The Evolution of Cannibalism in Lake Minnewaska

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Abstract

Cannibalism is the evolutionary anomaly where an organism consumes individuals of the same species. Through literature analysis, the conditions that foster cannibalism are introduced and explained with principles of evolution. The different types of cannibalism are identified with examples that cover a variety of invertebrate and vertebrate organisms. The cultural and biological evolution of cannibalistic practices observed in humans are also discussed. The scope of cannibalism and its adaptations are narrowed by case studies of fish, and specifically the largemouth bass. An experimental design was proposed by the Richardson lab in order to determine the health of largemouth bass in the New York lake, Lake Minnewaska. The largemouth bass were the only fish species to inhabit Lake Minnewaska since 2014, so the health of this population was determined from data acquired by mark and recapture, scale analysis, and standard measurement techniques. The relatively stable population trends and below average growth of the largemouth bass were consistent with the literature on cannibalistic largemouth bass and supported the hypothesis that cannibalism was an evolutionarily adaptive means of survival for the largemouth bass in Lake Minnewaska. The evolution of cannibalistic practices under starvation environments was exemplified in the largemouth bass population of Lake Minnewaska and may be used to understand the state of natural ecosystems.

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Introduction

The predation of intraspecifics, or cannibalism, is a relatively taboo area of study (Fox, 1975). The idea of consuming the flesh of one's own species in order to improve one's own chance of survival does not sit right with our altruistic human nature. Despite the many potential deleterious effects of cannibalism on individual organisms and species alike, cannibalism is still observed in a variety of circumstances today, even in local NY environments. The underlying motivations for cannibalism can be traced through evolutionary history. Through the analysis of cannibalism research and implementation of evolutionary theory, the adaptive mechanisms of cannibalism have been demonstrated in Lake Minnewaska.

Hamilton's Rule & Cannibalism

Altruism is explained by Hamilton's theory of *inclusive fitness,* or the idea that the direct fitness of an individual's reproductive success to pass on alleles, paired with the individual's indirect fitness from the reproductive success of close kin with similar genes, both contribute to an individual's total fitness level. Nepotism or altruism directed towards kin, is especially important in species with sterile or subfertile populations as observed in ants, bees, naked mole rats, and many other organisms, because their inclusive fitness, in terms of genetic transference, is entirely dependent on the success of their close kin (Pfennig, 1997).

The conceptualized interpretation of Hamilton's mathematical formula for altruism is that when the relatedness between conspecifics, multiplied by the consequential births due to an

altruistic act, is greater than the cost to the actor of altruism, then the individual will perform an altruistic act (Pfennig, 1997). This theory is also known as *kin selection* and relies on the assumption that organisms are able to identify their conspecifics and kin (Pfennig, 1997). Hamilton's theory can be used to explain cannibalism with the rearranged formula where r is the relatedness, V is the fitness measured in potential offspring produced by the victim, and (C - C') is the difference in reproductive success or offspring produced by the cannibal post cannibalizing. When V < (C - C') and r > V / (C - C'), cannibalism is most favorable and expected to occur. Pfennig (1997) notes that cooperation is almost always met according to empirical data. Under the circumstances that the victim cannot reproduce, V=0, cannibalism will be favored and this may induce sacrificial cannibalism in accordance with Hamilton's mathematical rule for kin selection and inclusive fitness (Pfennig, 1997).

Hamilton's theories of kin selection support the common trend that organisms with the ability to recognize kin will likely cannibalize non-kin or heterospecifics before kin in order to increase their genetic influence on future generations (Pfennig, 1997). Even with Hamilton's theory emphasizing altruistic behavior, this does not rule out the possibility for kin cannibalism. As Pfennig (1997) speculates of both vertebrates and invertebrates, kin selected cannibalism may provide an organism more benefits than costs in certain situations. Even sacrificial cannibalism may be practiced in order to indirectly improve their inclusive fitness by aiding in the survival and reproduction of close kin (Pfennig, 1997).

Cannibalism of Non-Kin

The different classifications of cannibalism are the product of the species behaviors and environmental conditions. The first distinguishing method of cannibalism is kin versus non-kin cannibalism. Non-kin cannibalism is most directly beneficial to the cannibal, as there is less genetic similarity and therefore a lesser indirect harm on an individual's fitness in passing on genes to the next generation (Pfennig, 1997). An example of this form of cannibalism is found in tiger salamanders. There are different morphs of tiger salamanders: a regular morph and a cannibalistic morph which is induced in crowded population environments. Both morphs are able to identify kin, and as a result, the cannibalistic tiger salamanders will consume non-relatives before kin, even opting to save a second cousin of ⅛ relatedness when non-kin are available (Pfennig, 1997). Another rare form of non-kin cannibalism is sexual cannibalism, or a cannibalistic act post copulation, expected to aid in fecundity (Birkhead, 1988). This form of cannibalism is sacrificial for a male when the likelihood of copulating with more females is low. The primary case study of sexual cannibalism behavior is of the praying mantis. In order to aid in female survival and fecundity post-copulation, the female praying mantis will decapitate and consume the male's head (Birkhead, 1988).

Cannibalism of Kin

Heterospecific cannibalism is often favorable to conspecific cannibalism, or cannibalism of close kin, in many organisms. One explanation for this observation is the genetic component

or inclusive fitness supported by Hamilton's mathematical rule. When an organism is in a starvation state with equal access to both kin and non-kin victims, the cannibal will likely prey on the heterospecific. Pfennig explains this logic by comparing intraspecies cannibalism to the redistribution of muscle tissue throughout the body in order to acquire needed protein to ensure the survival of the germline while in starvation state as a form of "self-cannibalism" (Pfennig, 1997). When intraspecific cannibalism occurs, there is a redistribution of energy between closely related cannibal and victim which secures the reproduction of the cannibal. Contrastingly, inter-species cannibalism is the cannibalism of non-kin and isn't based on cooperation of the species as a unit, but rather conflict.

Sibling Cannibalism

Kin-based or intraspecific cannibalism is the predation of an organism of close genetic similarity or kin (Fox, 1975). One form of kin cannibalism is observed between siblings. In Eurasian perch and European seabass, partial cannibalism is common at the larval stage when there is a variation in sibling sizes. This cannibalism is classified by the method of cannibalism. Type one is when the cannibal attacks from the victim's tail end, and is indicative of a slight difference in larval size. Type two is a cannibalistic attack from the front, observed when the cannibal is significantly larger than its prey which will not be a threat (Kestemont, 2003). Another example of non-random sibling cannibalism is observed in certain marine species such as the *Crepidula coquimbensis* (Brante, 2013). During the early embryonic stages of this marine gastropod's life, cannibalism between sibling embryos is common, but the study showed that

strains with the most genetically similar sibling embryos were less likely to be cannibalized, indicating the early development of kin selection in this species (Brante, 2013).

Filial Cannibalism

A subunit of kin cannibalism is filial, or the cannibalism of part or all of an organism's offspring (Manica, 2002). Filial cannibalism is highly common in aquatic, egg-laying species and can occur at differing levels of development from eggs to juveniles (Matsumoto, 2018). Infanticide is the killing of offspring in order to control the population and diminish competition. It is commonly practiced by a variety of organisms which produce many offspring. Many bird species will practice infanticide as a biproduct of the "insurance hypothesis", or the incubation of backup eggs for the single egg they will raise (Bartlett, 1987). Infanticide paired with cannibalism is less common, but is observed in insects such as the burying beetle, *Nicrophorus vespilloides,* which kill, bury, and later consume their own larvae offspring. The burying beetle will cannibalize up to half of their offspring, also known as partial filial cannibalism (Bartlett, 1987). A study on the burying beetle showed that the cannibalism of offspring primarily occured in the larval stage of development (Bartlett, 1987).

The ability of organisms to recognize kin is an important factor in the practice of cannibalistic practices. Pfennig indicates that the three critical steps for kin recognition are the production of signals for recognition, the interpretation of the signal to the conspecific, and the resulting action of the conspecific based on the interpreted signal (Pfennig, 1997). The realization of these steps is highly time sensitive and can be influenced by locational or

phenotypic changes. For example, the signs for cannibalistic behavior in female hamsters will cease at the time of pregnancy and resume after weaning offspring due to the hormonal timing. The perception of cues for kin recognition is either learned from relatives, environment, or themselves and is then saved as a "template" (Pfennig, 1997).

Cannibal Characteristics

Although cannibalism is found in a wide array of species, the majority of cannibalistic communities must fulfill a certain set of criteria. In a study observing the documentation of cannibalism, they found a "large proportion of known cannibalistic species that are predators living in freshwater, primarily fish and insects" (Fox, 1975). Both fish and insects generally share the same r-selected life strategy, meaning they overshoot the production of offspring, expecting many to die, and provide little to no care for the offspring, increasing the likelihood of "familial cannibalistic competition" for survival (O'Dor, 1998). The lack of parental care in a species is an evolved trait and is most common in species like fish with high fecundity. Cannibalism was also likely linked to the evolutionary history of high fecundity and low parental investment as all are common factors in the organisms exhibiting filial cannibalism.

Oftentimes partial-clutch filial cannibalism is carried out as a means for nutrient redistribution, while whole-clutch cannibalism is correlated to the sunk cost of caring for an inadequate amount of offspring (Hoelzer, 1992). The species which commonly utilize part or whole-clutch cannibalism are often r-selection species. The term r-selection represents the life situation where organisms bring offspring into harsh environments where many won't survive,

therefore, parental care would exert too much effort for the minimal benefit. In order to account for these trials, r-selection species will produce large groups of offspring in order to increase the odds of survival considering their high mortality rate and quick development, etc. (Pianka, 1970). Contrastly, the cannibalism of r-selected species is less common. The reproduction strategy of K-selected species is to have a low number of offspring, slow development, and high parental care. Therefore, filial cannibalism would be an extreme loss of energy for the parents who already invest so much into their offspring's survival (Pianka, 1970).

Evolution of Human Cannibalism

The motivations and evolved practices of cannibalism fall into three major categories: survival cannibalism, ritualistic cannibalism, and warfare cannibalism (Engelhaupt, 2017). These motivations behind cannibalism can be observed in a wide variety of organisms, including humans. The unusual practice of human cannibalism has been recorded in human lineage as early as the *Homo antecessor*, nearly 800,000 years ago (Engelhaupt, 2017). In the Gran Dolina cave site in Spain, dozens of pre-human skulls and bones were discovered in the same prepared manner as other animals they would eat for food, suggesting the regular cannibalism of smaller, vulnerable pre-humans (Engelhaupt, 2017). The evidence of regular cannibalism in the Gran Dolina caves indicates that cannibalism was not practiced for survival due to lack of food, but possibly as a means of strategy to keep outsider *Homo antecessor* groups from challenging them (Engelhaupt, 2017).

One of the most well-known documentations of modern human cannibalism is the Donner Party of 1846. The Donner Party was a group of 87 pioneers, only forty of which survived, traveling west through the Sierra Nevada in order to fulfil the Manifest Destiny. When the Donner Party was faced with a brutal snowstorm, cannibalism of the deceased was their only chance of survival (Worall, 2017). According to David Buss' research published in *Evolutionary Psychology*, those individuals with more genetic relatives in the colony had a greater chance at survival from cannibalism (Buss, 2015). This research makes sense when considering evolutionary psychology, because according to Hamilton's kin selection theory, the greater the genetic similarity, the more altruistic behavior between individuals, so conversely, the less genetic similarity, the greater likelihood for cannibalistic practices (Rachlin, 2008). Therefore, individuals in the *out-group*, or not close kin or community, are most likely to be victims of cannibalism due to their lack of genetic similarity and lack of contribution to the *in-group's* fitness, or the fitness of close kin or community (Geher, 2015b).

Despite the public's horrified response to the Donner Party, a recent paper by Mead *et al.* suggests cannibalism is in our DNA (Stoneking, 2003). A genetic analysis of 30 cannibalistic women of the Fore people of New Guinea showed that a majority exhibited heterozygosity for an amino acid polymorphism at codon 129. This polymorphism or heterozygosity at codon 129 is significant because it inhibits various prion diseases which are commonly contracted from eating human brains. These findings of heterozygosity did not follow the expectations of the Hardy-Weinberg principle, indicating a balancing selection acting on the prion protein gene as 23/30 individuals studied were protected from the prion disease, kuru. A similar study was conducted on individuals from populations around the

world, and the heterozygosity at codon 129 was still observed at a higher frequency than expected from the Hardy-Weinberg principle, indicating its universal genetic selection due to a common cannibalistic pre-human ancestor (Stoneking, 2003).

Evolutionary psychology would suggest that cannibalism of kin observed in early humans would be beneficial only in the extreme circumstances of starvation. Cannibalism of individuals in the out-group would be more likely executed in ritualistic or sacrificial scenarios, because killing close kin decreases the likelihood of passing down an individual's genes, a driving subconscious motivator for an individual's peak fitness (Geher, 2015b). Today, the idea of cannibalism, whether in dire or traditional settings, is extremely disturbing to discuss. This distaste may be explained by our expanding sense of an in-group as well as our greater access to nutrients, making cannibalism for survival an *evolutionarily mismatched* trait, or a trait evolved to fit a different early-human environment, as compared to our modern environment (Geher, 2015a).

Cannibalism in Fish

Despite the strong shift away from cannibalism in modern human society, cannibalism is still a common practice in many other species. For example, filial cannibalism is highly common and even necessary in aquatic, egg-laying species with short brood cycles, like fish. Filial cannibalism can be further categorized as embryocide or infanticide depending on the timing of cannibalism (Matsumoto, 2018). An example of embryocide, the filial cannibalism of embryos, is observed in a study looking at fish exhibiting primary paternal care of offspring such

as observed in bass, stickleback, minnow, and blenny fish. In a study analyzing these paternal caregiving fish species, the likelihood of filial cannibalism was drastically increased when the cost of taking care of the clutch increased, in terms of food needed. Fatality rates also increased when the personal costs to the male was increased due to the cost of feeding himself. It was observed that filial cannibalism was most favorable when the chances of clutch survival were low despite paternal care. This indicates that the filial cannibalism was carried out in hopes for a new more successful clutch in the next breeding season rather than for nutritional value (Schmoetzer, 1995).

Filial cannibalism is also observed in fish species with maternal care. In Renn's study conducted at Reed College, the pressures for cannibalistic practices were observed in Astatotilapia burtoni cichlid fish (Renn, 2009). Filial cannibalism was significantly higher in the laboratory stock of fish rather than the wild stock, despite the controlled settings. These results indicate that the wild stock fish, as well as their first generation offspring, had a "good mother" gene which both improved maternal care and therefore reduced filial cannibalism (Renn, 2009).

In genus blenniid fish, particularly the *Rhabdoblennius nitidus* males, filial cannibalism is also observed, primarily as total filial cannibalism. The observation of the male fish showed that the eggs were not always completely consumed, but sometimes spat out indicating the purpose of the cannibalism was not for nutrients but an act of infanticide or embryocide. The purpose of this behavior was determined to be a method for controlling the hormonal levels of testosterone and 11-ketotestosterone in androgen which impact the male blenniid's spawning phase. After the first day of egg acquisition, male androgen levels drop and parental care behavior spikes.

Therefore, courtship behavior is low, and it is unlikely to produce more offspring as long as any eggs are around. This illustrates why cannibalism is necessary when there is a small brood. Most males were observed to re-mate the day after total filial cannibalism. In this study, total filial cannibalism was defined as "an adaptive form of offspring abandonment" due to the low cost on long term reproductive success (Matsumoto, 2018).

Cannibalism in Largemouth Bass

Some fish species are always cannibalistic, no matter the environmental factors, while other fish species are only cannibalistic under a specific set of conditions. The *Micropterus salmoides,* or largemouth bass species, is an example of a conditionally cannibalistic species. The diet of largemouth bass is mainly small invertebrates like zooplankton. When largemouth bass are fully developed adults, these piscivorous fish primarily consume other smaller fish. According to DeAngelis' research, the largemouth bass will resort to cannibalism of their own fry, called youth of the year (YOY), depending on the degree of size dispersal, the presence of alternative prey, and the 'aggressiveness' or willingness to resist among the YOY (DeAngelis, 1980). Largemouth bass have been discovered to use olfaction, or their sense of smell, in order to recognize kin (Dufour, 2015). With olfactory senses, largemouth bass are able to track the pheromones in urine, and chemical cues deposited on their nests or eggs in order to trace their way back to their kin (Dufour, 2015). This theory was tested by observing largemouth bass homing activity, or ability to return home, after being removed up to a kilometer away from their site of spawning (Dufour, 2015).

More evidence of largemouth bass recognition may be in their tendency to prefer consuming other species before their own, even when the accompanying species is the same size as the smaller largemouth bass. In Clady's study of lakes in Michigan, the cannibalistic fish included the adult smallmouth bass, yellow perch and juvenile largemouth bass (Clady, 1974). Interestingly, the adult largemouth bass and yellow perch alike would eat the small yellow perch before the small largemouth bass (Clady, 1974). This was likely due to the size dispersal between the largemouth bass and the yellow perch. The size of largemouth bass was also an essential component in observing cannibalism of largemouth bass. The bimodality between cannibal and victim would benefit the cannibal and the potential victims in largemouth bass populations as cohort cannibalism was discovered to be a mechanism for producing necessary variations in seasonal environments (Huss, 2010).

Lake Minnewaska Study

The cannibalistic behavior of largemouth bass (LMB) has been observed across the globe under a variety of conditions. In New Paltz, New York, the unique conditions and biological history of Lake Minnewaska have influenced the cannibalistic behaviors of the largemouth bass population. Lake Minnewaska is located in Minnewaska State Park, on the Shawangunk Ridge in New Paltz, New York. Over the past century, the chemistry and biology of Lake Minnewaska have undergone changes. There were no fish inhabiting the lake from 1922 until 2008 when the small minnows (Golden Shiner) were unintentionally introduced to Lake Minnewaska (Charifson et al., 2015). The Golden Shiners primarily feed on zooplankton, a herbivorous heterotrophic

plankton which is an intermediate trophic level between the Golden Shiners and phytoplankton. The trophic cascade caused by the Golden Shiners resulted in a spike in algae blooms and decrease in water clarity following 2008 (Richardson et al., 2016). Another disturbance of trophic levels occurred in 2012 when the largemouth bass was unintentionally introduced into Lake Minnewaska. The largemouth bass, a piscivorous species with no natural predator in Lake Minnewaska, ate through the entire Golden Shiner population by 2014. Today, the largemouth bass are the only fish species in Lake Minnewaska.

The chemical and biological changes in Lake Minnewaska have been recorded by Richardson for years, in tandem with monitoring the implications of the largemouth bass' presence on the ecosystem. Richardson obtained evidence for the recovery of water clarity as a result of the decrease in phytoplankton after the introduction of the largemouth bass, but more research on how the largemouth bass population will change in Lake Minnewaska was needed (Richardson et al., 2016). In the summer of 2018, the overarching goal was to examine the trajectory, age, and health of the largemouth bass population in Lake Minnewaska in comparison with national and local largemouth bass standards.

Methods

In order to collect a history of fish data, the recordings from as early as 1896 were obtained from the observations and recordings of fish populations in Lake Minnewaska by the Smiley family, owners of the Mohonk Mountain House. This data was cross-referenced with the NY Department of Environmental Conservation and ecologists before being incorporated into

the population data timeline produced by the *History of Fish Presence and Absence Following Lake Acidification and Recovery in Lake Minnewaska, Shawangunk Ridge, NY* study (Charifson et al., 2015).
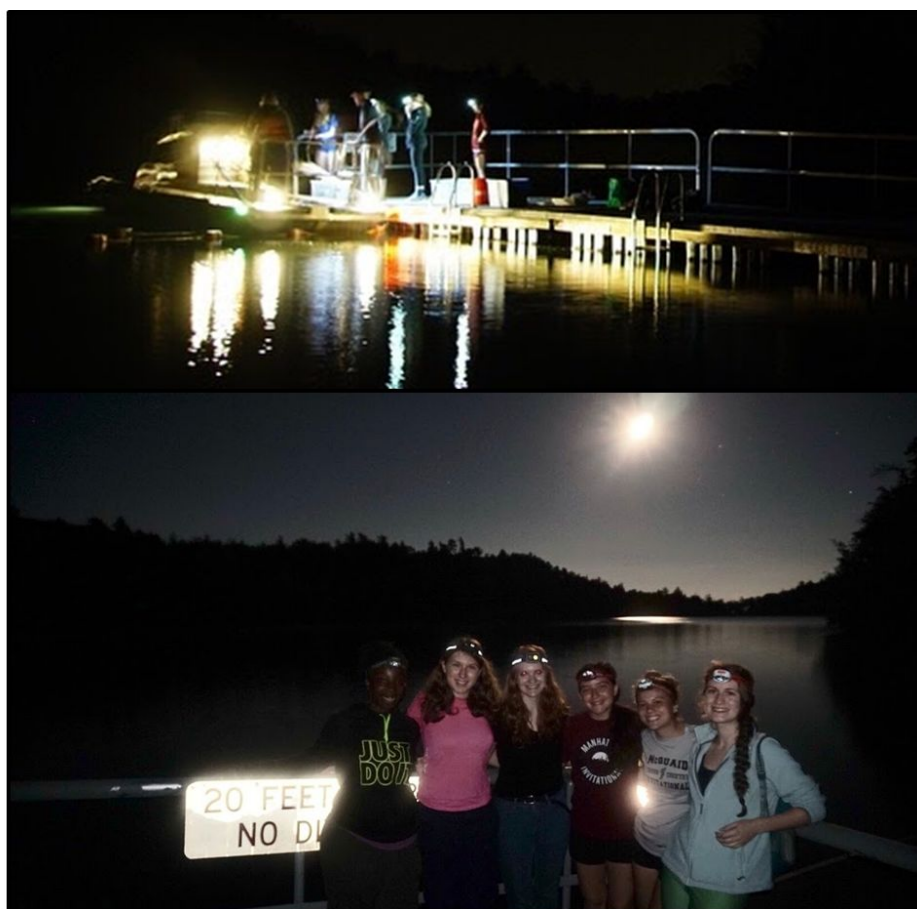

Picture 1a (top): DEC electrofishing at Lake Minnewaska
1b (bottom): Richardson's lab team night fishing at Lake Minnewaska

Recent fish data was obtained from Richardson's lab in collaboration with the NY Department of Environmental Conservation (DEC). This data was obtained through mark and recapture methods. The same mark and recapture method was performed in the summer of 2018 fish data collection. In collaboration with the DEC, we caught largemouth bass by electrofishing

on two nights during each summer from 2012 to 2018 (Picture 1a). We marked the caudal fin of

the largemouth bass, and two weeks later recaptured largemouth bass to determine population

size using Peterson's method. In 2012, largemouth bass were present, however, we did not catch

enough (n = 4) for mark and recapture calculations. In 2018, we measured individual lengths

tip-to-tail (Picture 2), girths, and masses using a scale or Boga Grip (Picture 3). To estimate age,

10-20 scales were scraped from behind the dorsal fin and below the lateral line, then stored in

paper envelopes. The scales were later observed under a microscope to determine the fish age

from the annuli growth rings, which indicate a year of growth (Picture 4).

Picture 2. Minnewaska LMB length measured tip to tail
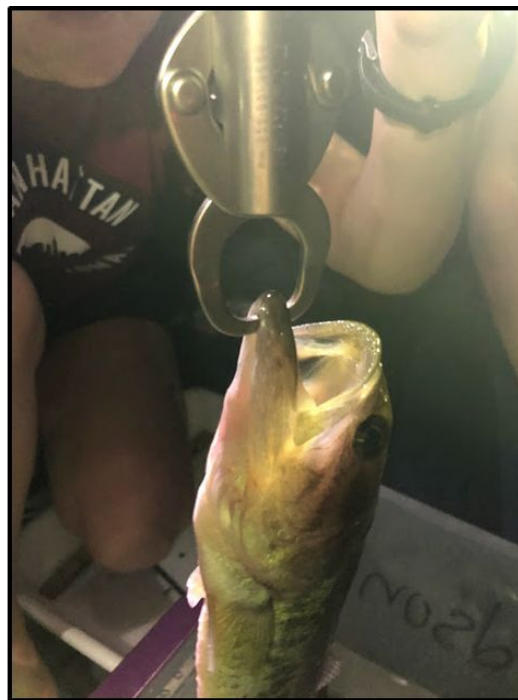
Picture 3. Minnewaska LMB mass measured using a Boga Grip
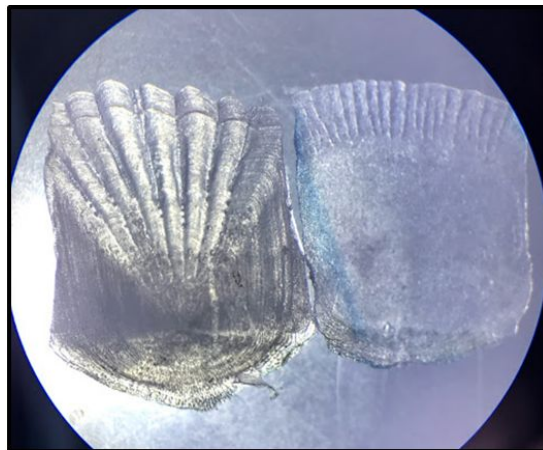
Picture 4. LMB scales under a compound microscope. Left: scale rings show 3+ years of growth.
Right: regenerated scale, rings cannot be used to determine fish age
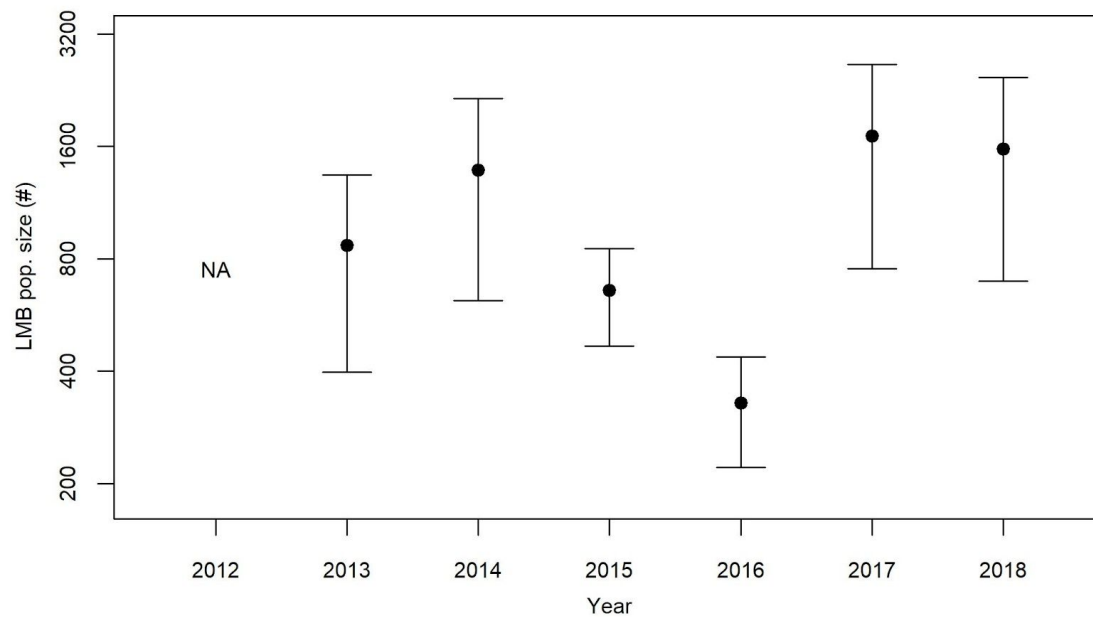
Results

Figure 1. The largemouth bass population size over the last 6 years. The largemouth bass population increased from 2013 to 2014. After a population boom in 2017, with over 1600 largemouth bass, there was little change to 2018. Error bars, representing standard error, are larger when the recapture population size is small. Note the logarithmic y-axis.
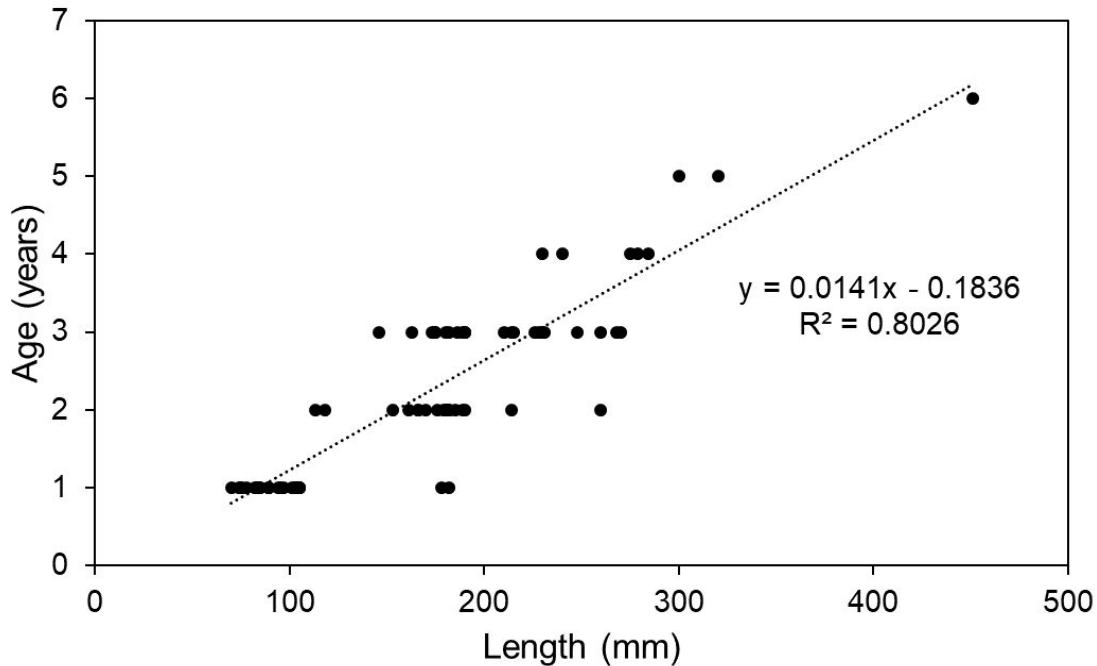
Figure 2. The age and length of largemouth bass along with the best fit linear relationship (dotted line). The relationship indicates that largemouth bass grow 71 mm each year they are alive, although there is some variability within each age.
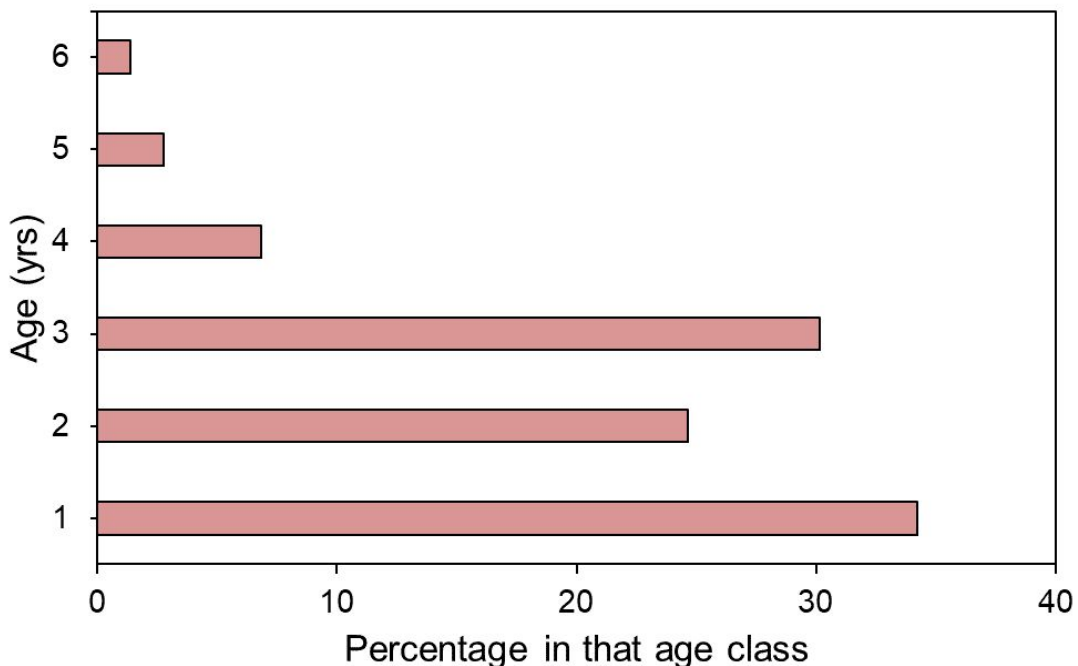

Figure 3. The population distribution graph displays a large density of younger largemouth bass in Minnewaska. Over 80% were born within the last 3 years, and less than 5% are over 6 years old. The graph displays a growing population where the younger generation outnumbers the older with high reproductive rates and lower survival of older, larger fish.
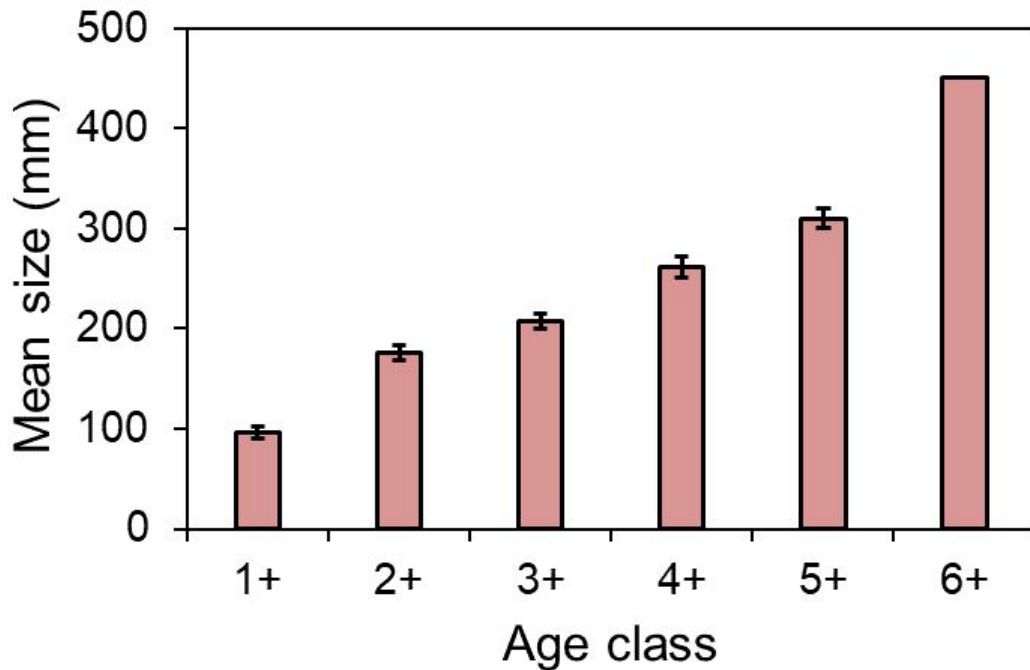
Figure 4. The mean size of the largemouth bass at given age groups. The age class with the most individuals, 1+, has a mean length of less than 100 mm. Only one largemouth bass in the 6+ age class was identified, hence the lack of error bars. Error bars represent standard error within each age class.
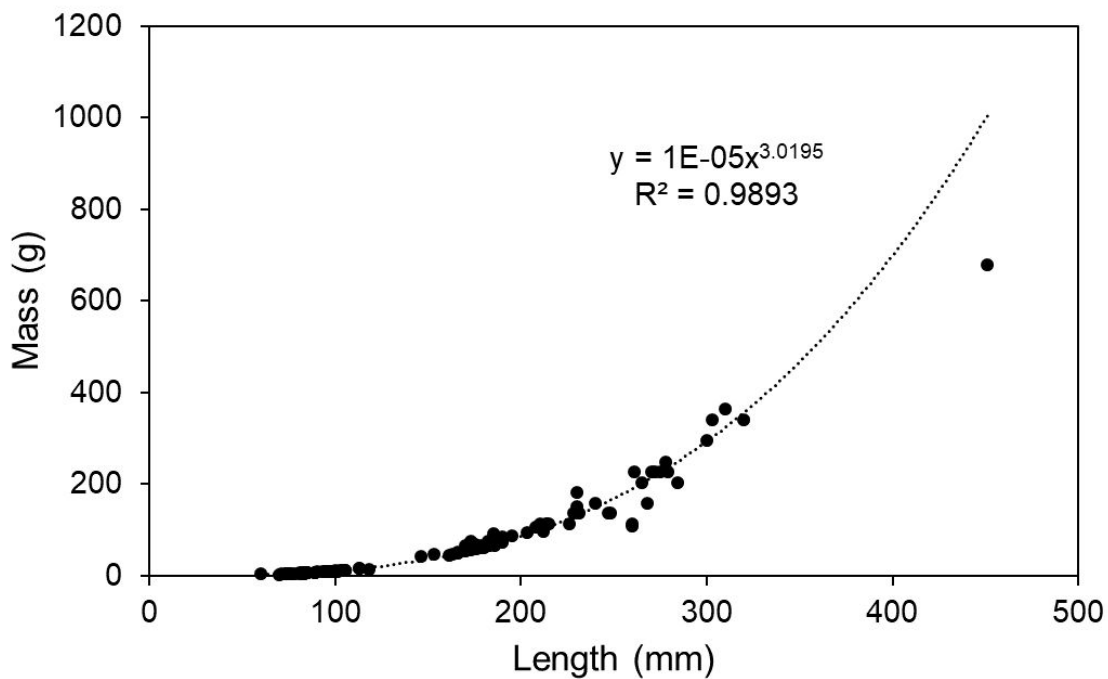

Figure 5. A comparison of the Minnewaska largemouth bass length to mass. The best fit power relationship is represented by the dotted line.

Table 1a (top) and 1b (bottom). Comparison of Minnewaska largemouth bass sizes to New York State (DEC) and national averages.

	DEC		Minnewaska
Length (mm)	Mass (g)		Mass (g)
254	227		183
305	397		317

	National Average largemouth bass at 3+ Years	Minnewaska largemouth bass at 3+ Years
Average Length (mm)	318	207
Average Mass (g)	454	102

A substantial amount of information was collected for the largemouth bass population and synthesized in figures. The Minnewaska largemouth bass data from 2013 to 2018 shows that the population significantly increased from 2016 to 2017 and has maintained from 2017 to 2018 (Fig. 1). The average length of a 3+ Minnewaska largemouth bass (Fig. 4) was below the national standard for 3+ largemouth bass indicating delayed growth. The Minnewaska largemouth bass population has more young individuals than old and is expanding with 89% of largemouth bass between 1+ to 3+ years old (Fig. 3). The average mass of a largemouth bass in Lake Minnewaska at each given length was below the mass of the DEC healthy standard. This indicates that the largemouth bass are not properly nourished (Table 1a). Although the largemouth bass population continues to survive in Lake Minnewaska, the largemouth bass fail to reach "healthy" developmental and nutritional standards of state and national guidelines. When largemouth bass are large, they are exclusively piscivorous. Given the lack of prey

species, their delayed growth and below average masses may be explained by limited nutrition, especially for the bigger fish. The expanding largemouth bass population, with no other fish species as competitors or as a food source, indicates that the larger fish are reproducing, and smaller largemouth bass are thriving.

Discussion

The results from the local Lake Minnewaska study held many similarities to the previously mentioned largemouth bass studies. The similar conditions of size dispersal and population trends observed provide basis for the conclusion that the largemouth bass in Lake Minnewaska are surviving due to their cannibalistic nature. A future study, including gut analysis of the largemouth bass, would provide the determining evidence to support this claim that cannibalism is being practiced in Lake Minnewaska.

Even without the definitive evidence of cannibalism from a gut analysis, there is plenty of cross-reference data from other largemouth bass studies to support this claim of cannibalism. For example, the study of cannibalism in a controlled lab setting showed that cannibalistic tendencies only occurred when another food source was not readily available, similar to the lack of food source in Lake Minnewaska (DeAngelis, 1980). Additionally, in the lab experiment, the largemouth bass populations without any other food source would experience an initial decrease in population size due to cannibalism, followed by a brief stabilization period before dying out. This was a stark contrast to the lab largemouth bass study where the control group was provided an alternative fish species as a food source. The largemouth bass with a consistent alternative

food source did not resort to cannibalism, and the population remained stable over time (DeAngelis, 1980). The conditions of the largemouth bass in Lake Minnewaska more closely mirror the conditions of the cannibalistic largemouth bass population due to the lack of other fish species to consume. The largemouth bass population in Lake Minnewaska does not show a decreasing trend like the initial trend in the cannibalistic lab largemouth bass, but the Minnewaska largemouth bass population data cannot be used to rule out cannibalism due to the large standard of error incorporated with the small recaptured population.

Another largemouth bass study similar to the Minnewaska largemouth bass was conducted using a physiologically structured population model (Huss, 2010). The cannibalistic largemouth bass populations were most likely to survive when the hatching periods of largemouth bass were long enough to create significant bimodal size distributions between cannibal and victim largemouth bass. When the bimodal ratio is large enough, then the cannibalistic largemouth bass will grow faster and thin out the population enough to decrease competition of resources, therefore sustaining the cannibalistic community (Huss, 2010). The same trends were observed in DeAngelis' study of largemouth bass when the cannibal-victim ratio was above 2.4 (DeAngelis, 1980). There is no significant bimodal size distribution observed in the Minnewaska largemouth bass, but the data did suggest delayed development in largemouth bass compared to state and national averages. The same stunted development was observed in the physiologically structured population model study in largemouth bass populations where the cannibalistic largemouth bass did not have enough victims to significantly increase their biomass and achieve a bimodal size distribution needed to reduce resource

competition (Huss, 2010). The same lack of victims is likely the reason there is a notable lack of nutrients for the largemouth bass, thus contributing to their stunted growth in Lake Minnewaska.

Although the largemouth bass population appears to be stable from the research obtained, similar largemouth bass studies suggest that this temporary sustenance on zooplankton, other invertebrates, and minimal cannibal victims will eventually result in a crash or cyclical trend in the Minnewaska largemouth bass population (Richardson, 2019).

The evolution of cannibalism is important for understanding the full story of Lake Minnewaska. The largemouth bass inhabiting Lake Minnewaska are the product of years of evolutionary pressures which can be used to explain anomalies, such as their survival in a lack of biodiversity. The literature analysis of largemouth bass populations in similar circumstances can be used to support the conclusion that largemouth bass cannibalism has evolved as a universally constant survival mechanism under the observed conditions. The study of cannibalism, the environmental and biological pressures which motivate it, and the underlying evolutionary benefits and costs for it, will allow for a holistic understanding of the unique ecosystems in which cannibalism plays a role.

Cannibalism is often practiced as a response to a stress signal. An understanding of the evolutionary terms under which cannibalism was implemented for that species may help determine and strategize for the correction of various man-made changes in natural environments. This can help with conservation efforts and direct attention to needed areas of correction with a proper understanding of situational cannibalistic triggers. Additionally, the understanding of cannibalism's evolutionary history will ultimately provide us with a deeper understanding of our holistic phylogenetic tree.

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