

Determining the Effects of Climate-Induced Range Shifts on Caddisfly Population Dynamics

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Abstract

The geographic distribution of many freshwater insects is restricted in part by timing of snowmelt and the temperature of the water. Because of this, climate change is having a significant effect on the distribution of aquatic species around Gothic, Colorado. Scientists have documented that species typically found in lower elevation have begun to expand their range into higher alpine ponds. However, it is unknown how elevation will affect their population dynamics and rate of nutrient recycling. Caddisflies are a species of aquatic detritivores that are fundamental in providing nutrients to the ecosystem. Understanding how elevation affects caddisfly growth and population size is key to understanding how climate change will affect alpine communities globally. To have a better understanding of this concept, I studied 37 ponds ranging from 2,347 to 3,505 meters in elevation and looked at how elevation affected population density, adult body size, and adult emergence time of four species of caddisfly: *Limnephilus externus*, *Limnephilus picturatus*, *Grammotaulius lorretae*, and *Asynarchus nigriculus*. I took density samples of these species in each pond throughout the summer. Pupae were placed in emergence chambers, and adults were collected and measured. Elevation had a significant effect on the emergence time of *Asynarchus*. Elevation also positively affected *Asynarchus* density while it negatively affected *Grammotaulius* density. Pond type had a significant effect on *Asynarchus* thorax and abdomen weight at the Mexican Cut. This study was important because understanding how climate change affects foundational species may help us better understand its far-reaching effects on ecosystems.

Introduction

The geographic distribution of many aquatic insect populations in mountainous regions is likely to be influenced by the characteristics of snowfall from previous winters and the temperature of the water (Barnett et al. 2005). Their range in elevation is limited in part by colder water at higher elevation and the permanence of the ponds in which they live. The beginning of the snowmelt determines the start date of aquatic growth and development in insects that overwinter as eggs, such as caddisfly larvae (Wissinger et al. 2003). Earlier snowmelt means that these species can get a jumpstart on their path to adulthood, but also exposes ponds to sunlight for longer periods of time (Lund, Wissinger, and Peckarsky, 2016).

Ponds in mountainous regions with an early snowmelt may experience higher temperatures, and if they are temporary ponds, may also dry earlier (Wissinger et al. 2016).

Climate change has had a large impact on the distribution of freshwater insects. As the planet continues to warm, the snow has begun to melt earlier in high elevation habitats, and the temperature in the surrounding pools has begun to increase (Clow 2010). This increase in temperature is likely contributing to the upslope shift in geographic distribution that has been documented in many freshwater species, though the exact mechanism behind the shift has yet to be determined (Chen et al. 2011). These range shifts have the potential to impact the population dynamics of the migrating species, which could significantly impact ecosystem function since many of these shifting species are detritivores, and detritus is the primary source of energy in shallow standing water habitats (Batzner et al. 2014).

Detritivores are species that eat decaying plants and leaves that fall into the water (Wissinger et al. 1999). They also play a major role in nutrient recycling in high elevation systems. These alpine ecosystems are characteristically nutrient limited, and because of this, they rely heavily on the nutrients recycled by detritivores (Elser et al. 2009). These detritivores ingest nutrients that are trapped in the detritus, decaying plant material, and excrete usable nutrients back into the water – turning particulate nutrients into dissolved nutrients (Moore et al. 2004). Once the dissolved nutrients have been released back into the water, they can then be used by other plants and animals to stimulate growth and life in these nutrient-limited systems (Klemmer et al. 2012). Changes in the population size or growth rate of detritivores therefore have the potential to influence the rate at which nutrients are recycled, which could impact the alpine ecosystem as a whole (Balik et al. 2018). For this reason, we need to determine the effect that elevation has on the different detritivore species now found in these high elevation ponds.

One of the most common detritivore species in montane ponds are caddisflies – (Order: Trichoptera), a group of aquatic insects that can be found all over the world (Wissinger, Brown, and Jannot 2003). Caddisfly larvae of the family Limnephilidae are classified as detritivores and are commonly found in alpine and subalpine water systems such as the ponds located in the East River Valley around Gothic, Colorado. Caddisflies start their lives out in streams or ponds where most species go through five different larval stages while forming a case around them before metamorphosing into an adult (Wissinger, Brown, and Jannot 2003). Once they have reached their adult stage, the caddisflies will emerge from their pond or stream and spend the rest of their short lives on land where they mate. Eventually, the females return to the water to lay their eggs. Caddisflies are also the biomass dominant detritivore species in many high elevation ponds, meaning that they are the main species in high elevation ecosystems that recycle nutrients (Balik et al. 2018). Since they are the biomass dominant species, a loss in their populations could have a greater impact on the functioning of the ecosystem than if another detritivore species was lost. Caddisflies can be considered a keystone species in providing nutrients to plants and animals and are therefore a foundational part of alpine habitat.

In ponds around the Rocky Mountain Biological Laboratory (RMBL) in Gothic, *Limnephilus externus* and *Asynarchus nigriculus* have been the dominant species of caddisfly in subalpine ponds for many years (Greig 2018), and the range of *L. externus* extends down-valley to montane elevations. However, in 1998, a new species of caddisfly, *Limnephilus picturatus*, began moving into subalpine ponds, and in 2009, another species, *Grammotaulius lorretae*, was found for the first time in subalpine ponds (Wissinger et al. 2016). We hypothesize that the warming caused by climate change may have been a trigger in this movement of species. This shift could have significant impacts on the population size and growth rate of resident species as

well as range-shifting species, yet scientists are unsure how this shift is currently impacting caddisfly population dynamics.

In order to better understand the effect of elevation on caddisfly population dynamics, I examined their population density, mortality rate, emergence time, and adult body size across an elevation gradient. Based on my knowledge of nutrient limitation in high elevation areas and the fact that caddisflies are more of an r-selected species, I predicted that the density of a given caddisfly population would decrease over its development time in permanent ponds (i.e. from early to late instar). I hypothesized this decrease in density because as caddisflies grow and develop, the intraspecific competition for resources should increase throughout time as individuals accrue mass and resources become more limited (Klemmer et al. 2012). Also, in permanent ponds, caddisflies experience predation from tiger salamanders (*Ambystoma tigrinum nebulosum*), which would decrease the caddisfly population density of these pools over time. However, in temporary pools, it was likely that changes in population density may depend on how quickly the pool dries (Lund et al. 2016). If the pond remained filled for an extended period of time, we might have seen a decrease in population density, but if there was rapid drying in temporary ponds, the density of the population might increase as the caddisflies are confined to a smaller space. I predicted that the mortality rate would also decrease in more permanent ponds because caddisflies are more of an r-selected species (Rafferty 2011). This means that they put more energy into high rates of reproduction instead of investing energy into parental care. These types of species tend to have initial high rates of density-dependent mortality that eventually decrease as some individuals make it to adulthood (Rafferty 2011). However, in temporary ponds, we might have expected to see the mortality rate increase as the pond size shrank and the effects of density-dependent mortality increased. This is particularly likely in temporary pools

that dry up earlier in the summer, and therefore, not all caddisflies are likely to survive because of death by desiccation. Across the elevation gradient, I expected to find a higher density of caddisflies of a given species at lower elevation of its range because of a greater abundance of nutrients (Wissinger et al. 1999). This higher availability of nutrients at lower elevations could decrease the mortality rate of young caddisflies because of a decrease in competition for resources.

I also expected to find that the average adult body size was greater at higher elevation and that emergence times occurred earlier at lower elevations because of earlier snowmelt, hence longer growing season before ponds dry. I predicted this difference in adult body size because past data has shown that *Asynarchus* adults found at Mexican Cut are larger than those found down-valley (Greig unpublished data). Adult body size is highly connected to the number of eggs a female can release. Larger, adult females can allocate more energy into creating more, and larger eggs (Wissinger et al. 2004). Understanding how climate change affects the fecundity rates of adults will help us understand the impact climate change will have on future generations. I also predicted an earlier emergence at lower elevations because if there is an earlier snowmelt, then the caddisflies at those ponds have the potential to begin their lifecycles earlier, and therefore could reach adulthood and emerge before caddisflies at higher elevation ponds that are locked beneath snow for a longer period of time.

Methods

Some of the main caddisflies found in ponds near Gothic that supply nutrients to the surrounding ecosystem are the species of *Limnephilus externus*, *Limnephilus picturatus*, *Grammotaulius lorretae*, and *Asynarchus nigriculus* (Wissinger, Brown, and Jannot 2003). These focal species were chosen for this study because of the specific ways that climate change

is impacting their populations. *Asynarchus* is usually found in subalpine temporary, pools that tend to dry out in the summer while *L. externus*, *L. picturatus*, and *Grammotaulius lorretae* are usually found in more subalpine and montane, permanent ponds that are less likely to dry out throughout the year (Wissinger, Brown, and Jannot 2003). However, while *Asynarchus* is limited to subalpine elevations, *L. externus* is more broadly distributed from lower montane to subalpine ponds. This created an interesting contrast between the two species that allowed us to study how elevation affects these species at different ranges. Both species have faced new competition from the recent climate-induced range shifts the shifting range of *L. picturatus* and *Grammotaulius* (Greig 2018).

I sampled 37 ponds found near and around Gothic, Colorado. These ponds were in an elevation range of 2,347 to 3,505 meters and were easy to access from The Rocky Mountain Biological Laboratory (RMBL) where the study was based. These ponds range from elevations around Crested Butte township up to the Mexican Cut Nature Preserve (MCNP). The Mexican Cut is a high elevation site where there around 60 ponds divided into the upper and lower cut (Greig 2010). The ponds used in the study had one or more of the four species of caddisflies that were the focus of this project. While many of these ponds are mapped, GPS data were collected for my Judd Falls sites in order to create a GIS map. The parameters of the Wilderness Boundary Pond and Shooting Star Pond were collected in the morning using a GPS receiver, and points were taken at each pond to show the location of the emergence chambers. After processing, the data was uploaded to ArcMap where additional layers were added to show trails, streams, and the boundary of the wilderness area (Figure 1).

At each pond, between two and four replicate $1/3 \text{ m}^2$ D-net sweeps (depending on pond size and accessibility) were taken in order to collect an accurate sample of the population size of

the caddisfly species found in that pond. The samples were then examined live, pondside, and each caddisfly found was categorized according to species and larval instar. If there was a question on determining species or instar size, replicate individuals (1-3) were brought back to the lab where they were identified. Repeating this sampling method 3 times allowed us to calculate how caddisfly population density and mortality rate change over time for each species. These second and third samples were usually taken two or three weeks after the first sample.

Pupae were placed inside emergence chambers in the ponds. These chambers were checked 2-3 times a week and time of emergence was recorded at each site. Once the adults emerged, they were collected, returned to the lab, and euthanized. Dead caddisflies were examined under a microscope to determine species, sex, wing length, and body length. The right wing was measured from tip to wing joint on each caddisfly on a stereomicroscope under 6.5X. Total body length was measured from the tip of the head to the end of the abdomen. I separated the caddisfly abdomen from the body and dried both in a drying oven at 60°C for 48 hours. Once removed from the oven, dried caddisflies were kept in a desiccation chamber and weighed on a Cahan microbalance to the nearest 0.001mg.

I was able to sample 10 of the 37 ponds three times, 14 ponds twice, and 13 ponds once. I found the density of caddisflies per m^2 by adding the total number of caddisflies counted for each $1/3\text{m}^2$ sweep and multiplying by 3. For the ponds that were sampled three times, I was able to run a linear regression on the density of caddisflies over time in order to determine if there was a significant relationship for each species. Mortality was calculated for species identified in each round of sampling from ponds that were visited either 2 or 3 times. To measure mortality, I would subtract from the percentage of survivors from 1.0. This survivorship was calculated by dividing the density of caddisflies from the later sample by the density of caddisflies of the

earlier sample. These rates of mortality were then analyzed by regressing against time and elevation.

For adults, I was able to place emergence chambers in 24 ponds and collected adults from 16 of them. Mean emergence time (date) was calculated for each pond by species and graphed along the elevation gradient to test for correlation using another linear regression. Adult body size was calculated by adding the individual's thorax and abdomen weight. These weights were graphed for each species along the elevational gradient, and a linear regression was run to test for a significant relationship.

Results

In many of the ponds that were sampled 3 times, there was a significant negative relationship between time and population density. *Asynarchus* in pond K7 experienced a significant decrease in density over time ($p = 0.0078$, Figure 2). *Asynarchus* populations also experienced a significant decrease in density in the Shooting Star pond ($p = 0.0048$). Similarly, *L. externus* population density significantly declined over time in ponds Marsh 2, K1, Schutt South, and High School ($p = 0.0051$, <0.001 , <0.001 , and 0.0035 respectively), and *Grammotaulius* experienced a significant decrease in population density in pond K1 ($p < 0.001$). Elevation also had a significant impact on the density of caddisflies. *Asynarchus* experienced a significant increase ($p = 0.041$) in mean population density as the elevation gradient increased while *Grammotaulius*' population density significantly decreased at higher elevation ($p = 0.019$). However, there was also a marginally non-significant decrease in *Asynarchus* density between the lower and upper cut elevations at Mexican Cut ($p=0.058$) suggesting a trend towards declines in density at the highest elevations.

Elevation did not have a significant effect on the mortality rate across species ($p=0.43$) or on species-specific mortality rates of *Asynarchus* ($p=0.78$), *L. externus* ($p=0.70$), or *Grammotaulius* ($p=0.29$). There was also no significant effect of time on the mortality rate of the caddisfly species as a whole or the individual species of *Asynarchus*, *L. externus*, or *Grammotaulius* ($p = 0.189, 0.515, 0.949$, and 0.119 respectively).

Elevation had a significant impact on the mean emergence time of *Asynarchus* ($p = 0.044$, Figure 3). As elevation increased, *Asynarchus* adults emerged significantly later in the summer. However, elevation did not have a significant effect on *Asynarchus* adult body weight across its total range ($p = 0.734$, Figure 4). However, looking at *Asynarchus*' elevation range from their lowest site to the lower cut at Mexican Cut, there was a suggested trend in an increase of male body size across this range, but this relationship wasn't significant ($p = 0.192$). Though there wasn't a significant effect of elevation on *Asynarchus* male body size across the total elevation, there was an almost significant negative effect of elevation on male adult body size as elevation increased from the lower cut to the upper cut ($p = 0.0528$). At the Mexican cut, comparisons of *Asynarchus* body mass between semi-permanent and temporary ponds indicated shorter hydroperiod ponds had a significant decrease of adult thorax and abdomen (Ttest: $p < 0.001$ for both).

Few data was collected on *L. picturatus* because these caddisflies were far along in their development at lower elevations and at lower abundance in the ponds I sampled at the Mexican Cut. Because of this, I could not collect data on their emergence or adult size across the elevation gradient. However, I was able to collect data on their density across elevation, and there was found to be an insignificant relationship between this data with a p of 0.66 .

Discussion

I found that elevation has a significant effect on *Asynarchus* and *Grammotaulius* density, which might provide a clue to which elevations are optimal for these species. Based on the theories of optimal habitat, population density should be highest in the center of their range where they are best suited for their habitat (Geber 2008). Thus, I conclude that *Asynarchus*'s central range occurs at a higher elevation since its density increases with elevation. I also conclude that *Grammotaulius*'s presence is at the upper edge of its range since its density decreases with elevation. This knowledge can help us understand what future populations might look like. As climate change keeps forcing caddisflies to move into higher elevation areas, either their central range will shift, or they will be forced to move into less suitable habitat. If their central range shifts, then it could be likely that the habitat they are moving into has changed to become more like their habitat at lower elevation. If this is the case, then studying what lower elevation sites are currently like may help us understand what higher elevation sites might look like in the future under the effects of climate change.

However, caddisflies are undergoing elevational range shifts may encounter less suitable habitat as they travel up in elevation. For example, lower food availability in nutrient poor high elevation ponds could cause a decrease in female adult body size and emergence time (Jannot, Wissinger, and Lucas 2008) In some caddisfly species, growth and development decreases as density increases (Klemmer 2012). This makes understanding how elevation and time affect caddisfly population density more important because as caddisfly density increases, so does competition for resources and instances of cannibalism (Lund 2016). This is especially apparent in temporary ponds that dry during the summer. This makes sense because as density increases, there will likely be more intraspecific competition for food which would increase aggression and decrease the amount of food available to individual caddisflies. As aggression and growth rate

are negatively correlated with larval survival, adult body mass, and adult reproduction output (Jannot 2005), an increase in density could have a significant negative effect on the fitness and survival of the adult caddisflies, which could have a negative effect on their population as well as the ecosystem as a whole.

Another reason population density is an important trait to understand is because changes in population density can help us determine how caddisfly mortality rate is changing. Caddisflies in areas of high mortality will be less likely to reach adulthood and therefore have lower fitness (Lund et al. 2016). Studying changes in mortality rate can also help us understand the health of the populations as places of high mortality could imply unsuitable habitat. From my research, I found that neither time nor elevation had a significant effect on mortality. However, more data on mortality across time and elevation is needed in order to come to a conclusive decision on their relationship. To gather a good estimate on the effects of time on mortality, I think that ponds should be sampled five to six times throughout the caddisfly's development beginning at the very early instars (1st and 2nd) so that there is sufficient power to detect trends. This would also make the elevation analysis more rigorous since some ponds only had one mortality point which cannot account for variation or a possible change in time. If my data, showing that there is no relationship between mortality and time/elevation, is consistent with what this additional research might show, then my results would tell us that caddisflies experience a relatively constant rate of mortality. This would mean that there would be less pressure to develop quickly since the threat of mortality would remain constant. However, this doesn't seem likely which is why more data should be collected before a conclusion can be made.

The impact of elevation on emergence time is also important because time of emergence impacts both survivability and fecundity (Lund et al. 2016). In areas that dry quickly, having an

earlier emergence time can increase a caddisfly's chance of survival by avoiding desiccation. An earlier emergence time also implies a faster growth rate which can be helpful in avoiding predation from salamanders or beetle larvae (Greig and Wissinger 2010). However, an earlier emergence time may also have a negative impact on fecundity because of the focus of energy allocation to growth instead of reproduction (Lund et al. 2016). Because of these different factors, understanding elevation's impact on emergence time can give us insight onto the possible success of different caddisfly populations. Learning how elevation effects emergence time can also give us insight into the structure of caddisfly populations. Caddisflies that experience an earlier emergence to avoid desiccation tend to have a smaller body size which leads to a lower adult fitness (Lund et al. 2016). This could help explain why in the past, there have been larger adults found at higher elevations when compared to adults from lower elevation ponds.

From my results, there seemed to be a suggested increase in male *Asynarchus* adult body size from its lowest elevation to the lower cut, though it was not significant. If more research were to show that this trend was significant, then we could know that up to a certain elevation, *Asynarchus* adult body size would increase. This increased body size would significantly affect future populations because a caddisfly's size is highly correlated to its fecundity (Wissinger et al. 2004). Individuals with a higher fecundity can lay more eggs or have an increased number of mates which could lead to increased population density in the future, so understanding how elevation affects adult body size may give us insight to how the future population levels with change or grow. While there wasn't a significant effect of elevation on adult body size, there was a lot of variation in *Asynarchus* adult body size across elevations, and this might be in part attributed to pond type. The ponds that I collected adults from at Mexican Cut were either semi-

permeant or temporary, and the male adults from the temporary ponds were significantly smaller than those from the semi-permeant ponds. This variation could be caused by how quickly the ponds dried this summer. The effects of pond drying have shown to significantly slow growth rates and cause delayed development (Jannot 2005). This could significantly affect future populations since a later emergence across a season can cause a decrease in the average adult body size (Jannot 2005). Temperature could also explain some of the variation at Mexican Cut since studies have shown that warmer water produces fewer and smaller adult caddisflies (Jannot 2009). However, I have not yet analyzed the effect of temperature per pond, so I will have to wait to make further conclusions.

Unfortunately, I was not able to collect many adults for the upper shelf of Mexican Cut or from Galena Lake. Possibly because of this lack of data, my results for the effect of an increase in elevation from the lower cut to the upper cut were not significant. However, if further research were to show that *Asynarchus* adults were smaller at elevations above the lower cut, this finding could help us better understand what future populations may look like. Smaller body size has significant effects on the fitness of both males and females. Smaller males are less likely to procure females and mate successfully (Jannot et al. 2009). For females, a smaller body size means that an individual is more likely to lay a smaller clutch of eggs which leave the eggs more vulnerable to predation (Bovill, Downes, and Lancaster 2015). This vulnerability to predation can have disastrous results to the fitness of the female by loss of offspring as well as to the population because of a loss of recruitment. If climate change continues to force caddisflies to move into higher elevation ponds, there is the potential that their population size could be at risk.

One of the difficulties that I faced with the research for the project was that upon my arrival, I discovered that the caddisfly populations were three weeks ahead in their normal

development timeline as compared to other years (Wissinger et al. 2003). This meant that populations at lower elevations were already in their fourth or fifth instar stage. Luckily, another group of caddisfly researchers had arrived a few weeks earlier and had been able to sample many of the populations that I would be studying. This allowed me to still have around three samples of the lower elevation ponds before the caddisflies pupated even though I was only able to conduct two of those sample times myself. This could have been disastrous to my project, and in fact, a few group projects that were planned for the summer had to be edited or shifted to next summer because the caddisflies were simply too far along in their development. Thankfully, with the help of Scott Wissinger's lab group, the early development of the caddisflies didn't have too big of an impact on the structure of my project – it just meant that the first few weeks were super busy for us trying to get a first sample of the ponds before the caddisflies were too far along in development.

If I were to do this study again, I think that I would focus more specifically on one of the three species, which would allow me to sample less ponds and therefore be more thorough in my analysis. I think that it would be really interesting to study *L. picturatus* in more detail because it is one of the species that is currently shifting its range. This year was a difficult year for *L. picturatus* which is why I wasn't able to get many pupae in emergence chambers or do many density samples of ponds they were in. It would be interesting to better understand what causes shifting species to experience a good year vs a bad year and the factors behind the scenes that allow them to colonize in the first place. Invasive species on the front line of their range tend to invest significantly more energy into reproduction and dispersal than other species or even individuals of the same species that live in the center of the range (Phillips, Brown, and Shine 2010). Because of this, I would like to see if *L. picturatus* is following this trend and determine if

it invests more in dispersal or reproduction. This could give us insight into why *L. picturatus* is experiencing varied years of success at Mexican Cut. If they are investing more in reproduction, then that might suggest that their populations could have a better chance at asserting themselves, while a larger investment in dispersal might explain why their population levels are lower this year since there would be lower energy allocated to egg production.

Conclusions

As climate change continues to warm the planet, sporadic drying of ponds is expected to become a more common event (Jannot 2009). This variability in pond duration may have a significant impact on caddisfly species as a whole. As mentioned before, the effects of drying have been found to have many negative impacts on the growth and development, including emergence time, of caddisflies (Jannot 2005). A delay in emergence would leave pupae vulnerable to desiccation, and a smaller body size would have a negative impact on the adult's fitness. Drying also causes pupae to allocate less energy to reproduction (Jannot 2005). This would also decrease adult fitness. This effect may be coupled by the fact that there are minimum thresholds in size that caddisflies must reach before they pupate (Jannot 2005). This limitation may stop caddisflies from being able to adapt to climate change in their current locations and instead may force them to continue to migrate into higher elevation ponds. The problem with this is that caddisflies have a limit on the extent to which they can move into higher elevation. Once they reach the top of the mountain, there aren't many more places for them to go. Increased drying is not the only effect that climate change will have on caddisflies. As climate change continues, global temperatures are predicted to rise (Lund 2016). These rising temperatures will lead to increased water temperatures and in turn, fewer and smaller adult caddisflies (Jannot 2009). This could be devastating to future populations.

Because caddisflies provide the majority of the readily usable nutrients that are needed in high elevation, alpine systems (Klemmer et al. 2012), it is very important to understand how their population dynamics are changing since a loss of the niche they fill could impact the plants and animals that rely on them. Without the role played by caddisflies, much of the diversity and life found in high elevation pond ecosystems (predatory insects, salamanders, bird predators on pond insects) could be lost. Because these systems are so limited by the availability of nutrients, the loss of a key link in the food chain could cause a cascade of changes in how high alpine ecosystems function. By studying the effect of climate change on these foundational organisms, we may be able to determine the current and future effects that climate change is having on alpine ecosystems. Also, because caddisflies are found worldwide, their connectivity can help scientists better understand the long-reaching effects of climate change. This could help us be better prepared for the future changes we may face and could help us learn how to better protect the delicate balance that is alpine ecosystems.

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Figures

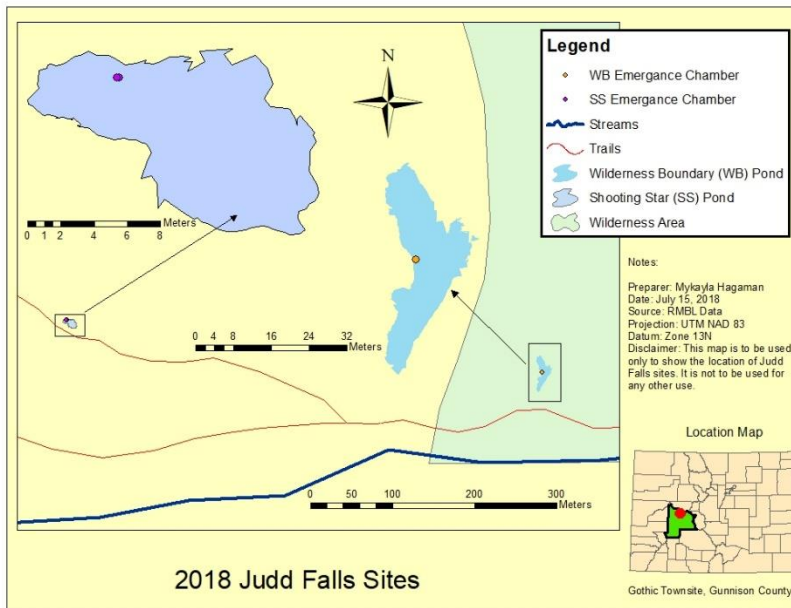


Figure 1. Map of Judd Falls Sites: Shooting Star and Wilderness Boundary. Points collected by hand-held GPS by Mykayla Hagaman.

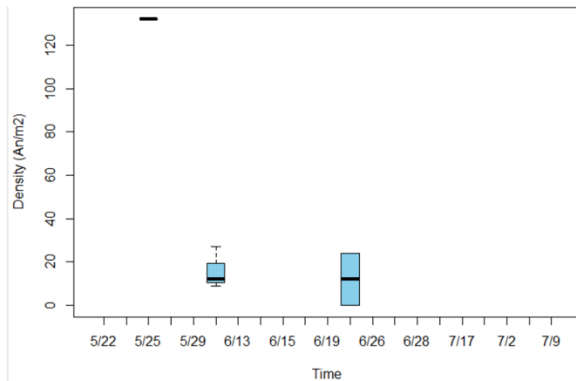


Figure 2. The changes in mean density of *Asynarchus nigriculus* per m² in pond K7 over May and June 2018. $p = 0.0078$; $r^2 = 0.93$

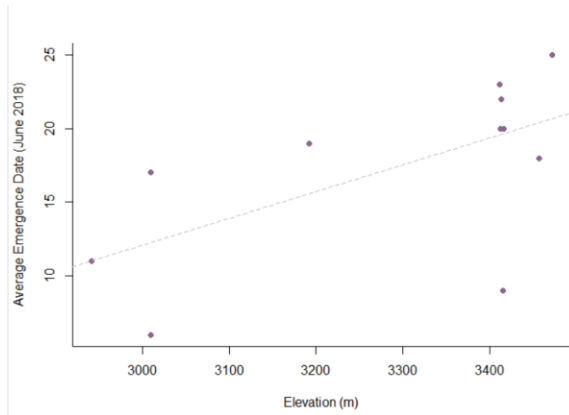


Figure 3. Mean emergence time of adult *Asynarchus nigriculus* across an elevation gradient. $p = 0.044$; $r^2 = 0.31$

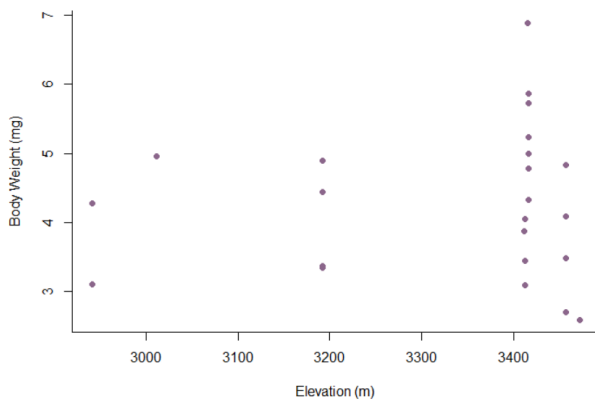


Figure 4. The changes in male *Asynarchus nigriculus* adult body weight across an elevation gradient. $p = 0.734$; $r^2 = -0.038$