PREY CAPTURE AND OPTIMAL HABITAT SELECTION OF WILD RAINBOW TROUT (ONCORHYNCHUS MYKISS) IN A SOUTHERN APPALACHIAN STREAM

by

KIERAN MERRITT

(Under the Direction of GARY GROSSMAN)

ABSTRACT

Rainbow trout (*Oncorhynchus mykiss*) are members of the salmonid family which have been introduced worldwide. Because of their popularity as a species, knowledge of their habitat utilization could be essential in managing their populations. Net energy intake (NEI) models have been successful in predicting optimal holding velocity in young-of-year rainbow trout and other salmonids but have fallen short of doing the same in others Using the Grossman et al. (2002) model, we found that rainbow trout were holding in water that was 1cm/s slower than the prediction of the optimal microhabitat, and that water velocity had a negative effect on prey capture, little to no effect on reactive distance, and a positive effect on holding velocity. We also found that dominance had a significant effect on the prey capture success of subordinate fish but not on their dominant counterpart.

INDEX WORDS: Rainbow Trout, Microhabitat, Habitat selection, Net energy intake, Foraging models, Drift-feeding

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KIERAN MERRITT

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KIERAN MERRITT

Major Professor:	Gary Grossman
Committee:	Martin Hamel Brian Irwin

Electronic Version Approved:

Ron Walcott
Vice Provost for Graduate Education and Dean of the Graduate School
The University of Georgia
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DEDICATION

I dedicate this work to Jolene Gale for her extensive research assistance and the Merritt family, who have provided me with moral and emotional support in all my work and have always inspired me to challenge myself and explore my curiosities of the natural world.

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CHAPTER 1

GENERAL INTRODUCTION

Rainbow trout (*Oncorhynchus mykiss*) are members of the salmonid family native to the Pacific Rim Slope from northeast Asia, through Alaska, Canada, and the continental United States, and south into northwestern Mexico (Page and Burr 1991; Behnke 2002). They have been introduced to water bodies around the world due to their desirability as both angling and aquacultural species (Fausch, 1988, Cambray, 2003b; Copp et al., 2005). Naturalized populations of Rainbow Trout currently exist on six of the seven continents (Behnke 2002). Despite their importance and widespread distribution, managing wild *O. mykiss* populations is not as straightforward as one would expect, because outside of their native range they may become a pest species. Introduced Rainbow Trout have negatively affected the endangered humpback chub (*Gila cypha*; Healy et al., 2022), cutthroat trout (*Oncorhynchus clarkii*; Seiler and Keeley 2009, Young 1995), and Southern Brook Charr (*Salvelinus fontinalis*; Kanno et al. 2017). According to the Eastern Brook Trout Joint Venture (EBTJV 2006), 96% of subwatersheds historically inhabited by Brook Charr in Georgia and South Carolina have been negatively affected by the introduction of nonnative Rainbow Trout (EBTJV 2006). Despite both the potential and actual deleterious impacts of Rainbow Trout, management efforts to suppress non-native populations frequently are met with resistance by the angling community (Rahel 2004).

Notwithstanding its widespread transplantation and establishment, surprisingly little is known about the mechanisms determining the use of ecological resources by wild Rainbow Trout. This is unfortunate because Rainbow Trout face the same threats of habitat loss and habitat fragmentation as other trout species across their native and nonnative range. In the

Southern Appalachians, computer modeling based on water and air temperatures suggest that 53% of Brook Charr habitat and 97% of Rainbow Trout habitat will be lost due to climate change (Flebbe et al. 2006). This reinforces the need for a better understanding of the requirements and mechanisms by which trout choose habitat. Ultimately, trout in the Southern Appalachians could become restricted to a series of high-elevation habitat islands.

The complexities of Rainbow Trout management, whether for minimizing impacts of an invasive, or ensuring that fishable populations are maintained, require the development of predictive habitat models applicable to a variety of geographic regions. One method that has proven successful in gaining insight into habitat selection by Rainbow Trout is the development of net energy intake (NEI) models (Hill and Grossman 1993; Fausch 2014; Grossman 2014; Piccolo et al. 2014; Rosenfeld et al. 2014). NEI modeling allows us to draw connections between microhabitat use by individuals and its potential effect on fitness via energy intake. NEI models for drift-feeding fishes aim to quantify the relationship between holding velocity and net energy intake to identify the most "profitable" microhabitats within a stream and determine whether fish are choosing these microhabitats. NEI modeling has successfully been used to predict optimal holding positions for various salmonid species(Table 1.1) including Arctic Grayling (*Thymallus arcticus*; Hughes and Dill 1990), Brown Trout (Salmo trutta; Fausch 1984; Hayes et al. 2007), Northern Brook Charr (Fausch 1984), Southern Brook Charr (Sliger and Grossman 2021), Coho Salmon (*Oncorhynchus kisutch*; Fausch 1984), young-of-the-year, and yearling Rainbow Trout (Hill and Grossman 1993), and four species of cyprinids (Grossman et al. 2002).

Quantifying the characteristics of high-quality holding positions in a stream and their availability is crucial for habitat preservation and population maintenance. To this end, we parameterized the Grossman et al. (2002) NEI microhabitat model using laboratory experiments for wild Rainbow Trout and tested the predicted optimal holding velocity of this species in Twentymile Creek. This creek is a third-order stream in the North Carolina portion of the Great Smoky Mountains National Park.

Table 1.1 Previous Grossman NEI model iterations showing species, optimal holding velocity predictions, occupied holding velocity (95% Confidence interval), and degree of success on drift-feeding fishes.

Author and Year	Species	Season	Predicted Holding Velocity (cm/s)	Occupied Velocity (cm/s, 95% CI)	Prediction Degree of Succuss
Hill & Grossman 1993	*O. mykiss*(Small)	Winter	13.4	7.8 - 17.8	Successful
		Spring	13.6	8.2 - 18.1	Successful
		Summer	17.1	12.4 - 21.5	Successful
		Fall	15.5	11.3 - 19.3	Successful
	O. mykiss(Medium)	Winter	16.1	9.9 - 20.9	Successful
		Spring	17.2	11.2 - 22.2	Successful
		Summer	22.1	17.1 - 26.4	Successful
		Fall	19.3	14.5 - 23.6	Successful
	C. funduloides(Medium)	Winter	7.7	3.2 - 11.4	Successful
		Spring	10.2	5.9 - 14.3	Successful
		Summer	16.5	12.4 - 20.2	Successful
		Fall	11.9	8.8 - 14.9	Successful
	C. funduloides(Large)	Winter	11.8	6.8 - 15.6	Successful
		Spring	13	8.3 - 17.1	Successful
		Summer	18.1	13.6 - 22.3	Successful
		Fall	14.6	11.3 - 17.5	Successful
Grossman 2002	*C. funduloides*	NA	13.9	11.2 - 13.4	Successful
	L. coccogenis	NA	13.4	12.5 - 14.8	Successful
	N. leuciodus	NA	11.8	13.2 - 18.0	Partial Success
	N. lutipinnis	NA	11.0	8.3 - 15.1	Successful
Bozeman & Grossman 2019a	*T. arcticus*	NA	41.2; 36.2; 34.7	20.7 - 27.9	Partial Success
Bozeman & Grossman 2019b	*S. Malma*	NA	24	24.9 - 29.3	Semi-Success

					(within 1cm/s)
Sliger and Grossman 2021	*S. fontinalis*	NA	18.5	13.5 - 20.5	Successful

CHAPTER 2

A GENERALIZED OPTIMAL HABITAT SELECTION MODEL FOR DRIFT-FEEDING FISHES: RAINBOW TROUT (ONCORHYNCHUS MYKISS)

Introduction

Understanding the mechanism driving habitat selection for a species is a topic of interest to both behavioral ecology and fisheries management. Streams provide an interesting arena for such studies, because of their high microhabitat heterogeneity (Grossman and Freeman 1987; Hill and Grossman 1993; Grossman 2014). In many temperate North American streams, drift-feeding fishes typically hold a position facing upstream and capture prey as it approaches from upstream.

One of the most productive approaches to quantifying microhabitat selection in drift-feeding stream fishes has been the development and application of net energy intake (NEI) models (Hill and Grossman 1993; Fausch 2014; Grossman 2014; Rosenfeld et al. 2014). NEI modeling uses both descriptive and experimental data to parameterize a model that predicts the holding velocity at which an individual will maximize their net energy gain (a parameter directly related to fitness via its impact on growth, fecundity, and disease resistance), and typically tests that prediction via *in situ* measurements of fish-holding velocities in the stream of interest. This approach has been used to predict optimal holding positions for various salmonid species including Brown Trout (*Salmo trutta*; Fausch 1984; Hayes et al. 2007), Northern Brook Charr (*Salvelinus fontinalis*; Fausch 1984) Coho Salmon (*Oncorhynchus kisutch*) and (*Thymallus arcticus*; Hughes and Dill 1990). Grossman and Hill (1993) developed and tested an NEI model for young-of-the-year and yearling Rainbow Trout (*Oncorhynchus mykiss*) and Rosyside Dace (*Clinostomus funduloides*). These models successfully predicted the focal-point velocities occupied by these species. This model was further refined by adding curve fitting constants to better fit the nonlinear relationship between prey capture and water velocity (Grossman et al. 2002) and successfully predicted holding velocities of four species of cyprinids, although there were some failed seasonal predictions, correlated with small sample sizes. Subsequent studies have produced further refinements in the model by removing variables found not to aid in prediction accuracy and expanded successful predictions to Arctic Grayling (Bozeman and Grossman 2019a), Dolly Varden Char (*Salvelinus malma*, Bozeman and Grossman 2019b), and Southern Brook Charr (Sliger and Grossman 2021).

With drift-feeding fishes attempting to maximize their NEI, the effect of dominance favors more aggressive and typically larger individuals and plays a role in habitat selection by subordinate fish. Dominance has been shown to occur both between members of the same species (David et al 2007) and across members of different species (Cunjak et al. 1984). Dominant fish frequently occupy the most profitable feeding positions, with lower-ranked fish-holding correspondingly less profitable locations (Bachman 1984; Hughes 1992; Nakano 1995). With dominant fish forcing subordinates to occupy less than optimal locations in a stream, the effect of dominance could be significant on Rainbow Trout habitat selection and understanding it better could partially explain differences in predicted optimal holding velocities and occupied holding velocities.

In this study, we parameterize the Grossman et al. (2002) model for wild Rainbow Trout residing in Twentymile Creek in Great Smokey Mountain National Park. Specifically, we quantify the relationship between velocity and: 1) prey capture success, 2) reactive distance, and 3) holding velocity, as well as the effects of dominance, a larger fish holding at or close to the center of the test chamber, on these parameters. Finally, we test whether adult wild Rainbow Trout occupy the predicted optimal holding velocity in the natural environment.

Materials and Methods:

Field data collection

We captured 27 wild adult (minimum size 165mm SL) Rainbow Trout from Twentymile Creek within the North Carolina portion of the Great Smokey Mountain National Park (GSMNP). We used backpack electrofishing to capture fish. We chose Twentymile Creek for specimen collection because it is one of few locations in the southeast with a substantial population of wild Rainbow Trout. We gave the fish two weeks to acclimate to laboratory conditions in temperature-controlled recirculating holding tanks (10°-13°C). After completion of experiments and model generation of the predicted optimal holding velocity, we returned to Twentymile Creek on June 13th, 2022, to collect holding velocity data between 9 am and 7 pm. As a test of the NEI model, we compared fish mean holding velocities in Twentymile Creek to the optimal holding velocity predicted by the NEI model. Finally, on the same day we collected fish data, we made 45 random measurements of mean water column velocity using a random number table to locate longitudinal and latitudinal positions in the stream.

All fish were collected under GSMNP and North Carolina Collecting Permits and humanely treaded under AUP# A2020 10-012-Y2-A0 and approved by the IACUC of the University of Georgia.

Experimental Flume and Procedures

A complete description of the experimental flume and procedures are presented in Bozeman and Grossman (2019a) and Sliger and Grossman (2021). In brief, the flume measured 3.5m L x 0.75m W x 1.0m H and was constructed out of clear plexiglass, facilitating observations. Test fish were placed in the upper portion of the flume in a 1.5m L x 0.75m W x 0.5m H arena (i.e., the test chamber) isolated on both upstream and downstream ends by mesh netting. A PVC collimator, located just above the test chamber minimized variation in water velocity during experiments.,

Prior to the experiment, the tank was filled with dechlorinated water, to a depth of 40cm in the test chamber. The flume was drained and refilled after every fourth fish trial or once a week, whichever came first. A network of bamboo rods was attached to the collimator to mimic natural structure and prevent fish from holding directly below one of the three feeding tubes. Feeding tubes were evenly spaced across the width of the test chamber, at a depth of 8cm below the surface. Water velocity was controlled via two 24V continuous-speed trolling motors placed side by side at the back of the flume. An electronic chiller at the back of the test flume maintained a temperature between 10°-12°C. The test chamber was shrouded with black plastic to minimize disturbance and visually isolate the observer from the experimental subject. All experiments were recorded with video cameras placed at the side of the test chamber.

Experimental Design

We conducted both single fish and dominance experiments following the design of Bozeman and Grossman (2019a) and Sliger and Grossman (2021). We quantified the relationship between treatment velocity (cm/s) measured at three evenly spaced points across the width of the experimental chamber at a depth of eight cm (i.e., feeding tube depth), and three response variables: 1: prey capture (frozen blood worms, *Glycera* sp.), 2: reactive distance, and 3: holding velocity. We also estimated the effects of fish length (standard length, mm), mass (g), and days in captivity on these response variables. Treatment velocity, rather than prey velocity, was used in all analyses because these two variables are strongly correlated in the experimental flume (Sliger and Grossman 2021). We recorded whether a prey item was captured or missed via visual observation and video. Holding velocity was measured at the nose of the fish (cm/s). We used video recordings of trials to record reactive distance, which was defined as the distance from the nose of the fish to the prey when the fish first oriented to the prey. Measurements of reactive distance were made using the methods of Bozeman and Grossman (2019) and the VidSync video analysis program which yields a measurement of the distance between a prey item and the Rainbow Trout at the video frame that the fish first reacts to the prey item (www.vidsync.org; Neuswanger et al. 2016).

A test specimen was fasted overnight to ensure that feeding motivation would be high during a trial. We first measured the mass (gm, electronic scale) and standard length (mm, SL) of the test specimen and then placed them in the test chamber. Water velocities (± 0.1cm/s) were measured using a HACH FH950 flow meter. Before beginning a trial, the test fish was acclimated in the test chamber for 15 minutes at a water velocity of 5 cm/s. We then tested for feeding motivation by pipetting several bloodworms (mean length ± sd = 8.8 ± 1.4, n = 50, Bozeman and Grossman 2019a) and liquid down the middle feeding tube. If the fish initiated foraging behavior, we began the feeding trial. All fish showed strong feeding motivation in experiments. A trial began by increasing water velocity to the first treatment velocity of 10 cm/s and releasing a prey item from a randomly selected (random number table) feeding tube. Rainbow Trout were eager feeders, and it was easy to score prey as captured or missed. On rare occasions where fish were distracted and did not orient to a prey, we released another prey. We continued this process until a total of nine responses were recorded at a given test velocity. After the 10 cm/s treatment was concluded, the water velocity was reduced back to 5 cm/s and allowed the fish to rest for 30 minutes. We then slowly increased water velocity to the next treatment velocity (20 cm/s) and the procedure was repeated (test velocities increasing in 10 cm increments) until the test specimen failed to catch at least three of the nine released prey. The fish was then returned to the holding tank, to be used later for dominance trials.

We were interested in the effects of behavioral dominance (i.e., dominant versus subordinate) on our three output variables: 1) prey capture, 2) reactive distance, and 3) holding velocity, as well as the effects of fish length (standard length, mm), mass (gm), and days in captivity on these variables, so we repeated experiments using two fish in a trial. As per Bozeman and Grossman (2019a, b) and Sliger and Grossman (2021), the dominant fish was defined as the fish that spent the greatest amount of time at the central holding position within the test chamber. To keep a constant prey/fish ratio, we released 18 prey items (two fish X nine prey) per treatment velocity and ended the trial once the fish failed to capture a cumulative six prey items. All other methods were identical between experiments.

Model Overview

We used the modified version of the Grossman et al. (2002) model developed by Sliger and Grossman (2021). This modification involved calculating a holding velocity for test specimens in the tank rather than treatment velocity and was obtained using the following linear equation $H_x=\beta_0+ \beta_1 V_x$ where β_0 is the intercept and β_1 is the slope where H = holding velocity and V = treatment velocity (Sliger and Grossman 2021). We parameterized the Grossman et al. (2002) NEI model using our experimental data on the relationship between prey capture success and treatment velocity. In this formula, (x) represents measurements at a specific velocity, and I (net energy gain) at velocity x can be expressed as follows:

(**Equation 1**) $I_x = (E_x * P_x) - S_x$, where:

E = prey encounter rate,

P = prey capture success,

and S = the metabolic cost of swimming S.

Prey encounter rate may be expressed as:

(**Equation 2**) $E_x = D_x * A_x * V$

In this equation, D is the energy content of the prey in the drift (J/m^3) at velocity x, A is the visual reactive area of the fish at velocity x (cm^2, Hughes and Dill 1990), and V is water velocity (cm/s, Hughes 1998).

Prey capture success may be represented as:

(**Equation 3**) $P_x = 1 / [1 + e^{(b + cV)}]$

where V is water velocity and b and c are curve-fitting constants derived from the prey capture success – treatment velocity curve (Sliger and Grossman 2021).

Thus, the NEI at microhabitat x may be expressed as

(**Equation 4**) $I = \{(D_x * A_x * V) * (1 / [1 + e^{(b+cV)}])\} – S_x$.

The variables D, A, and S are relatively constant across the range of microhabitats used by drift-feeding fishes (Grossman et al. 2002; Bozeman and Grossman 2019a); and can be dropped from the equation, yielding

(**Equation 5**) $I = V * (1 / [1 + e^{(b+cV)}])$.

We used the R package nlstools (Baty et al. 2015) to obtain curve fitting constants b and c.

These constants were used to fit the nonlinear relationship between prey capture(P) and water velocity (V) in equation three. This equation was then used iteratively to calculate the value of V in Equation 5 that maximizes net energy gain (R Core Team 2019). Fish typically hold at slightly lower velocities than that at which they forage (Hill and Grossman 1993; Liao 2007), and we calculated the predicted optimal holding velocity by inputting the predicted optimal foraging term in the linear equation describing the relationship between the treatment velocity and holding velocity. The resulting value was the predicted optimal holding velocity.

We tested the prediction of Grossman et al. (2002) model by measuring holding velocities occupied by adult Rainbow Trout in Twentymile Creek, North Carolina. We measured holding velocities using the methods of Sliger and Grossman (2021) and calculated a mean and 95% confidence interval for these measurements. As per previous tests (Grossman et al 2002; Bozeman and Grossman 2019), we considered the model prediction to be successful if it fell within the 95% confidence interval of the mean holding velocities occupied in the field. We also collected mean water velocities from 45 randomly selected habitat data points to assess the availability of velocities in Twentymile Creek. We measured mean velocity at 0.6 water column depth because all depths were less than 75 cm (Grossman and Ratajczak 1998). Velocity availability measurements and fish holding velocities were collected from the same section of the creek.

Statistical Analysis

We used generalized linear models (link = logit) and simple linear models to assess the effects of predictor variables on prey capture success, holding velocity, and reactive distance in both experiments using the methods of Sliger & Grossman (2021). For the single fish experiment, we constructed a global model using: 1) treatment velocity, 2) fish length, 3) fish mass, and 4) days in captivity, and also assessed all possible reduced models. For the dominance experiments, we added fish rank (dominant or subordinate) as a binary categorical variable (1=dominant, 0=subordinate). We ranked models using Akaike's Information Criterion for small sample sizes (AICc, Burnham and Anderson 2002) and only interpreted models with a w_i value of at least 10% of the highest w_i (Burnham and Anderson 2002; Bozeman and Grossman 2019a). We used model-averaged parameter estimates to quantify the explanatory power of each variable because the ratio of samples to predictor variables was large, and our models were biologically plausible, reducing the possibility of inaccurate information (Burnham and Anderson 2002). To avoid loss of information caused by multicollinearity (Cade 2015), we standardized parameter coefficients by their partial standard deviations. All model averaging was conducted with the MuMIn package (Bartoń 2019) in R (R Core Team 2019).

Results

Measured Fish Variables

Test specimens ranged from 160 to 191mm in length (mean = 179mm; n = 27) and 31.1 to 78.4g in mass (mean = 59.2g; n = 27) for single fish experiments. Fish were held for between 17 and 158 days (mean = 113 days, n = 27). Dominant fish differed from the subordinate fish by 13mm in mean length and10.9g in mean mass. Dominance trials began after single fish trials ended with days in captivity ranging from 162 to 217 days (mean = 194; n = 13)

Prey Capture Success

The prey capture success model with the greatest explanatory power included fish length and velocity (Table 2.1) with a w_i of 0.41 and the model with the next highest value had a w_i =

0.19 (mass + velocity; Table 2.1). Velocity was included in every interpretable model and had the highest explanatory power based on its model-averaged parameter estimate (Table 2.2) for single fish experiments. Treatment velocity negatively affected prey capture success in both experiments but had a significantly larger effect size in the single fish trials (slope β_i = -0.88, 95% CI = -0.95 to -0.80: Table 2.2, Figure 2.1). Fish length had a small effect (slope β_i =0.1, 95% CI = 0.007 to 0.29, Tables 2.1 and 2.2). Model averaging parameter estimates ($w_{+)}$ for velocity and length were high (i.e., 1.0 and 0.74 respectively; Table 2.2). The remaining parameter estimates had confidence intervals that overlapped zero and hence, may not be interpreted with confidence.

None of the predictor variables had interpreted explanatory power with respect to reactive distance in the single fish experiment and remained relatively constant across all treatment velocities (Figures 2.2). In the single fish experiment, only one model had a w_i greater than 0.20 (length + mass model, w_i = 0.25, Table 2.1). However, because confidence intervals for both predictor variables overlapped zero (length β_i = -0.09, 95% CI = -0.37 to 0.07, mass β_i = 0.10, 95% CI = -0.37 to 0.36; Table 2.2) it is unlikely that they had a strong effect on this response variable.

The interpretable models for holding velocity for the single fish experiment all included treatment velocity, with the strongest model (velocity + days in captivity) having a w_i = 0.36 (Table 2.1). Treatment velocity had a strong positive correlation with holding velocity (β_i = 0.97, 95% CI range = 0.95 to 1.0; Table 2.2, Figure 2.3) in single the single fish experiment.

Effect of Dominance

In dominance experiments, velocity was included in three of four interpretable models for prey capture success (Table 2.2). Both velocity (slope βi = -0.25, 95% CI = -0.31 to -0.18,) and rank (slope βi = 0.56 CI = 0.034 to 1.1) had high parameter estimates and high relative variable importance for prey capture success in the dominance experiment (Tables 2.1 and 2.2). Velocity had a smaller effect size on prey capture success (slope βi = -0.25, 95% CI = -0.31 to -0.18,) in dominance trials, than in the single fish experiment (slope βi -0.88 CI = -0.95 to -0.80; Table 2.2, Figures 2.4-2.6). In the dominance experiment, only one reactive distance model had a w_i greater than 0.2 (rank + velocity model, w_i = 0.411, Table 2.1). Velocity had a negative effect (slope βi = -0.52, 95% CI = -0.62 to -0.37) and rank had a positive effect (βi = 0.39, 95% CI = 0.08 to 0.70) on reactive distance in dominance trials (Table 2.2). As was found in single the single fish experiment, holding velocity increased with treatment velocity in the dominance experiment (βi = 0.97, 95% CI range = 0.94 to 1.0; Table 2.2). Velocity also had high relative variable importance $w+$ = 1.0 for velocity (Table 2.1, Figures 2.4-2.6). Parameter estimates for all other predictor variables had confidence intervals that overlapped zero (Table 2.2) and were not interpretable.

In conclusion, dominant fish captured the vast majority of prey items and consequently had higher prey capture success across all treatment velocities than subordinate fish (Figures 2.4). Dominance had little cost, because there were no significant differences prey capture success between dominant fish in single fish experiments and dominance trials (Figure 2.5). By contrast, the cost of being subordinate was high and capture success of subordinate fish was markedly higher in single fish experiments (Figure 2.6). Dominance behavior also affected the reactive distance of fish. Subordinate fish had significantly lower reactive distances than dominant fish at all velocities except at 30 cm/s where their 95% CI overlapped (Figure 2.7). Holding velocity between dominant and subordinate fish did not differ at velocities between 10 and 40cm/s but were slightly higher for subordinates at 50 cm/s (Figure

2.8).

Optimal Holding Velocity

We fit the mean prey capture from each treatment velocity of the single fish experiment to Equation 3 of the Grossman et al. (2002) optimal foraging model (RSS = 1.42), which yielded curve fitting values of b = -4.69 and c = 0.092. Inputting these values into Equation 5 and solving for the value of V that maximizes I, yielded a value of 40.1cm/s. Inputting this value as the treatment velocity term in the linear equation of the relationship between treatment and holding velocity for the Rainbow Trout single fish experiment (holding velocity = 1.38 + 0.59[treatment velocity], n = 96, $R^2 = 0.67$, p << 0.001) yielded an optimal holding velocity value of 33 cm/s. The mean holding velocity of individuals at Twentmile Creek was 27.1cm/s with a 95% confidence interval of 22-32cm/s. The prediction fell 1 cm/s outside the upper confidence limit of the field data which is within measurement error for our velocity meter. Velocity availability within the study site in Twentymile Creek ranged from 0 to 270cm/s (Figure 2.9).

Discussion

Water velocity had a strong effect on prey capture success and holding velocity for adult Rainbow Trout in both single fish and dominance trials. Dominance also affected prey capture success, with dominant fish having substantially higher capture success than subordinates. Only water velocity affected reactive distance, but this effect was small ad only occurred in the dominance experiment. Holding velocity was affected by water velocity, dominance, and days in captivity.

Water velocity has been shown to influence the foraging of drift-feeding fishes, especially salmonids, in multiple ways (Fausch 2014; Grossman 2014; Piccolo et al. 2014;

Rosenfeld et al. 2014). At lower stream velocities, drift-feeders may catch most prey present but may be unable to meet energy demands due to low prey availability (Bozeman and Grossman 2022). Prey abundance in streams is typically thought to increase with water velocity because high-velocity water is able to carry greater quantities of drift as well as prey with greater mass (Bozeman and Grossman 2022). However, recent analyses indicate this relationship is not universal (Sliger and Grossman 2021). At the other extreme, at high velocities prey are moving so fast that fish may become physically unable to detect and capture them (Hill and Grossman 1993). This results in the frequently observed negative exponential relationship between velocity and prey capture success (Hill and Grossman 1993; Grossman et al 2002; Grossman 2014; Bozeman and Grossman 2022); a result observed in our experiments. In addition, we observed a positive relationship between treatment velocity and holding velocity in previous work (Bozeman and Grossman 2019a, b; Sliger and Grossman 2021). We also observed Rainbow Trout in Twentymile Creek foraging at slightly velocities than their held position, which also has been observed previously in both laboratory and natural settings (Jenkins 1969; Everest and Chapman 1972; Liao 2007; Bozeman and Grossman 2022).

There were no clear patterns in the potential factors affecting reactive distance. Although treatment velocity and rank were identified as variables having explanatory power in dominance trials, their effect sizes overlapped zero, which also has been observed in earlier research (Donofrio et al. 2018; Bozeman and Grossman 2019a, b; Sliger and Grossman 2021). Nonetheless, in other drift-feeding fishes, reactive distance may be affected by factors such as 1) light intensity (Vogel and Beauchamp 1999), and 2) turbidity (Barrett et al. 1992; Vogel and Beauchamp 1999; Hazelton and Grossman 2009)

Our finding that dominance affected multiple aspects of foraging behavior is consonant with the current consensus that intraspecific competition manifested by dominance is the likely mechanism producing density-dependent effects observed in many salmonid populations (Utz and Hartman 2009; Grossman et al. 2010; Huntsman and Petty 2014; Grossman and Simon 2020). Although subordinate Rainbow Trout experienced greatly reduced prey capture success, this effect might be lessened in stream habitats, where subordinates are likely better able to avoid dominants than is possible in the testing flume. Nonetheless, Rainbow Trout in Twentymile Creek only were observed near each other once. In addition, the lack of physical proximity of Rainbow Trout in Twentymile Creek and other streams may indicate that subordinates have been displaced into lower quality microhabitats. Despite the benefits conferred by dominance, recent studies with other salmonid species show that prey capture success of dominants may be slightly lower when a subordinate is present than when they are the sole fish in an experiment (Bozeman and Grossman 2019a, b, Sliger and Grossman 2021).

In conclusion, we have shown that water velocity and behavioral dominance have significant impacts on the foraging behavior of Rainbow Trout. In addition, Rainbow Trout held positions in Twentymile Creek that were only one cm/s greater than that predicted by Grossman et al (2002) optimal foraging model, despite a range of possible holding velocities that totaled over two meters per second. The Grossman et al. (2002) model also predicted an optimal holding position that was less than 1 cm/s outside the upper confidence interval for Dolly Varden Char in Panguingue Creek, Alaska, however, this species coexisted with a strong potential competitor (Bozeman and Grossman 2019b) and because of its shallow depth also may be exposed to avian and terrestrial predators, which are not accounted for in the model. Nevertheless, this NEI-based, habitat selection model is one of the few models that has been tested with multiple species, at multiple sites and in multiple years (Grossman et al. 2002).

Fitness-based optimality models have contributed greatly to our understanding of how animals choose habitats. Although they are not necessarily designed for management purposes, the Grossman et al. (2002) model does yield the predicted optimal holding positions for species, and that information is useful in both habitat management (stream rehabilitation or modification) as well as predicting the impacts of water abstraction or impoundment. From a management perspective, our results indicate that habitat management or stream modifications should ensure that holding velocities between 25 and 35 cm/s are common within the stream.

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Tables

Table 2.1. AICc values and Akaike weights (w_i) for interpretable models with explanatory power for all response variables (Resp. Var.) in both experiments. Experiment titles are Single Fish and Dominance, respectively. Predictor variables are abbreviated as follows: treatment velocity = Velocity, fish length = Length, days in captivity = Days, Rank = dominance rank. We only present interpretable models (i.e., those with w_i greater or equal to 10% of the w_i of the best model). Values in parentheses represent the likelihood of the model with the highest value being "true" given the data, in comparison to models with lower but interpretable w_i values

Response Variable	Experiment	Model	AICc	w_i
Prey Capture Success	Single Fish	Length + Velocity	226.0	0.40
		Mass + Velocity	227.5	0.19 (2.1)
		Length + Mass + Velocity	228.1	0.14(2.9)
		Days + Length + Velocity	228.1	0.14(2.9)
	Dominance	Rank + Velocity	101.0	0.22
		Days + Rank + Size +Velocity	101.8	0.15(1.5)
		Days + Rank	101.9	0.15(1.5)
		Rank + Length + Velocity	102.0	0.14(1.6)
Reactive Distance	Single Fish	Length + Mass	496.5	0.26
	Dominance	Rank + Velocity	270.5	0.41
		Days + Rank + Velocity	272.6	0.15(2.7)

		Rank + Velocity + Mass	272.7	0.14(2.7)
		Rank + Length + Velocity	272.7	0.05(8,2)
Holding Velocity	Single Fish	Velocity + Days	-107.8	0.36
		Velocity + Days +Mass	-106.9	0.23(1.6)
		Velocity +Days + Size	-106.3	0.17(2.1)
		Global	-105.3	0.10(3.6)
	Dominance	Velocity + Rank + Days	-63.91	0.25
		Velocity +Rank	-62.50	0.12(2.1)
		Velocity + Length + Days	-62.48	0.12(2.1)
		Velocity + Rank + Length + Days	-62.13	0.10(2.5)
		Velocity + Rank + Days + Mass	-62.00	0.10(2.5)
		Velocity + Rank + Mass	-61.70	0.08(3.1)

Table 2.2 Model-averaged parameter coefficients standardized by partial standard deviations (with 95% confidence intervals) and relative variable importance (*w*+) for predictor variables and response variable combinations in all experiments. Variables described in table 2.1. Confidence intervals marked by * overlap 0.

Response Variable	Predictor Variable	Experiment	Estimate (95% CI)	w+
Prey Capture	Velocity	Single Fish	-0.88(-0.95 to -0.80)	1.0
		Dominance	-0.25(-0.31 to -0.18)	1.0
	Length	Single Fish	0.21(0.0068 to 0.29)	0.74
		Dominance	0.014(-0.032 to 0.026)*	0.38
	Mass	Single Fish	0.045(-0.079 to 0.29)*	0.45
		Dominance	0.0033(-0.045 to 0.10)*	0.34
	Days	Single Fish	0.041(-0.073 to 0.071)*	0.26
		Dominance	-0.023(-0.11 to 0.10)*	0.48
	Rank	Dominance	0.56(0.034 to 1.1)	1.0
Reactive Distance	Velocity	Single Fish	0.063(-0.17 to 0.17)*	0.26
		Dominance	-0.52(-0.62 to -0.37)	1.0
	Days	Single Fish	0.0078(-0.16 to 0.21)*	0.28
		Dominance	0.014(-0.14 to 0.10)*	0.26
	Length	Single Fish	-0.099(-0.37 to 0.07)*	0.57
		Dominance	0.0021(-0.13 to 0.13)*	0.25
	Mass	Single Fish	0.10(-0.37 to 0.36)*	0.6

		Dominance	0.0093(-0.13 to 0.13)*	0.25
	Rank	Dominance	0.39(0.085 to 0.70)	1.0
Holding velocity	Velocity	Single Fish	0.97(0.95 to 1.0)	1.0
		Dominance	0.97(0.94 to 1.0)	1.0
	Days	Single Fish	0.03(0.013 to 0.054)	0.85
		Dominance	0.02(0.0061 to 0.06)	0.73
	Length	Single Fish	0.00(-0.031 to 0.027)*	0.31
		Dominance	-0.01(-0.11 to 0.034)*	0.39
	Mass	Single Fish	-0.013(-0.040 to 0.010)*	0.37
		Dominance	-0.011(-0.12 to 0.045)*	0.33
	Rank	Dominance	-0.044(-0.11 to 0.012)*	0.71

Figures

Figure 2.1: The relationship between prey capture success and treatment velocity in the single fish experiments. Error bars represent 95% confidence intervals. Point labels represent the number of trials run.

Figure 2.2: The relationship between prey capture success and velocity for dominant and subordinate Rainbow Trout. Error bars represent 95% confidence intervals. Point labels represent sample sizes

Figure 2.3: The relationship between holding velocity and treatment velocity in the single fish experiments. Error bars represent 95% confidence intervals. Point labels represent sample sizes

Figure 2.4: Dominant fish make up nearly all of the successful prey captures in the paired trial. Error bars represent 95% confidence intervals. Point labels represent sample sizes.

Figure 2.5: Dominant fish prey capture success was not significantly different from single fish prey capture success. Error bars represent 95% confidence intervals. Point labels represent sample sizes.

Figure 2.6 Subordinate fish prey capture success was drastically lower than that of single fish prey capture success Error bars represent 95% confidence intervals. Point labels represent sample sizes

Figure 2.7: Mean reactive distance was consistently lower for subordinate Rainbow Trout at all velocities except at 30cm/s and was negatively affected by velocity. Error bars represent 95% confidence intervals. Point labels represent sample sizes

Figure 2.8: Mean holding distance was only different between dominant and subordinate Rainbow Trout at the highest recorded velocity. Error bars represent 95% confidence intervals. Point labels represent sample sizes

Figure 2.9: Predicted optimal foraging velocity fell 1cm/s outside of the observed range. All Rainbow Trout we observed below mean available stream velocity. Error bars represent 95% CI for observed holding velocity.

Figure 2.1

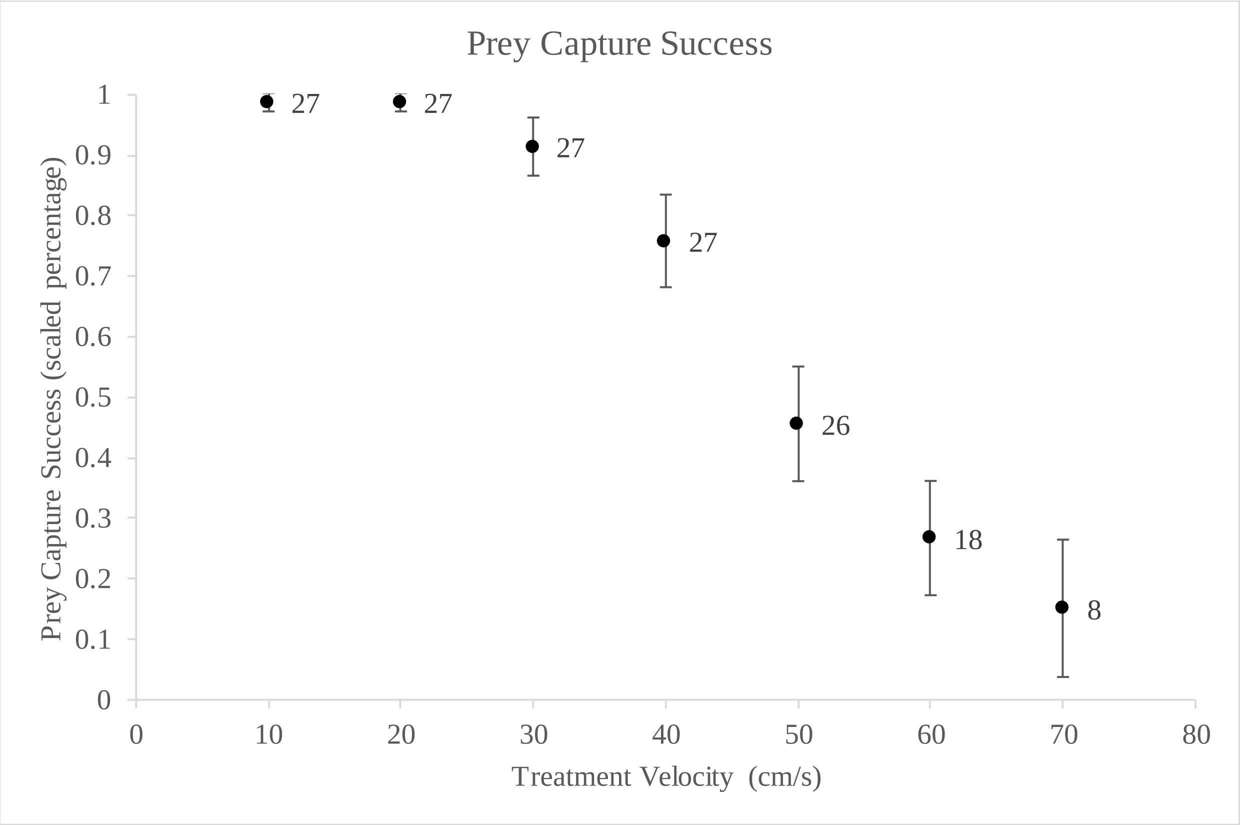

Prey Capture Success
Prey Capture Success (scaled percentage)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
27
27
27
27
26
18
8
0
10
20
30
40
50
60
70
80
Treatment Velocity (cm/s)

Figure 2.2

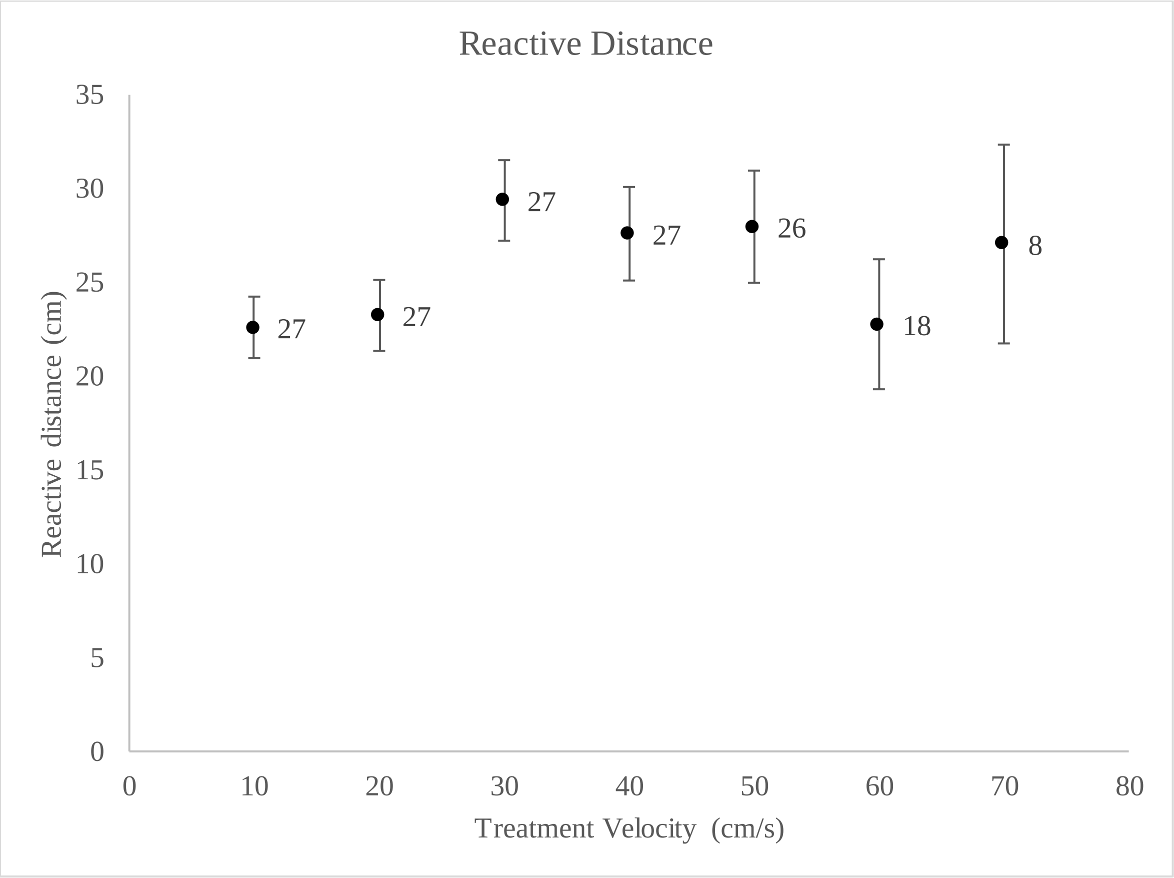

Reactive Distance
Reactive distance (cm)
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
Treatment Velocity (cm/s)
27
27
27
27
26
18
8

Figure 2.3

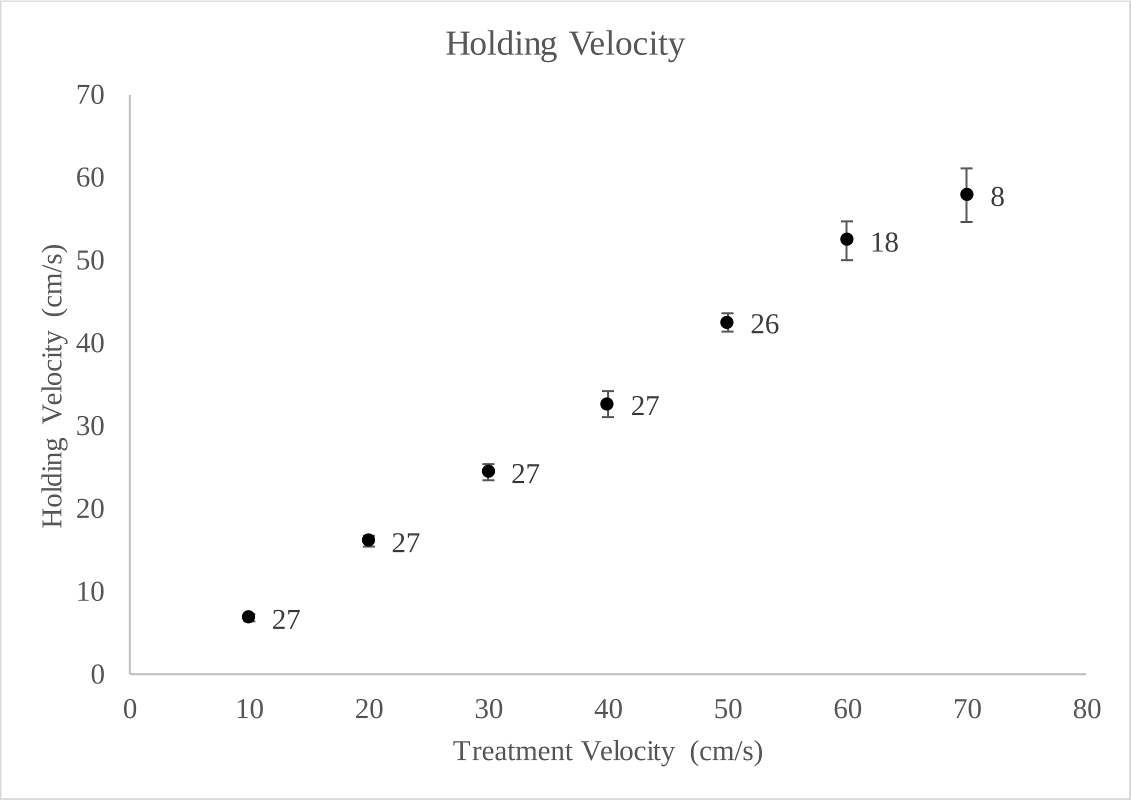

Holding Velocity
Holding Velocity (cm/s)
Treatment Velocity (cm/s)
0
10
20
30
40
50
60
70
0
10
20
30
40
50
60
70
80
27
27
27
27
26
18
8

Figure 2.4

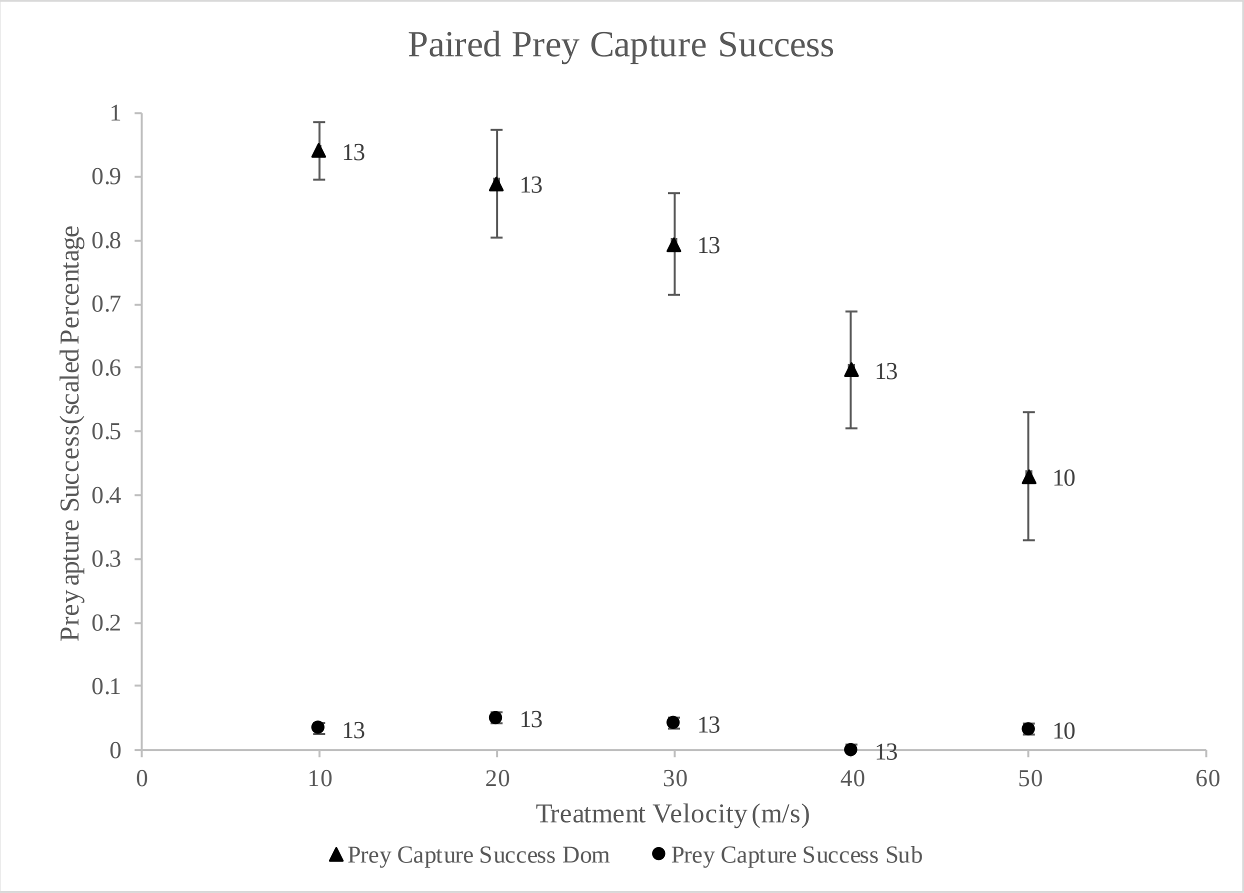

Paired Prey Capture Success
Prey apture Success(scaled Percentage
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
60
Treatment Velocity (m/s)
13
13
13
13
10
13
13
13
13
10
▲ Prey Capture Success Dom
● Prey Capture Success Sub

Figure 2.5

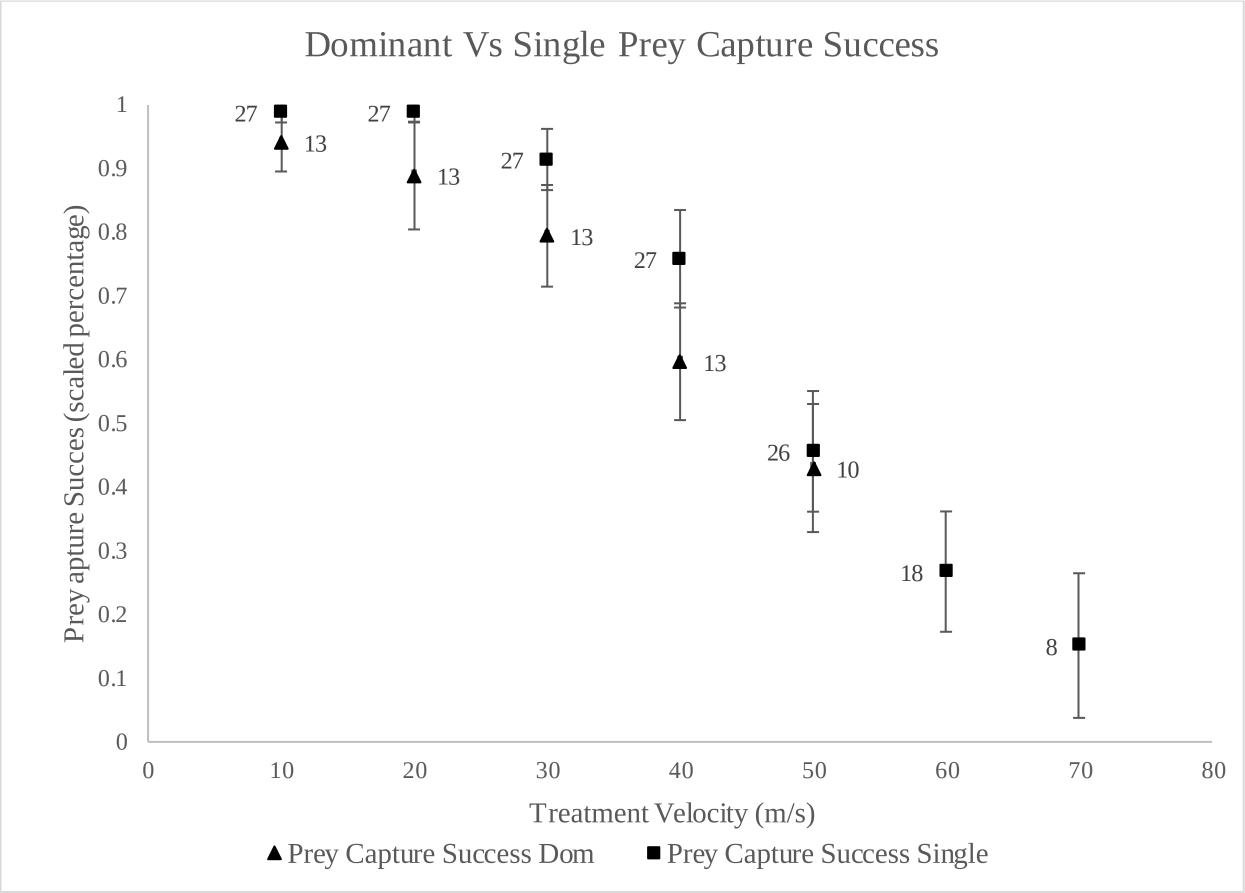

Dominant Vs Single Prey Capture Success
Prey apture Succes (scaled percentage)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
27
13
27
13
27
13
27
13
26
10
18
8
0
10
20
30
40
50
60
70
80
Treatment Velocity (m/s)
▲ Prey Capture Success Dom
■ Prey Capture Success Single

Figure 2.6

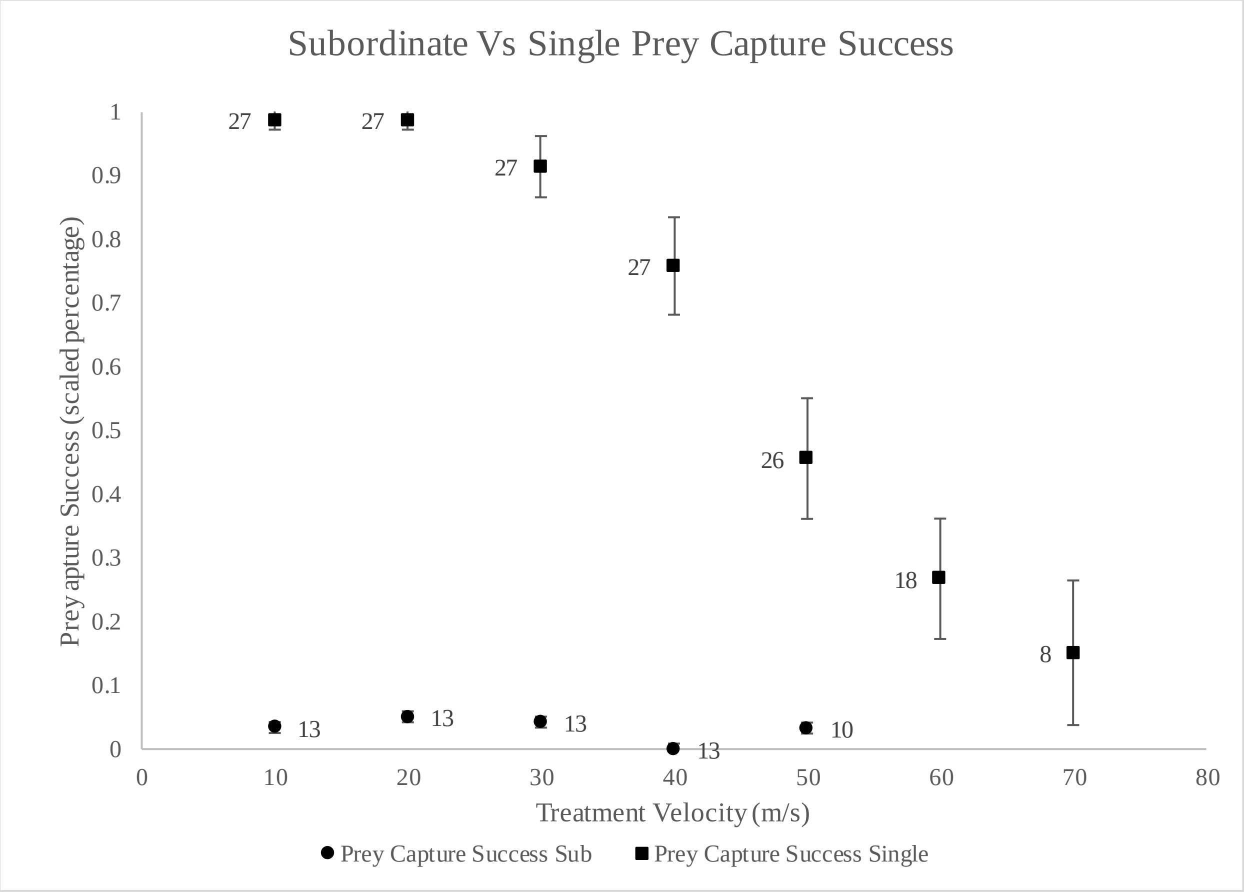

Subordinate Vs Single Prey Capture Success
Prey apture Success (scaled percentage)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
60
70
80
Treatment Velocity (m/s)
27
27
27
27
26
18
8
13
13
13
13
10
● Prey Capture Success Sub
■ Prey Capture Success Single

Figure 2.7

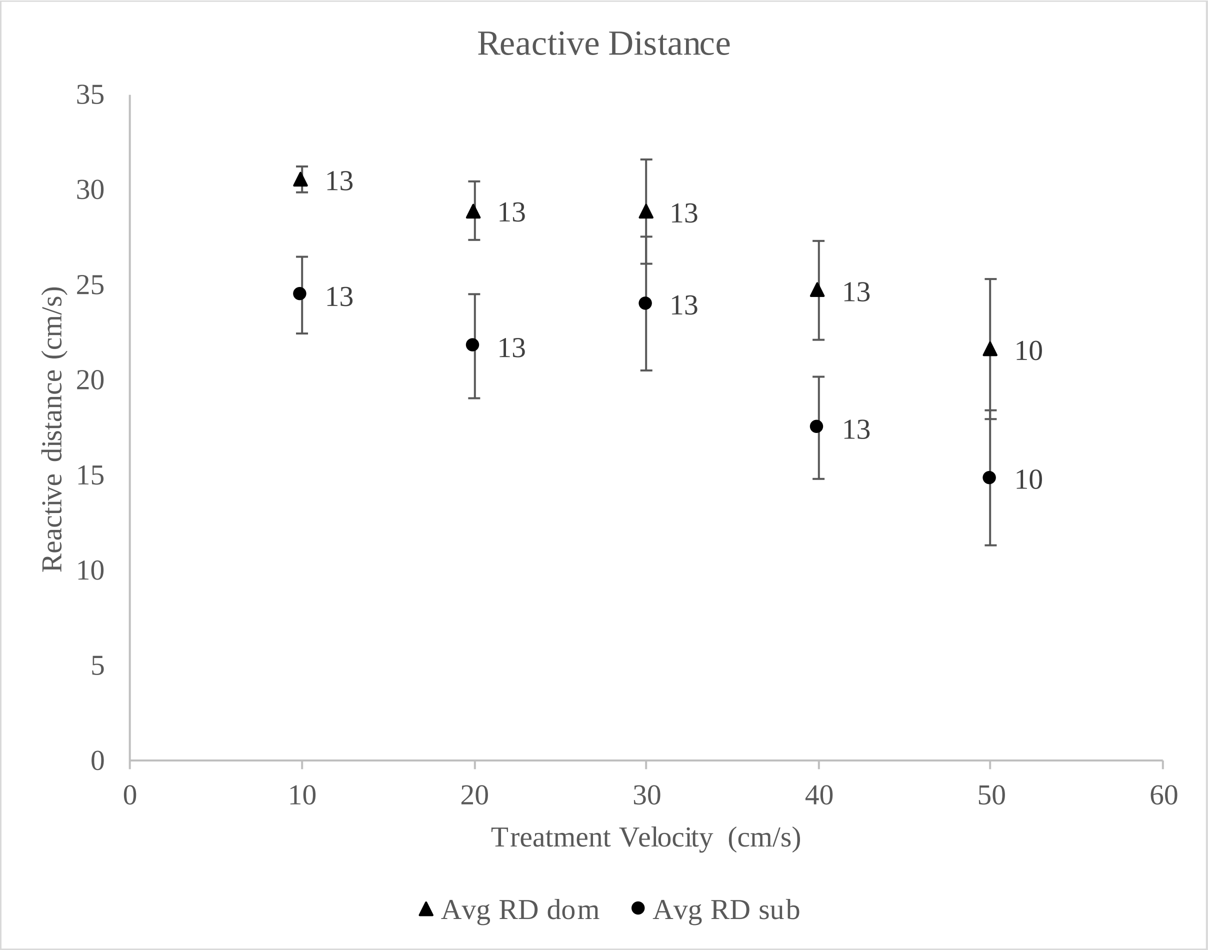

Reactive Distance
35
30
25
20
15
10
5
0
Reactive distance (cm/s)
0
10
20
30
40
50
60
Treatment Velocity (cm/s)
13
13
13
13
13
13
13
13
10
10
▲ Avg RD dom
● Avg RD sub

Figure 2.8

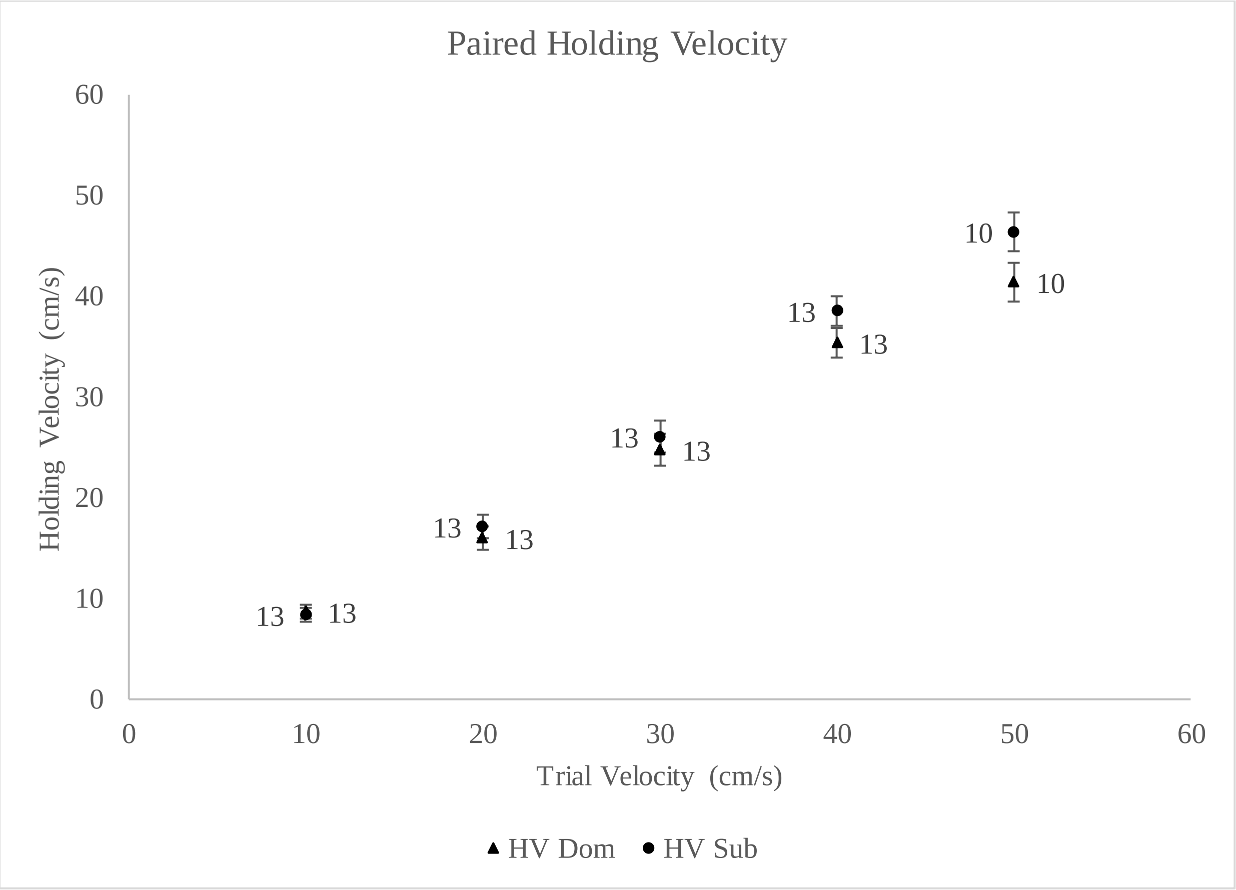
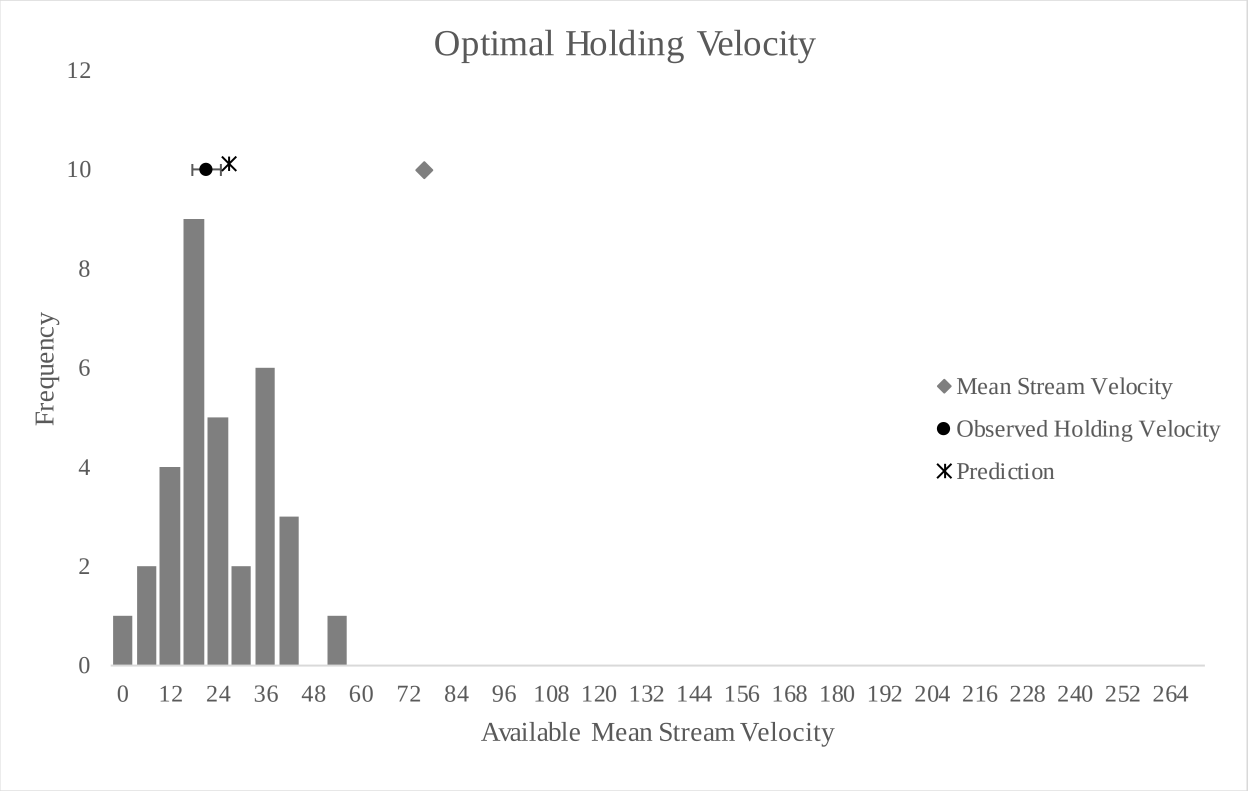

Paired Holding Velocity
Holding Velocity (cm/s)
0
10
20
30
40
50
60
Trial Velocity (cm/s)
0
10
20
30
40
50
60
13
13
13
13
13
13
13
13
10
10
▲ HV Dom
● HV Sub

Figure 2.9


Optimal Holding Velocity
12
10
8
6
4
2
0
Frequency
0
12
24
36
48
60
72
84
96
108
120
132
144
156
168
180
192
204
216
228
240
252
264
Available Mean Stream Velocity
◆ Mean Stream Velocity
● Observed Holding Velocity
✳ Prediction