant spinescence was nearly significantly higher than island plant spinescence ( $p=0.098$ ). **(b)** Number of spines per leaf area compared between island and mainland plants ( $n=3$ ). Mainland plant spinescence was nearly significantly higher than island plant spinescence ( $p=0.098$ ). **(c)** Leaf mass per area compared between island and mainland plants ( $n=10$ ). There is no significant difference between the two locations ( $p=0.112$ ). **(d)** Leaf toughness measured with a leaf penetrometer compared between island and mainland plants ( $n=9$ ). Mainland plants had a significantly higher leaf toughness ( $p=0.003$ ).

### *Individual Species Comparison*

When comparing total spine length per leaf area between individual species pairs, all three had significantly higher spinescence in the mainland plants (Table 3, Figure 2a). *Prunus* had the greatest mean difference because the island plants have completely lost their spines.



**Table 3.** Summary of the paired t-tests comparing individual species pairs for total spine length per leaf area (n=5-6). The difference in means is calculated by island – mainland.

Taxa	t value	p value	Difference in means
<i>Heteromeles</i>	-5.57	0.003	-0.14
<i>Rhamnus</i>	-5.33	0.003	-0.32
<i>Prunus</i>	-16.7	1.95e-5	-0.41

All three species pairs had significantly higher numbers of spines per leaf area in the mainland plants (Table 4, Figure 2b). Once again, *Prunus* showed the greatest difference because the island plants have completely lost their spines.

**Table 4.** Summary of the paired t-tests comparing individual species pairs for number of spines per leaf area (n=5-6). The difference in means is calculated by island - mainland.

Taxa	t value	p value	Difference in means
<i>Heteromeles</i>	-2.66	0.028	-1.37
<i>Rhamnus</i>	-3.20	0.024	-3.42
<i>Prunus</i>	-22.7	4.65e-6	-5.23

*Cerastes* was the only pair out of 10 species pairs that had significantly higher leaf mass per area on the mainland than on the island (Table 5, Figure 2c). Though not statistically significant, *Heteromeles*, *Rhamnus*, *Cercocarpus*, *Prunus*, and *Ceanothus* all had higher leaf mass per area on the mainland than the island (Table 5).

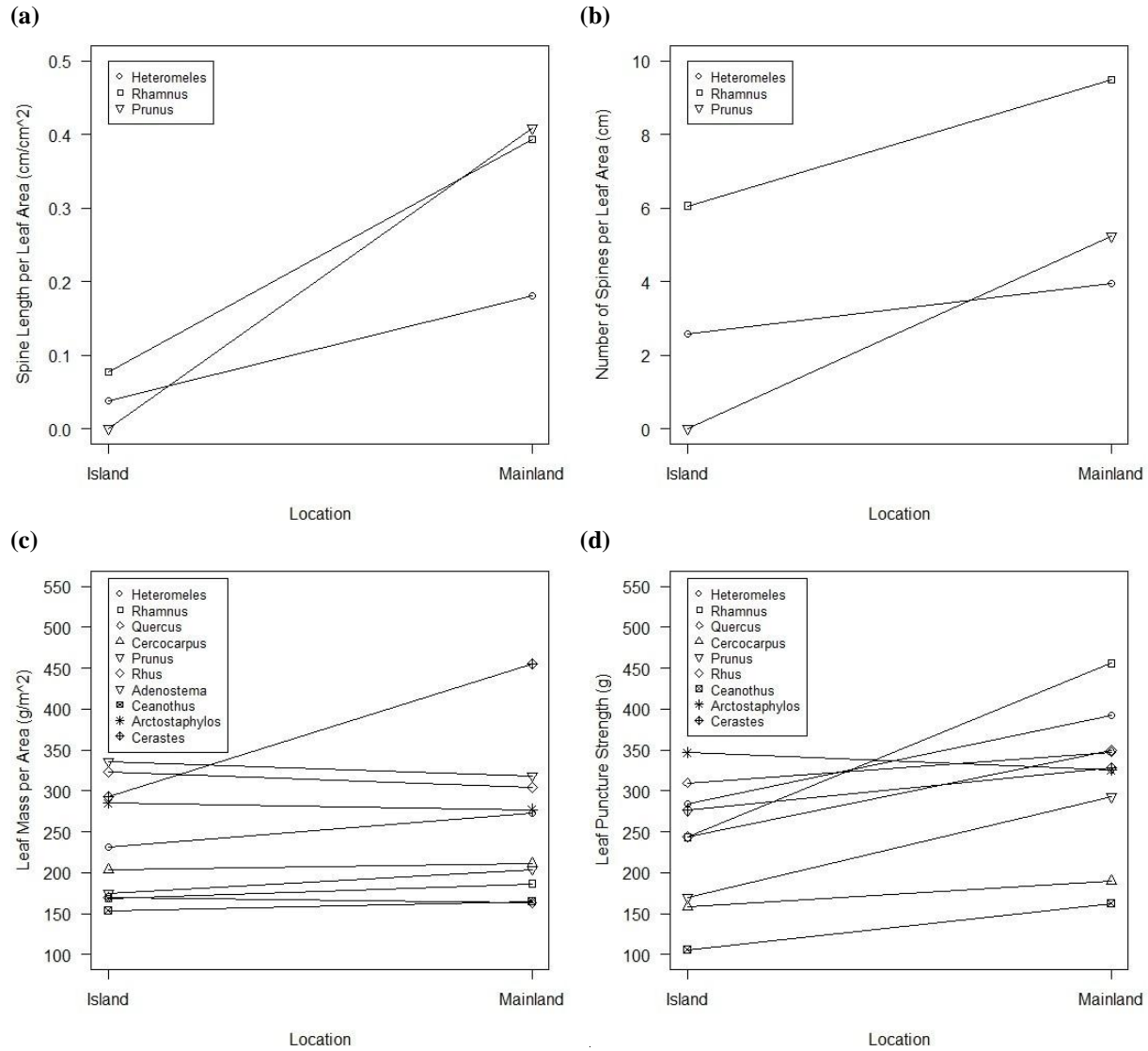
**Table 5.** Summary of the paired t-tests comparing individual species pairs for leaf mass per area (n=8-10). The difference in means is calculated by island - mainland.

Taxa	t value	p value	Difference in means
<i>Heteromeles</i>	-1.82	0.39	-39
<i>Rhamnus</i>	-1.20	0.79	-18
<i>Quercus</i>	0.66	1	7.1
<i>Cercocarpus</i>	-0.47	1	-7.7
<i>Prunus</i>	-2.28	0.22	-29
<i>Rhus</i>	0.51	1	11
<i>Adenostema</i>	0.54	1	17
<i>Ceanothus</i>	-2.21	0.25	-22
<i>Arctostaphylos</i>	0.79	1	9.7
<i>Cerastes</i>	-12.4	2.87e-6	-160

Of nine species pairs, only *Rhamnus* had significantly higher leaf puncture strength on the mainland (Table 6, Figure 2d). *Prunus* and *Rhus* were nearly significantly different ( $p=0.08$  for each), with both having higher toughness in mainland samples than in island ones. *Arctostaphylos* was the only genus exhibiting a higher leaf toughness on the island than on the mainland, though this was not statistically significant ( $p=0.68$ ).

**Table 6.** Summary of the paired t-tests comparing individual species pairs for leaf puncture strength ( $n=6$ ). The difference in means is calculated by island - mainland.

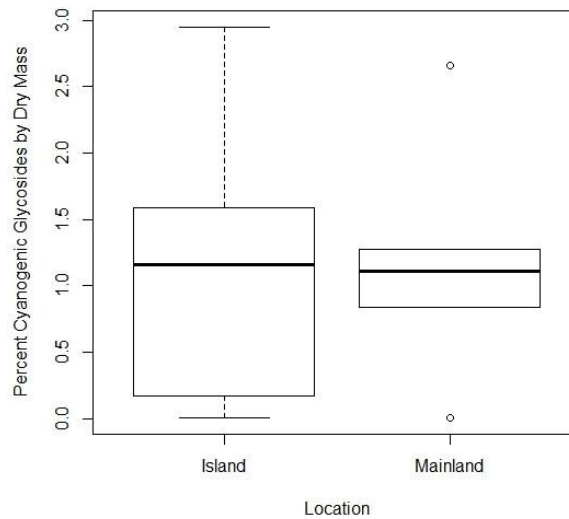
<b>Taxa</b>	<b>t value</b>	<b>p value</b>	<b>Difference in means</b>
<i>Heteromeles</i>	-2.17	0.23	-110
<i>Rhamnus</i>	-7.36	0.003	-210
<i>Quercus</i>	-1.08	0.45	-38
<i>Cercocarpus</i>	-1.16	0.45	-32
<i>Prunus</i>	-3.27	0.08	-120
<i>Rhus</i>	-3.40	0.08	-110
<i>Ceanothus</i>	-2.24	0.23	-57
<i>Arctostaphylos</i>	0.48	0.68	22
<i>Cerastes</i>	-1.88	0.24	-52



**Figure 2.** (a) Comparison of spine length per leaf area between individual species pairs between island and mainland sites. All three pairs had statistically significantly higher spinescence in the mainland plants than in the island plants ( $p < 0.05$ ). (b) Comparison of number of spines per leaf area between individual species pairs between island and mainland sites. All three pairs had statistically significantly higher spinescence in the mainland plants than in the island plants ( $p < 0.05$ ). (c) Comparison of leaf mass per area between individual species pairs between island and mainland sites. Six of the ten pairs had higher leaf mass per area in the mainland plants than in the island plants. *Cerastes* was the only pair with significantly higher leaf mass per area in the mainland plants than the island plants ( $p = 2.87 \times 10^{-6}$ ). (d) Comparison of leaf puncture strength between individual species pairs between island and mainland sites. Eight of the nine pairs had higher leaf puncture strength in the mainland plants than in the island plants. *Rhamnus* was the only pair with significantly higher leaf mass per area in the mainland plants than the island plants ( $p = 0.003$ ).

## Chemical Traits

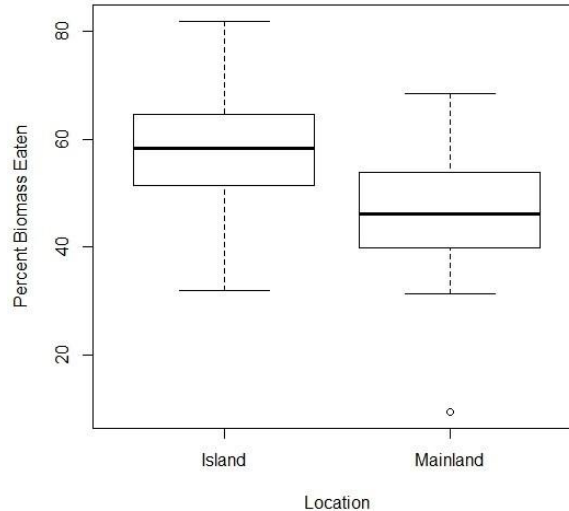
I found no difference in percent cyanogenic glycoside by dry mass in *Heteromeles arbutifolia* from the mainland plants ( $1.18\% \pm 0.43\%$ ) and island plants ( $1.17\% \pm 0.45\%$ ) ( $p=0.99$ ; Figure 3).



**Figure 3.** Cyanogenic glycoside concentration compared between island and mainland plants ( $n=5-6$ ). There was no difference in cyanogenic glycoside concentration between the island plants and mainland plants ( $p=0.99$ ).

## Feeding Trials

The feeding trials resulted in the goats having a preference for island plants over mainland plants. The goats ate a statistically significantly greater percentage of biomass of island plants ( $57.9\% \pm 4.7\%$ ) than mainland plants ( $44.6\% \pm 4.8\%$ ) ( $p=0.02$ ; Figure 4).



**Figure 4.** Percent biomass eaten compared between island and mainland plants. Goats ate significantly more island plant biomass than mainland plant biomass ( $p=0.02$ ).

## DISCUSSION

The aim of this project was to characterize any differences in herbivory defense traits between two study sites: Santa Catalina Island and the Santa Ana Mountains. My data suggest that, in general, herbivory defense traits were higher in the mainland site than in the island site. Furthermore, results of feeding trials with goats suggest a greater preference for island plants. This pattern may implicate selection for reduced herbivory defense on Santa Catalina Island related to the historical absence of mammalian herbivores over evolutionary time. Future management decisions regarding introduced herbivores on Santa Catalina Island should be mindful of the reduced defenses and increased palatability of native island plants.

### Morphological Traits

Spinescence and leaf puncture strength measurements suggest that mainland plants are better defended than close relatives on the island, while leaf mass per area was only moderately higher in mainland plants. Similar studies have found comparable spinescence differences between island and mainland plant communities (Bowen and Van Vuren 1997). Differences in spinescence were especially apparent in *Prunus*, as the island plants no longer have any spines.

Lack of herbivory has been shown to greatly reduce spines, even within a single generation (Young et al 2003). It may be that without the presence of herbivores on Santa Catalina Island until recent years, there was no need for plants to devote resources to produce spines. Producing spines unnecessarily might interfere with the biomechanics in the leaf (Brown et al 2012). Instead of producing defenses, plants can instead allocate their resources towards growth (Mole 1994).

Leaf toughness is a much more variable trait that has many secondary functions including resistance to wilting, water and nutrient conservation, and total assimilation efficiency (Hanley et al 2007). Both measurements of leaf toughness I used (leaf mass per area and puncture strength) were higher in specimens from the mainland site. For leaf mass per area, most species pairs were similar between the two sites with the exception of *Cerastes*, whose leaves were much tougher on the mainland than on the island. The difference in leaf mass per area can be explained by the difference in appearance of sclerophylly. The difference in sclerophylly is much more pronounced to the naked eye in *Cerastes* than any other species pair. For puncture strength the only species pair that had a higher mean on the island was *Arctostaphylos*, though this difference in means was relatively small. The puncture strength of *Arctostaphylos* may be relatively similar between the two sites because both species are isofacial, with equal amounts of stomata on both sides of the leaf (Howell 1945). Isofacial leaves may have a more specialized structure, which may limit the variation in leaf toughness over evolutionary time. The more important trend is that 8 of the 9 species pairs showed higher puncture strength on the mainland than on the island, which indicates that island plants are less defended, in general. Leaf toughness has been shown to be positively correlated with phenolics, chemical compounds known to deter herbivores (Read et al 2009). A decrease in leaf toughness on Santa Catalina Island could mean there is also a decreased level in phenolics.

### **Chemical Traits**

I found no difference in cyanogenic glycoside concentration in the *Heteromeles arbutifolia* from Santa Catalina Island than the *Heteromeles arbutifolia* from the Santa Ana Mountains. However, higher concentrations were found in mainland plants in a previous study of cyanogenic glycosides between Santa Catalina Island and the Santa Monica Mountains (Helms

*unpublished data*). Tannins and phenols were shown to be less indicative of herbivory defense in a study between Santa Cruz Island and the Santa Ynez Mountains (Bowen and Van Vuren 1997). Cyanogenic glycosides are widely accepted to be antiherbivore compound (Hruska 1988), which suggests that a lack of herbivores would cause a decrease in cyanogenic glycoside production. Although there has been some argument that cyanogenic glycosides in small quantities have a limited role in nitrogen assimilation, the more common belief is that it is primarily used as a defense compound (Jones 1979). Without herbivores present until recent years, there has been no need for large quantities of cyanogenic glycosides. Production of defenses is costly, and takes resources that could otherwise be allocated towards plant growth (Herms and Mattson 1992).

### **Feeding Trials**

Goats preferred to eat vegetation from Santa Catalina Island over vegetation from the Santa Ana Mountains. The reduced morphological herbivory defense traits of the plants on Santa Catalina Island likely influenced the feeding preferences. Similar results were found in feeding preference tests between Santa Cruz Island and the Santa Ynez Mountains using sheep (Bowen and Van Vuren 1997). In other feeding trials of ungulates comparing the palatability of spinescent and non-spinescent species, it was found that less herbivory occurred in the plants with spines (Cooper and Owen-Smith 1986). Tannins proved to be a more important factor than spinescence for deer in a feeding trial testing various defenses (Schindler et al 2003). In general, it appears that morphological and chemical traits both influence the browsing behavior of large herbivores. As my results show that the plant communities on Santa Catalina Island have fewer defenses, island plants may be more palatable than mainland plants.

### **Causes and Implications of Reduced Defenses**

My study shows that plants on Santa Catalina Island have fewer defenses and are more preferred by goats than close relatives from the mainland. This phenomenon may be, at least in part, explained by the lack of natural herbivores throughout most of the island's history. Large herbivores were introduced approximately 150 years ago (Minnich 1982), which is very recent compared to the 300,000 year history of the island (Shoenherr et al 1999). Over evolutionary

time plants on Santa Catalina Island evolved in the absence of large mammalian herbivores, which may have reduced the need for plants to maintain defenses against such herbivores (Marquis 1991).

An alternative interpretation is that reduced herbivory defense of Santa Catalina Island plants is a consequence of adaptations to the unique island climate. Herbivory defense traits may have additional functions and may be influenced by multiple factors. For example, high leaf toughness is also associated with nutrient poor soils, full sunlight, high elevations, and dry climates (Hanley et al 2007). Production of chemical defenses, such as cyanogenic glycosides, may also be associated with water stress (Gleadow and Woodrow 2002) and nitrogen availability (Gleadow and Woodrow 2000). The island climate is cooler and more mesic than adjacent areas on the southern California mainland, and these conditions are associated with reduced drought tolerance in island plants (Ramirez et al. *unpublished data*). Therefore, it is possible that some of the observed reductions in herbivory defenses like lower leaf toughness may be due to adaptations to the island climate.

### **Broader Implications**

Regardless of which evolutionary path has gotten them there, plants on Santa Catalina Island have fewer defenses and increased palatability. It may be that by the time large herbivores were introduced to Santa Catalina Island, the reduction in herbivory defenses had rendered them particularly sensitive to browsing, thus adding to the magnitude of overgrazing by the exotic herbivores. The legacy of these herbivore introductions is a drastically altered and degraded landscape (Coblentz 1978).

More intensive management strategies may be needed to restore Santa Catalina Island back to the lush chaparral community it was before the introduction of herbivores. While goat and pig populations have already been removed from the island, there are still about 1,000 deer that provide a heavy browsing pressure on the native plant communities (Stapp and Guttilla 2006). As several other studies have also shown reduced herbivory defenses in island ecosystems (Bowen and Van Vuren 1997; Vourc'h et al 2000), this may be a more general characteristic of island ecosystems.



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