Characteristics of Terrestrial Invertebrate Populations in Western and Central Montana

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Abstract

Examining invertebrate availability as a driver of North American Deer Mouse *(Peromyscus maniculatus)* abundance may provide a more detailed understanding of the potential for local invertebrate abundance to affect Sin Nombre Hantavirus (SNV) transmission. This study assessed invertebrate availability as a forage source for deer mice populations known to carry SNV. The study was conducted during repeated five-month spans (June through October) at two study sites in central and western Montana from 2000 to 2016. The study sites (Polson and Cascade) encompass two habitat categories of sagebrush and grassland which consistently supported deer mice populations. The objectives of the study were to determine how invertebrate types and their availabilities varied by habitat, weather conditions, and temporally. We collected invertebrates using pitfall traps and identified 24 separate categories of invertebrates (20 orders, 1 sub-order, 2 classes, & 1 miscellaneous category). Five orders that were consistently captured at both sites include Hymenoptera (Ants & Wasps), Araneida (Orb Weaver Spiders), Orthoptera (Grasshoppers & Crickets), Coleoptera (Beetles), and Diptera (Flies). Most orders had their highest abundance during July and August of each year with invertebrate numbers declining during October. At both the Polson and Cascade sites, the grand mean invertebrate abundance and biomass was significantly correlated with the average monthly temperature. This study is part of a larger project examining the transmission of SNV within deer mouse populations.

Keywords: Deer Mouse, Hantavirus, Invertebrates, Populations, Sin Nombre Virus, Terrestrial, Weather Data

INTRODUCTION

The North American Deer Mouse (*Peromyscus maniculatus*) is the main reservoir host for Sin Nombre hantavirus (SNV), a directly transmitted zoonotic pathogen (Nichol et al., 1993). Deer mice are distributed across most of North America and occur in a variety of habitats, including grasslands, upland forests, arid desert, rainforests, tundra, and shrublands (King 1968, Hall and Kelson 1981, Kays and Wilson 2009). SNV is maintained in natural deer mice populations horizontally through both intraspecific aggressive behavior and communal nesting (Mills et al. 1999, Calisher et al. 1999). Spillover to humans can occur where it causes Hantavirus Pulmonary Syndrome (HPS), a serious illness with a high mortality rate (Nichol et al. 1996, CDC, 2009). Humans can become infected by inhaling aerosolized virus shed in an infected rodent's feces, urine, or saliva. Most human exposure to the virus occurs in mouse-infested peridomestic environments such as human dwellings and associated out-buildings, garages, sheds, and barns (Armstrong et al. 1995, Zeitz et al. 1995, de St. Maurice et al. 2017). One of the most well-known outbreaks of HPS infections occurred in the Four Corners region of the U.S. in 1993 (Childs et al. 1994). This outbreak followed El Niño events, which is thought to have increased deer mouse density and human-deer mouse interactions (Yates et al. 2002).

Deer mice population densities have been linked to various factors including changes in food availability and plant productivity (Gorosito and Douglass 2017, Lack 1954, Schnurr 2002). Loehman et al. (2012) suggested a theoretical bottom-up precipitation driven trophic cascade in which increased precipitation levels in temperate low moisture climates results in a higher abundance of edible plant produce (seeds, grains, mast, grasses, and leaves). This increase in available forage may result in higher abundance of deer mice. Luis et al. (2010) found that deer mouse population numbers correlated with precipitation with up to a five-month time lag. Since

SNV is directly transmitted from mouse to mouse, increased population density can lead to increased prevalence of infection within the deer mouse populations and subsequently increased risk of human infection. A positive relationship between deer mouse density and SNV seroprevalence has been observed when incorporating time lags (Luis et al. 2015). Additionally, frequencies of encounters, and therefore physical contact, between individual rodents may depend on the interaction of rodent density and habitat-related variables, including food availability (Biggs et al. 2000). Thus, an understanding of food availability may be important to understand the SNV-deer mouse system.

Deer mice are omnivorous and eat a wide variety of food items including invertebrates, fruits, seeds, and nuts, with lesser amounts of green vegetation and fungi (Whitaker 1966, Wolff 1985, Wolff 1996). Invertebrates have been shown to be an important food source for deer mice, but their importance has been found to vary with season and habitat type (Pearson & Calloway, 2006, Jameson 1952, Whitaker 1966). Jameson (1952) found that arachnids and lepidoptera larva were frequently found within the stomach contents of deer mice and comprised nearly 1/5th of all stomach contents during the winter months (Jameson 1952). A variety of habitat types (plowed fields, soybean stubble, upland woods, river-bottom woods, and brushy fields) produced differing percentages of invertebrates (juvenile lepidoptera, coleoptera, earthworms, arachnids, hemiptera, and chilopods) in the stomach contents of House Mice (*Mus musculus*), Prairie Deer Mice (*Peromyscus maniculatus bairdi*), and White Footed Mice (*Peromyscus leucopus*) (Whitaker 1966).

Little is known about the diversity and abundance of invertebrate populations in Montana. Since many studies show that terrestrial invertebrates make up a large percentage of deer mice diet, an understanding of invertebrate abundance and how abundance changes with time are an important component of understanding the dynamics of deer mouse populations and potential hantavirus transmission.

The overall goal of this study was to describe the terrestrial invertebrate communities that could potentially affect deer mouse abundance. This study was part of a larger long term (1994-2016) study on deer mice and SNV dynamics in Montana (Douglass et al. 1996, 2001, Kuenzi et al. 2001, 2005). Our specific objectives were to: 1) Determine an estimate of abundance and biomass (grams) of different types of invertebrates at each study site monthly. 2) Compare estimates of abundance and biomass between months and years within each study site. 3) Compare abundance and biomass (grams) between sites. 4) Examine the relationship between monthly abundance and biomass with monthly average temperature and monthly total precipitation at each study site.

METHODS

Study sites

We studied terrestrial invertebrates at two sites located near Polson and Cascade in west central Montana. The sites were originally selected due to their high deer mouse abundance and because they represented two separate habitat types (Douglass et al. 1996, Figure 1). The Cascade site is characterized as grassland habitat and contained a variety of native and non-native grasses and forbs. The Polson site is characterized as sagebrush habitat dominated by sage brush (*Artemesia sp.*) (Figure 1). Topography varied among the sites with elevations ranging from 815 meters at the Polson site to 1,430 meters at Cascade.

Invertebrate sampling

Invertebrates were sampled using pitfall traps. At each site we placed 10 pitfall traps within one of the 1-hectare (100 m X 100 m) small mammal trapping grids originally established during a long-term longitudinal hantavirus research study (Douglass et al. 1996, 2001, Lonner et al. 2003). Pitfall traps remained in the same location for the duration of the study and were situated diagonally across the small mammal trapping grid at 15.7-m intervals. The pitfall traps were constructed by placing two 355-ml (12-oz) disposable cups into a hole dug into the ground. The lips of the cups were flush with the surface of the ground. The outer cup provided a foundation for ease of removal of the inner cup. The inner cup was partially filled with propylene glycol antifreeze to kill any invertebrate that fell in and to keep samples from freezing during the cooler nights without posing a risk to any vertebrates that might accidentally ingest the fluid. A 15-cm wire, mesh metal ladder was also placed inside the cup to allow small vertebrates that may fall into pitfall traps an escape route. Pitfall traps were covered with a 30cm x 30cm ceramic tile, supported approximately 3-cm off the ground with small rocks to allow access of invertebrates while protecting traps from precipitation and disturbance from livestock and other fauna.

At each site, invertebrate sampling was initiated in May 2000 and was conducted monthly from June through October of each year. Cascade was sampled through September of 2013 for a total of 67 sampling periods. Polson was sampled through October of 2016 for a total of 83 sampling periods. Traps remained open the entire month resulting in 30 – 31 trap nights per month for each individual trap. Each month, invertebrate contents of pitfall traps were separated from the antifreeze with a tea strainer, then placed in labeled plastic vials filled with isopropyl alcohol. Pitfall traps were then reset. Due to logistical issues, insect sampling was not done in June 2001 at both sampling sites.

Invertebrate identification

In the lab, we identified invertebrates using a dissecting microscope. We used a classification strategy based on a previous study of invertebrate abundance and biomass trends (Lonner et al. 2003). We sorted invertebrates into five taxonomic classes consisting of 20 taxonomic orders. Invertebrates in classes Chilopoda (Centipedes) and Diplopoda (Millipedes) were not categorized to order. Order Lepidoptera (Butterflies/Moths/Caterpillars) was divided into two sub-groups (Lepidoptera Adult & Lepidoptera Larvae). A miscellaneous category was included to account for non-arthropod invertebrates such as snails & worms. This study used a total of 24 invertebrate classification categories (Table 1). The invertebrates from each pitfall trap were counted, dried, and then weighed, using a ± 0.01-g digital scale, to obtain 2 measures of insect availability, abundance (counts) and biomass (weights) for each of the 24 invertebrate categories.

Data analysis

Abundance and biomass in each invertebrate category were averaged across the 10 pitfall trap stations at each study site to obtain monthly averages for both measures of insect availability. Grand mean abundances and grand mean biomasses for each study site were calculated by averaging individual monthly averages across all years, all monthly averages within a year and for all months and years combined. One-way ANOVAs were used to determine if there were differences in estimates of abundance and biomass between months and years. Tukey's honest significance difference (HSD) tests were used to determine which estimates differed from one another. Two-sample T-test (two sample, two-tail, unequal assuming) analyses were used to compare measures of insect availability (abundance and biomass) over the course of the entire study between study sites.

We used multivariable linear regression models to examine the relationship between grand mean abundance and grand mean biomass with average monthly temperature and total monthly precipitation at both sampling sites. These correlations were performed using MINITAB, version 21.1 (Minitab, 2010). Weather data were set to assume our independent variables while invertebrate abundance and biomass were set as dependent variables. Model reduction was accomplished through either forward selection or backward elimination of environmental variables in order to maximize model fit parameters. Three points of unusual leverage were identified through model selection and excluded from subsequent regression analysis. Model assumptions were assessed through visual analysis of diagnostic plots. Deviance, Homer-Lemeshow goodness of fit, variance inflation factor, and Akaike information criteria were all used to verify the ability of the final model to describe the relationship between model classifiers and insect biomass and abundance. Weather data were obtained from the National Oceanic and Atmospheric Administration (NOAA)/National Weather Service database (https://www.weather.gov/wrh/climate). We used data from the weather stations closest to the Polson and Cascade sampling sites (SSE SKQ DAM & CASCADE 20).

RESULTS

Abundances and Biomasses (grams)

Four orders of invertebrates were found to be the most abundant throughout the study. These orders were Hymenoptera (Ants/Wasps) at both Polson (= 19.16) and Cascade (= 15.23), Thysanura (Silverfish) at Polson (= 21.19), Phalangida (Harvestmen/Daddy longlegs) at Cascade (= 17.31), and Araneida (Orb weaver spiders) at Polson (= 13.61) with all other orders and classifications having averages ranging from < 0.01 – 8.99 for the entirety of the study

(Tables 2 & 3). In terms of biomass, the orders with the highest grand mean biomass at both Polson and Cascade were Orthoptera (Grasshoppers/Crickets) (0.93g & 1.73g) and Coleoptera (Beetles) (0.50g & 1.41g) (Tables 4 & 5). The lowest grand mean abundance and grand mean biomass at both sites were the orders Diplura (Bristletails) and Ephiminoptera (Mayflies). Araneida was the only order to be sampled at both sampling sites, during all sampling periods.

Insect availability as estimated by abundance differed between months for both study sites (Polson: P-value = <0.001, Cascade: P-value = 0.002) (Figure 2). At both sites, abundances increased over the summer peaking in July and then declining into the fall. At the Polson site abundances in July were significantly differed from those in Oct (Table 6). At Cascade, July abundances were significantly higher than both September and October (Table 6).

Insect availability as measured by biomass also differed significantly between months at both the Cascade (P-value = 0.001) and Polson (P-value = 0.042) sites (Figure 3, Table 6). Biomass followed a similar pattern as abundance, increasing over the season, peaking in July or August before dropping off in September and October. At Cascade, insect abundance as measured by biomass was significantly different between July and October with no differences found between other months. While the ANOVA indicated a just barely significant difference in biomass between months at the Polson site, the Tukey's HSD test failed to find significant differences between individual months (Table 6).

Insect availability as measured by abundance differed significantly between years at the Cascade site (P-value = 0.002) but not the Polson site (Figure 4, Table 6). At Cascade abundance was significantly higher in 2011 when compared with 2001, 2003, 2006, and 2013. Trends in abundance tended to show a gradual increase over the years with much variation within each year.

Insect availability as measured by biomass was highly variable between years (Figure 5, Table 6). No significant difference in biomass was found between years at Cascade. At the Polson study site, biomass in 2008 was significantly higher than biomass in 2005 and 2016 (Figure 5, Table 6).

Over the course of the whole study (years and months combined), insect availability as measured by abundance did not differ between the Polson and Cascade sampling sites (P-value = 0.914, Figure 6). Insect availability as measured by biomass were significantly higher at Cascade compared to Polson (P-value = < 0.001, Figure 7).

Correlation with Weather

The multiple regression analysis for both the Polson and Cascade sampling sites found a significant positive correlation between the grand mean abundance and the average monthly temperature (Polson, R^2 = 29.80%; S-value = 1.93; P-value = <0.001 & Cascade, R^2 = 17.76%; S-value = 2.134; P-value = 0.001). Grand mean biomass and average monthly temperature were also positively correlated at both study sites (Polson: R^2 = 16.46%; S-value = 0.059; P-value = <0.001 & Cascade: R^2 = 7.88%; S-value = 0.141; P-value = 0.021). No significant relationship between total monthly precipitation and either biomass or abundance was found at either study site.

DISCUSSION

Over the course of the study, individuals in all 24 invertebrate categories were identified. Twenty-two of the categories were identified at each sampling site at least once. These categories include all except for Ephiminoptera (Mayflies) and Diplura (Bristletails). Araneida (Orb weaver spiders) was the only category that at least one individual was found at each sampling site, during every sampling period. This diversity of invertebrate populations may point to healthy ecosystems at both sites, suggesting more diverse plant and animal communities. In terms of biomass, Orthoptera (Grasshoppers/Crickets) and Coleoptera (Beetles) produced the heaviest biomass at both sites. This was primarily due to the overall size of the individuals and being the two orders with the most robust exoskeleton. The overall grand mean abundances tended to be higher, for both sites, during the month of July whereas biomass peaked later in the summer. This may be due to the additional month for individuals to grow and exoskeletons to strengthen.

Several of the invertebrate categories were found almost exclusively at one particular site. Thysanura (Silverfish) were found almost completely at the Polson sampling site, which is sagebrush habitat. Silverfish tend to prefer habitats of high humidity (Brimblecombe & Querner 2021) therefore, this suggests the Polson sampling site has a higher average humidity due to lower elevation and higher abundance of Silverfish. The grassland habitat at Cascade produced almost all the collected Daddy Long-legs. Grasshoppers and crickets were also more abundant at Cascade.

Craig et al. (1999) found that certain grasshopper species were dependent on open grassland for reproductive success, so it makes sense that few orthoptera and other field-dependent species were observed at Polson, a sagebrush habitat classification. The greatest diversity of invertebrate categories was found at the grassland site. The Cascade sampling site produced the greatest variety of categories with at least one individual from every category being collected from there at least once. This may be due to the Cascade site being a natural grassland setting with a wide diversity of shrubs, forbs, and grasses. Specific habitats can be advantageous to certain species of invertebrates while also unfavorable to other species (McNett and Rypstra, 2000). Invertebrate distribution relies heavily on food/prey availability and the overall biodiversity of the habitat. Site based differences in invertebrate diversity observed in this study are likely due to a combination of altitude, type of vegetative forage available, and weather conditions.

Weather conditions may be a stronger driving factor behind both invertebrate abundances and biomass rather than habitat type. This is indicated by the significant differences between months for both sites. Polson also shows an insignificant difference when compared by years in terms of abundance, possibly due to a more stable climate west of the Continental Divide. Cascade shows a significant difference in abundance over all the years suggesting climate may be more variable on the eastern side of the divide.

Monthly weather data at the Polson and Cascade sampling sites were compared with the grand mean invertebrate abundance and biomass at each site. Both sampling sites show increasing invertebrate abundance with increasing average monthly temperature. This is expected due to the ectothermic nature of most terrestrial invertebrates and the temperature-related increase in plant productivity. When compared with total monthly precipitation, invertebrate abundance at both sampling sites shows more variability and weak relationship with amount of precipitation. This suggests that invertebrate abundance may be influenced by precipitation only after a time lag (Loehman et al. 2012).

Polson and Cascade were sampled for a longer time-period, from June 2000 until September 2016, so time-based trends at these sampling sites could be examined in more detail. Both sampling sites had comparable levels of invertebrate abundances although the grand mean biomass for the Polson sampling site was lower. While the grassland sampling site at Cascade produced larger-mass invertebrates (grasshoppers, crickets, beetles, and daddy long-legs), the sagebrush sampling site at Polson produced small-mass invertebrates (orb weaver spiders, silverfish, and ants/wasps).

This study was part of a larger longitudinal study that encompasses a broader scope of ecological aspects that involve invertebrates, deer mice, weather, vegetation, and Sin Nombre Virus. This study provided us with a greater understanding of how biomass and diversity of invertebrates differ between individual sites and habitat types. It also suggests that seasonal invertebrate abundance is linked to temperature across both sites. Our data suggests that any relationship between precipitation and invertebrate abundance or biomass is not immediate but may be a time delayed effect. In addition, we show that at the two sites located within two habitat types there has been no notable change in invertebrate abundance or biomass over a span of 16 years suggesting that invertebrate populations for at least some sites are relatively stable.

In the future, analysis of the collected samples into more detailed species categories and further study of the difference in invertebrate diversity between habitat types would provide a greater understanding of preferred habitats for certain species. A more in-depth look into the drivers for plant production and vegetative forage availability may also provide a deeper understanding of how climate change and agricultural practices might affect deer mouse populations. Invertebrate abundance and biomass data from this thesis is currently being used to model the effect of invertebrates on deer mouse abundance as part of a separate study.

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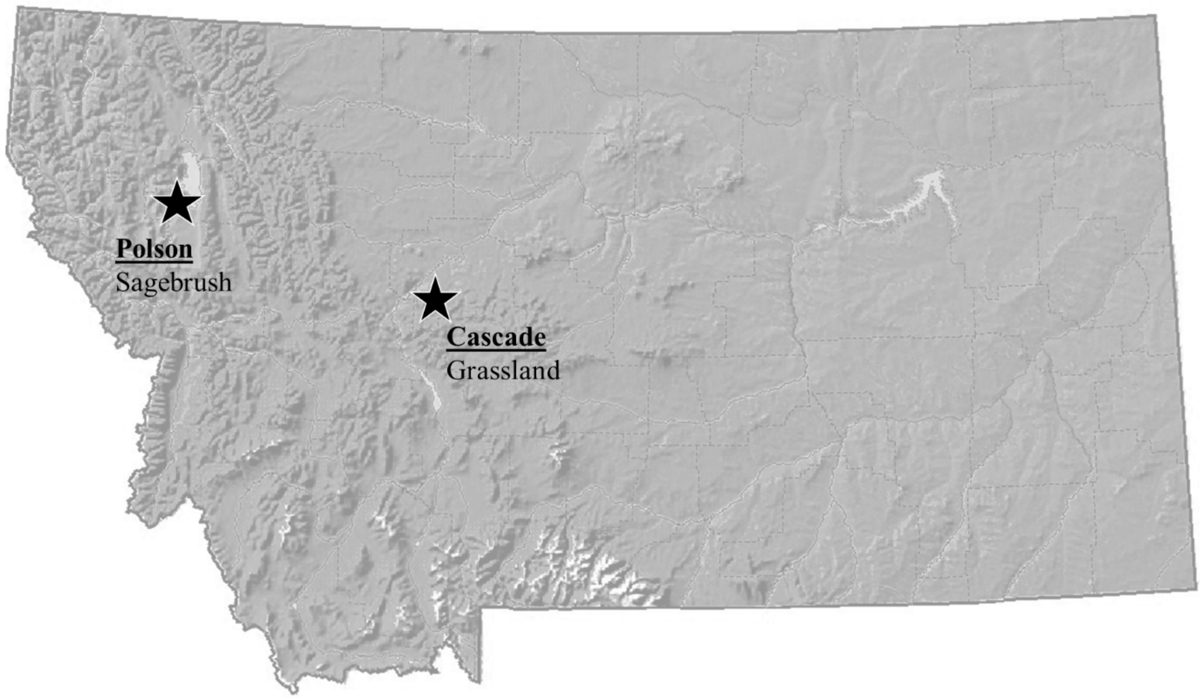

Figure 1: Locations and habitat types of invertebrate collection sites. Locations are part of long-term longitudinal study of hantavirus research (Douglass et al. 1996). Invertebrates were sampled at all sites starting 06/2000. Sampling periods ended at Cascade in 09/2013, and Polson in 10/2016.

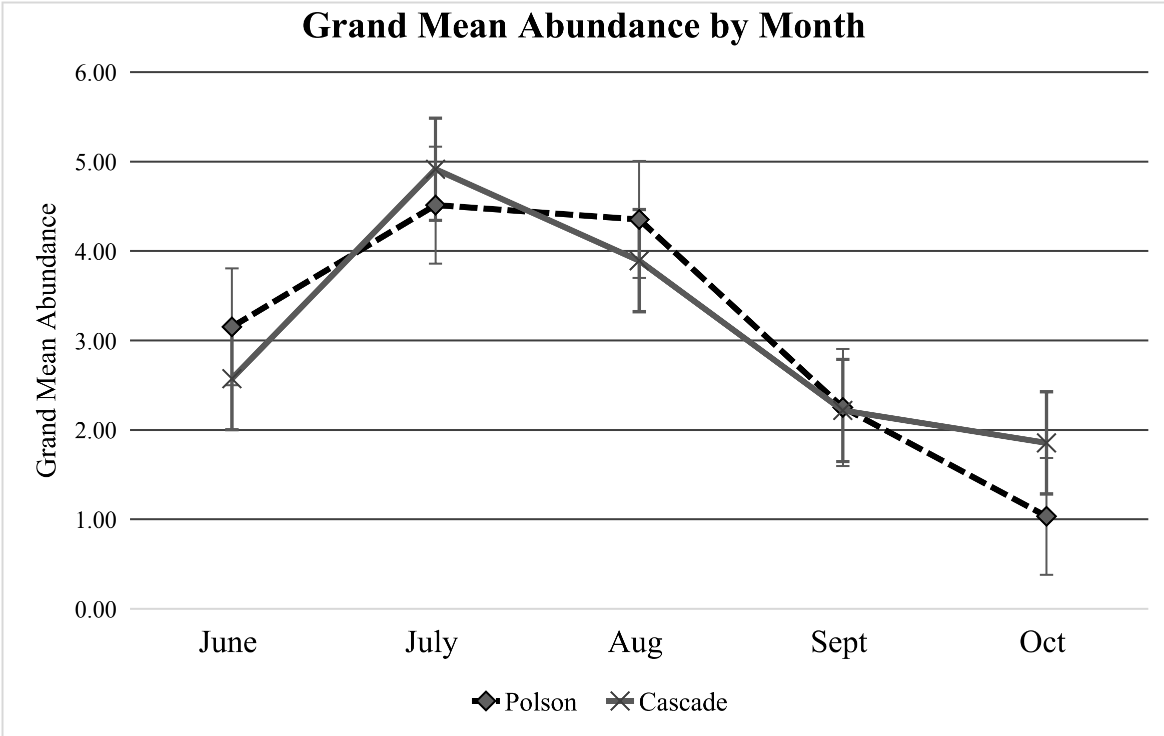

Figure 2: Grand mean abundance by month at the Cascade and Polson study sites in central and western Montana from June/2000 until October/2016. The mean was calculated for each order, using the total of all 10 pitfall traps, per sampling period. A one-way ANOVA analysis was used to compare significance between months for both sites. Both sites showed significant correlations (Polson: P-value = <0.001, Cascade: P-value = 0.002). Tukey's HSD test was used to determine differences between specific months. The Polson site showed significance between July/October (P-value = 0.048). Cascade showed significance between two monthly comparisons of July/Sept (P-value = 0.011) and July/Oct (P-value = 0.003).

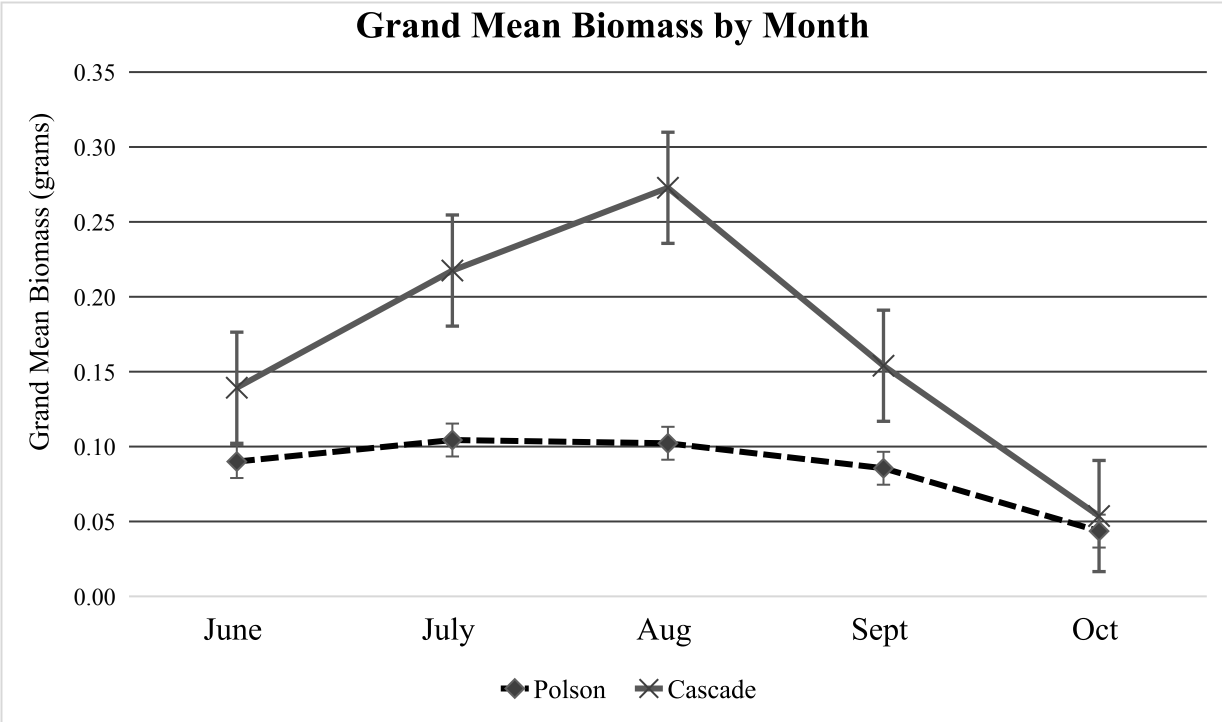

Figure 3: Grand mean biomass by month collected at Polson and Cascade study sites in central and western Montana from June/2000 through October/2016. The mean was calculated for each order, using the total of all 10 pitfall traps, per sampling period. A two-way ANOVA analysis were used to compare significance between months for both sites. Both sites showed significant correlations (Polson: P-value = 0.042, Cascade: P-value = 0.001). Tukey's HSD test was used to determine which months were significant. The Polson site showed no significance between individual months. Cascade showed significance between the monthly comparison of July/Oct (P-value = 0.016).

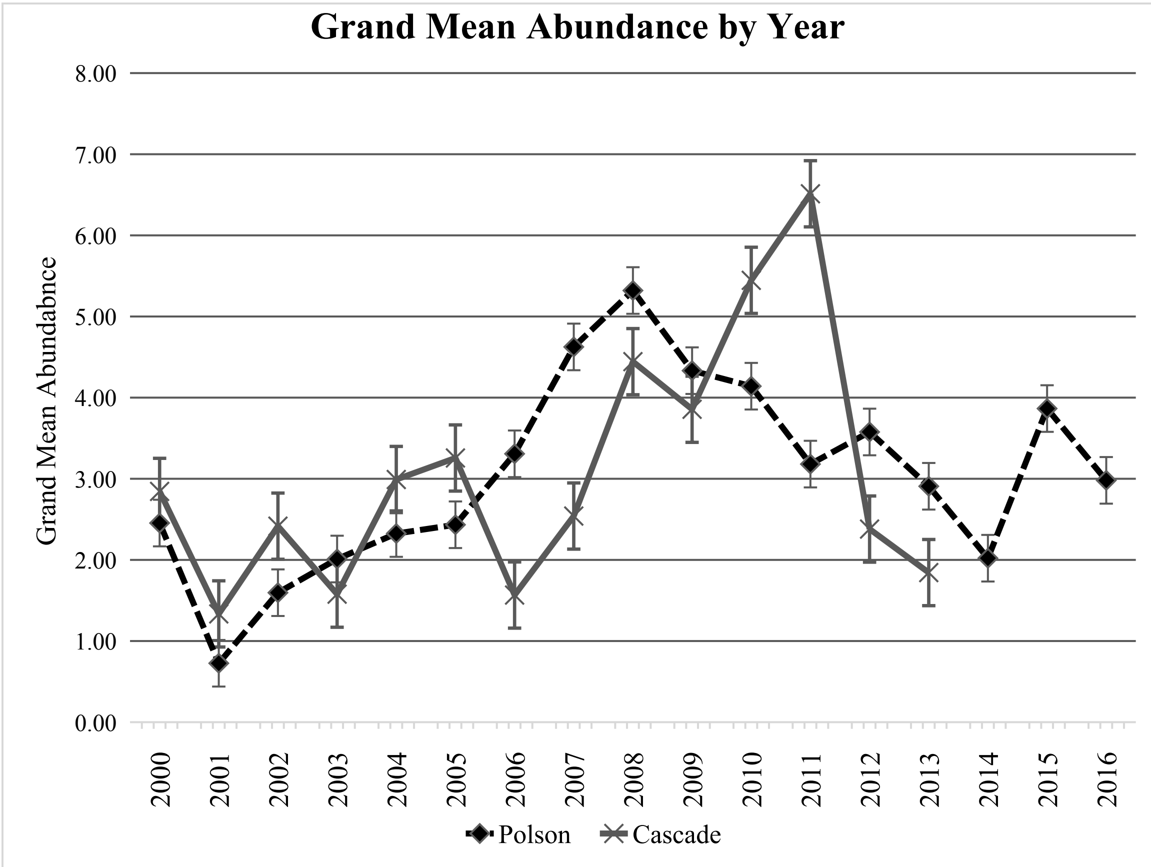

Figure 4: Grand mean abundance by year at the Cascade and Polson study sites in central and western Montana from June/2000 until October/2016. The mean was calculated for each order, using the total of all 10 pitfall traps, per sampling period. A two-way ANOVA analysis were used to compare significance between years for both sites. Only the Cascade site showed significant correlations when compared between years (P-values = 0.002). The Polson site showed no significance when compared between years. Tukey's HSD test was used to determine which years were significant. Cascade showed significance between four yearly comparisons of 2011/2001 (P-value = 0.014), 2011/2006 (P-value = 0.012), 2011/2003 (P-value = 0.012), and 2011/2013 (P-value = 0.042).

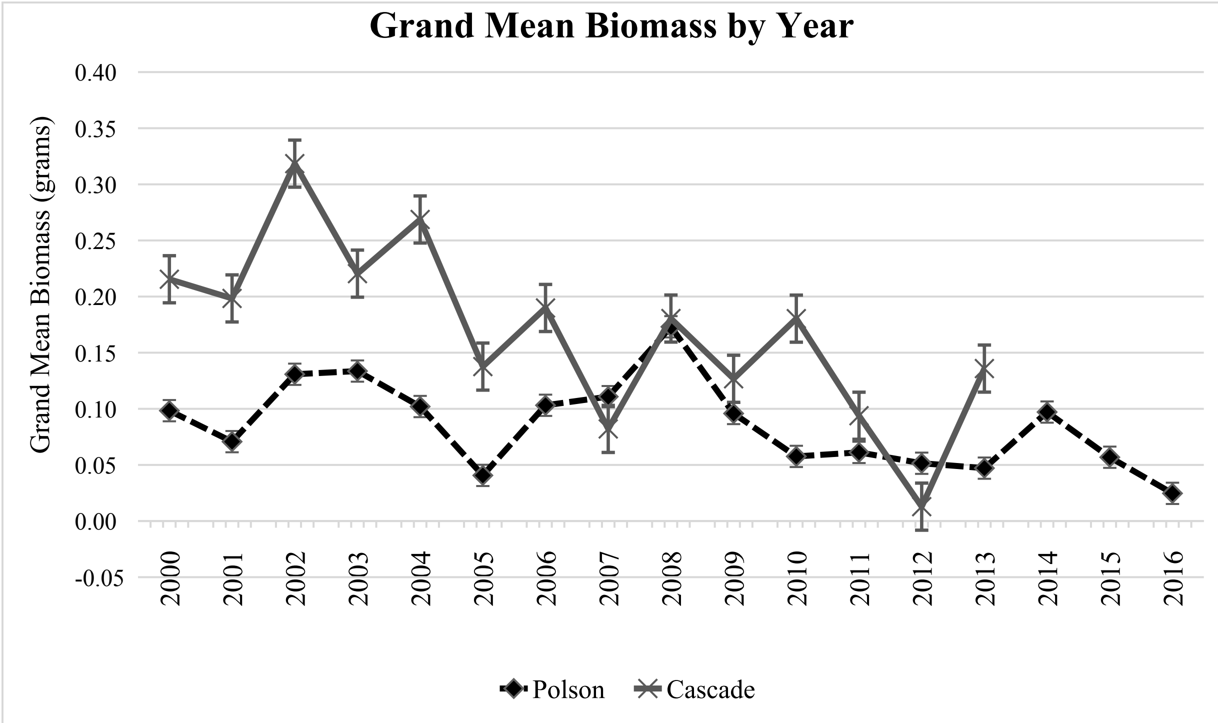

Figure 5: Grand mean biomass by years collected at Polson and Cascade study sites in central and western Montana from June/2000 through October/2016. The mean was calculated for each order, using the total of all 10 pitfall traps, per sampling period. A two-way ANOVA analysis were used to compare significance between years for both sites. Only the Polson site showed significant correlations when compared between years (P-values = 0.008). The Cascade site showed no significance when compared between years. Tukey's HSD test was used to determine which years were significant. Polson showed significance between two yearly comparisons of 2008/2016 (P-value = 0.011) and 2008/2005 (P-value = 0.040).

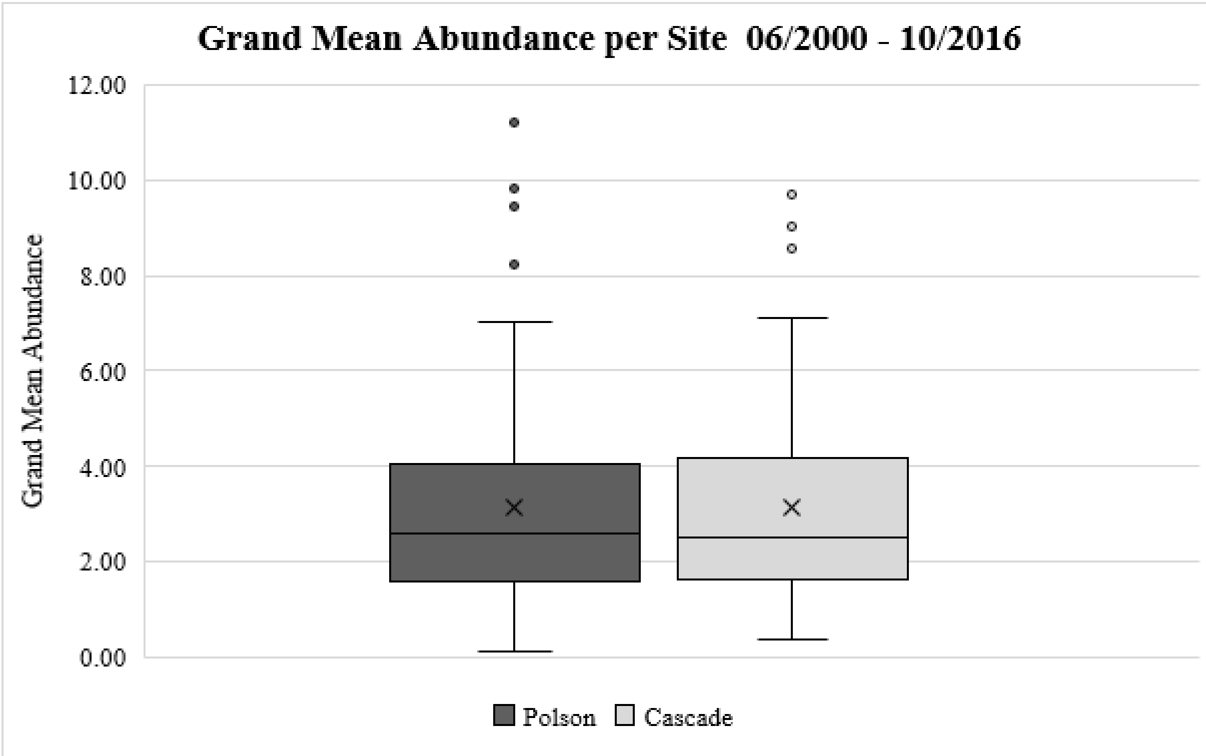

Figure 6: Grand mean abundance for Polson and Cascade sites from June/2000 until October/2016. T-tests were conducted to show any significance of difference comparing between sites. No significance in difference was shown (P-value = 0.914). The mean was calculated for each order, across all 10 pitfall traps, per sampling period. This mean calculation is the same for both individual abundance and biomass (grams). Error bars show the minimum and maximum values of the sample sites data set. The mean and median are represented by the “X” and the middle line, respectively. Any outliers are shown by the small circle.

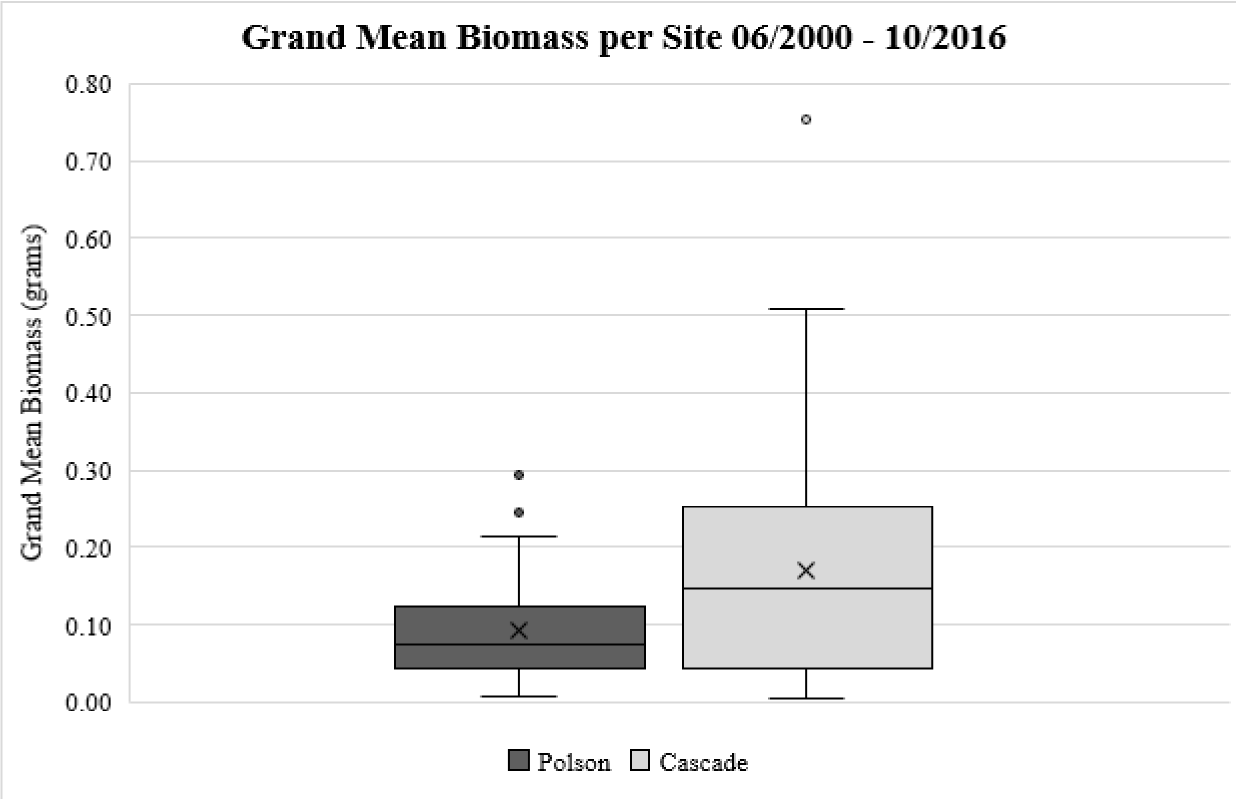

Figure 7: Grand mean biomass for Polson and Cascade sites from June/2000 until October/2016. T-tests were conducted to show any significance of difference comparing between sites. A significance in difference was shown when compared (P-value = <0.001). The mean was calculated for each order, across all 10 pitfall traps, per sampling period. Error bars show the minimum and maximum values of the sample sites data set. The mean and median are represented by the “X” and the middle line, respectively. Any outliers are shown by the small circle.

Table 1: Class, Order, and Common Name of the 24 categories of invertebrate identification. (*) Indicates categories that were categorized by class and not to order.

Class	Order	Common Name
Arachnida	Araneida	Orb weaver spiders
	Phalangida	Harvestman/Daddy long legs
Insecta	Hymenoptera	Ants/Wasps
	Thysanura	Silverfish
	Coleoptera	Beetles
	Diptera	Flies
	Orthoptera	Grasshoppers/Crickets
	Auchenorrhyncha	Cicadas/Treehoppers
	Hemiptera	True Bugs
	Isoptera	Termites
	Collembola	Springtails
	Homoptera	Aphids/Leafhoppers
	Dermaptera	Earwigs
	Pscoptera	Booklice
	Sternorrhyncha	Whiteflies
	Neuroptera	Antlions
	Diplura	Bristletails
	Ephiminoptera	Mayflies
	Lepidoptera (Adult)	Butterflies/Moths
	Lepidoptera (Juv)	Caterpillars
Crustacea	Isopoda	Pillbugs
Chilpoda*		Centipedes
Diplopoda*		Millipedes
Misc*		Worms, Snails, Etc

Table 2: Grand mean abundance collected at the Polson sampling site in western Montana for all sampling periods. Standard deviation calculated over 83 samples (n=83).

Grand Mean Abundance - Polson

Order	Common name	Grand Mean	St. Dev ($\bar{x}$ = +/-)
Thysanura	Silverfish	21.19	**31.94**
Hymenoptera	Ants/Wasps	19.16	**15.36**
Araneida	Orb weaver spiders	13.61	**13.07**
Coleoptera	Beetles	4.59	**3.45**
Diptera	Flies	3.96	**4.89**
Orthoptera	Grasshoppers/Crickets	3.86	**4.90**
Lepidoptera (Adult)	Butterflies/Moths	1.69	**4.13**
Isoptera	Termites	1.17	**3.71**
None	Misc	1.11	**4.96**
Hemiptera	True Bugs	0.82	**3.47**
Lepidoptera (Juv)	Caterpillars	0.59	**0.96**
Auchenorrhyncha	Cicadas/Treehoppers	0.53	**0.81**
Phalangida	Harvestman/Daddy long legs	0.50	**1.68**
Isopoda	Pill bugs	0.50	**0.59**
Pscoptera	Booklice	0.24	**1.56**
Collembola	Springtails	0.20	**0.93**
Sternorrhyncha	Whiteflies	0.13	**0.70**
Homoptera	Aphids/Leafhoppers	0.06	**0.53**
Neuroptera	Antlions	0.03	**0.15**
Dermaptera	Earwigs	0.02	**0.09**
None	Centipedes	0.01	**0.04**
None	Millipedes	0.00	**0.02**
Ephiminoptera	Mayflies	0.00	**0.00**
Diplura	Bristletails	0.00	**0.00**

Table 2: Grand mean abundance collected at the Cascade sampling site in central Montana for all sampling periods. Standard deviation calculated over 67 samples (n=67).

Grand Mean Abundance - Cascade

Order	**Common name**	**Grand Mean**	**St. Dev ($\bar{x}$ = +/-)**
Phalangida	Harvestman/Daddy long legs	17.13	**18.94**
Hymenoptera	Ants/Wasps	15.23	**15.23**
Diptera	Flies	8.99	**9.02**
Coleoptera	Beetles	8.48	**8.94**
Araneida	Orb weaver spiders	6.84	**5.77**
Orthoptera	Grasshoppers/Crickets	6.58	**7.08**
Auchenorrhyncha	Cicadas/Treehoppers	4.59	**10.61**
Lepidoptera (Juv)	Caterpillars	1.98	**3.65**
Hemiptera	True Bugs	1.52	**2.17**
Homoptera	Aphids/Leafhoppers	1.06	**6.71**
None	Misc	0.68	**1.7**
Lepidoptera (Adult)	Butterflies/Moths	0.58	**1.13**
Dermaptera	Earwigs	0.50	**1.07**
Isoptera	Termites	0.31	**0.66**
Thysanura	Silverfish	0.26	**0.85**
None	Centipedes	0.07	**0.23**
Sternorrhyncha	Whiteflies	0.06	**0.17**
Collembola	Springtails	0.05	**0.33**
Isopoda	Pill bugs	0.05	**0.18**
None	Millipedes	0.01	**0.04**
Pscoptera	Booklice	0.00	**0.03**
Neuroptera	Antlions	0.00	**0.01**
Ephiminoptera	Mayflies	0.00	**0.01**
Diplura	Bristletails	0.00	**0.01**

Table 4: Grand mean biomass collected at the Polson sampling site in western Montana for all sampling periods. Standard deviation calculated over 83 samples (n=83).

Grand Mean Biomass (grams) - Polson			
Order	**Common Name**	**Grand Mean**	**St. Dev ($\bar{x}$ = +/-)**
Orthoptera	Grasshoppers/Crickets	0.93	**1.25**
Coleoptera	Beetles	0.50	**0.53**
Araneida	Orb weaver spiders	0.16	**0.16**
Hymenoptera	Ants/Wasps	0.15	**0.20**
Thysanura	Silverfish	0.10	**0.19**
Sternorrhyncha	Whiteflies	0.04	**0.24**
Diptera	Flies	0.04	**0.07**
Lepidoptera (Juv)	Caterpillars	0.03	**0.15**
Lepidoptera (Adult)	Butterflies/Moths	0.03	**0.09**
Collembola	Springtails	0.03	**0.15**
None	Misc	0.02	**0.06**
Isoptera	Termites	0.01	**0.04**
Isopoda	Pill bugs	0.01	**0.01**
Hemiptera	True Bugs	0.00	**0.01**
Pscoptera	Booklice	0.00	**0.01**
Neuroptera	Antlions	0.00	**0.00**
Phalangida	Harvestman/Daddy long legs	0.00	**0.00**
Homoptera	Aphids/Leafhoppers	0.00	**0.00**
None	Millipedes	0.00	**0.00**
None	Centipedes	0.00	**0.00**
Auchenorrhyncha	Cicadas/Treehoppers	0.00	**0.00**
Dermaptera	Earwigs	0.00	**0.00**
Ephiminoptera	Mayflies	0.00	**0.00**
Diplura	Bristletails	0.00	**0.00**

Table 5: Grand mean biomass collected at the Cascade sampling site in central Montana for all sampling periods. Standard deviation calculated over 67 samples (n=67).

Grand Mean Biomass (grams) - Cascade			
Order	**Common Name**	**Grand Mean**	**St. Dev ($\bar{x}$ = +/-)**
Orthoptera	Grasshoppers/Crickets	1.73	**2.48**
Coleoptera	Beetles	1.41	**1.62**
Phalangida	Harvestman/Daddy long legs	0.38	**0.42**
Hymenoptera	Ants/Wasps	0.20	**0.56**
Araneida	Orb weaver spiders	0.11	**0.12**
Diptera	Flies	0.07	**0.20**
Lepidoptera (Adult)	Butterflies/Moths	0.04	**0.15**
Lepidoptera (Juv)	Caterpillars	0.04	**0.07**
Homoptera	Aphids/Leafhoppers	0.02	**0.16**
None	Misc	0.02	**0.07**
Hemiptera	True Bugs	0.01	**0.03**
Collembola	Springtails	0.01	**0.06**
Isopoda	Pill bugs	0.01	**0.09**
Dermaptera	Earwigs	0.01	**0.03**
None	Centipedes	0.01	**0.03**
Thysanura	Silverfish	0.00	**0.02**
None	Millipedes	0.00	**0.01**
Auchenorrhyncha	Cicadas/Treehoppers	0.00	**0.00**
Sternorrhyncha	Whiteflies	0.00	**0.00**
Isoptera	Termites	0.00	**0.00**
Neuroptera	Antlions	0.00	**0.00**
Pscoptera	Booklice	0.00	**0.00**
Ephiminoptera	Mayflies	0.00	**0.00**
Diplura	Bristletails	0.00	**0.00**

Table 6: Analysis summary values displayed for one-way ANOVA's used to compare grand mean abundance and grand mean biomass at both sampling sites, between months and years for the entire study. Tukey's Honestly Significance Difference (HSD) test shows precisely which months and years significantly differ. P-values are displayed to show level of significance.

Grand Mean Abundance by Month

	n	DF	St. Dev	Adj R^2	Pr > F	F	Pr > |t|	t
Polson	83	77	2.296	0.311	**<0.001**	8.397	**<0.001**	6.614
Cascade	67	61	2.291	0.199	**0.002**	4.270	**<0.001**	4.437

Grand Mean Biomass by Month

	n	DF	St. Dev	Adj R^2	Pr > F	F	Pr > |t|	t
Polson	83	77	0.064	0.081	**0.042**	2.440	**<0.001**	5.867
Cascade	67	61	0.146	0.217	**0.001**	4.649	**<0.001**	3.733

Grand Mean Abundance by Year

	n	DF	St. Dev	Adj R^2	Pr > F	F	Pr > |t|	t
Polson	83	66	2.296	0.063	0.199	1.343	**0.004**	2.998
Cascade	67	53	2.291	0.281	**0.002**	2.986	0.063	1.899

Grand Mean Biomass by Year

	n	DF	St. Dev	Adj R^2	Pr > F	F	Pr > |t|	t
Polson	83	66	0.064	0.207	**0.008**	2.342	0.336	0.968
Cascade	67	53	0.146	0.100	0.125	1.567	0.055	1.962

Tukey's HSD test

	Differing Months
Polson Abundance by Month	Jul/Oct
Cascade Abundance by Month	Jul/Oct
	Jul/Sept
Polson Biomass by Month	----
Cascade Biomass by Month	Jul/Oct
Polson Abundance by Year	----
Cascade Abundance by Year	2011/2001
	2011/2006
	2011/2003
	2011/2013
Polson Biomass by Year	2008/2016
	2008/2005
Cascade Biomass by Year	----