EFFECTS OF ENVIRONMENTAL CONDITIONS ON SIZE DISTRIBUTIONS OF LEPIDOPTERA IN TWO CONTRASTING ECOSYSTEMS: THE CHIHUAHUAN DESERT AND THE EDWARDS PLATEAU

by

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I. INTRODUCTION

A central focus in ecology is understanding how organisms interact with their environment. The mechanisms by which individuals, species and populations respond to abiotic factors, such as weather, are not fully understood. These mechanisms are the basis for understanding ecosystem dynamics, predicting how ecosystems will respond to climate change, and developing methodologies for conservation efforts. Comparative studies in ecosystems that differ strongly in climate could be especially powerful for understanding how individuals, species, and populations respond to abiotic factors, and predicting how the ecosystems will respond to the effects of variable or changing climate. As climate varies seasonally, inter-annually or over longer time periods, temperature and evaporation rates interact with the amount, frequency, intensity, and type of precipitation (Trenberth 2011).

Comparative studies can address a wide range of hypotheses and questions. Do closely-related organisms, for example of the of the same family or order, respond similarly to abiotic factors? Does the response to these factors change with the size of the organism? For example, in the Chihuahuan Desert the insects as well as the plants are under-studied, which is a knowledge gap that complicates research because many of the species are unidentified, and the natural histories of most species are not well known.

To investigate how organisms respond to abiotic factors and how those responses vary with changes of weather patterns due to climates change, we took advantage of the strong precipitation gradient across Texas and initiated research at two contrasting locations along that gradient.

Given the near absence of information on insects of the Chihuahuan Desert in West Texas, we began a long-term study to establish a baseline for the moth fauna. For comparison, we also studied insects on the Edward's Plateau, at Freeman Ranch near San Marcos, where moth species and their life history properties are better known. Both of these ecosystems have high rates of plant endemism and a strong contrast in the amount and timing of rainfall.

Body Size Relationships

Even for species that cannot be identified, measurements of their size can provide useful information about differences between species, as well as variation with the population of a single species. Even for an environment where species are understudied body size is an easily quantified dependent variable, and has been found to be correlated with various independent variables, such as metabolism, temperature, primary productivity, precipitation and nutrient availability (Peters 1986; Huston and Wolverton 2011). Body size patterns provide ecologists a starting point for investigating poorly-characterized systems, and can be readily quantified for virtually all types of animals (Wainwright 1994).

The idea that abiotic factors affect morphology has played a major role in the fields of evolution and ecology (LaBarbera 1989). Abiotic factors vary spatially and temporally, as does animal body size. In the mid-1800's, various ecologists took notice of body size patterns and established eco-geographic rules (e.g., Bergmann's and Allen's Rule) to describe the patterns at the intraspecific and interspecific levels (Bidau et al. 2012). Both of these scales of analysis were traditionally applied to endotherms and attempted to explain why the individuals of many species tended to be larger at higher elevation and/or latitudes. This relationship was described in 1839 as the result of metabolic demand based on total animal body size (Robiquet 1839). They explained that this was due to larger animals having a lower surface-to-volume ratio and are consequently more efficient at maintaining internal body temperatures that are advantageous for colder climes (Bergmann 1848; Kivelä et al. 2011; see however Huston and Wolverton 2011).

These eco-geographic rules, while simple in concept and general in application, created a baseline for future ecological research. Some species of endotherms show discrepancies from these predictions (Wolverton et al. 2009, Huston and Wolverton 2011). This suggests that body size distributions are more complex than thermoregulation alone and are possibly due to a combination of abiotic and biotic factors (Huston and Wolverton 2011). When originally applied to ectotherms, some of the observed patterns were inconsistent between vertebrate and non-vertebrates (Angilletta et al. 2004; Klok and Harrison 2013). Many arthropods, specifically insects, demonstrate a Bergmann's cline for body size variance along latitude and altitudinal gradients, while they show an inverse cline in response of their developmental time – as larval development rate increased, growth rate decreased with increasing latitude (Ray 1960; Kivelä et al. 2011).

Study System

We chose nocturnal insects in the order Lepidoptera as our study system to evaluate the variation of population responses and body-size distributions due to differences in environmental conditions such as temperature, growing degree days, and precipitation. This area of study is important because these factors potentially affect the productivity of plants on which herbivorous insects feed, and are likely to shift spatially and temporally as climate changes. We compared the patterns of lepidopteran body-size distributions between two contrasting ecosystems, the Chihuahuan Desert and Edward's Plateau.

Night-flying lepidoptera are an ideal study system due to the ease of capturing adults. Adults can be caught passively through the use of ultraviolet light traps, are easily processed, and are in high abundance in most ecosystems. They are also used as an umbrella species for biodiversity conservation (New 1997) and as indicator for ecosystem health (Hilty and Merelender 2000). Night-flying lepidoptera, specifically microlepidoptera, are not well-documented in the Chihuahuan Desert and many other ecosystems, and using them as a study system helps develop a baseline for future research in the region.

Abiotic Factors and Lepidoptera Responses to Environmental Conditions

We used nocturnal lepidoptera surveys in two ecosystems to address the following questions: 1) Do abiotic factors predict the overall abundance of lepidoptera; 2) Do lepidoptera that differ in size respond similarly to abiotic factors, and 3) Do abiotic factors affect the number of lepidopteran species in different areas. For abiotic factors, we focused on precipitation, temperature, and growing degree-days, because these factors are strongly influenced by climate and both plant growth and lepidopteran abundance are influenced by them.

The vast majority of Lepidoptera are herbivores that feed on plants during their larval stage. Variation in body size within and between species of Lepidoptera is affected by many different environmental factors, including the quantity and quality of the plant material they eat, rainfall, and temperature. It is important to note that other factors such as top-down predation, life-history strategy, dormancy, and sexual selection also influence body size (Klok and Harrison 2013).

Temperature is one of the strongest direct influences on body size of lepidoptera. Temperature is crucial for development. It influences feeding rates, individual development, movement, and population dynamics. Individuals that are reared in higher temperatures are often smaller, in comparison to ones that are reared in lower temperatures (Klok and Harrison 2013, Kingsolver and Huey 2008).

In addition to its effects on larval growth and activity, temperature also affects movement of adult lepidoptera (Raimondo et al. 2004;De Freitas et al. 2005). Numerous studies have demonstrated that as temperature increases more individuals are attracted to light traps (Williams and Bell 1940;Yela and Holyoak 1997; Williams and Bell 1940; Muirhead-Thompson 2012). The same pattern occurs with precipitation – as precipitation increases so do the number of individuals at traps (Butler et al. 1999). Precipitation also has been found to have a positive effect on individual body size of populations between sampling years (Maelzer and Zalucki 1999).

To standardize temperature and to account for intra-annual variation, we used growing degree-days (GDD). Growing degree-days are a temporal accumulation of heat and are calculated by calculating the daily average temperature based on the daily maximum and minimum temperatures, then subtracting temperature base, often 50°F (10°C), from the total temperature. GDD are widely used in horticulture and agriculture to determine planting dates, and have been demonstrated to be a reliable predictor of phenological responses to temperature for lepidopteran host plants and larval emergence (Baker et al. 1984, Damos and Savopoulou-Soultani 2011; Baker et al. 1984; Cayton et al. 2015) While temperature can affect insect development, precipitation can alter its effects.

Ecosystems are highly complex and have multiple levels of interactions between organisms and abiotic factors, and among the organisms themselves. Ecological comparative studies can be limited by the amount of knowledge of how organisms respond to their environment. The lack of information of the lepidopteran community in the Chihuahuan desert imposes limitations what types of research are feasible. It is important to establish a baseline on which future research can be based. Lepidoptera are an ideal study group because they are indicators for biodividersity and ecosystem health. We identified abiotic factors for which data are relatively easy to gather to evaluate whether and how the body size distribution of lepidoptera varies in response to the chosen abiotic factors. By doing so we are establishing a methodology that can be used in other under-studied ecosystems. This work should lead to a better understanding of how lepidoptera respond to their environment and how that response changes due to climate change.

II. METHODS

Sampling and Sorting Methods

The analysis is based on monthly sampling of a specific subset of the Lepidopteran communities within two contrasting ecosystems, the Chihuahuan Desert and the Edwards Plateau, in 2013. To develop a quantitative and reproducible sampling method, we standardized a light-trap procedure after multiple trials in the field. Traps were suspended from three telescoping legs that raised the trap above vegetation, with the top of the trap about 1.75 m about the ground surface. Trap design consisted of a cylindrical container with one side cut away to create a 90° field of light projected from a 15-w tubular UV light bulb that was attached to the inside of the trap. The bottom of the trap funneled into a plastic bucket charged with ethyl acetate, a common entomological killing agent. The UV-light attractant was indiscriminate of order of insect, and collected only species that were attracted to UV light.

Criteria for acceptability of the monthly sample included controlling for UV light competition from moonlight by sampling only during the new moon (Nowinszky 2004), and by only sampling when wind gusts were less than 5 mph and ambient temperatures were above 50^{o} F (McGeachie 1989). Sampling was started 30 minutes after sunset for a duration of 90 minutes, thus capturing only a subset of the total moth fauna, and collecting no information on moths that become active later than two hours after sunset. To eliminate sampling bias due to local vegetation composition, we chose two sites per location, each comprised of different vegetation mosaics. Both sites were sampled simultaneously with identical traps.

We sorted samples into morphospecies and pinned or stored them in dry vials. We defined morphospecies by visible differences between individuals based on morphological characteristics as color, wing pattern (e.g., reniform spot, fringe, and margin), and size. To analyze body mass, we dried collections of morphospecies at 140°F (60°C) for 24 hours, and immediately weighed them to the nearest mg. We chose to sort samples to morphospecies, because the Chihuahuan Desert lepidopteran community is not well-characterized, with incomplete species lists, and with many species having multiple morphs that are not easily identifiable without dissection of genitalia.

Site Descriptions

Chihuahuan Desert

We sampled the Chihuahuan Desert near Terlingua Ranch Headquarters, at the base of the Christmas Mountain Range, adjacent to Big Bend National Park located in Brewster County, Texas. We chose the site due to the proximity of the Christmas Mountains which are owned and maintained by the Texas State University System. We obtained weather data for the area from Panther Junction in Big Bend National Park. Panther Junction receives an average of 33.53cm (13.22inches) of rain per year, with most of the precipitation occurring during the monsoon season – beginning in May and peaking between July and October. Average annual temperature is 66.3°F (19.05°C).

The two different sampling sites were 1) mesquite (*Prosopis pubescens)* and creosote (*Larrea tridentate)* flats, and 2) a mountain hillside that was dominated by Sotol , Yucca, tarbush (*Flourensia cernua)*, and various other shrubs. One temperature station was used for both sites during sampling. However, it should be noted that the two sites have microclimatic differences. The mountain hillside (west slope facing afternoon sun) is warmed from the sun during the late afternoon, while the flats (lower elevation) are affected by cool-air drainage that occurs shortly after sunset.

Edwards Plateau

The Edwards Plateau sampling site is located at Freeman Ranch in San Marcos, Texas. Freeman Ranch is managed by Texas State University, and has been used as a site for cattle management and forensic research. The area that was sampled has not been used for grazing cattle for over 20 years. Weather data for the area were obtained from a weather station in San Marcos, Texas. San Marcos, Texas receives an average of 90.81cm (35.75 in) of precipitation per year with the majority of the rain falling during the spring, May and June, and the fall, September and October. This bimodal distribution of rainfall, with the rainy periods separated by a hot, dry summer is similar to a mediterranean climate. Average annual temperature is 68.45°F (20.25°C).

The two sites sampled are an open oak savannah and a juniper thicket (29.935140, -98.014092). The juniper thicket tended to stay warmer than the open savannah (29.935458, -98.013853).

Analysis

I calculated individual weights for each morphospecies by dividing the total mass of all individuals by the number of individuals. Body size classes were defined using a log 2 scale of average morphospecies weight in milligrams: 1,2,4,8,16,32,64, and 128.

The effects of environmental factors (precipitation, temperature, growing degree days, photoperiod) on the abundance of the various body-size classes (evaluated using both the total number of individuals and total weight per size class) were evaluated using a correlation matrix. Because of small sampling size (9 months) the significance level was set at $p < 0.05$.

III. RESULTS

I analyzed a total of 11,060 individual lepidoptera in 9 monthly samples at both the Christmas Mountains (6,884) and Freeman Ranch (4,176) Total dry weight of all samples was 56.92 grams (see Appendix B, Table 3 and 2). Christmas Mountains had a total of 39.82 grams, with Freeman Ranch having a total of 17.10 grams for the 9 sample months. At the Christmas Mountains there were more correlations (both positive and negative) among body-size classes and of body size classes with environmental factors than at Freeman Ranch (Table 1 and Table 2). The majority of the significant ($p < 0.05$) correlations were positive.

The number of morphospecies, total weight, and the number of individuals per size class all reach a maximum during the month when precipitation reaches a maximum (Fig 1 and 2). At Freeman Ranch this is during the spring and fall months, while at Christmas Mountains it is at the peak of the summer monsoon in late summer. Total annual distribution of morphospecies varies in peaks per size class at both locations (Fig. 7 and 8). The annual totals of the number of morphospecies by size class at both sites have a unimodal annual normal distribution (Fig. 3 and 4). The monthly distributions of morphospecies per size class differs greatly from month to month, and rarely matches the annual average. Annual weight by size class has a distribution that is skewed to the left at both locations, with most of the weight in the larger size classes (Fig 5 and 6). Weight by size class is greatest during months that had the highest amount of precipitation. i.e, March and September at Freeman Ranch, and August in the Christmas Mountains

All data are compiled in the Appendix. These data include monthly mean and cumulative values for precipitation, photoperiod and temperature, and temperature at time of sampling. These are the highlights of the most pertinent data for the study.

Freeman Ranch

Monthly precipitation in Central Texas typically has a bimodal distribution with most rain falling in the spring and fall. In 2013, there was heavy rainfall in March, some rain in June and moderate rainfall in August, September and October. Both the total number of individuals and total dry weight per month had a bimodal distribution, with peaks in March and September (Fig. 1b and c).

The total number of morphospecies was highest in March and remained relatively constant until dropping in October (Fig. 1c). March has the highest total of morphospecies coinciding with the major peak of precipitation.

Patterns of number of individuals and of weight per size classes, did not follow that of total morphospecies. The annual pattern of total weight was bimodal with peaks in March and September (Fig. 1c), and the annual pattern of the number of individuals was also bimodal, with the largest amount in the late summer (Fig. 1b). Months that had the highest total weight also had the largest number of morphospecies.

The summed annual distribution of morphospecies per size class is unimodal with the highest number in the median size class, size class 8 (Fig 3, bottom panel). This annual pattern breaks down at a monthly scale. June has the most dramatic difference among size classes, with 30 morphospecies in size class 8, and with size classes 2 and 16 following with 7 morphospecies, respectively. Size classes representing the ends of the spectrum, 1,2, and 128, are low in number of morphospecies in all months. In March, weight was centered on larger body size classes, 8, 16, and 32 (Fig. 3).

Annual distributions of morphospecies were not consistent between size classes (Fig. 7). Combined body-size classes 64 and 128 due to small sample size. Body-size classes 64 and 128 peaked in March, coinciding with spring rainfall. Body-size class 8 had varied distribution not coinciding with rainfall. Body-size classes 1 peaked in May, and in August coinciding with fall precipitation.

Annual distribution of total weight were not consistent between size classes (Fig. 9). Body-size classes 64 and 128 peaked in March, coinciding with increase in total number of morphospecies. Body-size class 8 peaked in September.

Pearson's Correlation Matrix

Numbers of individuals for body size classes 2, 8, 16, 32, 64 and 128, were positively correlated with one another (Table 1). Body-size class 16 was the strongest predictor of presence and total number of individuals for body-size classes 32, 64, and 128 ($p < 0.05$). No environmental factors were statistically significant ($p < 0.05$) as predictors for biotic, weight, response of the total sample and for all body size classes, although the three correlations greater than $r = 0.5$ were negative (Table 1).

Total weight of the monthly sample was strongly correlated with the weights of body-size classes 2, 16, 32, and 64, indicating that these comprise the majority of the total sample weight. Size class 64 was positively correlated with size class 16 and 32 ($p < 0.05$). Total monthly precipitation was negatively correlated with body size class 128

($p < 0.05$), while body-size class 1 had a similar negative correlation with cumulative precipitation over 2 and 3 months (Table 2).

Christmas Mountains

Precipitation in the Big Bend region has a unimodal distribution with increasing rainfall over the summer, peaking in September at the height of the monsoon season. Both total number of individuals and sample weight followed a unimodal distribution of precipitation, with the major peak occurring in August (Fig. 2 b and c). The number of morphospecies had a bimodal distribution, with the peaks occurring in April and July (Fig 2a).

The annual distribution of morphospecies per size class was concentrated in the median size class, size class 8 (Fig 4, lower panel). The smallest size class (1) had more morphospecies than size class 2. In August, where total number of individuals and weight were highest and amount of precipitation was the greatest, distribution was similar to the total annual distribution, with a minor peak in size class 1 and a major peak in size class 8. In June, size class 1 had the highest number of morphospecies of all size classes. The abundance of size class 1 was greater than in any other month and coincided with the minor peak of precipitation (Fig 2 and 4). July had the highest abundance of median body size classes, 8 and 16, more than any other month.

At the annual scale, weight per body size class was bimodal with a peak in size class 64 and a higher peak in size class 8. August had the greatest total weight per sample and also highest total weight per body size class The weight distribution in August differed from the annual pattern, with size class 8 and size class 16 having by far the highest total weight per size class. (Fig 6).

Annual distribution of morphospecies were not consistent between size classes (Fig. 8). Body size class 1 peaked with first on set of precipitation in June. Body-size classes 8, 64, and 128 peaked in July as total monthly precipitation increased. Body-size class 128 peaked in August when precipitation was greatest and when body-size classes 1 and 8 decreased.

Annual distribution for total weight was consistent between size classes (Fig. 10). All body-size classes peaked in August with increasing precipitation.

Pearson's Correlation Matrix

Similar to the results from Freeman Ranch, no environmental factors were statistically significant ($p < 0.05$) as predictors for number of individuals or weight of either the total sample or the individual body-size classes. All size classes were positively correlated with each other except for size class 2. Size class 2 was negatively correlated with all other size classes, with the correlations with size classes 4 and 128 being statistically significant

Sample temperature was positively correlated with the total weight of body size class 1 (Table 2). No other environmental factors in our analysis were significant as predictors for the response of the total sample or the body size classes ($p < 0.05$).

Total sample weight was significantly and positively correlated with the weight of all body-size classes except 2, which had a negative correlation that was not statistically significant and 4 which had a positive correlation greater than 0.5 that was not significantly significant at $p<0.05$ (Table 2). Increase in body weight in size class 1 was correlated with increases in body-size classes 8, 16, and 64 ($p < 0.05$).

IV. DISCUSSION

Despite the fact that there were few correlations between specific environmental factors and either the total number or weight of all lepidoptera or the number or weight of the individual size classes, there were strong differences in the patterns observed at Freeman Ranch in comparison to the Christmas Mountains. Specifically, there were many more correlations and stronger correlations among the abundance and weights of the body size classes at Christmas Mountains than at Freeman Ranch. This could be due to the contrasting seasonal patterns of precipitation at the two locations.

There are also more correlations between abiotic factors and body size classes at Christmas Mountains than at Freeman Ranch, which also likely due to the differences in the precipitation patterns at each location. Rainfall at Freeman Ranch has a bimodal distribution, peaking in the spring and in the fall, while Christmas Mountains has a unimodal distribution peaking in the late summer (Fig 1 and 2). Water is a much more limiting resource at the Christmas Mountains than at Freeman Ranch. In the desert, precipitation is the driving force behind ecosystem dynamics. It is a signal to animals to mate (Denlinger 1980), for plants to grow (Ogle and Reynolds 2004), and for seeds to germinate (Clauss and Venable 2000). We can conclude that body size classes 1, 4, 8, 16, 32, 64 and 128 are responding and utilizing the same type of resources as they are all strongly correlated with precipitation (Table 1). However, since the species composition and productivity of the plant communities were not quantified, it is difficult to say what resources are being utilized.

The lepidopteran community at Freeman Ranch is responding to a more complex precipitation pattern than in the Christmas Mountains. The total number of individuals at

Freeman did not respond in proportion to the magnitude of the precipitation peaks (Fig1). This could be due to the colder temperatures (and fewer growing degree days) in March than in September, or due to the difference in life history strategies between the different species abundant in the different seasons. Body size classes were not strongly correlated with each other at Freeman Ranch like they were at the Christmas Mountains. Morphospecies could have more opportunity for temporal niche partitioning, to reduce competition species utilize the environment in both space and time, or mating, eclosion, and emergence due to two peaks of precipitation at the Freeman Ranch.

The Christmas Mountains' single peak in precipitation had a strong influence over monthly weight and number of morphospecies per body size class (Figure 2). Temperature at time of sampling was strongly correlated with number of individuals and weights for body size class 1 and 16. Growing degree days were weakly correlated with body size classes. The lack of strong correlations between body size and GDD could be due to using the same base temperature for all morphospecies. Even though we observed in the field that 50°F (10°C) is when flight activity is limited for lepidoptera, GDD is known to be species-specific for both plants and insects. Also, GDD is drastically different between C3, C4, and CAM plants (Bonan 2015). The concentration and timing of emergence of these plants are different between the Christmas Mountains and Freeman Ranch and could have effects on lepidoptera population dynamics.

Annual distribution of morphospecies per body size class followed a unimodal curve described by Siemann et al. (1996). They had the same number of sample periods of 9 months, but many more locations, 48, in different types of vegetation, including grasslands and savannah. Their samples were comprised of Coleoptera, Hymnoptera, Diptera, Orthoptera, and Hemiptera. Results from our research show that lepidopterans follow the same unimodal distribution as the insect orders they sampled. They suggest that differences among modal body-size classes of the 6 orders they investigated are due to the common genetic heritage producing shared physiology and morphology within an order that limit related organisms to similar body sizes.

Siemanns et al. (1999) lumped all of their sampling locations and all of the time periods into a single analysis for each order, which produced a unimodal, normal size distribution for each order. While we found a similar unimodal size distribution when all months were summed to the annual scale. Our results show that the unimodal distribution of morphospecies, weight, and individuals does not hold at shorter monthly time scales with lower numbers of individuals and different seasonal climatic conditions and vegetation growth stages. While our annual distributions show a unimodal response of body size classes as an order the monthly distributions of size classes indicate that morphospecies are responding to different factors unique to a specific seasonal context. Thus, it may not be a shared genetic heritage between orders that causes a unimodal distribution,, as Siemann et al. suggest, but rather an artifact of combining multiple very different distributions into a single average distribution that reduces the variance and allows the distribution to approach the true mean of the large sample.

Siemann et al. also note that the weight and number of individuals would not necessarily be expected to follow a unimodal distribution, because there is no theory that predicts this pattern. The mechanisms that influence population numbers for species are complex, and there are a number of top-down controls such as predation and disease that affect population numbers and various life history properties such as fecundity and mating success also have effects.

Future considerations

This work has multiple lessons for future studies. First, meteorological data should be obtained directly from the sites at each location by a weather station. This is most important in the Christmas Mountains where microclimates are highly heterogeneous and may have a greater effect on local populations. It would also be important to analyze multiple years of data to determine if the body size responses are typical for the region, or vary from one year to the next. This would also lead to larger sample sizes and allow more complex statistical analysis to investigate nonlinear relationships.

A starting point for evaluating environmental biotic effects on body size distribution would be to catalog species and biomass of plants at each site during the sampling period. Collecting plant biomass synchronously with insect sampling would allow investigation of how plant productivity and diversity affect insect body size distributions. Productivity of plants determines the amount and type of herbivores, such as lepidopterans, that an ecosystem can support (Huston and Wolverton 2011), while diversity of plants determines the diversity of insect herbivores (Knops et al. 1999). Our results have shown that the Christmas Mountains have more insect biomass, more morphospecies, and more individuals than the Freeman Ranch, at least for the subset of moths that are active for the two hours after sunset. Evaluating variation in plant productivity and how variation in insect body size distribution responds might help answer why the insect communities at these two sites have patterns of abundance, total weight, and number of morphospecies that are negatively correlated with the amount of precipitation at each site, contrary to what would be expected.

We conclude that there is a need for future research in how lepidoptera respond to environmental factors. This study is a starting point for future comparative studies based on a precipitation gradient. It has been demonstrated that in an environment where water is limited, the Chihuahuan Desert, individuals across body-size classes respond to the influx of rain. In contrast in environment where rainfall is distributed throughout the year, Freeman Ranch, individuals do not respond consistently to precipitation. With the inclusion of more studies across the precipitation gradient it would be interesting to see if this response of individuals changes with increasing amounts of rainfall.

APPENDIX SECTION

APPENDIX A

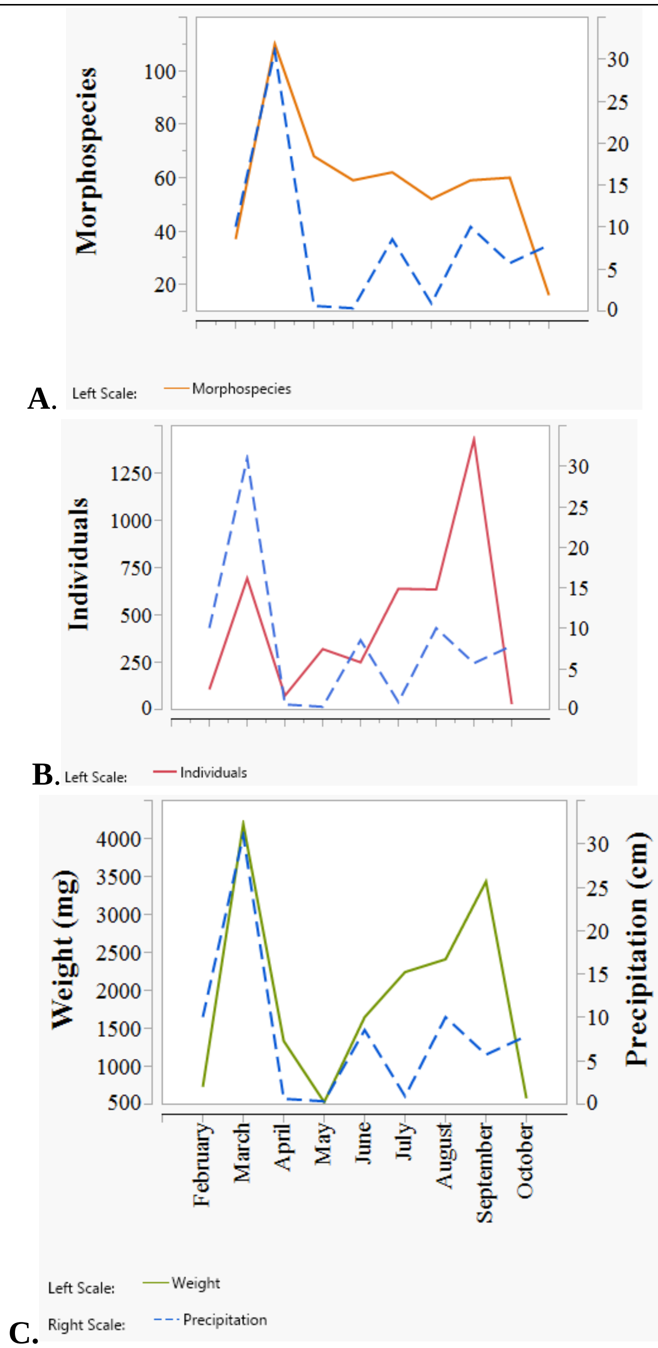

Figure 1. Freeman Ranch: 2013 Monthly Precipitation, Total Weight, Morphospecies, and Individuals of Lepidoptera.

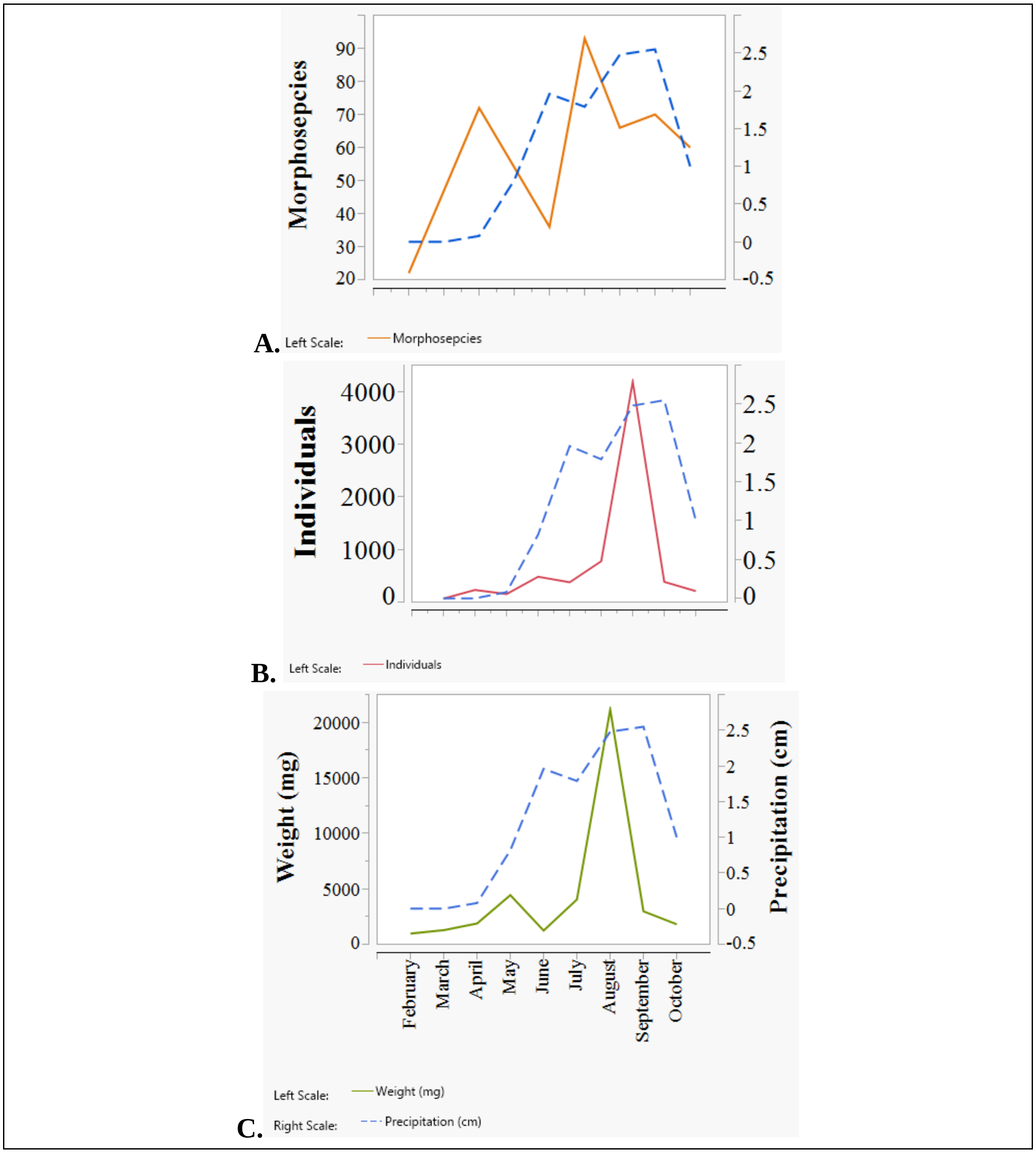

Figure 2. Christmas Mountains: 2013 Monthly Distribution of Precipitation, and Total Number of Morphospecies, Individuals, and Weight of Sample

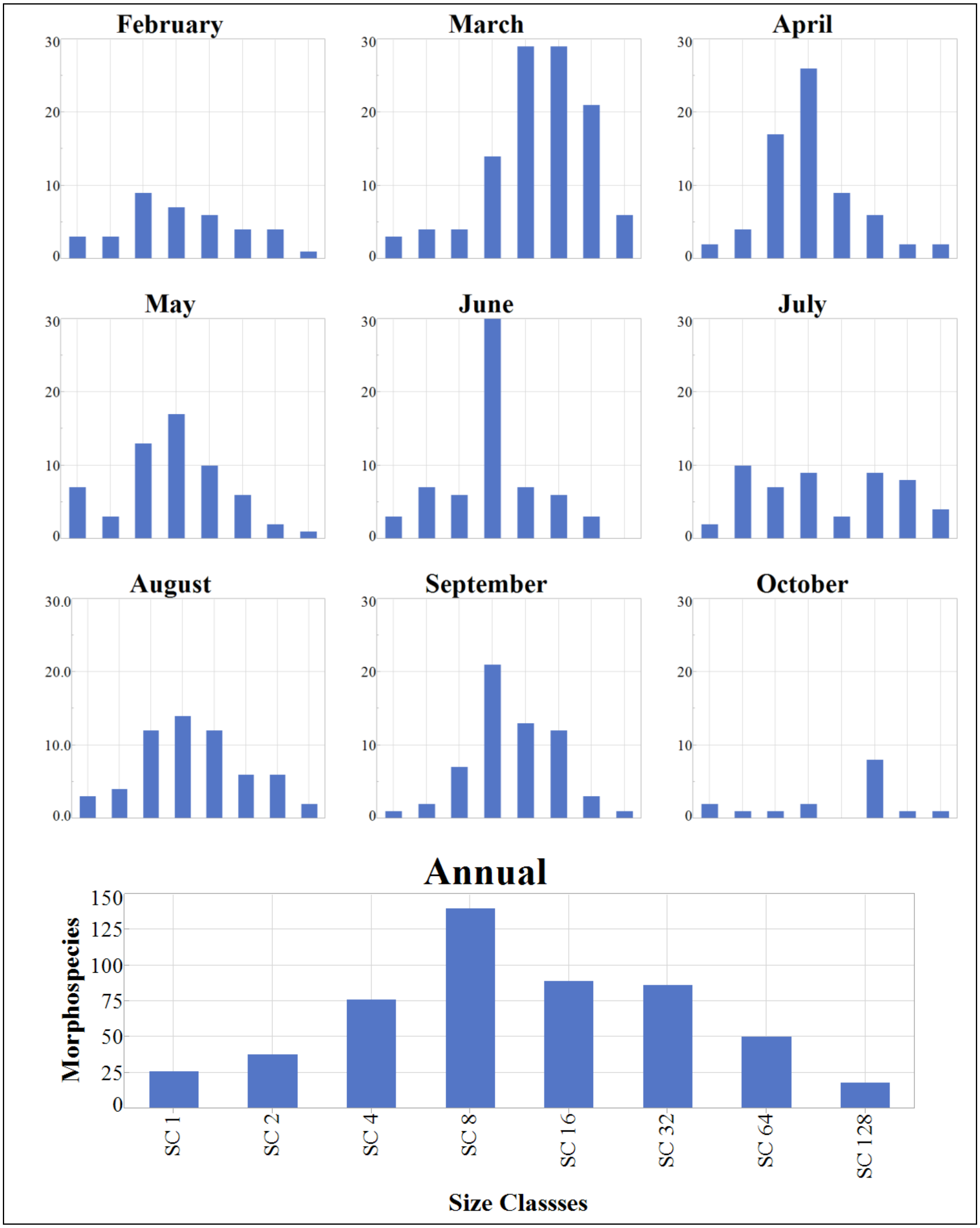

Figure 3. Freeman Ranch: Distribution of Morphospecies per Size Class

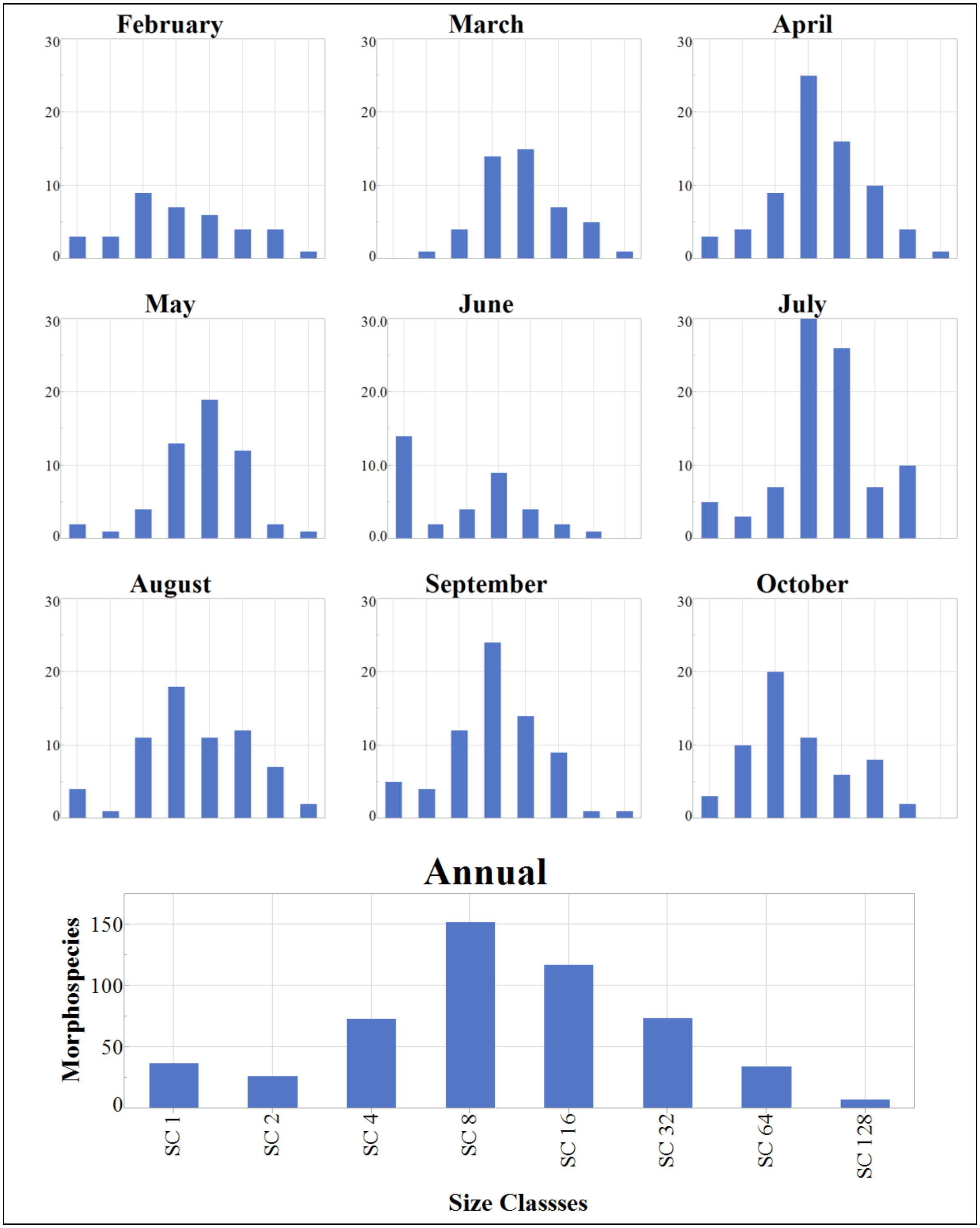

Figure 4. Christmas Mountains: Distribution of Morphospecies per Size Class

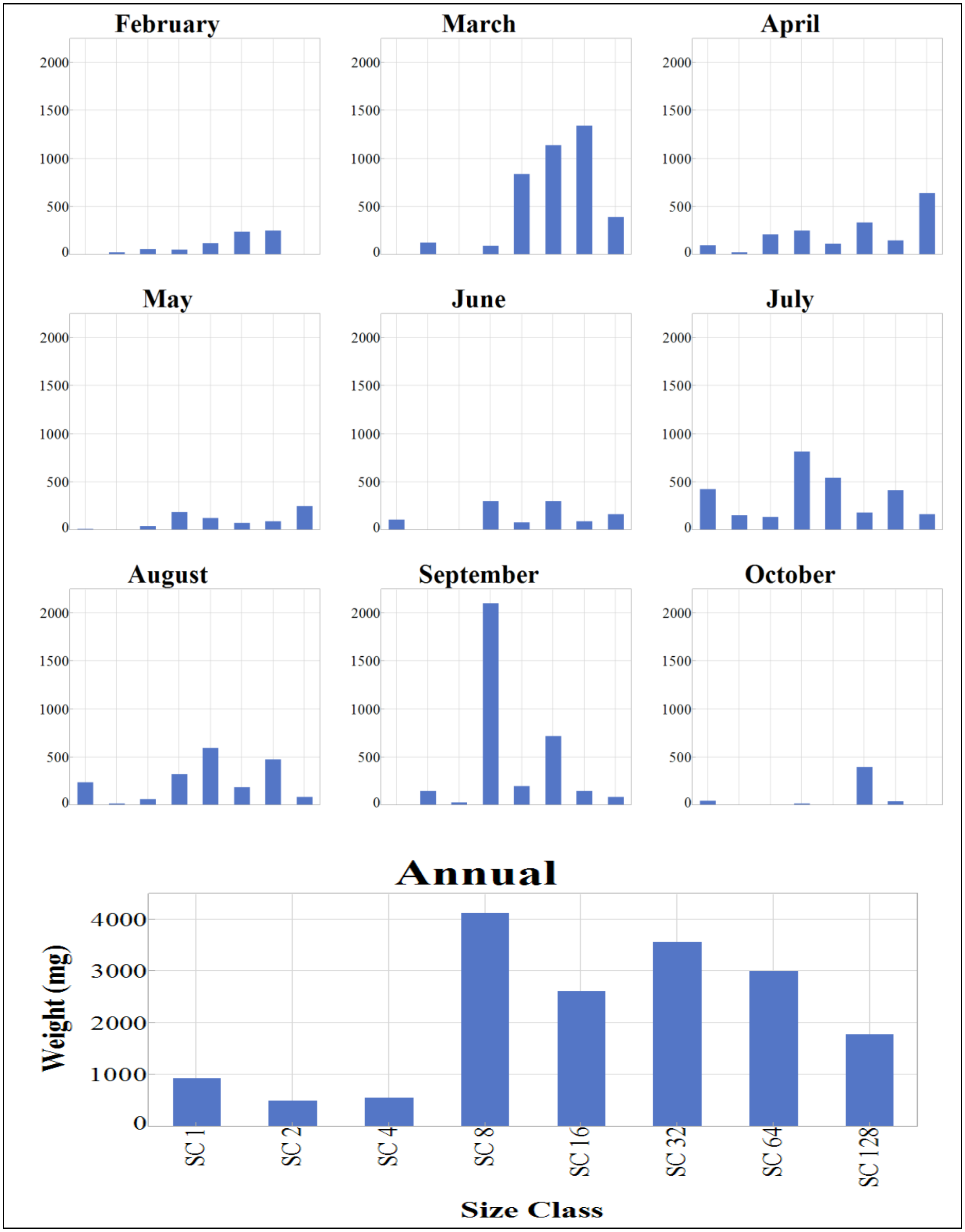

Figure 5. Freeman Ranch: Monthly Weight Distribution by Size Class.

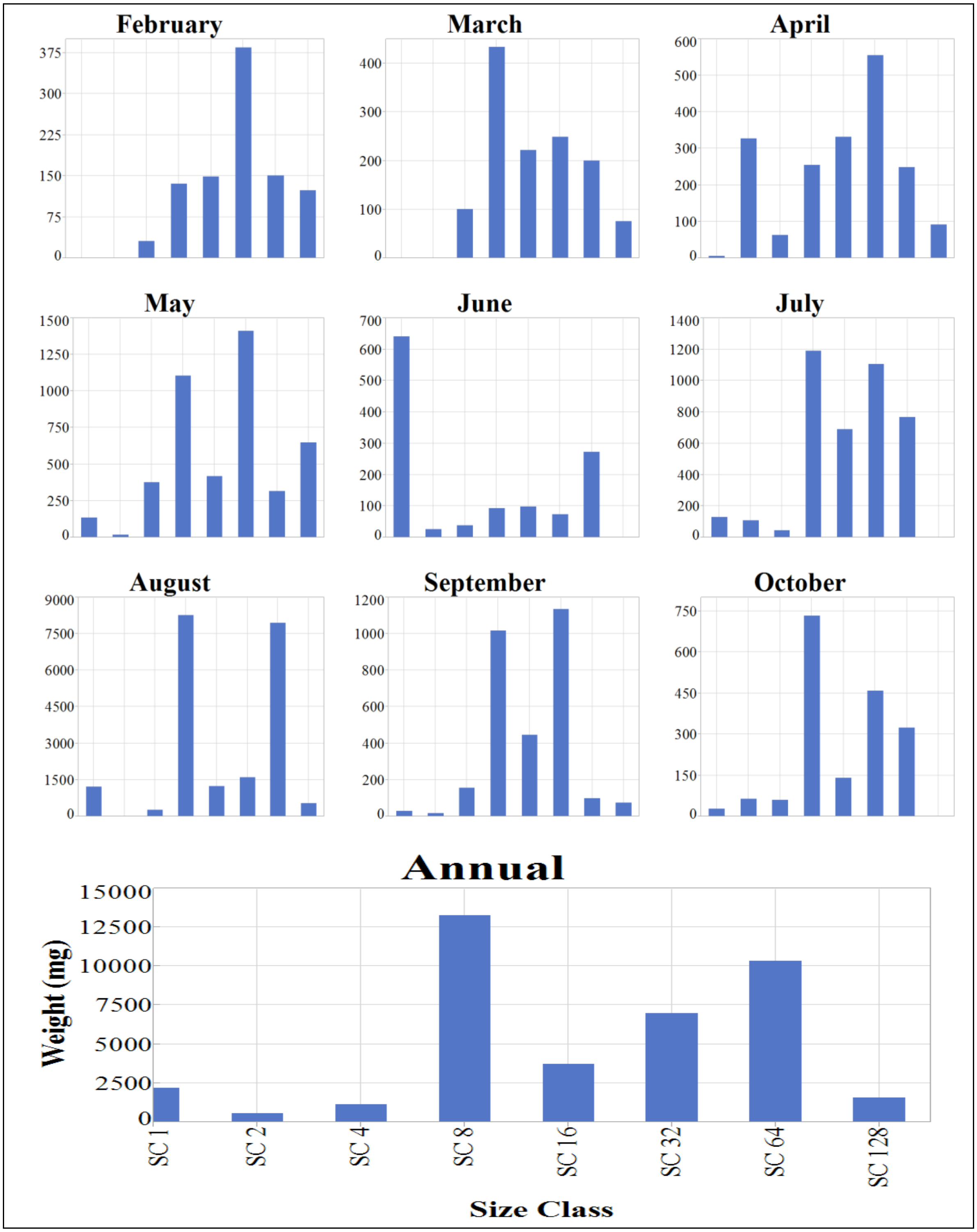

Figure 6 Christmas Mountains: Monthly Weight Distribution by Size Class.

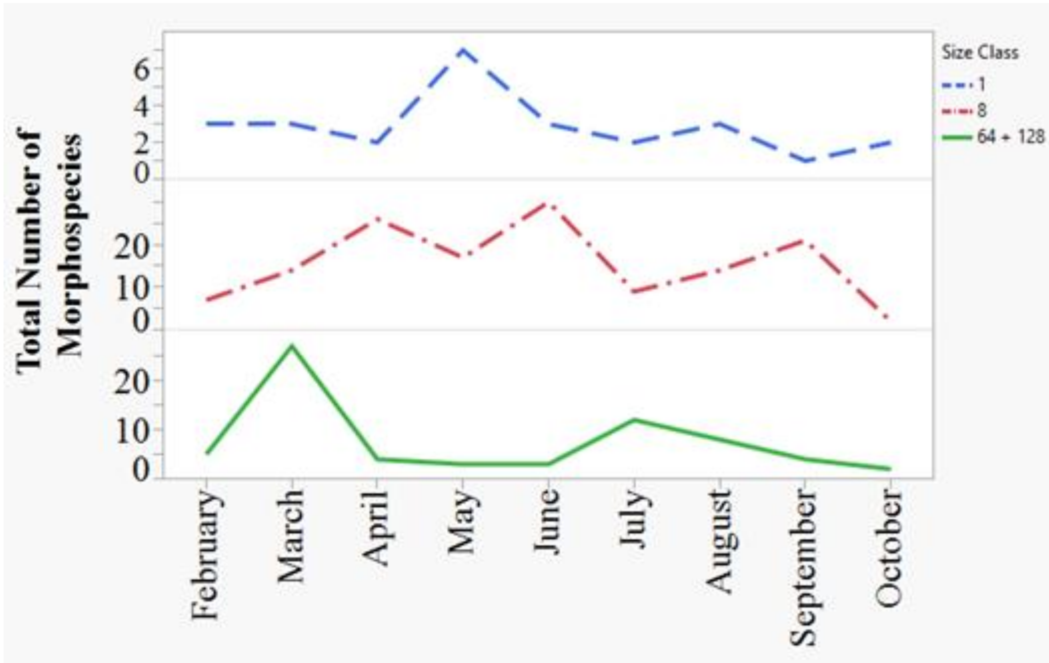

Figure 7 Freeman Ranch: Monthly Morphospecies Distribution per Size Class

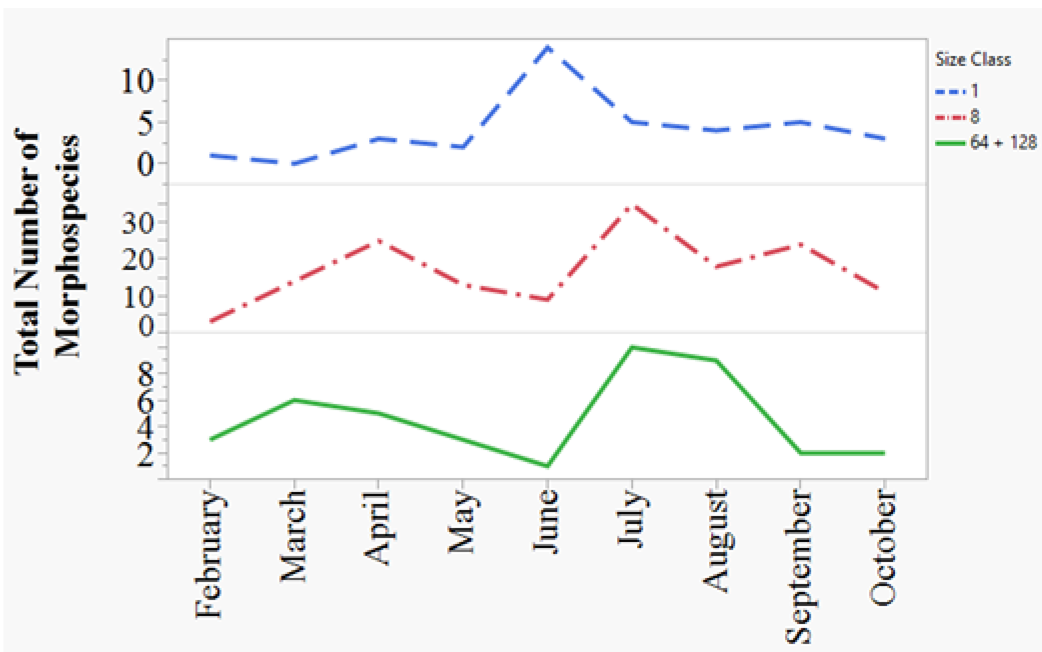

Figure 8 Christmas Mountains: Monthly Morphospecies Distribution per Size Class

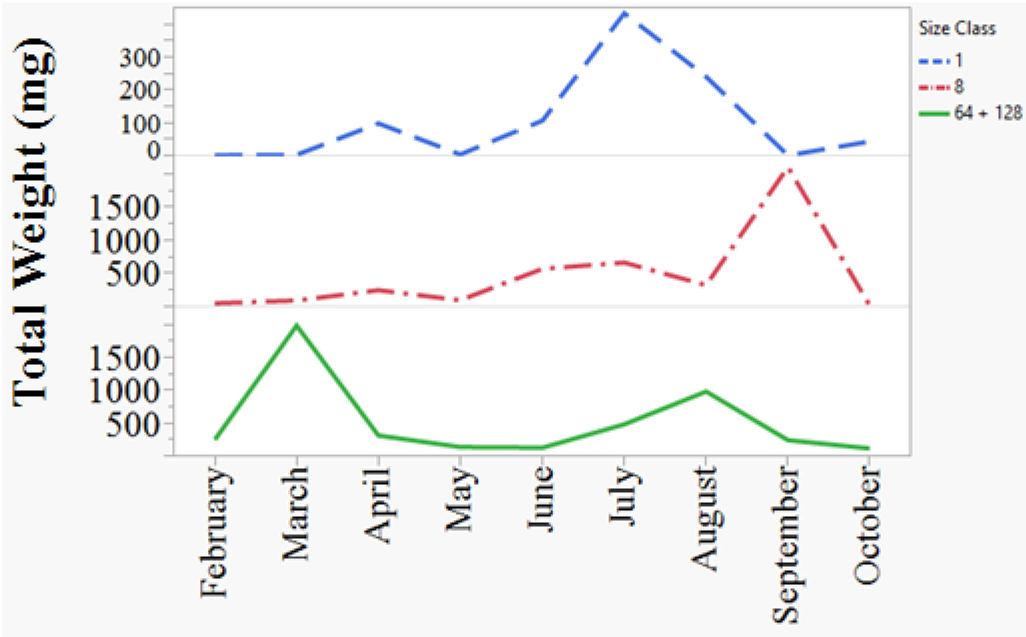

Figure 9 Freeman Ranch: Monthly Weight Distribution per Size Class

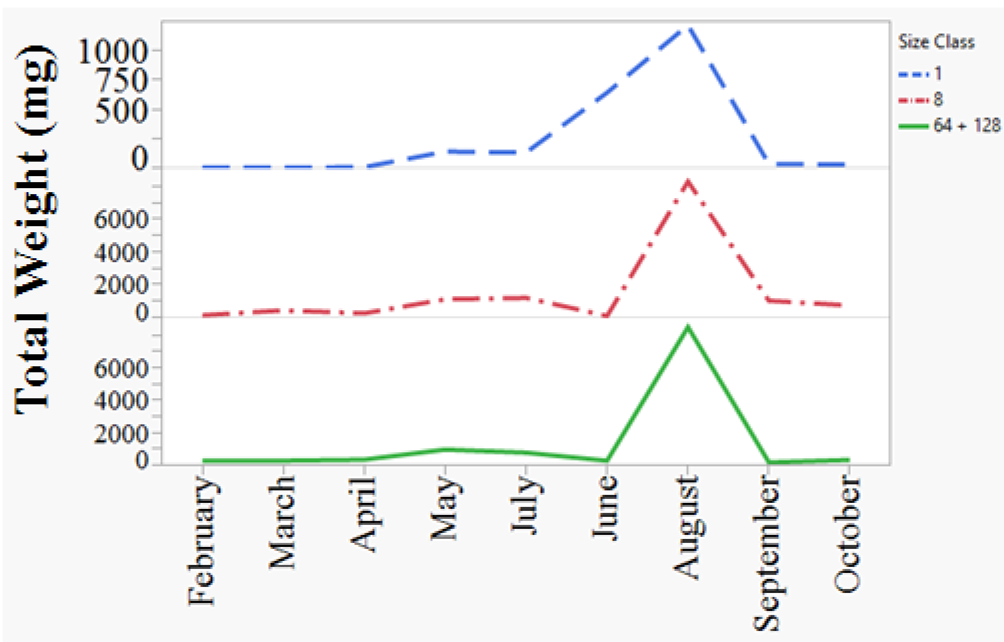

Figure 10 Christmas Mountains: Monthly Weight Distribution per Size Class

APPENDIX B

Table 1. Pearson's Product - Moment Correlation Matrix between Total Number of Individuals per Body Size Class and Abiotic Factors. Growing degree days and precipitation are cumulative up to 6 months. Photoperiod and temperature are calculated as an average for a calendar month. Temperature was also recorded at time of sampling. Cells that are highlighted in yellow are positive correlations that have r > 0.50. Cells that are highlighted in orange are negative correlations with r < .-0.50. Cells that are bolded have correlations that are significant at p < 0.05.

Freeman Ranch	Total Individuals	Size Class 1	Size Class 2	Size Class 4	Size Class 8	Size Class 16	Size Class 32	Size Class 64	Size Class 128
Total Individuals	1								
Size Class 1	-0.2875	1							
Size Class 2	0.371	0.3058	1						
Size Class 4	0.3756	0.4918	0.1199	1					
Size Class 8	0.0784	0.101	**0.7007**	-0.1433	1				
Size Class 16	0.1583	-0.2574	0.3341	-0.2163	0.1947	1			
Size Class 32	0.0202	-0.1395	0.5475	-0.3838	**0.7568**	**0.7445**	1		
Size Class 64	-0.11	-0.1092	0.2237	-0.2143	0.0724	**0.9501**	**0.6526**	1	
Size Class 128	-0.1211	-0.2766	0.115	-0.2999	0.1092	**0.9405**	**0.693**	**0.9614**	1
GDD 1 Months	-0.0875	0.3461	0.3841	-0.0147	0.3547	-0.3536	0.056	-0.3574	-0.3448
GDD 2 Months	-0.1043	0.2966	0.3295	-0.0755	0.342	-0.368	0.061	-0.3722	-0.3568
GDD 4 Months	-0.1289	0.2975	0.3478	-0.0823	0.3515	-0.3544	0.0724	-0.3484	-0.339
GDD 6 Months	0.1307	0.3732	0.3009	-0.0323	0.2424	-0.3725	-0.0007	-0.4298	-0.5002
Precipitation 1 Month	-0.4037	-0.1855	0.0045	-0.4101	0.1141	0.022	0.1765	0.1428	0.0858
Precipitation 2 Months	-0.4333	-0.4902	-0.3085	-0.375	-0.0931	0.2323	0.1365	0.3579	0.3969
Precipitation 3 Months	-0.2123	-0.6617	-0.6337	-0.2734	-0.3179	0.2772	0.0115	0.3202	0.4411
Precipitation 6 Months	-0.1716	-0.5157	-0.4675	-0.3088	-0.2752	0.2775	0.0443	0.3366	0.3309
Monthly Average Photoperiod	0.1493	0.4707	0.4033	0.1349	0.293	-0.3784	-0.0236	-0.444	-0.4626
Sampling Temperature	0.371	0.3163	0.1064	0.1596	0.0666	-0.3247	-0.1244	-0.4605	-0.4654
Monthly Average Temperature	-0.0914	0.3324	0.3684	-0.0299	0.3511	-0.3583	0.0566	-0.3628	-0.3481
Christmas Mountains	Total Individuals	Size Class 1	Size Class 2	Size Class 4	Size Class 8	Size Class 16	Size Class 32	Size Class 64	Size Class 128
Total Individuals	1								
Size Class 1	**0.996**	1							
Size Class 2	-0.2613	-0.2325	1						
Size Class 4	0.5914	0.533	-0.6113	1					
Size Class 8	**0.9969**	**0.9885**	-0.3165	0.6203	1				
Size Class 16	**0.8648**	**0.8357**	-0.0566	**0.6052**	**0.8574**	1			
Size Class 32	**0.732**	**0.6834**	-0.3201	**0.7194**	**0.7432**	**0.8601**	1		
Size Class 64	**0.9938**	**0.993**	-0.2767	**0.5589**	**0.9932**	**0.8195**	**0.6793**	1	
Size Class 128	**0.8769**	**0.8486**	**-0.5076**	**0.7776**	**0.8916**	**0.7601**	**0.8278**	0.873	1
GDD 1 Months	0.5252	0.5304	0.2916	0.2763	0.4832	0.6002	0.5243	0.4504	0.3597
GDD 2 Months	0.4961	0.4935	0.1832	0.1675	0.4816	0.5385	0.505	0.438	0.2289
GDD 4 Months	0.5081	0.5097	0.2696	0.1478	0.4827	0.5762	0.5317	0.4429	0.2547
GDD 6 Months	0.3932	0.3902	-0.1243	0.1429	0.4001	0.3669	0.432	0.3544	0.1608
Precipitation 1 Month	0.5491	0.5541	0.0508	0.1861	0.5337	0.578	0.536	0.4828	0.3076
Precipitation 2 Months	0.4187	0.4281	0.0424	-0.0525	0.4153	0.4385	0.4219	0.3768	0.1317
Precipitation 3 Months	0.4475	0.4431	-0.0602	0.1042	0.4598	0.4268	0.3937	0.4199	0.1584
Precipitation 6 Months	0.1687	0.1679	-0.1272	-0.1087	0.1958	0.0582	0.1715	0.1725	-0.0171
Monthly Average Photoperiod	-0.5073	-0.4939	-0.1239	-0.1137	-0.5107	-0.6161	-0.4822	-0.4807	-0.2043
Sampling Temperature	0.5672	0.5919	0.3762	0.1422	0.51	0.6209	0.4571	0.5049	0.3621
Monthly Average Temperature	0.4934	0.503	0.2998	0.2312	0.4503	0.5531	0.4754	0.42	0.3231

Table 2. Pearson's Product - Moment Correlation Matrix between Total Weight of Individuals per Body Size Class and Abiotic Factors. Growing degree days and precipitation are cumulative up to 6 months. Photoperiod and temperature are calculated as an average for a calendar month. Temperature was also recorded at time of sampling. Cells that are highlighted in yellow are positive correlations that have r > 0.50. Cells that are highlighted in orange are negative correlations with r < .-0.50. Cells that are bolded have correlations that are significant at p < 0.05

Freeman Ranch	Total Weight	Size Class 1	Size Class 2	Size Class 4	Size Class 8	Size Class 16	Size Class 32	Size Class 64	Size Class 128
Total Weight	1								
Size Class 1	0.1744	1							
Size Class 2	**0.8859**	0.2772	1						
Size Class 4	0.0726	0.4834	0.0668	1					
Size Class 8	0.546	0.0769	0.6563	0.0002	1				
Size Class 16	**0.7592**	0.3757	0.5863	-0.0021	0.0079	1			
Size Class 32	**0.7226**	-0.4173	0.5544	-0.3503	0.222	0.4812	1		
Size Class 64	**0.6991**	0.0238	0.498	-0.1487	-0.1682	**0.9029**	**0.7097**	1	
Size Class 128	0.295	-0.0393	0.0543	0.6077	-0.1723	0.1745	0.2284	0.2721	1
GDD 1 Months	0.0376	0.2348	0.0961	-0.1993	0.4678	-0.1251	-0.0569	-0.3406	-0.4528
GDD 2 Months	-0.0158	0.1853	0.0763	-0.2771	0.4456	-0.1806	-0.0486	-0.3654	-0.5256
GDD 4 Months	0.0015	0.1716	0.0886	-0.2749	0.4483	-0.1597	-0.0271	-0.3411	-0.5364
GDD 6 Months	-0.1438	0.3442	0.0526	-0.4551	0.3721	-0.177	-0.2457	-0.391	-0.7506
Precipitation 1 Month	-0.0685	-0.3847	0.0629	-0.4289	0.0024	-0.0647	0.2927	0.1002	**-0.6098**
Precipitation 2 Months	-0.0297	-0.6152	-0.0327	-0.0859	-0.2762	-0.043	0.4132	0.2758	0.0214
Precipitation 3 Months	-0.1434	-0.6129	-0.1826	0.1017	-0.49	-0.1589	0.2866	0.219	0.4761
Precipitation 6 Months	-0.1693	-0.512	-0.1063	-0.1508	-0.4456	-0.0626	0.2244	0.2724	0.0249
Monthly Average Photoperiod	0.0025	0.4519	0.0767	-0.1711	0.4595	-0.0982	-0.249	-0.3946	-0.4168
Sampling Temperature	-0.1691	0.4464	-0.05	-0.1803	0.2284	-0.1995	-0.3901	-0.4201	-0.2543
Monthly Average Temperature	0.0234	0.222	0.09	-0.2176	0.4622	-0.1413	-0.0551	-0.3489	-0.4679
Christmas Mountains	Total Weight	Size Class 1	Size Class 2	Size Class 4	Size Class 8	Size Class 16	Size Class 32	Size Class 64	Size Class 128
Total Weight	1								
Size Class 1	**0.8486**	1							
Size Class 2	-0.2033	-0.2728	1						
Size Class 4	0.5676	0.3614	-0.3081	1					
Size Class 8	**0.9965**	**0.8409**	-0.2314	0.5336	1				
Size Class 16	**0.9243**	**0.6863**	-0.0658	**0.5274**	**0.9106**	1			
Size Class 32	**0.7126**	0.3821	-0.1207	**0.7796**	**0.6829**	**0.836**	1		
Size Class 64	**0.9861**	**0.8762**	-0.1958	0.451	**0.99**	**0.8775**	0.5908	1	
Size Class 128	**0.6442**	0.4553	-0.2576	**0.9406**	0.6043	0.5605	**0.7283**	0.557	1
GDD 1 Months	0.5121	0.6404	-0.0395	0.3972	0.4796	0.5777	0.541	0.446	0.2888
GDD 2 Months	0.4822	0.4851	-0.2328	0.2147	0.4968	0.5253	0.5058	0.4346	0.0422
GDD 4 Months	0.4966	0.5301	-0.1475	0.2528	0.4957	0.5587	0.5473	0.4395	0.1016
GDD 6 Months	0.3781	0.3359	-0.56	0.1277	0.4184	0.3562	0.3751	0.3534	-0.0156
Precipitation 1 Month	0.5265	0.6108	-0.3044	0.2518	0.5275	0.5682	0.5211	0.4789	0.1106
Precipitation 2 Months	0.3982	0.3905	-0.3556	0.0091	0.4241	0.4335	0.4077	0.3757	-0.0942
Precipitation 3 Months	0.4266	0.3413	-0.4038	0.0221	0.4745	0.4305	0.3599	0.4183	-0.1191
Precipitation 6 Months	0.1654	0.0976	-0.3609	-0.0769	0.2227	0.0808	0.1263	0.1717	-0.2058
Monthly Average Photoperiod	-0.4986	-0.2584	0.1846	-0.0001	-0.5359	-0.6055	-0.5012	-0.482	0.0752
Sampling Temperature	0.54	**0.7062**	0.0382	0.2627	0.4985	0.6059	0.4733	0.5017	0.2657
Monthly Average Temperature	0.4761	0.6395	-0.0326	0.3603	0.4433	0.5332	0.4908	0.4151	0.2518

Table 3. Freeman Ranch Total Weight, Individuals, and Morphospecies by Body-Size Class**.** Both sites, oak-savannah and juniper thicket, were combined to calculate total abundance for each category.

Freeman Ranch									
Weight	**February**	**March**	**April**	**May**	**June**	**July**	**August**	**September**	**October**
1	1.13	2.72	98.08	12.91	109.60	426.29	240.28	0.89	43.23
2	22.12	126.70	21.34	7.42	4.29	153.87	16.44	145.00	1.60
4	55.29	7.88	209.58	41.71	7.34	137.70	63.87	26.87	4.57
8	50.30	91.56	246.84	186.27	298.24	815.88	323.31	2101.67	17.08
16	118.77	840.92	115.00	124.79	82.03	541.76	596.67	200.27	0.00
32	236.00	1137.98	332.13	76.39	297.81	183.44	188.55	718.05	397.73
64	247.62	1344.86	148.20	89.25	91.31	414.27	478.25	145.73	42.31
128	0.00	389.04	640.12	251.08	163.91	163.91	84.37	84.37	0.00
Individuals									
1	44	8	4	154	162	2	376	195	5
2	12	87	6	6	3	162	128	150	1
4	17	3	16	71	4	30	48	15	2
8	9	298	29	58	47	363	38	983	3
16	10	158	9	16	12	47	22	17	0
32	9	76	6	11	20	32	9	64	16
64	6	49	2	3	2	3	13	3	1
128	0	15	2	1	0	0	1	1	1
Morphospecies									
1	3	3	2	7	3	2	3	1	2
2	3	4	4	3	7	10	4	2	1
4	9	4	17	13	6	7	12	7	1
8	7	14	26	17	30	9	14	21	2
16	6	29	9	10	7	3	12	13	0
32	4	29	6	6	6	9	6	12	8
64	4	21	2	2	3	8	6	3	1
128	1	6	2	1	0	4	2	1	1

Table 4 Christmas Mountains Total Weight, Individuals and Morphospecies per Body-Size Class. Both sites, oak-savannah and juniper thicket, were combined to calculate total abundance for each category.

Christmas Mountains									
Weight	**February**	**March**	**April**	**May**	**June**	**July**	**August**	**September**	**October**
1	0.35	0.00	5.67	137.82	642.18	130.48	1218.52	31.68	27.96
2	0.00	1.00	327.79	17.20	26.26	109.22	3.29	17.29	64.18
4	31.28	100.69	63.07	379.00	38.79	45.23	279.07	158.56	59.47
8	135.57	433.87	255.58	1106.47	93.94	1193.04	8282.52	1018.26	734.35
16	149.21	222.00	332.80	421.01	98.55	692.23	1244.84	446.54	140.61
32	385.06	249.59	556.69	1414.23	73.76	1106.90	1619.76	1137.35	459.98
64	151.56	200.83	249.13	316.00	273.73	770.31	7961.40	98.37	323.99
128	123.81	76.13	92.68	649.00	0.00	0.00	542.73	74.38	0.00
Individuals									
1	1	0	1	98	246	343	2141	56	47
2	0	1	68	9	41	79	2	14	45
4	15	101	18	109	15	34	122	59	23
8	19	93	22	151	57	197	1515	167	57
16	13	21	26	40	9	64	97	40	12
32	18	11	13	66	3	41	83	48	19
64	2	5	6	7	8	20	220	2	8
128	1	1	1	4	0	0	8	1	0
Morphospecies									
1	1	0	3	2	14	5	4	5	3
2	0	1	4	1	2	3	1	4	10
4	2	4	9	4	4	7	11	12	20
8	3	14	25	13	9	35	18	24	11
16	6	15	16	19	4	26	11	14	6
32	7	7	10	12	2	7	12	9	8
64	2	5	4	2	1	10	7	1	2
128	1	1	1	1	0	0	2	1	0

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