

The University of Maine

DigitalCommons@UMaine

Honors College

Spring 2019

The Effect of Elevation on Factors Influencing Adult Body Size of *Asynarchus Nigirculus*

Mykayla Hagaman
University of Maine

Follow this and additional works at: <https://digitalcommons.library.umaine.edu/honors>



Part of the [Animal Sciences Commons](#)

Recommended Citation

Hagaman, Mykayla, "The Effect of Elevation on Factors Influencing Adult Body Size of *Asynarchus Nigirculus*" (2019). *Honors College*. 518.

<https://digitalcommons.library.umaine.edu/honors/518>

This Honors Thesis is brought to you for free and open access by DigitalCommons@UMaine. It has been accepted for inclusion in Honors College by an authorized administrator of DigitalCommons@UMaine. For more information, please contact um.library.technical.services@maine.edu.

THE EFFECT OF ELEVATION ON FACTORS INFLUENCING ADULT BODY SIZE
OF *ASYNARCHUS NIGRICULUS*

by

Mykayla B. Hagaman

A Thesis Submitted in Partial Fulfilment
of the Requirements for a Degree with Honors
(Wildlife Ecology)

The Honors College

University of Maine

May 2019

Advisory Committee:

Hamish Greig, Associate Professor of Stream Ecology, Advisor

Erik Blomberg, Associate Professor of Wildlife Ecology

Edith Elwood, Adjunct Assistant Professor in Sociology and Preceptor in the
Honors College

Amanda Klemmer, Assistant Research Professor of Food-web Ecology

Lindsay Seward, Instructor of Wildlife Ecology

ABSTRACT

Across the range of a species realized niche, individuals can face a range of environmental factors that change as you move from the central range towards the edge. These changes in environmental factors can have a significant impact on the fitness of an individual. In insects, one way to determine this impact is to study the difference in adult body size across the span of the species range. In western Colorado, caddisflies are the biomass dominant detritivores in alpine pond ecosystems. Caddisflies are fundamental in providing nutrients to the ecosystem because of the nutrients that they recycle as detritivores. Understanding how elevation and other factors affect caddisfly fecundity is key to understanding how climate change will affect alpine communities globally. To have a better understanding of this concept, I studied 23 ponds ranging from 2,347 to 3,505 meters in elevation and analyzed how elevation, density, sex, pond type and year affected the adult body size of the caddisfly *Asynarchus nigriculus*. I collected 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 positive effect while density had a significant negative effect on the adult body size of *Asynarchus*. The effect of pond type on *Asynarchus* body weight was almost significant in that adults were almost significantly larger in permanent ponds. Adults in 2004 were significantly larger than adults in other years, and females were significantly larger than males. These findings can help of have a better understanding of how alpine ecosystem processes may be changing in the future. In the past years, new

species of caddisflies have begun to shift their range into higher elevations. This movement could have a significant impact on the existing caddisfly populations as well as how energy is flowing through the system. This study is important because understanding how climate change affects species that are part of foundational guilds may help us better understand its far-reaching effects on ecosystems.

ACKNOWLEDGMENTS

I would like to thank my mentor Hamish Greig for his guidance and help in making this research run smoothly, Dr. Scott Wissinger for his knowledge and assistance, and Isaac Shepard for his help in collecting data and reviewing my papers. I would also like to thank Scott Wissinger's Caddisfly Crew – Grace O'Malley, Leah Franzluebbbers, Karly Studley, and Kylie Wirebach – for their assistance on collecting density data at Mexican Cut. I would like to thank RMBL for providing an amazing summer of research and the University of Maine for providing me with the funds to do this research. I would also like to thank the National Science Foundation for its support of the larger research project being run by Hamish Greig. I would like to say thank you to my thesis committee for their valuable input, suggestions, and assistance with this thesis. Also, I would like to thank the UMaine Composite Center for allowing me to use their microbalance. I would like to thank the Honors College for challenging me to do this research and for giving me the opportunity to work on this thesis instead of doing a capstone. I would like to thank everyone in the Gremmer lab for their helpful feedback. Finally, I would like to thank my family and friends, especially my mom and my brother for their love and support. I could not have done it without them. And, I would like to thank God for the strength He has given me to finish strong these four years of college and for all the amazing opportunities He has blessed me with.

TABLE OF CONTENTS

MANUSCRIPT	1
Introduction.....	1
Methods	5
Field Methods.....	5
Analysis.....	7
Results.....	7
Tables and Figures.....	10
Discussion	15
References.....	23
AUTHOR'S BIOGRAPHY	25

LIST OF FIGURES AND TABLES

Table 1	10
Table 2	10
Figure 1	11
Figure 2	12
Figure 3	13
Figure 4	14
Figure 5	15

MANUSCRIPT

Introduction

A species realized niche is the range of space where environmental conditions are optimal to allow for the survival and success of the species (Hutchinson 1957). This is also the range where the species is best fit to outcompete or coexist with other species, and future populations are able to persist (Tingley et al. 2014). Within this realized niche many species have what is called a central range within which resources are abundant enough and abiotic conditions are suitable to allow populations to increase in numbers, have higher survival, and have a greater fecundity (Geber 2008). Because of this, the density of populations found in the central range is often higher than populations on the outskirts of the range, and individuals from central populations often emigrate to outer populations and increase genetic flow between these groups (Geber 2008).

Although scientists often create models to show the effects of having central and edge populations, there has been a lack of studies on whether ecological factors and/or individual performance change in value across a species range from center to edge (Geber 2008). Across a spatial gradient, the abiotic factors that species encounter often vary from one location to another. Changes in these abiotic variables can have a significant impact on the community structure (Wissinger et al. 1999) which could in turn impact parameters of species' population dynamics such as individual growth rate, survival, and reproductive fitness (Lund 2016) that have consequences for population persistence.

A good indicator of an individual's fitness in insects is adult body size, which can be measured as the weight of an individual. In many species, adult body size is highly correlated to fecundity (Honěk 1993). Larger individuals typically lay more eggs, have more mates, or invest in larger, healthier eggs (Peckarsky et al. 2002). In many insect species, instead of investing more energy in larger eggs, females opt to invest in a greater number of eggs even if they are of a smaller size (Wissinger et al. 2004). This increased number of eggs decreases the chance of egg predation which increases offspring survival (Bovill et al. 2015). In general, females are larger than males (Wissinger et al. 2004) and one explanation for this could be that males allocate more energy into wing development rather than gametes. Though more research needs to be done on the effects of male body size on fecundity, it has been found that in some insect species, larger wings allow males to have greater success in carrying females during mating which could increase their reproduction success (Jannot, Bruneau, and Wissinger 2007)

Because of the importance of wing strength, males may invest more energy in wing muscle weight or in wing length. These factors make adult body size a good indicator of how an individual's lifestyle and the surrounding environment affect future populations through the individual's fitness. Also, for many aquatic insects, adults no longer eat once they emerge from the water (Wissinger et al. 2004). This means that all of the energy that is available for them to invest in reproduction comes from the time spent in their larval stage. Because of this, it is really the environmental factors during their larval stage that effect how much energy they have to invest in reproduction. Studying the environmental drivers of adult body size is a good way to understand how these factors also affect their fecundity and fitness.

In the West Elk Mountains located around Gothic, Colorado, many species of caddisflies occupy a range that spans a gradient of elevation and are therefore likely to exhibit variation in individual and population performance between the core and edge of this range. Caddisflies are a species of detritivores that are closely related to butterflies and these aquatic insects develop through a similar holometabolous lifecycle – the difference being that caddisflies start their lives in the water (Wissinger, Brown, and Jannot 2003). Being detritivores, caddisflies are fundamental in turning particulate nutrients into dissolved nutrients that can then be used by producers in these alpine ecosystems (Moore et al. 2004). Given that caddisflies are the biomass dominant detritivores in these nutrient-limited ponds, they are an important species to study as changes to their range and rate of nutrient excretion could impact how this ecosystem functions as a whole (Elser et al. 2009). Thus, understanding factors that influence caddisfly populations also provides insight on ecosystem-level processes.

Asynarchus nigriculus is one of the most abundant species of caddisflies to be found in this region. It is a species that is typically found in temporary ponds and is known for its fast as a way to avoid desiccation from drying ponds (Wissinger et al. 2003). Because of its quick development and abundance, researchers have often focused on this specific species. While much research has been conducted in order to understand the different population dynamics of *Asynarchus*, there has been a lack of research conducted to investigate how different factors influencing *Asynarchus nigriculus*' population dynamics change across their range. The collection of data from past years has allowed me to analyze what factors influence the adult body size of this species as well as how these factors change across the elevation gradient comprising this species' range.

In this study, my goal was to analyze how elevation, density of *Asynarchus* per pond, pond type (permanent, semi-permanent, and temporary), sex, and year affected the adult body size (measured as the total dry weight of the individual) of *Asynarchus nigriculus* individuals. For each of these factors, I looked at the direct impact on adult body size as well as how these factors influenced one another. I hypothesized that elevation would have a positive impact on adult body size up to a point and a negative effect on adult body size after this point has been exceeded. Past research has suggested that there might be an increase in adult body size to an elevation of 3400m and then a decrease in body size at elevations after this height (Greig unpublished data).

Looking at the impacts of density on adult *Asynarchus* body size, I hypothesized that a greater density of *Asynarchus* would decrease body size. With limited energy, caddisflies might have less available energy at higher densities to invest in reproduction (Klemmer et al. 2012). Since a larger body size is highly correlated with an increase in fecundity (Honěk 1993), I predicted that this relationship would be shown through a decrease in body size. Also, when densities are higher, *Asynarchus* caddisflies are more likely to participate in cannibalism (Lund 2016). This could increase the need to invest in aggression in order to avoid being eaten and could also increase stress levels. These increased demands for energy combined with the decreased amount of available food could have a negative effect on their growth rate and fecundity (Jannot 2005).

I hypothesized that adults from permanent or semi-permanent ponds would be larger than adults from temporary ponds. Temporary ponds are ponds that typically dry each year and are refilled in the spring by snowmelt, while semi-permanent ponds only dry up every couple of years (Wissinger et al. 1999). Because of this, semi-permanent

ponds are more likely to be filled with water for a longer time than temporary ponds and therefore enable a longer period of resource acquisition during the larval stage. Because of their short duration, I predicted that temporary ponds would have a shallower average water depth which would result in an increase in temperature. If a deeper, permanent pond has smaller surface area to volume ratio than a shallow, temporary pond, then, all else held equal, the temperature in the deeper pond should be lower (Xin and Kinouchi 2013). Warmer water temperatures in temporary ponds could cause caddisflies found in these ponds to be smaller. Experiments that have manipulated the temperature of the water during caddisfly development have shown warmer water typically decreases the adult body size of caddisflies (Jannot 2009).

Methods

Field Methods

To study the factors influencing adult body size of *Asynarchus*, I examined adults from 2004, 2006, 2017, and 2018. This data was all collected from ponds surrounding the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado during the summer of the specified years. Data from 2004, 2006, and 2017 was collected by – collaborators Hamish Greig and Scott Wissinger. During the summer of 2018, I sampled 12 ponds found near and around Gothic where *Asynarchus* was present. These ponds were in an elevation range of 2,877 to 3,472 meters and were easy to access. The highest elevation ponds were in the Mexican Cut Nature Preserve where around 60 ponds were divided into two elevational benches separated by ~200 m (Wissinger et al. 1999). The ponds used in the study were a mixture of temporary, semi-permanent, and permanent ponds.

Data loggers were placed in middle of ponds and would collect data on the temperature and depth of the water every two hours. Data loggers were placed in seven of the ponds that were used in this study. Data loggers were checked at least once a year when data was collected. There were no data loggers in ponds during 2004 or 2006 because they were not available at that time.

At each pond, I conducted between two and four replicate 1/3 m² D-net sweeps (depending on pond size and accessibility) in order quantify the density of the caddisfly species found in that pond. Each caddisfly found was categorized according to species and larval instar. If there was a question on determining species or instar size, voucher individuals (1-3) were brought back to the lab where they were identified. This sampling method was repeated typically 3 times over the larval life history of these species to calculate how caddisfly population density changes over time. These second and third samples were usually taken two or three weeks after the first sample.

Caddisflies nearing or in their pupae stage were placed inside emergence chambers in the ponds and reared to adulthood. 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 placed in a freezer to be 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 calculated the density of caddisflies per m² by adding the total number of caddisflies counted for each 1/3m² sweep and multiplying by 3. Adult body size was calculated by adding the individual's thorax and abdomen weight. Adults from 2004, 2006, and 2017 were collected and analyzed in a similar manner.

Analysis

Adult data from 2004, 2006, 2017, and 2018 was compiled into a single data set, and density for each pond, along with information from the data loggers, were added. Male and female mean body size was calculated for each, and ponds with 3 or less individuals for either males or females were not included in the analysis. These means were used as my unit of replication. Density was not collected for every pond in every year, so the data was also subset to only include ponds where density had been calculated. I ran linear regressions for multiple models to see how different combinations of factors effected adult body size. Predictor variables included elevation, elevation², larval density, pond type, sex, and year. In order to determine the best fitting model, I ran an AICc test. This allowed me to account for small sample sizes in the pond means.

Results

Across the four years, 436 caddisflies were analyzed, and 39 means from 23 ponds (some ponds had both male and female samples) were included in the analysis. The model that best fit the data was one of the most complex models (model 38) that included the added effects of elevation, sex, year, density, and the quadratic of elevation. This model had an AICc weight of 143, which was the lowest AIC score (Table 1). However, another model, which included pond type, had an AICc score that was less than 2 away from model 38 – model 39 which had an AICc score of 143.6 (Table 1). Because

these two models have AICc scores that are less than 2 apart, I cannot conclude that they are significantly different in how well they fit the data. However, model 38 is the best fit for the data 52 percent of the time whereas model 39 is the best fit model only 39 percent of the time based off of their weighted AICc scores (Table 1).

In model 39, elevation had a significant effect on adult body size in that when elevation increased, adult body size increased ($p=0.03$) (Table 2 and Figure 1). Sex also had a significant effect in that males were significantly smaller than females ($p<0.0001$) (Table 2 and Figure 2). Adults in 2004 were significantly larger than adults in 2006, 2017, and 2018 ($p<0.0001$) (Table 2 and Figure 3). As density increased, adult body size decreased ($p=0.02$) (Table 2 and Figure 4). The non-linear effect of elevation did not have a significant impact on adult body size ($p=0.24$), however, its effect did help explain some of the variance in the data as its inclusion in model 39 (AICc = 143) better fit the data than model 30 which was the same but without the effect of elevation² (AICc = 149.2) (Table 2 and Table 1). Pond type had an almost significant effect where adults in semi-permanent ponds were smaller than adults in permanent ponds, and adults in temporary ponds were larger than adults in permanent ponds ($p=0.07$) (Table 2). I used the p-values from model 39 instead of 38 because, since they had similar levels of support, 39 gives a better overall view of the factors since it includes pond type.

Elevation did not have a significant impact on caddisfly density, water temperature, or water depth (regressions: $p=0.24$, 0.79 , and 0.23 respectively). Pond type did not have a significant effect on density ($p=0.28$). Pond type did have a significant relationship with water depth in that temporary ponds were shallower than semi-permanent ponds ($p=0.027$), but pond type did not have a significant impact on water temperature ($p=0.28$). Caddisfly density varied significantly from year to year ($p=0.04$) whereby the density of caddisflies in 2004 was significantly less than the density of caddisflies in 2006 or 2017 ($p=0.008$ and 0.03 respectively).

Tables and Figures

Table 1. AIC selection of models predicting the adult body size of *Asynarchus nigriculus*. Factors included in each model are listed, and the final weighted AICc values are given. Data was collected during the summers of 2004, 2006, 2017, and 2018 from ponds around Gothic, Colorado.

model	factors	df	logLik	AICc	delta AICc	weighted AICc
38	elevation+ elevation ² + year + sex + density	9	59.388	143	0	0.527
39	elevation+ elevation ² + year + sex + density + pond type	11	55.887	143.6	0.57	0.397
39a	log(elevation) + year + sex + density + pond type	10	60.462	148.8	5.8	0.029
30	elevation + year + sex + density + pond type	10	60.669	149.2	6.21	0.024
36	elevation+ elevation ² *year + sex + density	12	57.233	150.5	7.48	0.012
37	elevation+ elevation ² *year + sex + density + pond type	14	53.233	152	8.98	0.006
35	elevation+ elevation ² *year + sex	11	60.253	152.3	9.3	0.005
32a	log(elevation) + sex	4	78.445	166.1	23.09	0
33	elevation + sex	4	78.468	166.1	23.13	0
34	elevation + sex + elevation ²	5	78.160	168.1	23.16	0
31	elevation	3	84.317	175.3	32.34	0
32	elevation+elevation ²	4	84.264	177.7	34.72	0

Table 2. The parameters included in the best model of adult body size of *Asynarchus nigriculus*. The factor's relationship effect on the data, the degrees freedom, sum of squares, mean squares, F value, and the p-value of this relationship. Data was collected during the summers of 2004, 2006, 2017, and 2018 from ponds around Gothic, Colorado.

Factor	Relationship	Degrees Freedom	Sum of Squares	Mean Squares	F value	p value
elevation	0.27	1	7.18	7.18	5.19	0.03
sex (male to female)	-2.02	1	44.67	44.67	32.30	<0.0001
year (2006 to 2004)	-2.49	3	69.62	23.21	16.78	<0.0001
year (2017 to 2004)	-2.29	3	69.62	23.21	16.78	<0.0001
year (2018 to 2004)	-3.64	3	69.62	23.21	16.78	<0.0001
density	-0.0082	1	8.08	8.08	5.83	0.02
pond type (semi to permanent)	-0.13	2	7.89	3.94	2.85	0.07
pond type (temporary to permanent)	1.12	2	7.89	3.94	2.85	0.07
elevation^2	-0.000041	1	2.00	2.00	1.45	0.24

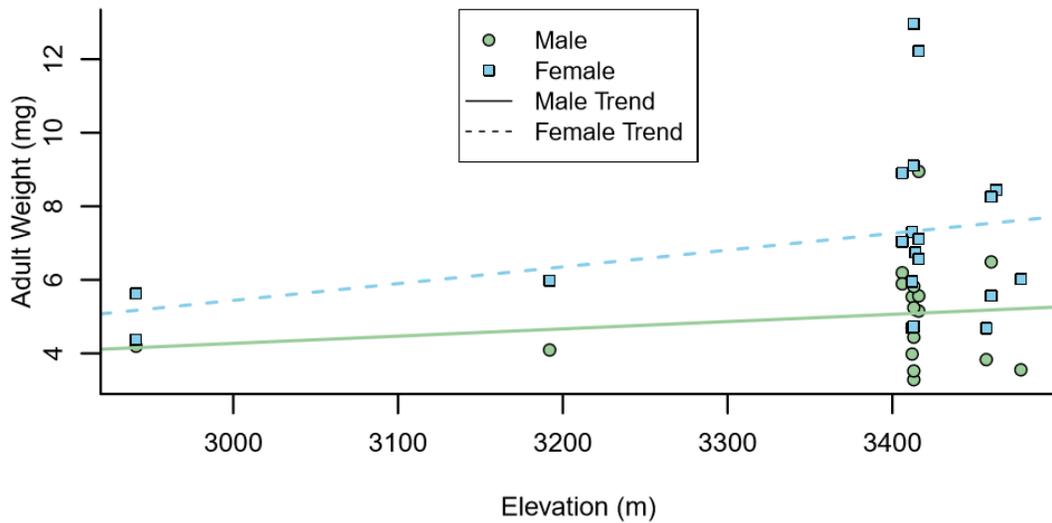


Figure 1. The effect of elevation, measured in meters, on mean *Asynarchus nigriculus* adult weight per pond, which is measured in mg. This shows a positive relationship between elevation and adult weight. Data was collected during the summers of 2004, 2006, 2017, and 2018 from ponds around Gothic, Colorado.

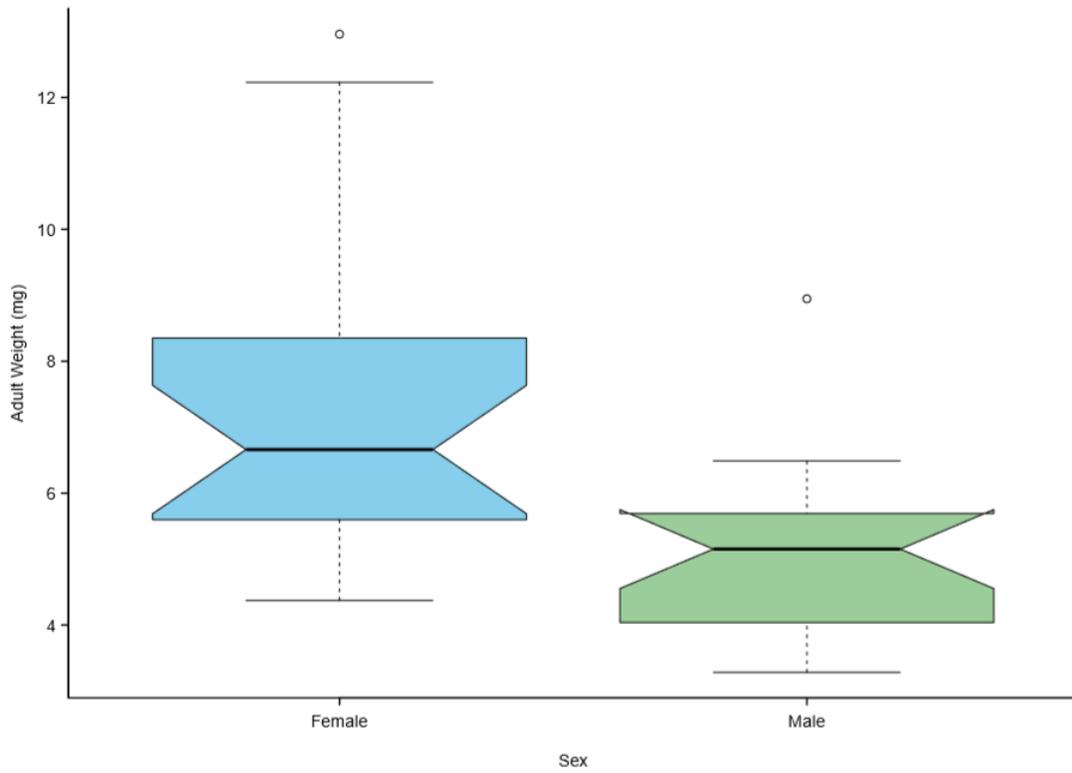


Figure 2. The effect of sex on *Asynarchus nigriculus* adult body weight, which is measured in mg. Data was collected during the summers of 2004, 2006, 2017, and 2018 from ponds around Gothic, Colorado.

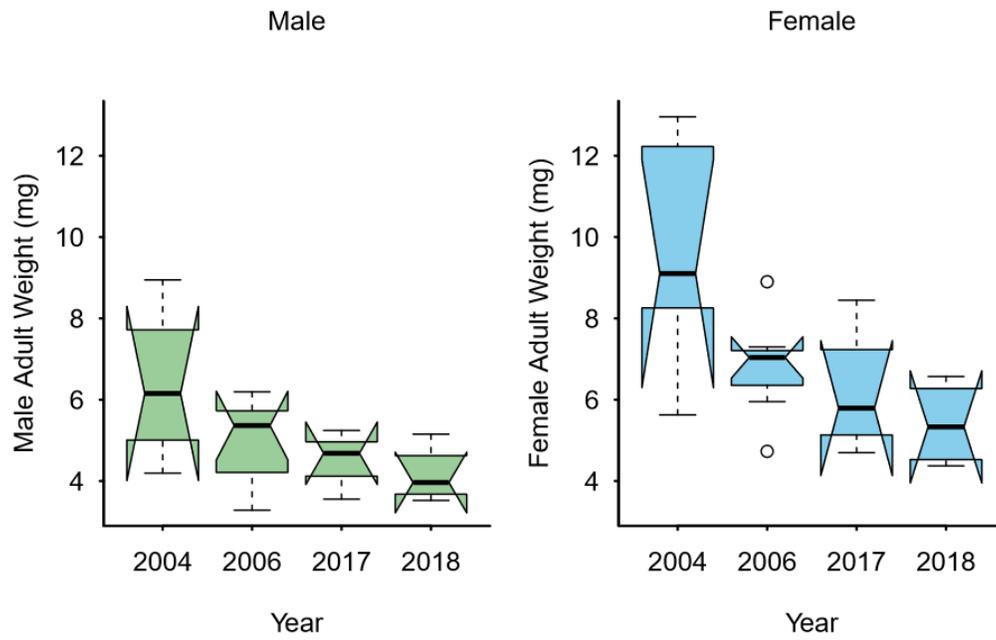


Figure 3. The effect of year on *Asynarchus nigriculus* adult body weight, which is measured in mg. Data was collected during the summers of 2004, 2006, 2017, and 2018 from ponds around Gothic, Colorado.

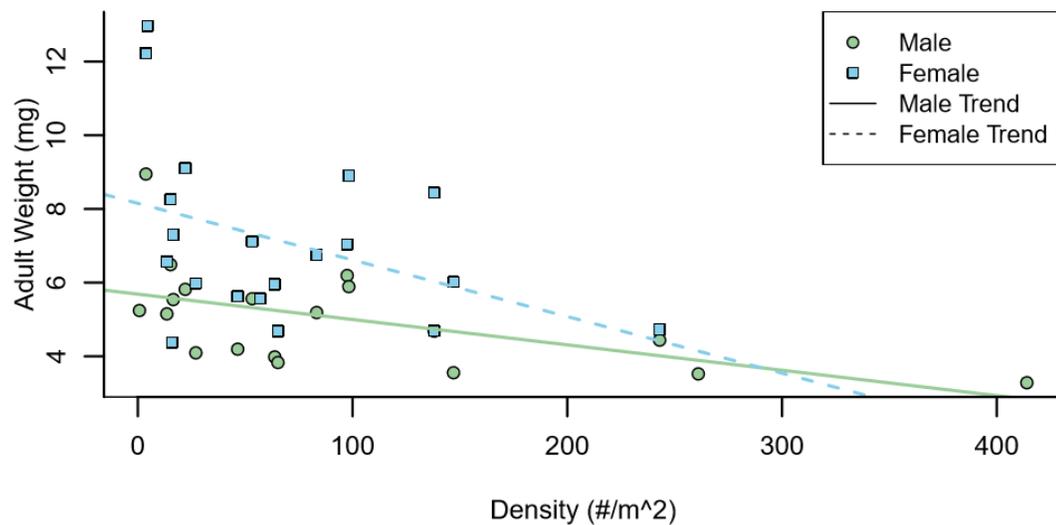


Figure 4. The effect of density, measured in the number of *Asynarchus nigriculus* per m², on *Asynarchus nigriculus* adult body weight, which is measured in mg. This figure shows a negative relationship between density and body weight. Data was collected during the summers of 2004, 2006, 2017, and 2018 from ponds around Gothic, Colorado.

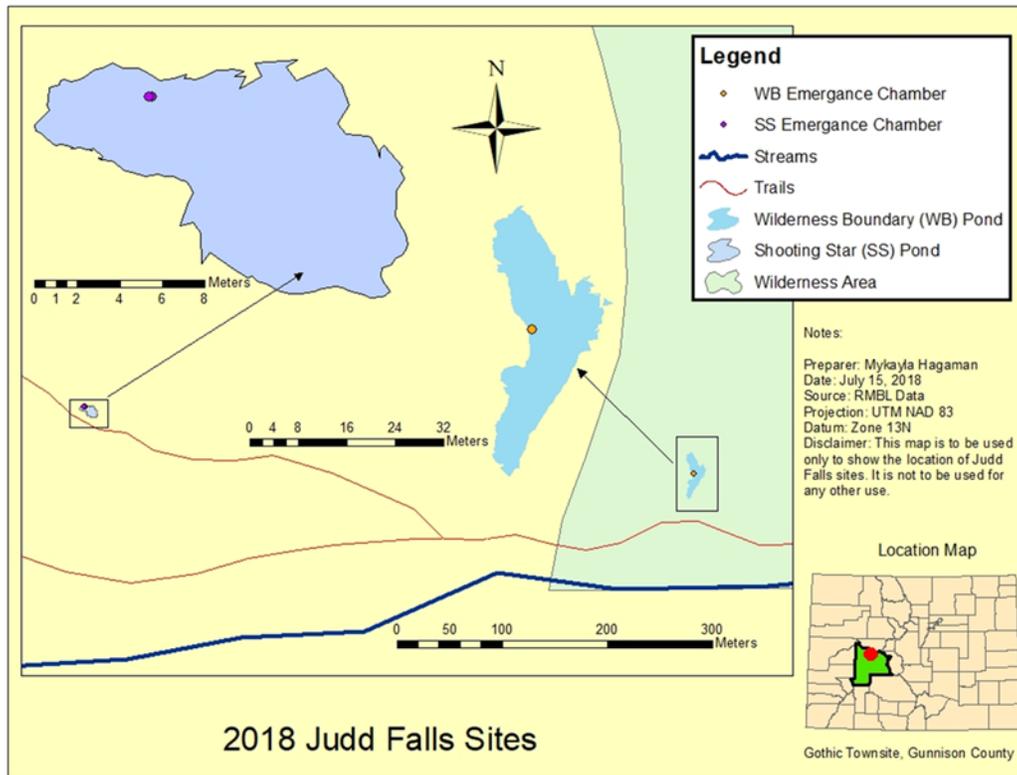


Figure 5. GIS map of ponds Shooting Star and Wilderness Boundary. Location of emergence chambers were also marked on the map. GID data was collected during the summer of 2018 in Gothic, Colorado.

Discussion

As mentioned before, scientists have been able to better understand and interpret the relationship between body size and fecundity, that body size is a good indicator of an individual's fitness (Wissinger et al. 2004). However, for caddisflies, there is a lack of knowledge on what environmental factors have a significant impact on adult body size, and how they affect adult body size. This research looked at how a selection of important factors, factors that either changed across the population's landscape or have been shown to effect growth rates in laboratory experiments, effect the adult body size of *Asynarchus nigriculus* in their natural range. I was specifically interested in how elevation, sex, year,

density, elevation², and pond type affect adult body size, and I found that elevation, sex, year, and density all have a significant effect, while elevation² and pond type are useful to help explain variation in the data.

Over the past two decades, scientists have discovered that some species of caddisflies are experiencing spatial disequilibrium which occurs when environmental conditions allow for a species to expand their range into new territory (Phillips, Brown, and Shine 2010). This is evident in the elevational range expansion of several species of caddisflies in Colorado. For many years, *Asynarchus* has been one of the dominant species of caddisfly in subalpine ponds around Gothic, Colorado (Wissinger et al. 1999), (Wissinger, Brown, and Jannot 2003). 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). And both have since become established (personal observation). Although *Asynarchus*'s range is not currently shifting, the movement of other species into higher elevation could impact *Asynarchus* populations and the interaction between different caddisfly species which could change how this foundational guild interacts with its environment. If other caddisfly species increase in body size as elevation increases, as seen in *Asynarchus* populations, this could increase their fecundity and possibly help them to persist in their new environment. This impact could be made possible if the change in elevation creates a gradient of habitat where other factors, such as temperature, detritus input, and timing of snow melt, may also be changing. More research should be done to test more specifically these factors change with elevation.

The effects of sex and density on adult caddisflies are consistent with other research that has been done in the past (Wissinger et al. 2004). Typically, females are larger than males for many insect species, including caddisflies (Wissinger et al. 2004). It is not surprising that sexual dimorphism between males and females explains much of the variation in the body size data set. Past research has also shown that caddisflies tend to have a decreased growth rate and therefore a smaller body size in higher densities (Klemmer 2012). This occurs because at higher densities, detrital resources become limiting factors, resulting in an increase in competition and reduced larval resource acquisition (Klemmer 2012). This could help explain why caddisflies in 2004 were larger on average. The density of caddisflies that year were significantly lower than in 2006 or 2017 ($p=0.04$), which could have allowed the larvae to acquire more resources and grow to a larger size. This impact of density could affect future populations as the introduction of new species and populations of caddisflies could increase the density in some ponds and therefore increase competition between individuals. While we don't have substantial evidence on how interspecific competition varies with density for *Asynarchus*, preliminary evidence from a study being conducted by Isaac Shepard, a PhD student advised by Hamish Greig, suggests that interspecific competition may be weaker than intraspecific competition, a concept that matches the expectations mentioned in broader competition literature. Understanding how these changes in different types of competition could affect future populations of *Asynarchus* can help us be better prepared for these changes in the future.

Even though the quadratic effect of elevation wasn't significant, it did help explain some of the variation in the data. Combining this with the positive effect

elevation had on adult body weight can give us a good picture of how adult body size changes across the elevational gradient. In general, as you travel up in elevation, *Asynarchus* adults grow larger in size. However, there is a suggestion that once you pass a certain elevation, adult body size decreases. One possible explanation for this change could be the quality of detritus across elevations. Visual change in the vegetation as elevation increased were common in this study area. Ponds at lower elevation varied in vegetation, from low, shrubby willows to forests of deciduous aspens (*Populus tremuloides*) or coniferous fir and spruce (*Picea pungens*) trees (Wissinger et al. 1999). However, as elevation increases, the forests shifted into a more conifer-dominated state, until there were no trees, and eventually a limited amount of grass or shrubs. This change in detritus input could affect the energy that is being transferred to caddisflies if some types of vegetation are more nutrient rich. This could help explain the possible decrease of body size at the highest elevations since a decrease in detritus would limit the resources available to larvae (Batzer et al. 2014).

Though elevation did not significantly impact water temperature in this study, more data from ponds at lower elevations should be collected in order to have a better estimate of the relationship. If water temperature decreased as elevation increased, this could help explain why adults at higher elevations are larger since adults raised in cooler water tend to be larger than those in warmer water (Jannot 2009). Another explanation for the increase in body size across elevation could be the amount of interspecific competition. Since *Asynarchus* reaches the end of its range at lower elevations (Wissinger, Brown, and Jannot 2003), it may experience a greater amount of competition with other species that are better adapted for lower elevation ponds. Also, since species

who are shifting into higher elevations were already established at lower elevations before they moved into higher elevations, if interspecific competition is affecting *Asynarchus* populations at lower elevations, these migrating species could significantly impact adults in higher elevation ponds. For these reasons, researching more why *Asynarchus* adults increase in size across elevations could help us have a better idea of what populations will look like in the future since body size is correlated to fecundity (Honěk 1993).

I think that in some years, like 2018, the non-linear effect of elevation had a stronger influence than in other years. In order to determine if adult body size does decrease after a certain elevation, more research needs to be done that focuses on collecting an even spread of adults from across the elevation gradient, specifically from some of the higher elevation ponds – something that is logistically challenging. If there is a decrease in adults past a certain elevation, this could affect future populations because of climate change. Already, species of caddisflies have begun to move into higher elevation areas (Wissinger et al. 2016), if this shift continues, caddisflies may continue to move to higher elevations in the future. If at some point, the environment in higher elevation areas begins to have a negative impact on caddisflies, this could cause problems to future generations if the range of suitable habitat, or their realized niche, begins to shrink.

The effect of pond type was almost significant in our more complex model (0.07) (Table 2) and it contributed to explaining the variation in the body mass since its inclusion made it the best fitting model 40 percent of the time (Table 1). I was surprised to find that adults in temporary ponds were larger than permanent ponds (Table 2),

although this does makes sense as temporary ponds are *Asynarchus*' stronghold (Wissinger, Brown, and Jannot 2003). In order to get a better understanding of this relationship between different pond types, a greater number of permanent ponds should be sampled with the quantity and quality of detritus being considered. This may be challenging, though, since it is rare that *Asynarchus* larvae will survive to adulthood in permanent ponds because of predation (Wissinger, Brown, and Jannot 2003).

The fact that temporary ponds were found to have a significantly lower water depth (0.027) could affect future caddisfly populations. As climate change continues, global temperatures are predicted to rise (Lund 2016). These rising temperatures will lead to increased water temperatures (Clow 2010), and in turn, could lead to fewer and smaller adult caddisflies (Jannot 2009). This could be devastating to future populations. With this increase in temperature, sporadic drying of ponds is expected to become a more common event (Jannot 2009). This variability in pond duration may affect caddisfly species as a whole, and we know that whole cohorts of *Asynarchus* in temporary ponds die before pupation in exceptionally dry years. Drying also causes pupae to allocate less energy to reproduction (Jannot 2005) which might 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).

One aspect that was not quantified in this study was the quantity and quality of detritus in these ponds. Because caddisflies acquire the energy for reproduction during their larval stage (Wissinger et al. 2004), the detritus found in their ponds can be a determining factor of their fecundity and fitness. For this reason, studying the input in detritus across the elevational gradient could help us better understand why caddisfly

body weight changes across elevation. I would also collect more data on characteristics of the water in the ponds, such as water chemistry, temperature, and depth. I was able to collect some preliminary data on temperature and depth, but it would be helpful to have this information on more of the ponds.

Species that are experiencing a shift in their range tend to increase their allocation of towards reproduction and distribution (Phillips, Brown, and Shine 2010). This allows them to be able to travel further into newly opened territory and increases the likely hood of their survival and persistence (Phillips, Brown, and Shine 2010). As caddisfly species begin to move into new elevations, it is important to understand how their allocation of energy is changing as an increase in reproduction and distribution could help us understand what future populations may look like. If individuals invest more in distribution, this decision would help us to possibly predict that the species range would continue to advance at an increasing rate as the highest dispersers would mate and increase dispersal abilities even further (Phillips, Brown, and Shine 2010). These individuals on the leading edge often also experience exponential population growth as they invest more in reproduction and are freed from density-dependent growth (Phillips, Brown, and Shine 2010). However, as allocation of energy to these demographics increases, investments to other population dynamics, (growth, survival, or aggression being possible options) will be decreased (Phillips, Brown, and Shine 2010). With increasing global temperatures, it is important to know where future populations of caddisflies will be found and what those populations will look like in order to properly conserve them.

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. In these shallow, standing water habitats, detritus is often the primary source of energy (Batzer et al. 2014). Furthermore, the majority of energy found within the surrounding plants is not passed on to other species through herbivores but enters the food chain in the form of detritus (Moore et al. 2004). Often, the energy moving from detritus through the food web can equal or even exceed the energy moving through herbivores (Moore et al. 2004). Because of this, detritivores play a key role in the recycling of not just nutrients but also energy back into their ecosystem. Since 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 (Balik et al. 2018). 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, understanding how caddisflies are being affected in one area may help scientists better understand the long-reaching effects of climate change if similar shifts are happening in other areas of *Asynarchus*' geographic distribution.

References

- Balik, J.A., B.W. Taylor, S.E. Washko, and S.A. Wissinger. 2018. High interspecific variation in nutrient excretion within a guild of closely related caddisfly species. *Ecosphere* 9:1-17.
- Batzer, D. P., R. Cooper, and S. A. Wissinger 2014. Wetland animal ecology. Pages 242-284 in D. P. Batzer and R. R. Sharitz (Editors). *Ecology of freshwater and estuarine wetlands*. University of California Press, Berkeley, CA.
- Bovill, W.D., Downes, B.J., and Lancaster, J. (2015). Caddisfly egg mass morphology mediates egg predation: Potential cost to individuals and populations. *Freshwater Biology* 60, 360-372.
- Clow, D.W. 2010. Changes in the timing of snowmelt and streamflow in Colorado: a response to recent warming. *Journal of Climate* 23, 2293-2306.
- Elser, J.J., Andersen, T., Baron, J.S., Bergstrom, A.K., Jansson, M., Kyle M., Nydick K.R., Steger L., and Hessen, D.O. (2009). Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science* 326:835-837.
- Geber, M. (2008). To the edge: Studies of species' range limits. *The New Phytologist*, 178(2), 228-230.
- Greig, H. (2018). *REU supplement proposal for 2018*.
- Honěk, A. (1993). Intraspecific Variation in Body Size and Fecundity in Insects: A General Relationship. *Oikos*, 66(3), 483-492. doi:10.2307/3544943
- Hutchinson, G. E. (1957). Cold spring harbor symposium on quantitative biology. *Concluding remarks*, 22, 415-427.
- Jannot, J.E. (2005). Developmental thresholds, life history trade-offs, and resource allocation in wetland caddisflies. *Purdue University*.
- Jannot, J.E. (2009). Life history plasticity and fitness in a caddisfly in response to proximate cues of pond-drying. *Oecologia* 161(2), 267-277.
- Jannot, J.E., Bruneau, E., and Wissinger, S.A., (2007). Effects of larval energetic resources on life history and adult allocation patterns in a caddisfly (Trichoptera: Phryganeidae). *Ecological Entomology* 32, 376-383.
- Klemmer, A.J., Wissinger, S.A., Greig, H.S., and Ostrofsky, M.L. (2012). Nonlinear effects of consumer density on multiple ecosystem processes. *Journal of Animal Ecology*, 81(4): 770-780.
- Lund, J.O., Wissinger, S.A., and Peckarsky, B.L. (2016). Caddisfly behavioral responses to drying cues in temporary ponds: implications for effects of climate change. *Freshwater Science*, 35(2), 619-630.

- Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, Q. Dong, P.C., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J., and Wall, D.H. (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters* 7:584-600.
- Peckarsky, B. L., et al. (2002). "Swarming and mating behavior of a mayfly *Baetis bicaudatus* suggest stabilizing selection for male body size." *Behavioral Ecology and Sociobiology* 51(6): 530-537.
- Phillips, B.L., Brown, G.P., and Shine, R. (2010). Life-history evolution in range-shifting populations. *Ecology* 91(6) 1617-1627.
- Tingley, R., Vallinono, M., Sequeira, F., and Kearney, M.R. (2014). Realized niche shift during a global biological invasion. *Proceedings of the National Academy of Sciences of the United States of America* 111 (28), 10233-10238. Retrieved from <http://www.pnas.org.prxy4.ursus.maine.edu/content/111/28/10233>
- Wissinger, S. A., et al. (1999). Subalpine wetlands in Colorado. Habitat permanence, salamander predation, and invertebrate communities. *Invertebrates in freshwater wetlands of North America: ecology and management*. D. P. Batzer, R. B. Rader and S. A. Wissinger. New York, USA, Willey: 757-790.
- Wissinger, S.A., Brown, W.S., and Jannot, J.E. (2003). Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorado (U.S.A). *Freshwater Biology*, 48, 255-270.
- Wissinger, S., Steinmetz, J., Alexander, J.S., and Brown, W. (2004). Larval cannibalism, time constraints, and adult fitness in caddisflies that inhabit temporary wetlands. *Oecologia*, 138, 39-47.
- Wissinger, S.A., B. Oertli, and V. Rosset. (2016). Invertebrate communities in alpine ponds IN: Batzer, D.P, and D. Boix (ed.) *Invertebrates in Freshwater Wetlands: An International Perspective on Their Ecology*. University of California Press.
- Xin, Z., and Kinouchi, T. (2013). Analysis of stream temperature and heat budget in an urban river under strong anthropogenic influences. *Journal of Hydrology* 489, 16-25. Retrieved from https://ac-els-cdn-com.prxy4.ursus.maine.edu/S0022169413001790/1-s2.0-S0022169413001790-main.pdf?_tid=9cc6d16e-ae48-4864-883d-870a8bde26c6&acdnat=1543345597_1990f7c38bb868b353932c20e8fffece

AUTHOR'S BIOGRAPHY

Mykayla Hagan was born on April 25, 1997, in Fairfield, Ohio. However, feeling that her true home was in Pickerington, Ohio, she moved there at the young age of three. Her life there was simple. It was easy to blend in. However, that could last for only so long. She was soon selected by the mysterious corporation known simply as the cake decorators, and they soon covertly began their brain-washing process. Mykayla's family tried to intervene by taking her on trips around the country, specifically to Yellowstone, in an attempt to show her that there was more to life than frosting. She became briefly conscious of reality after encountering a wolf in the park. However, the pull of the cake decorators was strong, and it would be another year before she was finally free of their grasp. Their first mistake was convincing her to get a job as a cake decorator working at Cold Stone. Failing at its intended effect of further brainwashing, this decision snapped Mykayla back into reality as she realized that she couldn't stand to work with these people, meeting their demands which were never satisfied.

Coming to this conclusion, Mykayla knew it was no longer safe to remain in her hometown as the cake decorators would surely come looking for her. So, remembering her friend the wolf, she made the decision to follow a new path in life and pursue a career working for animals (the least likely place the cake decorators would think to look for her). Yet, she could never be fully free from their clasp, as her lingering enjoyment for the Great British Baking Show can attest to.

Moving to Maine, Mykayla found that she was excited, yet unprepared for where this path would take her. As she traveled along her new journey, she had many diverse

adventures – returning to Yellowstone to reestablish her connection with the wolves, a daring escape from an island of infestation and mounting stress, surviving the swamp of seeping doom and planetary extinction, and finally arriving in the mountains of Colorado where she discovered friendship, hope, and managed to survive the stealthy hunt of the mountain lion. But these are stories for another day.

All in all, Mykayla can look back pleased and content with where her life has taken her. As she prepares for the adventures and challenges to come, she knows that she will succeed with the help of the friends she has found along the way.