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Size Selective Parasitism of Rainbow Trout (Oncorhynchus mykiss) by Chestnut Lampreys (Ichthyomyzon castaneus) in an Artificial Setting

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Abstract

Paradigms of optimal resource utilization by animals, both classical and more recent, were not originally developed in the context of parasitism. Though this oversight has slowly been reversed, little attention has been paid to optimal resource utilization by parasitic fishes, such as lampreys. Multiple explanations for host size selection by parasitic lampreys may be plausible, but results from previous studies have been inconsistent. We studied host size selection by Chestnut Lampreys (*Ichthyomyzon castaneus*) parasitizing Rainbow Trout (*Oncorhynchus mykiss*) in fish hatchery raceways in north central Arkansas during the late winter and early spring of 2013. Parasitized Rainbow Trout were significantly shorter than non-parasitized conspecifics. Using the relative weight metric of condition, evidence was found that parasitized Rainbow Trout were in better condition than non-parasitized Rainbow Trout. Our findings are not consistent with previous studies of parasitic lamprey host size selection, but do suggest that Chestnut Lampreys are capable of determining a fish's suitability as a host based on their plumpness even in a setting with low host size heterogeneity and high host density.

Keywords

Chestnut Lamprey, parasitism, optimal resource utilization, relative weight, Rainbow Trout

Cover Page Footnote

We would like to thank the staff of the United States Fish & Wildlife Service's Norfork National Fish Hatchery for permission to conduct this study in their facility with their fish. Further gratitude is extended to M. Jirka of the Friends of the Norfork National Fish Hatchery for his insights regarding historical mechanisms of lamprey access to the hatchery. Discussions with the late P. Cochran regarding parasitic lamprey feeding biology were indispensable. Field and laboratory assistance was provided by C. Allison, T. Mackey, J. Moore, L. Renoux, J. Royal, S. Shourd, D. Trotter, J. Wagner, and B. Williams. D. Gilmore and S. Trauth provided access to laboratory equipment necessary for specimen processing. This research was funded by a Conservation Grant from the North Arkansas Fly Fishers to the lead author.

INTRODUCTION

Although not originally included in initial discussions of optimal resource utilization (Royama 1971, Charnov 1976), size discrimination of hosts by parasites has been more recently studied, particularly among invertebrate taxa (Amin 1985, Dar et al. 2015, Gbankoto et al. 2001, Grutter and Poulin 1998, Knudsen et al. 1997, Lozano 1991, McKinney et al. 2001, Tekin-Özan et al. 2008, Walker et al. 2008)). Method of size-selectivity may be reasonably expected to differ based on whether the parasite in question is an ectoparasite or endoparasite. For example, as attached ectoparasites lampreys are subjected to selective pressures that endoparasites are not. These differing selective pressures include becoming prey themselves (Cochran et al. 1992, Grutter and Lester 2002, Cochran 2009), being dislodged/injured by their host (Wagner 1908, Cochran 1986, Weihs et al. 2007), having a greater foraging risk (Bateson 2002, Nonaka and Holme 2007), or compromising the host's dermal immune defenses (Sitjà-Bobadilla 2008, Esteban 2012).

It has been previously suggested that parasitic lampreys are size-selective (Berst and Wainio 1967, Cochran 1985, Swink 2003, but see Pelenev et al. 2008), with a tendency to parasitize larger hosts more frequently than smaller hosts (Johnson and Anderson 1980, Cochran 1985, Noltie 1987, Sepúlveda et al. 2012). Results of both lab (Cochran 1985, Cochran and Jenkins 1994, Edsall and Swink 2001) and field studies (Berst and Wainio 1967, Noltie 1987) suggest that lampreys may optimally forage. Lampreys even appear to be able to discriminate between hosts of similar size, even when those hosts are small (Cochran and Jenkins 1994, Swink 2003).

There are five possible explanations for size-selective parasitism by parasitic lampreys. The first explanation is the null hypothesis: that no size-selectivity exists and host selection is opportunistic (Cochran 1985). Cochran (1985) also suggested a second explanation where negative size selection may exist due to possible deleterious effects on lampreys which choose larger hosts, or a reduction in their ability to parasitize larger hosts. Third, positive selection may exist as a lamprey attempts to maximize its food source (Cochran 1985). Fourth, there may be a 'slot limit' approach by the lamprey in attempts to balance the costs and benefits of host selection. Were this explanation correct, both hosts too small to provide an adequate blood meal and hosts large enough to injure an attached lamprey would be avoided (Hume et al. 2013). The fifth explanation, as yet untested in the literature, is that host selection may instead be based on a host's condition, in that a lamprey may opt to parasitize a host that would be more likely to survive being parasitized and thus be available as a food source longer than would a compromised host, or a host that is heavier than would be expected for its length. In light of the mathematical relationship between body weight and surface area in fishes (Niimi 1975), this explanation is intuitive: an increase in a host's body weight and surface area would be expected to increase its blood volume, which in turn would be expected to increase the amount of blood that can be removed before severely harming the host (Duff et al. 1987, Nichols 1987, Brill et al. 1998, Lecklin et al. 2000).

The goal of this study was to investigate whether Chestnut Lampreys *Ichthyomyzon castaneus* exhibit size-selectivity in a study setting containing fish hosts largely homogeneous in size. Considering the above explanations, we hypothesized that Chestnut Lampreys would exhibit positive size-selectivity even with low host size variation within a fish hatchery raceway containing Rainbow Trout *Oncorhynchus mykiss*. A raceway provides the opportunity of identifying size selection on a small scale by lampreys on their hosts. Rainbow Trout within raceways are standardized within fine limits for length. If the data support this second explanation of fine-scale size-selectivity as suggested by Cochran and Jenkins (1994) and Swink (2003), then we would observe significant differences in length and/or mass of wounded vs. non-wounded Rainbow Trout hosts.

METHODS

Rainbow Trout were sampled from Norfork National Fish Hatchery (NNFH) in north central Arkansas, USA, over a three-month period from late January to mid-April 2013. This is a federally-owned and operated coldwater mitigation Rainbow Trout hatchery, though NNFH is also responsible for raising Brown Trout *Salmo trutta* and Cutthroat Trout *O. clarkii*. The hatchery rears Rainbow Trout from eggs to sizes ranging from 203 to 305 mm SL for stocking in tailwaters below dams in northern Arkansas and eastern Oklahoma. During the grow-out period following egg hatching, several attempts are made by NNFH personnel to 'grade' Rainbow Trout by both SL and mass to maintain a largely homogenous population of Rainbow Trout within individual raceways.

Parasitic lampreys have previously been reported by NNFH personnel (T. Anderson, pers. comm.) and by personal observation to occur in the hatchery, a phenomenon reported in the literature only once before (Lyons et al. 1994). For example, two specimens found in the hatchery's raceways by NNFH personnel before and after the completion of this study were identified by us as Chestnut Lampreys. Although the parasitic Silver Lamprey *I. unicuspis* has previously been identified from a single watershed in northwest Arkansas (Robison et al. 2011), only the Chestnut Lamprey has to date been found in other streams throughout the state, including those surrounding NNFH (Salinger et al. 2018). The method of entry for these lampreys into the hatchery has not been identified, but a greater frequency of parasitism in downstream raceways suggested a probable upstream entry from the hatchery's water discharge system into the adjoining Dry Run Creek

(Salinger and Johnson 2019). No lampreys were intentionally introduced to the hatchery for the purposes of this study.

A total of 15 raceways (raceway dimensions: 2.4 m x 28.3 m) containing Rainbow Trout were sampled per sampling trip ($n_{trips} = 9$, $n_{raceways} = 54$, $n_{raceway\ days} = 135$). Raceways sampled were selected using a random-number generator with replacement. As replacement was allowed in the random-number generator, some raceways were sampled multiple times on different sampling dates during the study. This gave each raceway equal probability of being selected. Raceways were excluded from selection if they contained Rainbow Trout whose average SL was less than 150 mm (minimum parasitic lamprey host length as suggested by Cochran and Jenkins 1994) or they contained Rainbow Trout being actively treated for disease. Observers trained to identify possible lamprey wounds and adult lampreys circled each raceway for approximately five minutes to locate lampreys and wounded Rainbow Trout. If a suspected wounded Rainbow Trout was observed in a raceway, blocking screens were inserted to isolate the wounded Rainbow Trout in a small area with as few conspecifics as possible. Targeted Rainbow Trout were collected with a dip net and examined for wounds; Rainbow Trout positive for lamprey parasitism were then held on ice for further study. Parasitized Rainbow Trout were measured to the nearest mm SL and g of mass. Monthly mean SL and mass records for Rainbow Trout in individual raceways are maintained by, and were provided to us, by NNFH personnel for the raceways that were sampled at the time said raceways were sampled. Mean lengths and weights were calculated ± standard error (SE) for all wounded fish collected. Standard length values were converted to total length (TL) values using the mean value of the conversion factor for Rainbow Trout provided by Fishbase (Froese and Pauly 2019), as most measures of condition incorporating length data require fish length to be expressed as TL (Pope and Kruse 2007). Condition was assessed using the relative weight (W_r) method (Wege and Anderson 1978) in the FSA R package (Ogle et al. 2018) with the standard weight (W_s) equation for Rainbow Trout of Simpkins and Hubert (1996).

Normality of the quantitative variables was assessed using a Shapiro-Wilk test. Mean wounded Rainbow Trout SL and mass data were compared to the extrapolated mean SL and mass of individuals in the raceway of collection using relativized one-tailed two-sample t-tests in R v 3.5.3 (R Core Team 2019). This approach compared the SL and mass of each wounded fish to the mean SL and mass of fish in that same raceway. As these data were not normally distributed ($p < 0.001$) and could not be normalized via transformation, relative weights of parasitized and non-parasitized fish were compared using a Mann-Whitney *U*-test. Results of all statistical tests were considered significant at $\alpha = 0.05$.

RESULTS

A total of 83 wounded Rainbow Trout were collected during the study. An inability to positively attribute wounds to a lamprey ($n = 1$) as well as five individuals determined to be outliers due to their masses being greater than two standard deviations from the mean led to the exclusion of these individuals from analysis. However, the Rainbow Trout considered to be outliers for mass analysis were included in length analysis. A further eight individuals were excluded from analysis for mass or length analysis due to a lack of comparative data provided by the hatchery. The wounded Rainbow Trout ranged in size from 140 to 267 mm SL ($n = 74$) and 44 to 481 g in mass ($n = 69$). Mean wounded Rainbow Trout SL was 218.9 ± 3.1 mm SE, and mass was 200.7 ± 12.9 g SE. Statistical analysis showed wounded Rainbow Trout were significantly shorter (32.5 mm shorter; $p < 0.0001$; Figure 1) than the means of non-wounded Rainbow Trout of the same sample. In contrast, wounded Rainbow Trout were insignificantly heavier (+6.6 g; $p = 0.24$; Figure 2) than non-wounded Rainbow Trout on average. The median W_r for parasitized Rainbow Trout was 91 (range: 42-218), indicating that parasitized individuals were in good condition. In contrast, median W_r of non-parasitized Rainbow Trout was 62 (range: 56-65), which is indicative of fish in poor condition (Figure 3). The median difference between parasitized and non-parasitized Rainbow Trout W_r was significantly different (+29; $p < 0.001$).

DISCUSSION

Our results were variable in regard to size selection. First, there was negative size selection relative to SL, yet the Rainbow Trout chosen as prey were heavier for their lengths, showing a greater relative weight. This indicates that Chestnut Lampreys may have been choosing their Rainbow Trout hosts on the basis of a fish's girth or body depth rather than for length alone. This selection within the raceways was despite both high host size homogeneity and density (mean Rainbow Trout per raceway = 11,000, range = 6,800 – 27,700).

A possible explanation for the choice of shorter hosts in a controlled setting such as a raceway may be that lampreys are sacrificing a potentially larger blood meal available from a longer host in exchange for a decreased risk of said host dislodging them via collision with the rough concrete raceway walls (Cochran 1986). Cochran's (1986) suggestion that a lamprey may be considering potential injury risk to itself when foraging is intuitively compelling; however, evidence to support this "traumatic dislodgement hypothesis"—first suggested by Wagner (1908)—has not been observed in either field or lab studies, as stated by Lennon (1954), and later by Farmer and Beamish (1973). However, as this hypothesis has not been previously studied, it bears future examination.

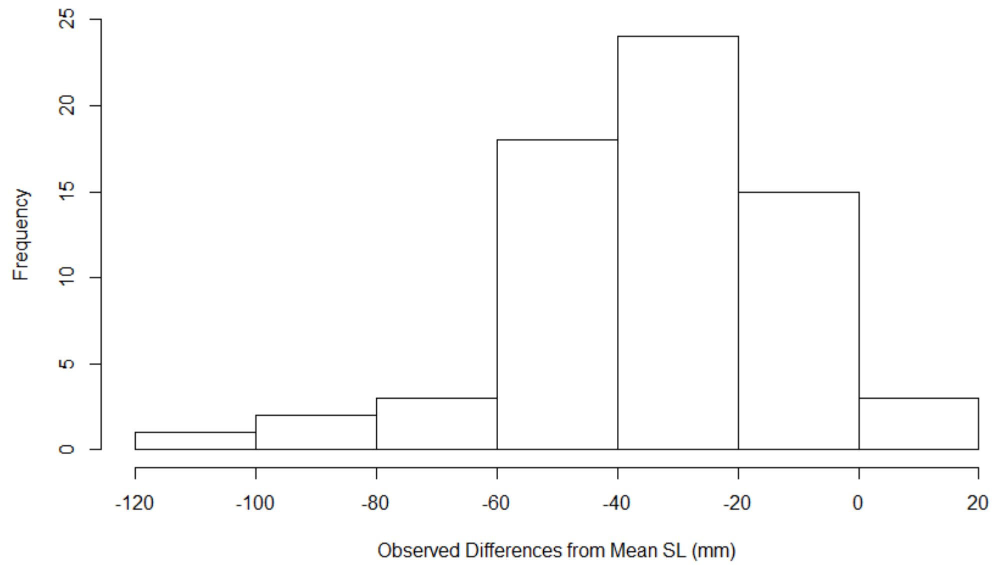

Figure 1. Frequency distribution of the observed differences from mean standard length of parasitized Rainbow Trout recovered from Norfork National Fish Hatchery, January-April 2013. The mean difference in SL between parasitized and non-parasitized Rainbow Trout was 32.5 mm.

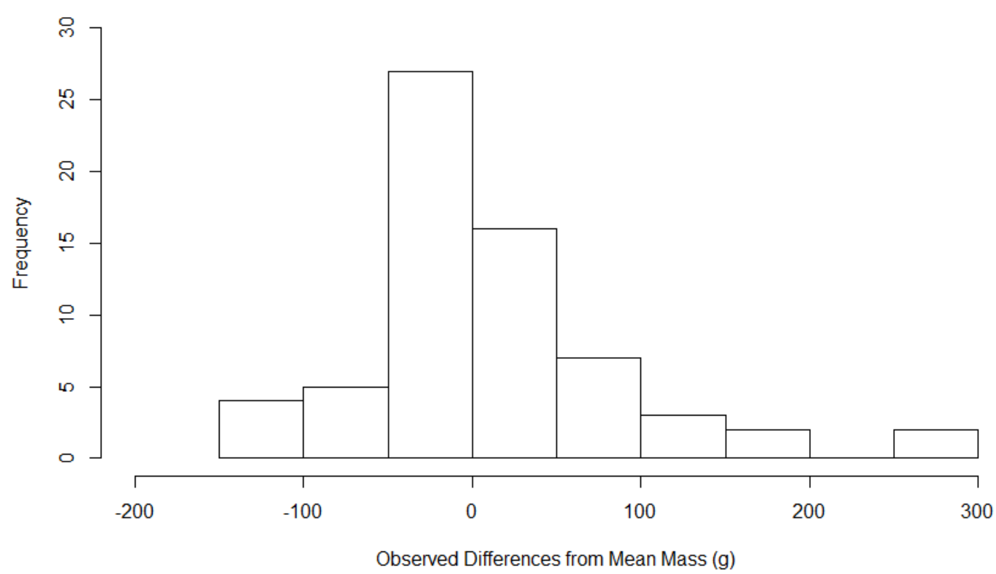

Figure 2. Frequency distribution (including outliers excluded from statistical analysis) of the observed differences from mean mass of parasitized Rainbow Trout recovered from Norfork National Fish Hatchery, January-April 2013. Mean difference in mass was 6.6 g.

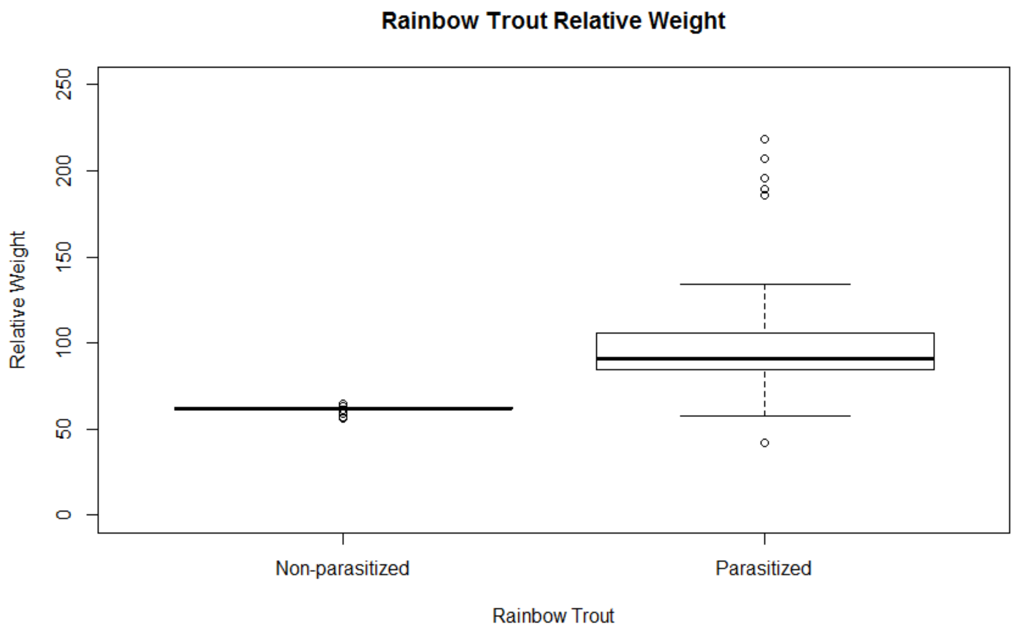

Figure 3. Distribution of relative weights (W_r) of parasitized (n = 69) vs. non-parasitized Rainbow Trout from Norfork National Fish Hatchery, January-April 2013. Whiskers represent standard error (SE). Relative weights were calculated after outliers for mass were removed.

To our knowledge, this study is the first to report on size-selective parasitism of fish by lampreys within a hatchery setting. Therefore, no direct comparison is possible of our results to work within hatcheries. Field study results of host size selection by lampreys are varied. For example, in contrast to our results of negative size selection for length, Pelenev et al. (2008) found no evidence of size selective attacks on North Pacific salmonids by Pacific Lampreys *Entosphenus tridentatus*. Likewise, there was no size selection for most parasitized host species, including multiple salmonids, by Western River Lampreys *Lampetra ayresii* residing in estuarine areas of the Columbia River (Weitkamp et al. 2015). Both of these studies provide evidence supportive of an opportunistic feeding hypothesis.

Several field studies have also shown negative length selection similar to our findings. In contrast with the findings for other parasitized species discussed by Weitkamp et al. (2015) above, Western River Lampreys more frequently parasitized shorter American Shad *Alosa sapidissima*. Similarly, Orlov et al. (2009), in studying Pacific Lamprey parasitism of commercially-important marine fishes in the North Pacific, found a negative association between host SL and incidence of parasitism, indicating a preference for smaller hosts. This association was observed regardless of host species, and included both pelagic (e.g., Pacific

Cod *Gadus macrocephalus*) and demersal (e.g., Pacific Halibut *Reinhardtius hippoglossoides*) hosts.

In contrast to our findings, multiple authors have demonstrated a positive relationship between incidence of parasitism and host length for lampreys parasitizing salmonids in field settings (Davis 1967, Noltie 1987), including Rainbow Trout (Berst and Wainio 1967). This positive relationship has also been observed in laboratory settings (see Swink 2003 and studies summarized therein). Cochran and Jenkins (1994) also found a positive relationship between host mass and incidence of parasitism for Sea Lampreys *Petromyzon marinus* parasitizing Rainbow Trout, indicating selection for heavier hosts. Cochran et al.'s (2003) finding for Silver Lampreys parasitizing Paddlefish *Polyodon spathula* suggests that combined host length and mass influence size selection, which is consistent with those of Silva et al. (2013b) for Sea Lampreys parasitizing Northern Straight-mouth Nase *Pseudochondrostoma duriense*. Both Cochran et al. (2003) and Silva et al. (2013b) found positive influences of host length and mass on incidence of lamprey parasitism. Among laboratory studies investigating size selectivity among non-salmonid hosts, Chestnut Lampreys parasitizing Northern Hogsucker *Hypentelium nigricans* showed a positive relationship of increased host mass, surface area, and length with increased incidence of parasitism (Cochran 1985). To our knowledge, the interaction of these three variables with respect to lamprey host selection has not been well-studied (Cochran 1985, Patrick et al. 2009), and bears further examination.

One possible balance between parasitizing smaller and larger hosts might take the form of a 'slot-limit' distribution, wherein the smallest hosts are not heavily targeted due to insufficient energy content versus the largest hosts being rejected because of their potential ability to harm a lamprey. Though this idea has not yet been addressed in the literature or by us in this study—due to relative host size homogeneity in raceways of a Rainbow Trout hatchery—such a slot distribution was observed in the case of European River Lampreys *L. fluviatilis* parasitizing Powan *Coregonus lavaretus* in Scotland (Hume et al. 2013). The hypothesis of a slot-limit distribution of hosts is intuitively compelling and is worthy of study.

The results of this study indicate that, even in a high host density environment such as a hatchery raceway, Chestnut Lampreys appear to exhibit behavior consistent with an optimal foraging hypothesis—in the form of parasitizing Rainbow Trout in better condition than their conspecifics. Given the dichotomy of our results pertaining to host length and W_r, and their inconsistency with prior studies of parasitic lamprey host size selection in an artificial setting, further study of this subject is necessary.

To our knowledge, our use of the relative weight metric to analyze parasitic lamprey host selection is novel, though both Cochran and Kitchell (1989) and Silva et al. (2013a) have used either Fulton's condition factor (Fulton 1904) or derivations of it for this purpose. Relative weight is easily and quickly computed and requires neither sacrificing specimens nor specialty training of personnel. Furthermore, the nature of the relative weight metric allows for comparisons of condition to be made across different populations and species, making it more versatile than other metrics for the investigation of size-selectivity (Pope and Kruse 2007). However, as morphometric characters (e.g., body girth or depth) included in condition factor analyses vary between species, further validation of the relative weight metric for the purpose of analyzing size-selectivity of lamprey parasitism among species is necessary. Specifically, size selection on hosts by lampreys for species having a large depth (i.e., crappie *Pomoxis* sp.) may differ from hosts having a greater girth (i.e., Largemouth Bass *Micropterus salmoides*).

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