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3 Foraging behavior and optimal microhabitat selection in Yukon River Basin nonanadromous

4 Dolly Varden Charr (*Salvelinus malma*)

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30

31 **Abstract**

32 Species conservation requires understanding the mechanistic processes of habitat selection and
33 their effects on fitness. Nonetheless, there are few fitness-based habitat selection models for
34 aquatic organisms. We examined multiple aspects of foraging behavior of nonanadromous Dolly
35 Varden Charr (*Salvelinus malma*) in Panguingue Creek, Alaska, USA and applied these data to
36 test a fitness-based microhabitat selection model. Velocity negatively affected prey capture
37 success, positively affected holding velocity, and had no effect on reactive distance. Dominance
38 was a better predictor of prey capture success than length difference between competitors, but
39 there was no relationship between these variables and holding velocity or reactive distance. We
40 used the velocity – prey capture success relationship to parameterize the microhabitat habitat
41 selection model and compared the predicted optimal holding velocity to the 95% confidence
42 interval (24.9 – 29.3 cm/s) of holding velocities occupied by Dolly Varden (N = 29) in
43 Panguingue Creek. The prediction of 24.0 cm/s fell just slightly (0.9 cm/s) outside the lower
44 limit of the confidence interval; the model barely failed to predict holding velocity for this
45 species in Panguingue Creek. Although this discrepancy fell within measurement error, model
46 failure also may have been due to influence of high turbulence on fish holding velocities in the
47 creek, low sample sizes imposed by permitting limitations, or field logistical issues. The
48 relationship between velocity and prey capture success is an important aspect of drift-feeder
49 habitat selection. Our optimal holding velocity prediction for Dolly Varden should aid in the
50 management and conservation of this species.

51

52 Keywords: Dolly Varden, net energy intake model, drift feeding, habitat selection, velocity

53

54

55 **Introduction**

56 Our ability to conserve species largely depends upon our understanding of how
57 organisms interact and select habitats. Temperate streams in the Northern Hemisphere are
58 dominated by fish species that feed on drifting invertebrates (i.e., drift-feeders; Grossman, 2014;
59 Piccolo, Frank, & Hayes, 2014), and many of these species, including the Salmonidae, are
60 economically important. Drift-feeding is a fairly stereotypical feeding behavior that involves: 1)

61 holding a relatively constant position in the stream (i.e., the holding position), 2) identifying
62 potential prey in the drift, 3) pursuing and capturing the prey, and 4) returning to the holding
63 position. Despite the substantial abundance and high diversity of lotic drift-feeders, little is
64 known about the mechanics of drift-feeding itself. Only over the past two decades have
65 ecologists begun to explore the relationships between velocity, reactive distance and prey
66 capture, and this just for a very few species.

67 The most common method used to quantify microhabitat selection (i.e., at the position of
68 the fish) in drift-feeders is by conducting correlational studies based on variables previously
69 shown to potentially influence habitat selection (e.g., velocity, depth, substrate composition).
70 Nonetheless, these methods only establish correlations not mechanisms, and may have limited
71 utility in identifying the causal relationships producing habitat selection (Grossman, 2014). In
72 recent decades, net-energy intake (NEI), fitness-based approaches have gained favor as an
73 alternative to correlational approaches because they estimate the energy gained by an individual
74 via occupying a given microhabitat (Rosenfeld, Bouwes, Wall, & Naman, 2014).

75 Several NEI models have been developed for drift-feeders since Fausch's (1984)
76 foundational model (Piccolo et al., 2014). These models vary in complexity and incorporate
77 different combinations of habitat variables, including: prey capture success and velocity (e.g.,
78 Grossman, Rincon, Farr, & Ratajczak, 2002; Piccolo, Hughes, & Bryant, 2008a; Piccolo,
79 Hughes, & Bryant, 2008b); invertebrate prey and habitat abundance (e.g., Rosenfeld & Taylor,
80 2009); turbidity (e.g., Harvey & Railsback, 2009); reach carrying capacity (e.g., Hayes, Hughes,
81 & Kelly, 2007); reactive distance (e.g., Hughes & Dill, 1990); intraspecific competition (e.g.,
82 Hughes, 1992; Railsback, Harvey, Jackson, & Lamberson, 2009); swimming costs (e.g., Hayes,
83 Stark, & Shearer, 2000); and woody debris (e.g., Wall et al., 2017). Furthermore, these models
84 potentially represent robust management tools because they can be linked to multidimensional
85 models of stream flow and used to produce more realistic estimates of habitat quality and
86 quantity at reach and watershed scales (Hayes, Goodwin, Shearer, Hay, & Kelly, 2016; McHugh
87 et al., 2017; Railsback, 2016).

88 Although NEI models show great promise in elucidating the causal mechanisms behind
89 microhabitat selection, few NEI models have been tested in multiple systems or with multiple
90 species (but see Bozeman & Grossman, 2019; Donofrio, Simon, Neuswanger, & Grossman,
91 2018). Likely, this is a result of the logistical difficulties of quantifying both the costs and

92 benefits at a given holding position; data required by many NEI models. Typically, costs are
93 estimated directly via swimming respirometry (Facey & Grossman, 1990, 1992), via published
94 data for surrogate species, or less commonly for the species of interest. However, Hill and
95 Grossman (1993) and Grossman et al. (2002) found that the inclusion of cost data (swimming
96 respirometry energy estimates) in an NEI model led to greater variance and reduced accuracy of
97 optimal holding velocity predictions. Consequently, they developed reduced models, based on
98 foraging costs alone. The reduced NEI model estimates an optimal holding position based on the
99 experimentally derived relationship between prey capture success and velocity, and has
100 successfully predicted field holding positions for four cyprinid species and two salmonids (small
101 Rainbow Trout, *Oncorhynchus mykiss*, and Arctic Grayling, *Thymallus arcticus*) (Bozeman &
102 Grossman, 2019; Grossman et al., 2002), although it failed to predict holding positions of
103 juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) and Arctic Grayling in Panguingue
104 Creek, Alaska respectively (Bozeman & Grossman, 2019; Donofrio et al., 2018). The Grossman
105 et al. (2002) model has several advantages including its logistical simplicity and tractability and
106 its successful testing in multiple habits with multiple species. Nonetheless, the robustness of the
107 model only can be determined by further testing in different habitats and with different species,
108 hence the present study.

109 Our overall objectives involved elucidation of the mechanics of drift-foraging and
110 microhabitat selection by an understudied, nonanadromous population of Dolly Varden Charr
111 (*Salvelinus malma*, henceforth Dolly Varden). Consequently, we quantified the relationship
112 between water velocity and prey capture success, holding velocity, and reactive distance, and
113 used portions of these data to parameterize and test the robustness of the Grossman et al. (2002)
114 NEI model, with this population.

115

116 ***Test Species***

117 Dolly Varden are widely distributed across the Pacific Rim from the Pacific Northwest
118 U.S.A. throughout the Alaskan Peninsula and Northwest Territories to eastern Asia and the
119 Northern Japanese archipelago (Armstrong & Morrow, 1980; Dunham et al., 2008; May-
120 McNally, Quinn, & Taylor, 2015; Reist, Johnson, & Carmichael, 1997; Reist, Low, Johnson, &
121 McDowell, 2002). Panguingue Creek contains a nonanadromous form of Dolly Varden that is
122 widely, but patchily, distributed in interior Alaska. Little is known about nonanadromous Dolly

123 Varden, but they are significantly smaller (maximum size in Panguingue Creek is ~ 260 mm in
124 length or 0.5 kg in mass) and perhaps younger (up to 10 years) than migratory forms (Armstrong
125 & Morrow, 1980; Bond, Miller, & Quinn, 2015; Koizumi, Yamamoto, & Maekawa, 2006;
126 Washington Department of Fish and Wildlife, 2000). Dolly Varden are opportunistic drift
127 feeders, although it is likely that the anadromous form is more piscivorous, given its much larger
128 maximum size (760 mm; Washington Department of Fish and Wildlife, 2000). Nonanadromous
129 Dolly Varden: 1) occupy small, harsh (i.e., typically iced over from October to April or May),
130 high-latitude, streams, 2) spawn during late summer and early fall, and 3) overwinter in gravel
131 and woody substrate (Armstrong & Morrow, 1980; Jonsson, Hindar, & Northcote, 1984;
132 Krueger, 1981). In Alaska, Dolly Varden are important subsistence and sport fish; some
133 populations supplement subsistence harvest in areas where salmon are less plentiful (Fall et al.,
134 2017; Harding & Coyle, 2011). Nonetheless, basic biological information is lacking for most
135 Dolly Varden populations in the Pacific Northwest (Washington Department of Fish and
136 Wildlife, 2000; Williams et al., 2015).

137 The taxonomic and ecological differences between nonanadromous Dolly Varden and the
138 four cyprinid and one salmonid species previously used to test the Grossman et al. (2002) NEI
139 model make the former an excellent candidate for testing model robustness. For example, Dolly
140 Varden are patchily distributed and occupy streams with harsh climate regimes; whereas, the
141 species previously used to test the Grossman et al. (2002) NEI model occupy a flashy but
142 climatically benign stream in the Southern Appalachian Mountains. Previous tests of the
143 Grossman et al. (2002) NEI model with Alaskan species yielded both positive and negative
144 results (Bozeman & Grossman, 2019; Donofrio et al., 2018), which indicates that further testing
145 of the model, especially with a species as ecologically distinct as Dolly Varden, is warranted.

146

147 **Materials and Methods**

148 *Experimental Procedures*

149 We used a methodology described in several recent papers (Bozeman & Grossman, 2019;
150 Donofrio et al., 2018); hence our descriptions will be brief. Dolly Varden were captured in
151 August 2015 and September 2016 in Panguingue Creek in central Alaska (Nenana River
152 drainage, WGS84 Coordinates: 63.906 N, 149.095 W). Panguingue Creek is a typical low-order,
153 relatively clear, interior Alaska stream that flows into the glacially-influenced, turbid Nenana

154 River of the Yukon River Basin. The reach of Panguingue Creek where specimens were
155 collected had an average water temperature of 10 °C, average depth of 35 cm, and average
156 velocity of 56 cm/s (range: 4 – 126 cm/s). The creek supports a migratory population of Arctic
157 Grayling (*Thymallus arcticus*), along with occasional sculpin (*Cottus* sp.) and whitefish
158 (*Coregonus* sp.). Due to permitting restrictions by Alaska Fish and Game, we only were able to
159 obtain 30 Dolly Varden (captured via hook and line). We then immediately (within two days of
160 capture) shipped fish (15 in 2015 and 15 in 2016) to the University of Georgia via air freight in
161 chilled, insulated containers. Transportation never lasted longer than 48 hours and there was no
162 evidence of mortality, disease, or impaired behavior from transport. We originally placed fish in
163 large holding tanks but their territoriality was sufficiently strong that ten fish were injured prior
164 to developing a satisfactory holding procedure (i.e., no more than five fish in a 700 l tank, with
165 substantial interior structure).

166 We assessed foraging behavior in experiments utilizing both individual fish (Single-Fish
167 Experiment, SFE) and pairs of fish (Dominance Experiment, DE). Specimens from the second
168 shipment were used in the SFE and the DE. Mean standard lengths (mm \pm SD) and masses (g \pm
169 SD) of experimental specimens were 165 \pm 24 mm and 52.9 \pm 21.1 g. We assumed all
170 experimental specimens were adults. We held fish in tanks at 10° C, which matched field
171 collection temperatures (10° C, N = 29). Holding times of specimens varied between 3 and 134
172 days before their use in single-fish experiments. We fed fish frozen blood worms (*Glycera*) *ad*
173 *libitum* during the holding period; however, rations were withheld one day prior to the start of a
174 trial to increase feeding motivation (Grossman et al., 2002).

175 We conducted experiments in a 3.5 m L x 0.75 m W x 1.0 m H artificial stream flume
176 (see Figure 1 in Bozeman & Grossman, 2019). Test subjects were confined to a 1.5 m L x 0.75
177 m W x 1.0 m H test chamber (top half of the stream flume), bounded upstream by a polyvinyl
178 chloride (PVC) collimator and downstream by a mesh and PVC barrier. The PVC collimator
179 reduced flow heterogeneity by distributing flow approximately evenly across the width of the
180 test chamber and allowed us to maintain accuracy in velocity trials. The downstream barrier
181 ensured that specimens remained in view of cameras and observer. We filled the stream flume
182 with dechlorinated tap water (turbidities < 0.001 NTU's, Athens-Clarke County) to a depth of 40
183 cm. We drained and refilled the stream flume approximately every five days to maintain water
184 quality and minimize debris accumulation. Water clarity and general conditions in the flume

185 (<https://youtu.be/zHbyNTxelxM>) were similar to those of the test stream, Panguingue Creek (see
186 <https://www.youtube.com/watch?v=HpGrtChuAHM>) although the substratum was much less
187 complex and water was clear rather than humic. We controlled water velocity with two 24V (80-
188 pound thrust), variable-speed trolling motors, and maintained water temperatures with an
189 electronic chiller placed behind the test chamber. Several thin strands of bamboo were attached
190 to the collimator which replicated natural stream cover and prevented fish from taking up a
191 holding position in front of the prey-delivery tubes. We made all observations from behind a
192 black plastic sheeting to minimize disturbance.

193 We used frozen bloodworms (8.8 ± 1.4 mm, $N = 50$) for test prey because they: 1)
194 resembled natural prey, 2) elicited natural foraging behavior in Dolly Varden, and 3) were
195 readily visible in videos of experiments. Logistically, it was impractical to obtain and use
196 Alaskan invertebrates as test prey. Fish were fed during experiments by an assistant who flushed
197 prey into the test chamber using water injected through one of three plastic tubes (6 mm
198 diameter) mounted at a depth of 8 cm (from surface) on the collimator. To ensure prey were
199 delivered naturally throughout the flume we spaced feeding tubes at 19 cm intervals across the
200 width of the test chamber. We filmed each trial with dual video cameras for subsequent video
201 analysis with VidSync 3D video analysis software (www.vidsync.com; Neuswanger, Wipfli,
202 Rosenberger, & Hughes).

203

204 *Velocity & Reactive Distance Measurements*

205 Our experimental design included three different velocity measurements: 1) treatment
206 velocity, 2) holding velocity, and 3) capture velocity. Treatment velocities ranged from 10 to 70
207 cm/s (10 cm/s increments) and represented the velocities at which prey were delivered to
208 specimens in the test chamber. Immediately prior to each velocity trial, we measured treatment
209 velocity across the width of the mid-point of the test chamber ($n = 3$) at 8 cm depth from the
210 surface (prey delivery depth) with an electronic velocity meter (± 0.01 cm/s).

211 Similar to most salmonids, Dolly Varden generally held position in a small and consistent
212 area from which they sallied forth to capture prey. We measured velocity at this position and
213 termed it “holding velocity”. Holding velocity was measured after completion of a trial using an
214 electronic velocity meter placed in fish locations identified via video recordings, observer
215 records, and benchmarks on the flume (Bozeman & Grossman, 2019). On rare occasions when

216 an individual held position at multiple locations during a trial, we calculated holding velocity as
217 the average velocity of those positions. In previous studies, holding velocity has been termed
218 focal-point velocity (Grossman, 2014; Grossman et al., 2002) and is the optimal velocity
219 predicted by the Grossman et al. (2002) NEI model.

220 Dolly Varden rarely failed to capture prey in experiments, and capture velocity
221 represented the velocity of drifting prey when caught by a test fish. We estimated capture
222 velocity by marking the prey item at any point where visible in trial videos and again at the point
223 of capture and used VidSync (Neuswanger et al., 2016) to calculate the elapsed time and distance
224 between those two points. The strong linear relationship and high correlation between prey
225 capture velocities and treatment velocities ($R^2 = 0.97$, $y = 0.89x + 3.47$) is evidence that our
226 treatment velocities delivered prey at the desired velocity throughout the duration of trials. All
227 velocities were recorded in cm/s.

228 Reactive distance represented the distance between the nose of a foraging drift-feeder and
229 a prey item when the fish first orients towards the prey to initiate pursuit and capture. We
230 estimated reactive distance using VidSync (Neuswanger et al., 2016), which calculated the
231 distance between the prey item and nose of the experimental specimen at the moment of fish
232 orientation towards the prey. Reactive distance was measured in three dimensions, with the
233 theoretical maximum reactive distance being the diagonal through the test chamber (i.e., from
234 low, near, rear corner to high, far, front corner). Given the dimensions of the test chamber with a
235 water depth of 40 cm, the main diagonal (i.e., maximum possible reactive distance) was 1.72 m.

236

237 *Single-Fish Experiment*

238 We quantified relationships between water velocity and: 1) prey capture success (proportion of
239 prey captured), 2) holding velocity, and 3) reactive distance, for each fish in the SFE. We used
240 standardized experimental methods from our laboratory (Bozeman & Grossman, 2019; Donofrio
241 et al., 2018; Grossman, 2014). For clarity, a velocity trial consisted of the results from an
242 individual Dolly Varden subjected to the 10-70 cm/s velocity treatment sequence and an
243 experiment comprised a set of velocity trials for a group of individually-tested Dolly Varden.
244 We replicated the SFE twice, once with a group of five fish and the second with a group of 15
245 fish.

246 Treatment velocities began at 10 cm/s and increased in 10 cm/s increments up to 70 cm/s
247 and fish were rested for 30-minute periods at low velocity (~5 cm/s) between treatment
248 velocities. We released 9 prey per treatment velocity (see below) and ended velocity trials when
249 fish exhibited a large reduction in prey capture success (i.e., captured 2 or fewer of the 9 prey
250 presented). Experiments typically lasted 3 – 4 hours depending on fish prey capture success
251 rates. We used a sequentially increasing design for velocity treatments because we were
252 concerned about potential carryover and stress effects imposed by a random design (e.g.,
253 carryover stress incurred by testing at 10 cm/s immediately after 70 cm/s). Unfortunately, our
254 collection permit did not allow us to take the number of fish required for a random design with
255 each fish tested at a single velocity. An additional justification for testing at a sequential velocity
256 regime is the fact that fish in natural streams typically experience velocity differences as
257 gradients rather than as the abrupt shifts in velocity that might occur with random treatment
258 orders (e.g., 10 cm/s after 60 cm/s). This methodology simplified experimental logistics, and it
259 is unlikely that specimens became tired or were fed to satiation over the course of the
260 experiments.

261 The day prior to a trial, we measured, weighed, and moved an experimental specimen to
262 the test chamber to acclimate overnight at zero velocity. On the day of the trial, we allowed the
263 individual to adjust to flow via a 15-minute low-flow (~5 cm/s) acclimation period. After the
264 acclimation period, we gradually increased treatment velocity to 10 cm/s, which represented the
265 first test velocity trial. To begin each velocity trial, we sequentially released five prey into the
266 test chamber to initiate foraging behavior. Once the individual captured one of the five prey, we
267 began the 9-prey release sequence of the velocity trial. Occasionally, an individual failed to
268 capture one of the first five prey released or behaved unusually (e.g., swam erratically). When
269 this occurred (< 5 times) we rested the specimen for 30 minutes at low flow levels before
270 initiating the velocity trial sequence again. If the individual continued to exhibit unnatural
271 behavior, it was eliminated from experiments (two fish).

272 We sequentially delivered prey in trials via the prey delivery tubes using a randomly
273 determined tube sequence. On occasion (i.e., ~ two or three times per trial) we eliminated a prey
274 from observations if it appeared to pass beyond the fish's field of vision, or if the specimen was
275 still trying to capture a previous prey. In these cases, we released an additional prey (i.e., same
276 tube and prey sequence) to ensure all fish were presented with nine prey in a similar manner.

277 After nine prey had been presented, we rested the individual for 30 minutes at 5 cm/s flow until
278 the following velocity trial. Velocity treatments increased in 10 cm/s increments until the
279 individual captured two or fewer of the nine delivered prey, at which point the trial was ended.
280 We recorded prey capture success and holding velocity during and immediately following each
281 velocity trial. We recorded reactive distance and capture velocity via 3D video analysis upon
282 completion of laboratory experiments.

283

284 *Dominance Experiment*

285 The Dominance Experiment (DE) quantified the effect of dominance and relative fish size on
286 prey capture success, holding velocity, and reactive distance by conducting velocity trials with
287 two Dolly Varden (N = 14) in the test chamber. We rested individuals between 1 and 52 days
288 between SFE and DE. The DE consisted of 7 pairs of individuals with an average standard
289 length of 170 mm (SD \pm 24 mm) and an average mass of 51.6 g (SD \pm 20.4 g). Individuals
290 within pairs differed in standard length by an average of 35 mm (range 75 – 5 mm) and in mass
291 by an average of 30.6 g (range 68.6 – 2.7 g).

292 We maximized the length difference between pairs of fish in the DE by sequentially
293 selecting the largest and smallest individuals from the holding tank. We continued this selection
294 method until all individuals had been selected (i.e., 75 mm size difference between pair 1 and 5
295 mm size difference between pair 7). We followed the same two-step acclimation process in the
296 DE as in the SFE.

297 Methods for the DE were nearly identical to the SFE, except that we delivered 18 prey
298 per velocity trial in the DE to maintain constant prey/velocity trial/fish ratio between
299 experiments. We ended trials when both fish cumulatively missed 6 or more of the 18 prey. We
300 used this criterion for ending velocity trials because we did not believe the stream flume was
301 capable of producing or sustaining velocities that would result in both fish missing 14 or more of
302 the 18 prey.

303 We added two categorical predictor variables to our analyses for the DE: holding position
304 and size rank. We recorded the holding positions of both fish during each velocity trial and
305 classified positions as “central” (approximate mid-portion of the test chamber on the x, y, and z
306 axes) and “peripheral” (any departure from the central position). We based this classification
307 system on more than 100 observations of fish holding positions during the SFE, where fish

308 almost always occupied the rear-central portion of the test chamber when alone (
309 <https://youtu.be/zHbyNTxelxM>). Salmonids preferentially rank and select holding positions via
310 dominance hierarchies in streams, with dominant individuals occupying ideal positions and
311 subordinate individuals occupying less favorable positions (Fausch, 1984; Jenkins, 1969).
312 Therefore, we classified the individual that occupied the rear-central or central position in the
313 test chamber as “dominant” and the individual that occupied the peripheral position as
314 “subordinate”. Size rank (i.e., larger and smaller) was determined based on size differences
315 between individuals in a pair. Finally, because we used individuals in the DE that also had been
316 part of the SFE, we were able to calculate the cost of competition by comparing individual prey
317 capture success in the DE with the corresponding individual’s prey capture success in the SFE,
318 as well as calculating the difference in prey capture success between dominant and subordinate
319 pairs in the experiment itself.

320

321 *Net Energy Intake Model Test*

322 We used the data from the SFE to parameterize and test the Grossman et al. (2002) NEI
323 microhabitat selection model. The NEI model prediction is based on the relationship between
324 water velocity and prey capture success, expressed as

325 (1)

$$P = 1/(1 + e^{(b+cV)})$$

326

327 where P is prey capture success (proportion of encountered prey captured), V is stream velocity
328 (cm/s), and b and c are curve fitting constants obtained from the prey capture success curve (i.e.,
329 P versus V) (Hill & Grossman, 1993). Although net energy intake for drift-feeders at a given
330 stream position is a function of swimming costs (S), fish visual reactive area (A), concentration
331 of prey in the drift (D), in addition to stream velocity (V), Grossman et al. (2002) found that D,
332 A, and S can be held constant across the range of velocities occupied by drift-feeders. Therefore,
333 the simplified NEI model is a function of the relationship between velocity and prey capture
334 success described as

335 (2)

$$e^{(b+cV)} = 1/(cV - 1)$$

336

337 which can be solved iteratively using curve-fitting constants b and c from the prey capture
338 success curve to yield a single NEI optimal holding velocity prediction. The value of V where
339 left and right sides of Equation 2 are balanced is the optimal holding velocity prediction for the
340 NEI model, or the velocity at which drift-feeders should theoretically be maximizing net energy
341 intake.

342 Our NEI model makes several assumptions: namely that energy content of prey in the
343 drift (D), fish visual reactive volume (A), and metabolic cost of swimming (S) all may be held
344 constant across the range of velocities occupied by our test species (Grossman et al., 2002).
345 Although we have not tested these assumptions directly, they have been indirectly validated by
346 the fact that the model has produced successful holding velocity predictions for five species
347 resident to Southern Appalachian streams (Facey & Grossman, 1992; Grossman et al., 2002; Hill
348 & Grossman, 1993) and Alaskan Grayling in the Richardson-Clearwater River (Bozeman &
349 Grossman, 2019). Previous studies found that turbulence and foraging maneuvers may cause
350 swimming costs to increase more rapidly with velocity compared to holding a steady position in
351 relatively laminar current (Enders, Boisclair, & Roy, 2003; Hughes & Kelly, 1996); however,
352 Hayes et al. (2007) did not include swimming costs in a subsequent NEI model due to difficulties
353 in accounting for these costs in foraging models. Both Facey and Grossman (1992) and Hill and
354 Grossman (1993) found that fishes did not occupy high cost holding velocities in a Southern
355 Appalachian stream; a finding similar to Hughes and Dill (1990) for Artic Grayling in an
356 Alaskan stream and Hayes et al. (2000) for Brown Trout (*Salmo trutta*) in a New Zealand River.
357 Additionally, Piccolo et al. (2008a) found swimming costs to be relatively unimportant in
358 determining optimal foraging velocities of two salmonids. Finally, quantification of A , D , and S
359 is logistically difficult and to our knowledge, there are no extant data for any of these variables
360 for Dolly Varden or other charr. Certainly, some of the main strengths of the Grossman et al.
361 (2002) NEI model are its simplicity, logistical tractability, and, consequently, potential utility to
362 managers. If the model succeeded in predicting holding velocities occupied by Dolly Varden in
363 Panguingue Creek it would be one more piece of evidence that model assumptions are robust,
364 whereas failure would suggest the reverse.

365 We tested the prediction of the NEI model by comparing the optimal holding velocity
366 prediction to holding velocities of drift-feeding Dolly Varden ($N = 29$) in Panguingue Creek
367 during the summer of 2015 and 2016. We considered the model prediction to be successful if it

368 fell within the 95% confidence interval of the holding velocities occupied by Dolly Varden while
369 drift-feeding in their natural habitat and unsuccessful if it did not (Grossman et al., 2002).

370 We measured the holding and capture velocities of Dolly Varden in Panguingue Creek
371 using two stereo video cameras and VidSync 3D video analysis software (www.VidSync.org).
372 We estimated holding velocities by locating a drift-feeding Dolly Varden in the camera
373 viewfinders and releasing Israeli couscous into the current upstream of this position. Most
374 couscous particles were neutrally buoyant, and we used these to estimate field holding velocities
375 of fish using VidSync. We averaged the velocities of the six tracers nearest to a drift-feeding
376 Dolly Varden. Capture velocities were estimated using the same method as laboratory
377 experiments. Holding and capture velocity measurements were based on an average of 99
378 measurable foraging attempts per drift-feeding Dolly Varden (N = 29).

379

380 *Statistical Analysis*

381 The SFE was comprised of identical laboratory experiments conducted on two separate
382 shipments of Dolly Varden (N = 5 and 15). We ran two-tailed t-tests to compare the values of all
383 response variables between the two groups of Dolly Varden at each treatment velocity. None of
384 the response variables differed significantly ($\alpha > 0.05$); therefore, we pooled data from both
385 SFE trials. Because of a camera malfunction, sample sizes were slightly smaller for reactive
386 distance analyses (N = 18) than prey capture success and holding velocity (N = 20) analyses in
387 the SFE.

388 We used an information-theoretic, multi-model inference approach (Burnham &
389 Anderson, 2002) to quantify the relative effects of three fixed, continuous predictor variables on
390 three response variables. The predictor variables were: 1) treatment velocity (cm/s), 2) fish size
391 (standard length, SL mm), and 3) days in captivity. The response variables were: 1) prey capture
392 success (proportion), 2) holding velocity (cm/s), and 3) reactive distance (cm). We analyzed
393 effects on response variables by constructing models containing all three predictor variables (i.e.,
394 the global model) and all possible reduced models, including an intercept-only model. For the
395 DE, we added categorical predictor variables of size rank (i.e., larger or smaller) and dominance
396 status (i.e., dominant or subordinate based on holding position) to our candidate model sets.

397 We used generalized linear models ('glm', link = 'logit') for prey capture success and
398 simple linear models ('lm') for holding velocity and reactive distance. We did not analyze our

399 data for interactions, because we were primarily interested in main effects and interaction terms
400 cannot be included in equal numbers of models as main effects which then biases model-
401 averaged coefficient estimates (Burnham & Anderson, 2002).

402 We used Akaike's Information Criterion for small sample sizes (AICc) to evaluate the
403 relative explanatory power of each model given the candidate set and the data (Burnham &
404 Anderson, 2002). Because AICc is a measure of the relative information lost from the data given
405 use of a specific model (Burnham, Anderson, & Huyvaert, 2010), the best model in a candidate
406 set has the least information loss, the lowest AICc value and the highest Akaike weight (w_i). We
407 ranked models based on w_i , which ranges from 1.0 (zero information loss) to 0.0 (complete
408 information loss). We estimated the comparative explanatory power of a given model by
409 dividing the w_i of the best model in a candidate set by the w_i of each subsequent competing
410 model, which produced the likelihood of a given model being "true" in comparison to the best
411 model given the data (Grossman et al., 2006). Finally, as per Burnham and Anderson (2002),
412 we only interpreted models in the candidate set that had w_i values $\geq 10\%$ of the model with the
413 highest w_i .

414 We used model-averaging to produce robust parameter estimates and 95% confidence
415 intervals (Burnham & Anderson, 2002). We averaged parameter estimates across all models
416 evaluated, including those where the variable was not present (Lukacs, Burnham, & Anderson,
417 2009). We determined the relative importance of each predictor variable (w_+) by summing the
418 model weights (w_i) across all models containing the predictor variable of interest (Burnham &
419 Anderson, 2002).

420 We used an information theoretic approach rather than a series of t-tests or other
421 frequentist approaches, because we were interested in evaluating the relative predictive value of
422 our predictor variables (Burnham & Anderson, 2002). A frequentist approach could not be used
423 to evaluate this nor would adjustment of p-values for multiple comparisons have permitted this
424 approach. The information theoretic approach produced parameter estimates with a directional
425 component, which allowed us to estimate the direction and magnitude of the effect of each
426 predictor variable on our response variables. We analyzed all models, manually built AICc
427 tables and checked their output against that of "AICcmodavg" (Mazerolle, 2016) and "MuMIn"
428 (Barton, 2016). Model-averaged parameter estimates (β) were created using package "MuMIn"
429 (Barton, 2016) in R 3.2.3 (<https://www.R-project.org>). This research was completed under

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431 specimens were euthanized and frozen for preservation upon completion of experiments.

432

433 **Results**

434 *Prey Capture Success*

435 Treatment velocities ranged from 10 to 70 cm/s, but few fish caught prey at velocities above 50
436 cm/s. Consequently, there was a strong negative relationship between treatment velocity and
437 prey capture success in both experiments ($\beta = -0.092$ and -0.034 , Table 2, Figures 1 & 2). For
438 the SFE, the model with the greatest explanatory power for prey capture success was the global
439 model ($w_i = 0.70$, Table 1, pseudo $R^2 = 0.498$). The only other interpretable model ($w_i \geq 10\%$
440 of the best model) was the velocity and fish size model, which was 2.3 times less likely to be true
441 given the data than the global model (Table 1). For the DE, the model with the greatest
442 explanatory power contained treatment velocity, fish size, size rank, and holding position ($w_i =$
443 0.76 , Table 1, pseudo $R^2 = 0.553$). Adding days in captivity to these variables, which produced
444 the global model, resulted in a 3.2-fold decrease in explanatory power ($w_i = 0.24$, Table 1).

445 In addition to treatment velocity, fish size (both experiments), holding position and size
446 rank (DE) all affected prey capture success, and each of these variables were included in every
447 interpretable model in experiments (Table 2). Fish size had a positive effect on prey capture
448 success in SFE and a negative impact in the DE ($\beta = 0.017$ in SFE & $\beta = -0.033$ in DE, Table 2).
449 Being subordinate and having a smaller size rank both negatively affected prey capture success
450 ($\beta = -3.210$ and -0.661 , Table 2, Figure 2A & B) in the DE. The other predictor variable, days in
451 captivity, had 95% confidence intervals that overlapped zero in both experiments, suggesting that
452 it had little explanatory power (Table 2).

453

454 *Holding Velocity*

455 Holding velocity increased with increasing treatment velocity in both experiments ($\beta =$
456 0.504 and 0.652 , Table 2), but at a slower rate than capture velocity (Figures 3 & 4). For the
457 SFE, the model including treatment velocity and fish size displayed the greatest explanatory
458 power ($w_i = 0.65$, Table 1, $R^2 = 0.664$), followed by the global and treatment velocity models
459 respectively ($w_i = 0.26$ and 0.09 , Table 1). For the DE, no single model contained more than
460 20% of the explanatory power (Table 1). The model containing treatment velocity, fish size, and

461 holding position and the treatment velocity model each accounted for 18% of the explanatory
462 power given the data ($R^2 = 0.507$), with the remaining 64% split amongst 12 models (Table 1).
463 Model averaging indicated that treatment velocity had the highest explanatory power with
464 respect to changes in holding velocity and was included in every interpreted model for both
465 experiments ($w_+ = 1.00$, Table 2). Every other predictor variable had confidence intervals that
466 overlapped zero, meaning they had little to no effect on holding velocity (Table 2).

467

468 ***Reactive Distance***

469 Analyses of reactive distance data indicated a lack of explanatory power for predictor
470 variables (Table 1, Figures 5 & 6). Oddly, the model with the greatest explanatory power in the
471 SFE was the intercept only model (i.e., no predictor variables included) ($w_i = 0.38$, Table 1).
472 Adding a single predictor variable to the models resulted in at least a 2.1-fold decrease in
473 explanatory power (Table 1). For the DE, only two candidate models contained more than 10%
474 explanatory power: the fish size model ($w_i = 0.16$, Table 1, $R^2 = 0.089$) and the treatment
475 velocity and fish size model ($w_i = 0.14$, Table 1). An additional 16 candidate models were
476 interpretable, but all contained 9% or less explanatory power (Table 1). All predictor parameter
477 estimates had 95% confidence intervals that overlapped zero, which confirms their low
478 explanatory power (Table 2).

479

480 ***Cost of Competition***

481 Dominance was a better predictor of prey capture success than size rank between
482 individuals (Figure 2A & B). Interestingly, size rank between competing individuals was not
483 necessarily a good indicator of dominance because smaller individuals were dominant in 27% (9
484 of 33) of DE trials, although this only occurred in pairs where size differences were small (< 1.5
485 cm). Subordinate and smaller individuals each captured fewer prey than their dominant and
486 larger counterparts; however, the magnitude of this difference was far greater for dominants and
487 subordinates than larger and smaller individuals ($\beta = -3.210$ versus -0.661 , respectively, Table 2;
488 Figure 2A & B). Furthermore, dominant individuals captured more prey than subordinate
489 individuals in 82% (27 of 33) of DE trials, whereas larger individuals captured more prey than
490 smaller individuals in 55% (18 of 33) of DE trials. Mean size difference between paired
491 individuals was 35 mm (SD \pm 29 mm, range: 75 mm – 5 mm).

492 Being dominant had a strong effect on individual fitness, because dominants captured
493 50% more prey than subordinates (across all velocities, Figure 7A). Nonetheless, there was a
494 cost to being either dominant or subordinate, because all fish captured less prey than they did in
495 the SFE, especially at low velocities (Figure 7B). Interestingly, dominant individuals exhibited
496 ~10% greater prey capture success than in the SFE at higher velocities (i.e., 40 and 50 cm/s) and
497 subordinate individuals displayed prey capture success rates equal to those in the SFE at the 50
498 cm/s treatment velocity (Figure 7B). Lastly, neither size rank nor dominance influenced holding
499 velocity or reactive distance (Figures 4A & B and 6A & B) and 95% confidence intervals for
500 both predictor variables overlapped zero for holding velocity and reactive distance (Table 2).

501

502 *NEI Model Field Test*

503 We obtained values for b and c of Equation 2 of 3.74 and 0.083, respectively, from the
504 prey capture success versus treatment velocity curve. Using these values, we iteratively solved
505 Equation 2 which yielded an optimal holding velocity of 24.0 cm/s. The 95% confidence
506 interval of holding velocities of Dolly Varden charr (N = 29) in Panguingue Creek was 24.9 –
507 29.3 cm/s (mean = 27.1 cm/s). Therefore, the prediction of the NEI model fell just outside (0.9
508 cm/s) the relatively narrow (4.4 cm/s) confidence interval for holding velocities occupied by
509 Dolly Varden in Panguingue Creek. This difference (0.9 cm/s) certainly was within
510 measurement error and also likely affected by the relatively small samples sizes of our
511 experimental (N = 20) and field data (N = 29). The narrow confidence interval and small
512 difference between the model prediction and the lower bound of the confidence interval are
513 particularly noteworthy, given that the range of possible velocities occupied in Panguingue
514 Creek was large (i.e., velocity range in Summer 2016 was 4 – 126 cm/s, n = 72).

515

516 **Discussion**

517 Little is known about the mechanics of drift-feeding for most lotic fishes. Nonetheless, our
518 results provide evidence that velocity affects holding velocity, reactive distance and capture
519 success in Dolly Varden from Panguingue Creek, Alaska. Nonanadromous forms of this species
520 are greatly understudied, with little published information available. Our results demonstrate
521 that treatment velocity was the variable with the greatest explanatory power; velocity was
522 included in 72% of all interpretable models (including all models for prey capture success and

523 holding velocity). In addition, fish size, dominance and size rank had interpretable explanatory
524 power for prey capture success in DE. Only treatment velocity possessed explanatory power for
525 holding velocity data. Dominance was a better predictor of prey capture success than size rank
526 between competitors, given that smaller individuals were dominant in more than 28% of DE
527 trials, although this only occurred when size differences were less than 15mm. The amount of
528 variability in top models for each experiment explained between 66% (SFE, treatment velocity
529 and fish size model to predict holding velocity) and 0% (SFE, reactive distance intercept only
530 model). Finally, the Grossman et al. (2002) NEI optimal holding velocity model prediction fell
531 just 0.9 cm/s below the 95% confidence interval of holding velocities occupied by Dolly Varden
532 in Panguingue Creek.

533 Our results show that water velocity is an important aspect of drift-feeder habitat
534 selection, substantiating existing literature on drift-feeder foraging mechanics (Fausch, 1984;
535 Grossman et al., 2002; Hill & Grossman, 1993). Net energy gain for stream fishes is strongly
536 tied to velocity via both benefits (i.e., prey encounter rates) and costs (i.e., metabolic swimming
537 costs). Therefore, drift-feeders may occupy holding positions with lower velocities to minimize
538 costs while foraging in nearby faster velocities where prey delivery rates remain relatively high
539 (Everest & Chapman, 1972; Kalleberg, 1958). We observed similar behavior because
540 individuals in the SFE and DE held positions at lower velocities than prey capture velocities as
541 treatment velocity increased (Figures 3 & 4).

542 Interestingly, neither dominance nor fish size affected holding velocity or reactive
543 distance; dominant and subordinate individuals occupied similar holding velocities throughout
544 the majority of trials. This was not due to lack of velocity refugia in the test chamber. At high
545 treatment velocities (i.e., > 30 cm/s), velocities beneath the bamboo structure near the front of
546 the test chamber remained near 10 cm/s (range: 1 – 24 cm/s). This was a product of the vertical
547 structure of water circulation in the experimental flume (i.e., water return chamber on bottom,
548 test chamber on top). Only rarely did subordinate individuals occupy low flow positions beneath
549 the bamboo structure, and only then due to aggressive behavior by dominant fish rather than
550 refuge from fast velocities. Subordinate fish typically were chased under the bamboo, waited
551 until the dominant fish returned to the ideal holding position, and then retreated to the rear of the
552 test chamber to hold position in areas of high velocity (personal observation). These flow

553 variations were much smaller in the portion of the test chamber most commonly occupied by fish
554 due to the presence of the collimator.

555 We did not anticipate the low explanatory power of predictor variables for reactive
556 distance in both experiments. It is reasonable to expect that reactive distance would decrease
557 with increasing treatment velocity; however, all parameter estimates in this analysis overlapped
558 zero. Although counterintuitive, this relationship mirrors similar observations in previous
559 experiments in our laboratory with juvenile Chinook salmon (*Oncorhynchus tshawytscha*)
560 (Donofrio et al., 2018) and Arctic Grayling (*Thymallus arcticus*) (Bozeman & Grossman, 2019).
561 It is possible that reactive distance measurements were constrained by the size of the holding
562 chamber; however, experimental specimens displayed a wide range of reactive distances in both
563 experiments (16.9 – 60.1 cm), which corresponds to expected reactive distances for Arctic
564 Grayling of similar size, but is slightly less than would be expected for ~8 mm prey (Hughes &
565 Dill, 1990). Piccolo et al. (2008b) observed reductions in prey detection distance with increases
566 in velocity for two salmonids in an experimental stream flume. Additional studies have shown
567 that reactive distance is negatively affected by turbidity for several drift-feeders (O'Brien,
568 Barfield, & Sigler, 2001), including the ecologically similar Brook Charr (*Salvelinus fontinalis*;
569 (Sweka & Hartman, 2001). Water quality data indicated that turbidity was basically nonexistent
570 in the test chamber (turbidities < 0.001 NTUs, Athens-Clarke County, personal communication),
571 as was suspended debris (personal observation), so it is unlikely that these variables could have
572 affected our results.

573 Our analyses also showed that size rank was a poorer predictor of prey capture success
574 than dominance status. In fact, smaller individuals were dominant in 28% of velocity trials, and
575 exhibited higher prey capture rates in 45% of trials. However, this effect was linked to size-
576 differences between individuals, because smaller fish were never dominant when the size
577 difference was greater than 15 mm. It appears likely that when size differences are below this
578 threshold, individuals either do not perceive the size difference or are willing to engage in
579 contests because the outcomes are less certain. It also is possible that instances of smaller fish
580 being dominant might be due to differences in sex (Johnsson, Sernland, & Blixt, 2001), which
581 was unmeasured.

582 Drift-feeders may select microhabitats based on fitness-based currencies other than net
583 energy intake optimization, including avoiding negative interactions such as predation or

584 interspecific competition (Fausch, 2014; Piccolo et al., 2014). Although we have no direct
585 evidence, it is possible that either or both interspecific competition or predation contributed to
586 the model prediction falling just outside the relatively narrow (i.e., 4.4 cm/s) 95% confidence
587 interval for holding velocities in Panguingue Creek. Nonetheless, Dolly Varden are strong
588 intraspecific competitors (personal observation) although it is unknown whether they are
589 competitively superior to the similarly sized (personal observation) Arctic Grayling also found
590 during summer and early autumn in Panguingue Creek. In addition, given the creek's shallow
591 depth, it also is possible that mammalian and avian predators affect holding positions and
592 velocities utilized by Dolly Varden as has been observed in other stream fishes (Lonzarich &
593 Quinn, 1995). Finally, differences between the stream flume and natural foraging habitat of
594 Dolly Varden in Panguingue Creek (e.g., visual complexity, laminar flow, prey size and density,
595 etc.) also may have contributed to the slight under-prediction by the model. Although further
596 testing and refinement are needed, results from the Grossman et al. (2002) likely are transferable
597 to other populations of nonanadromous Dolly Varden with similar size structure.

598 To our knowledge, the Grossman et al. (2002) NEI model is the most widely tested NEI
599 model (but see Hughes, Hayes, Shearer, & Young, 2003); it has been used to predict optimal
600 holding positions for a variety of salmonid and cyprinid species in streams in southern
601 Appalachia and Alaska (Bozeman & Grossman, 2019; Donofrio et al., 2018; Grossman et al.,
602 2002). The model, or an earlier variant, has shown mixed success, with accurate optimal holding
603 velocity predictions for cyprinids and Rainbow Trout occupying Southern Appalachian streams
604 (Grossman et al., 2002) and Arctic Grayling in the Richardson Clearwater river in Alaska
605 (Bozeman & Grossman, 2019). Nonetheless, its predictions have failed for juvenile Chinook
606 Salmon in the Chena River Alaska (Donofrio et al., 2018) and for Arctic Grayling in Panguingue
607 Creek, Alaska (Bozeman & Grossman, 2019). Similarly, Hughes et al. (2003) field tested a
608 foraging model for a drift-feeding salmonid in New Zealand, also with mixed success. Given
609 these mixed results, future testing of the model is warranted, especially tests that will examine
610 model assumptions as well as its predictive accuracy.

611 The confidence interval of holding velocities for Dolly Varden in Panguingue Creek ($n =$
612 29) was very narrow (i.e., 4.4 cm/s), which suggests that individuals in this population utilize
613 only a small portion of the available habitat in Panguingue Creek (i.e., velocity range in
614 Panguingue Creek in Summer 2016 was 4 – 126 cm/s, $n = 72$). Interestingly, a sympatric

615 population of Arctic Grayling ($N = 25$) occupied velocities of 21.0 – 27.5 cm/s in Panguingue
616 Creek (Bozeman & Grossman, 2019), which largely overlaps the confidence interval of holding
617 velocities occupied by Dolly Varden (24.9 – 29.3 cm/s). Given the large range of velocities
618 available to both species, this high habitat use specificity suggests that nonanadromous
619 populations of Dolly Varden may compete with migratory Arctic Grayling for favorable habitats
620 and also may be sensitive to natural or anthropogenic flow alterations. However, future studies
621 should consider temporal and spatial variation in nonanadromous Dolly Varden habitat use,
622 especially given that this species has been known to shift foraging strategies in response to
623 varying habitat quality (Nakano, Fausch, & Kitano, 1999). Interior Alaska nonanadromous
624 populations of Dolly Varden are largely understudied and should be protected to maintain
625 biodiversity and serve as reservoirs of recolonization in case of population extirpations in other
626 Yukon River Basin tributaries.

627 Despite their potential utility to both basic science and management, few fitness-based
628 habitat selection models have been tested with multiple species, locations, and seasons.
629 Nonetheless, the output of such models, the optimal holding velocity for a species, is an
630 important datum for basic scientists, conservationists and managers. These models may be
631 particularly useful tools for managers because they examine habitat selection from an
632 ecologically and evolutionarily meaningful perspective and likely are transferrable across
633 systems (Grossman, 2014). If accurate, predictions from NEI model will aid managers in
634 developing scientifically based habitat management strategies and aid reintroduction or
635 restoration efforts. In addition, when coupled with stream flow models, these predictions may be
636 used to assess future changes in habitat availability with climate change or anthropogenic flow
637 alteration (Jenkins & Keeley, 2010), on either the watershed or reach scale (Hayes et al., 2016;
638 Kawai, Nagayama, Urabe, Akasaka, & Nakamura, 2014; McHugh et al., 2017; Piccolo et al.,
639 2014; Railsback, 2016). This is especially applicable to Yukon (Tanana) River Basin Dolly
640 Varden, because glacial meltwater can be an important driver of daily and seasonal flow regimes
641 of the systems they inhabit (Wada, Chikita, Kim, & Kudo, 2018).

642

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835 Table 1: Model selection analysis for Single- and Dominance Experiments. Data include AICc

836 values, delta AICc values ($\Delta AICc$), and Akaike weights (w_i) for all response variables for both

837 experiments. The comparative likelihood that the top-ranked model is true compared to

838 subsequent models given the data is in parenthesis beside Akaike weight value (e.g., the Global

839 model is $2.3 \times$ more likely to be true given the data than the Velocity + Size model for prey

840 capture success in the Single-Fish Experiment). Predictor variables are abbreviated as follows:

841 Treatment Velocity = Velocity, Days in Captivity = Days, Fish Size = Size, Size Rank = Rank,

842 Holding Dominance = Dom.

Response Variable	Experiment	Candidate Model	AICc	$\Delta AICc$	w_i
Prey Capture Success	Single-Fish	Global	434.56	0	0.70
		Velocity + Size	436.22	1.66	0.30 (2.3X)
	Dominance	Velocity + Size + Rank + Dom	478.51	0	0.76
Holding Velocity	Single-Fish	Global	480.87	2.35	0.24 (3.2X)
		Velocity + Size	659.43	0	0.65
		Global	661.28	1.85	0.26 (2.5X)
	Dominance	Velocity	663.47	4.03	0.09 (7.2X)
		Velocity + Size + Dom	483.76	0	0.18
		Velocity	483.83	0.07	0.18 (1.0X)
		Velocity + Dom	484.58	0.83	0.12 (1.5X)
		Velocity + Days	485.54	1.78	0.08 (2.3X)
		Velocity + Size	485.79	2.04	0.07 (2.6X)
		Velocity + Size + Rank + Dom	485.88	2.13	0.06 (3.0X)
Velocity + Size + Days + Dom	486.06	2.30	0.06 (3.0X)		

FORAGING BEHAVIOR & OPTIMAL MICROHABITAT SELECTION OF DOLLY VARDEN

		Velocity + Rank	486.08	2.33	0.06 (3.0X)
		Velocity + Rank + Dom	486.34	2.58	0.05 (3.6X)
		Velocity + Days + Dom	486.36	2.60	0.05 (3.6X)
		Velocity + Size + Days	487.71	3.95	0.03 (6.0X)
		Velocity + Days + Rank	487.87	4.11	0.02 (9.0X)
		Velocity + Size + Rank	487.95	4.19	0.02 (9.0X)
		Velocity + Days + Rank + Dom	488.19	4.43	0.02 (9.0X)
Reactive Distance	Single-Fish	Intercept Only	578.90	0	0.38
		Days	580.45	1.55	0.18 (2.1X)
		Size	580.96	2.07	0.14 (2.7X)
		Velocity	580.99	2.09	0.13 (2.9X)
		Size + Days	582.50	3.60	0.06 (6.3X)
		Velocity + Days	582.63	3.74	0.06 (6.3X)
		Velocity + Size	583.12	4.22	0.05 (7.6X)
	Dominance	Size	-130.75	0	0.16
		Velocity + Size	-130.51	0.23	0.14 (1.1X)
		Velocity + Size + Dom	-129.66	1.09	0.09 (1.7X)
		Size + Dom	-129.55	1.19	0.09 (1.8X)
		Size + Days	-129.12	1.63	0.07 (2.3X)
		Velocity + Size + Days	-129.04	1.71	0.07 (2.3X)
		Size + Rank	-128.60	2.15	0.06 (2.9X)
		Velocity + Size + Rank	-128.28	2.47	0.05 (3.4X)
		Velocity + Size + Days + Dom	-128.01	2.74	0.04 (4.0X)
		Size + Days + Dom	-127.76	2.99	0.04 (4.5X)
		Velocity + Size + Rank + Dom	-127.32	3.43	0.03 (5.6X)
		Size + Rank + Dom	-127.31	3.44	0.03 (5.6X)
		Intercept Only	-127.03	3.72	0.03 (6.5X)
Rank	-126.82	3.93	0.02 (7.0X)		
Size + Days + Rank	-126.76	3.98	0.02 (7.4X)		
Velocity	-126.73	4.01	0.02 (7.4X)		
Velocity + Size + Days + Rank	-126.57	4.17	0.02 (8.1X)		

Velocity + Rank -126.47 4.27 0.02 (8.5X)

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854 Table 2: Model-averaged parameter estimates, 95% confidence intervals, and relative variable
855 importance (w+) for all experiments. Confidence intervals that overlap zero are denoted †.

Response Variable	Predictor Variable	Experiment	Estimate ± 95% CI	w+
Prey Capture Success	Treatment Velocity	Single-Fish	-0.092 ± 0.013	1.00
		Dominance	-0.034 ± 0.011	1.00
	Fish Size	Single-Fish	0.017 ± 0.008	1.00
		Dominance	-0.033 ± 0.011	1.00
	Days in Captivity	Single-Fish	-0.002 ± 0.004†	0.70
		Dominance	0.001 ± 0.020†	0.24
	Holding Position (Peripheral)	Dominance	-3.210 ± 0.450	1.00
	Rank (Smaller)	Dominance	-0.661 ± 0.417	1.00
Holding Velocity	Treatment Velocity	Single-Fish	0.504 ± 0.074	1.00
		Dominance	0.652 ± 0.164	1.00
	Fish Size	Single-Fish	0.059 ± 0.061†	0.91
		Dominance	-0.037 ± 0.125†	0.55
	Days in Captivity	Single-Fish	-0.002 ± 0.014†	0.26

		Dominance	$-0.049 \pm 0.356\ddagger$	0.25
	Holding Position (Peripheral)	Dominance	$-2.537 \pm 6.365\ddagger$	0.42
	Rank (Smaller)	Dominance	$0.010 \pm 3.044\ddagger$	0.24
Reactive Distance	Treatment Velocity	Single-Fish	$0.002 \pm 0.039\ddagger$	0.24
		Dominance	$0.000 \pm 0.001\ddagger$	0.49
	Fish Size	Single-Fish	$0.002 \pm 0.029\ddagger$	0.25
		Dominance	$0.001 \pm 0.001\ddagger$	0.91
	Days in Captivity	Single-Fish	$0.003 \pm 0.018\ddagger$	0.30
		Dominance	$0.001 \pm 0.003\ddagger$	0.26
	Holding Position (Peripheral)	Dominance	$0.010 \pm 0.041\ddagger$	0.32
	Rank (Smaller)	Dominance	$0.001 \pm 0.030\ddagger$	0.24

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862 **Figure Legends**863 **Figure 1:** Mean prey capture success versus treatment velocity for the Single-Fish Experiment.864 Error bars represent SD. N represents sample size (number of fish trials completed) at each
865 treatment velocity.866 **Figure 2:** Mean prey capture success versus treatment velocity for the Dominance Experiment867 by fish size rank (A) and dominance (B). Error bars represent SD. N represents sample size
868 (number of fish pair trials completed) at each treatment velocity.869 **Figure 3:** Mean holding velocity versus treatment velocity for the Single-Fish Experiment.870 Mean capture velocity also is displayed. Error bars represent SD. N represents sample size
871 (number of fish trials completed) at each treatment velocity.872 **Figure 4:** Mean holding velocity versus treatment velocity for the Dominance Experiment by

873 fish size rank (A) and dominance (B). Mean capture velocity also is displayed. Error bars

874 represent SD. N represents sample size (number of fish pair trials completed) at each treatment
875 velocity.

876 **Figure 5:** Mean reactive distance versus treatment velocity for the Single-Fish Experiment.

877 Error bars represent SD. N represents sample size (number of fish trials completed) at each
878 treatment velocity.

879 **Figure 6:** Mean reactive distance versus treatment velocity for the Dominance Experiment by
880 fish size rank (A) and dominance (B). Error bars represent SD. N represents sample size
881 (number of fish pair trials completed) at each treatment velocity.

882 **Figure 7:** Mean difference in dominant and subordinate prey capture success (i.e., Dominant –
883 Subordinate PCS) versus treatment velocity (A). Mean difference in prey capture success
884 between dominant and subordinate fish in a pair and the corresponding individuals in the Single-
885 Fish Experiment versus treatment velocity (B). PCS = Prey Capture Success. Error bars
886 represent SD.

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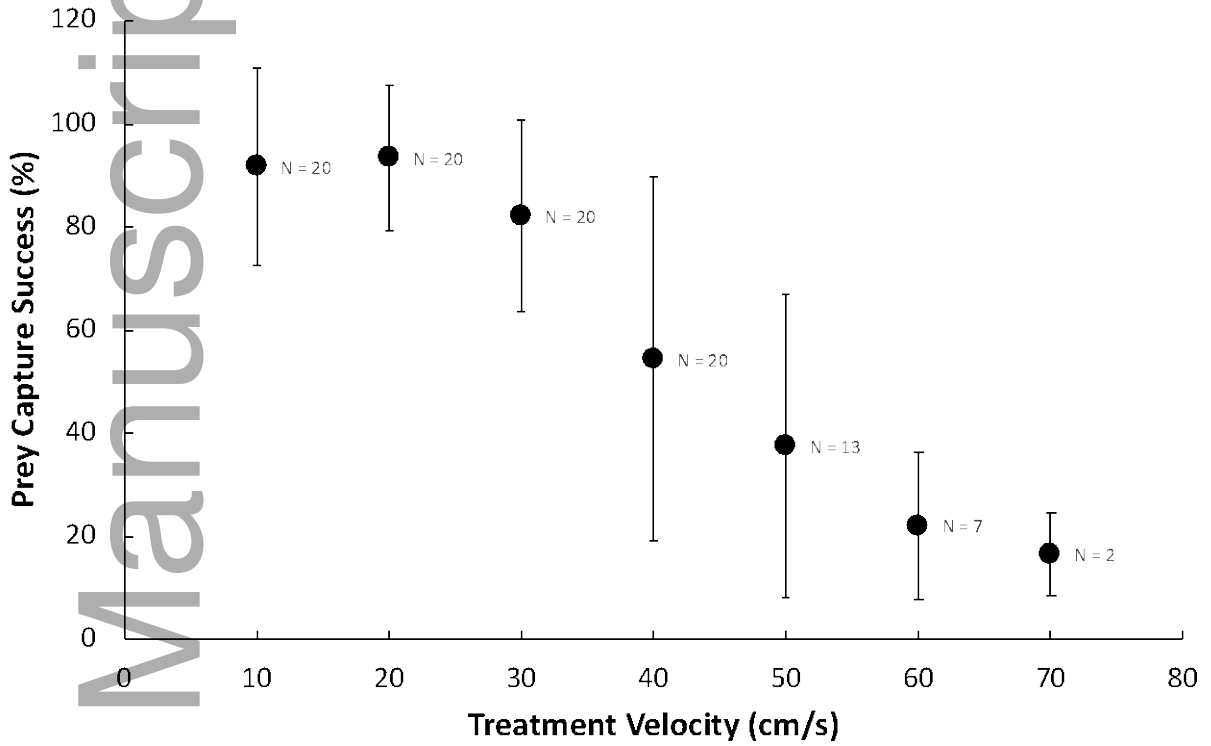
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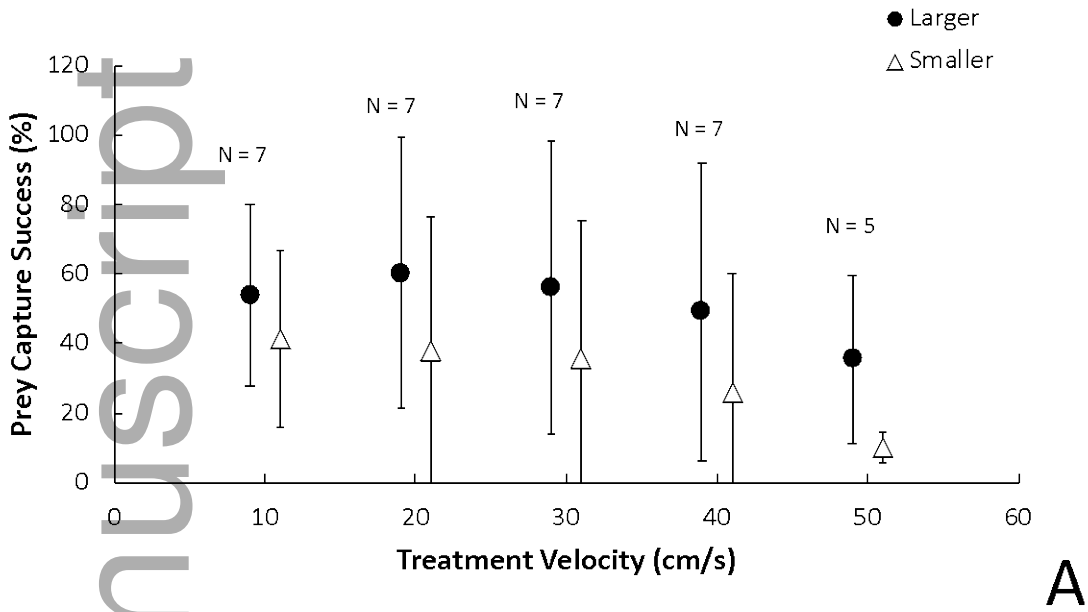
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Figure 1

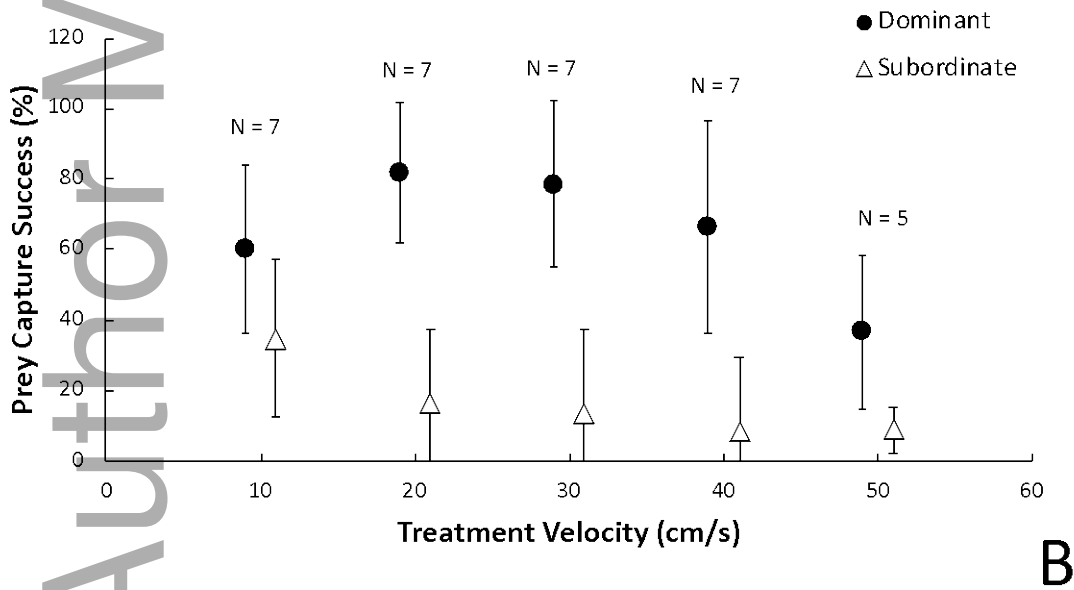


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923 Figure 2



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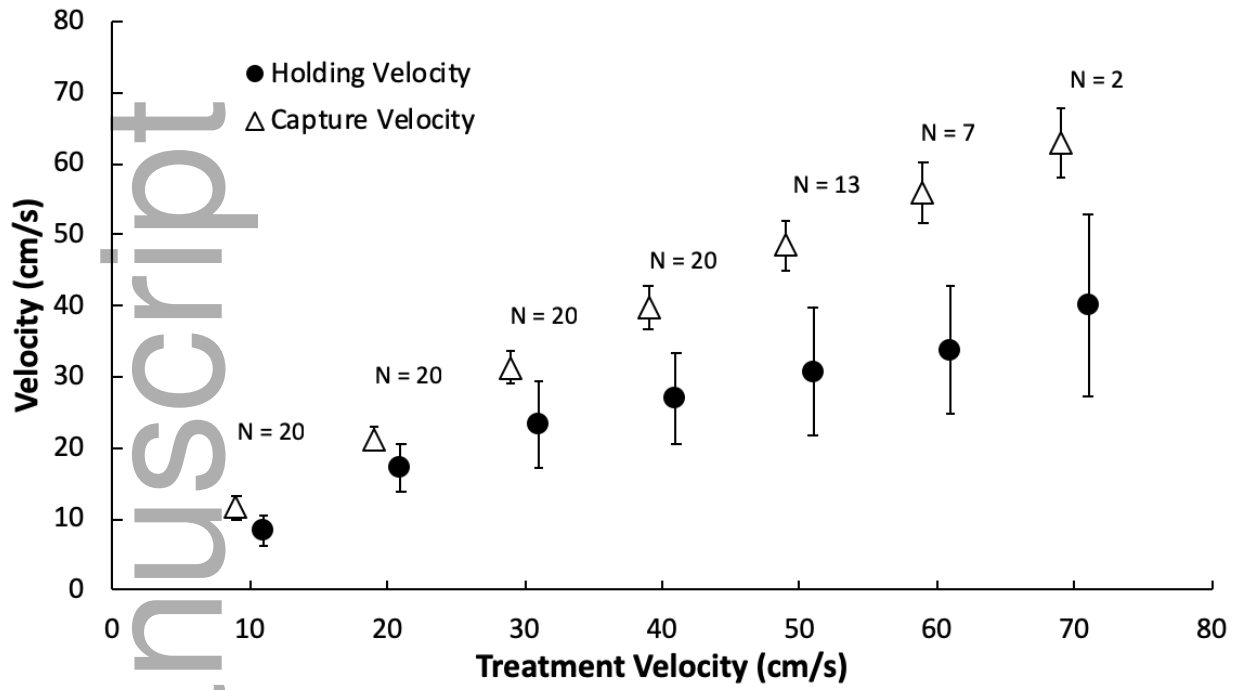


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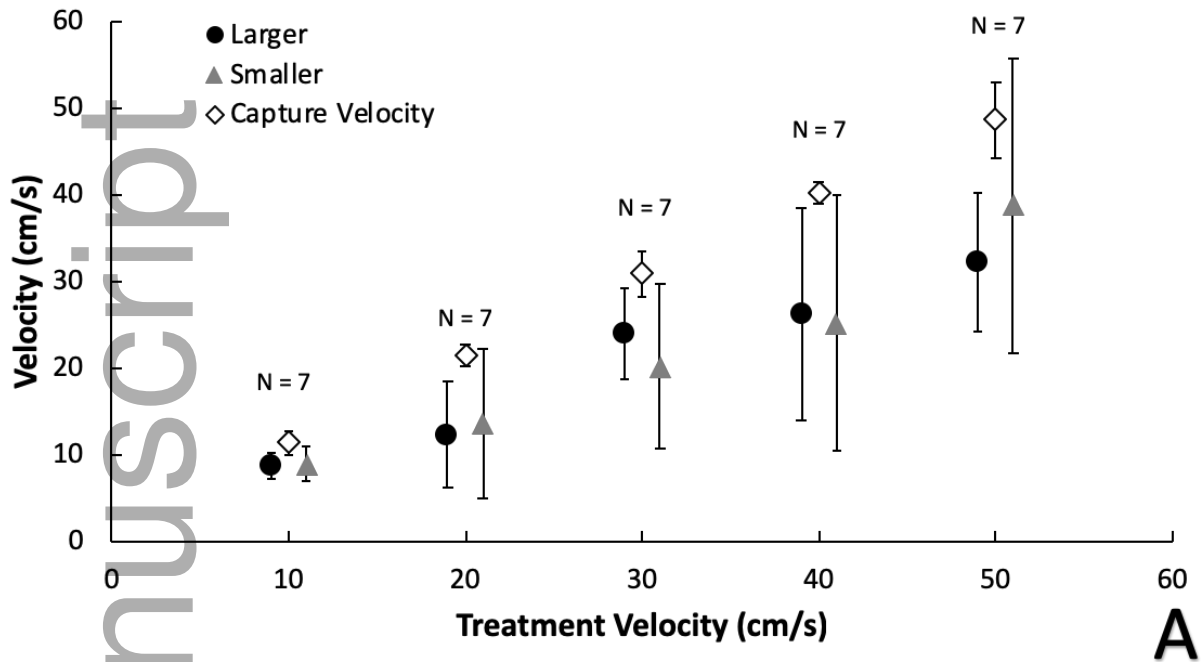
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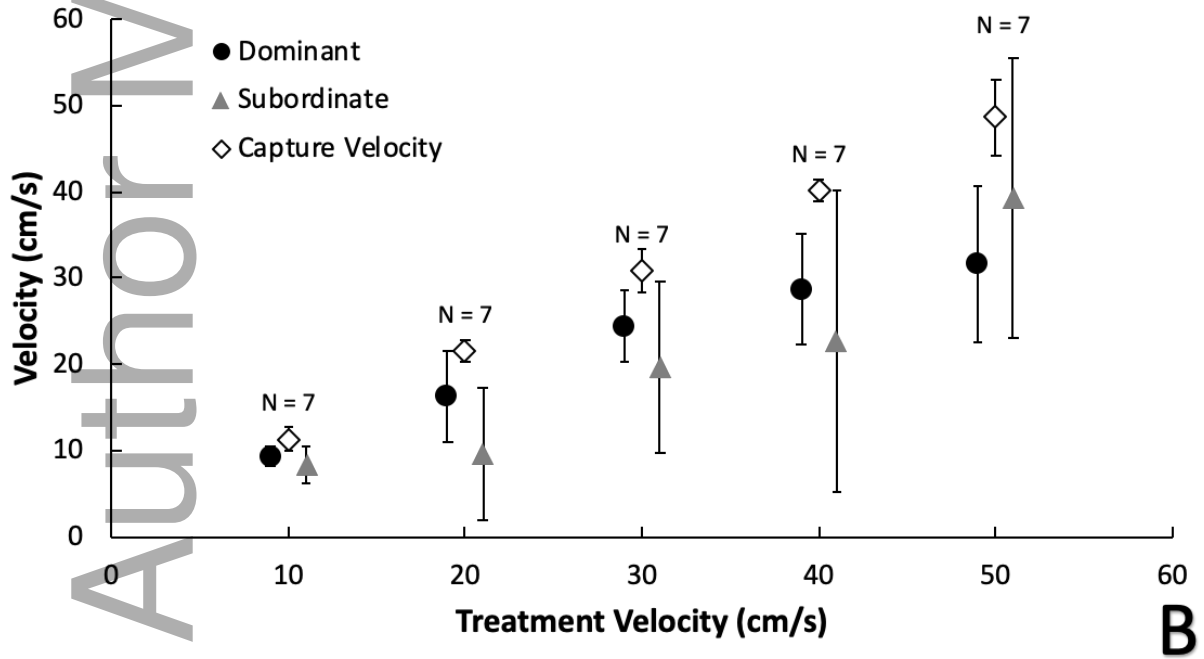


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Figure 4

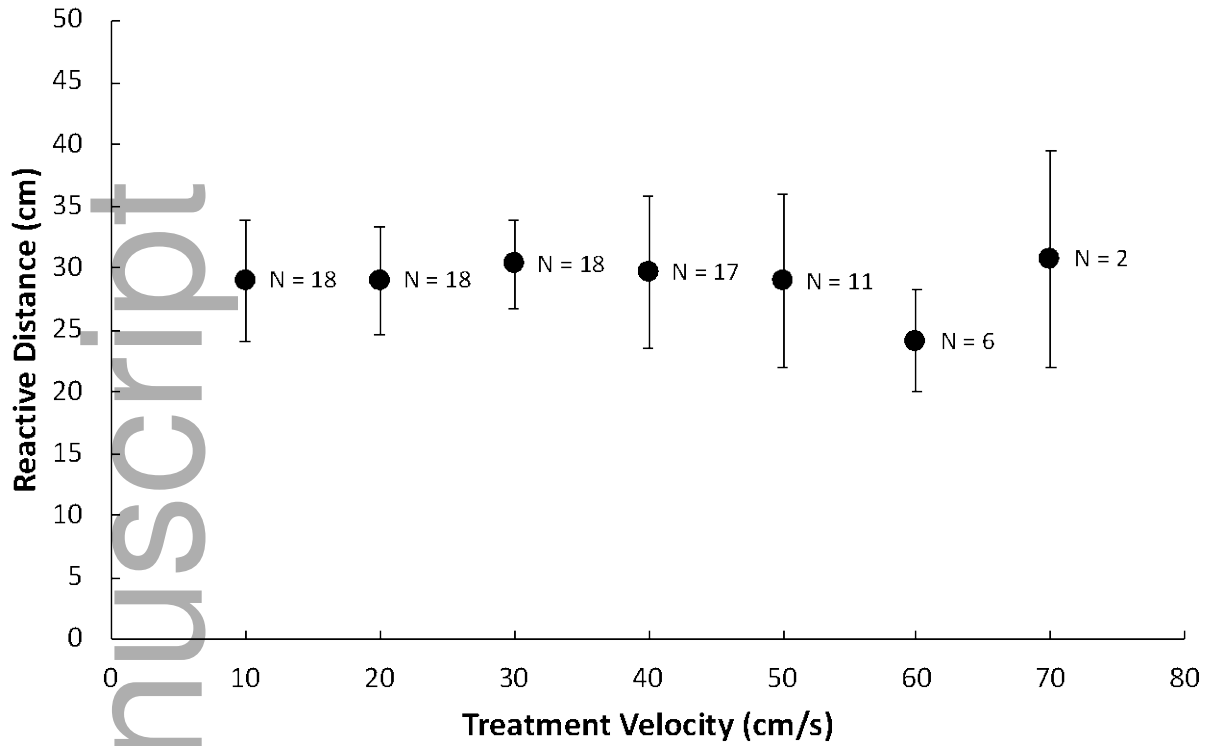


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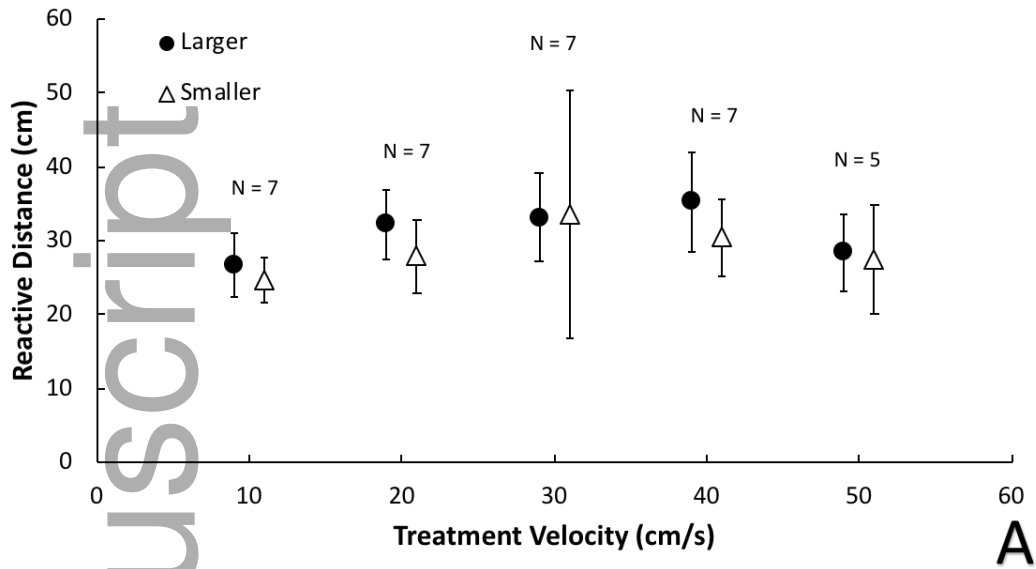
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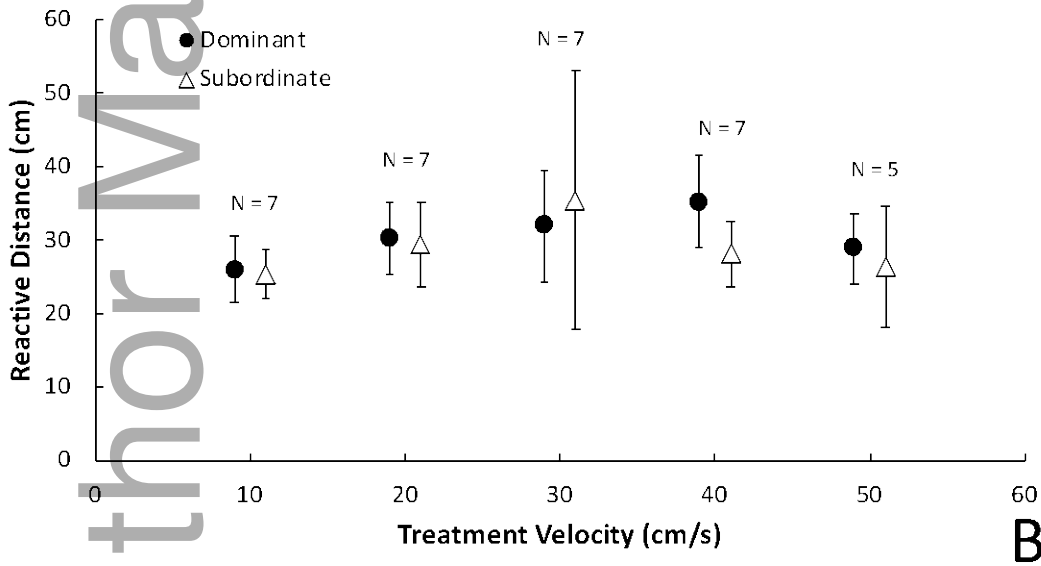


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Figure 6



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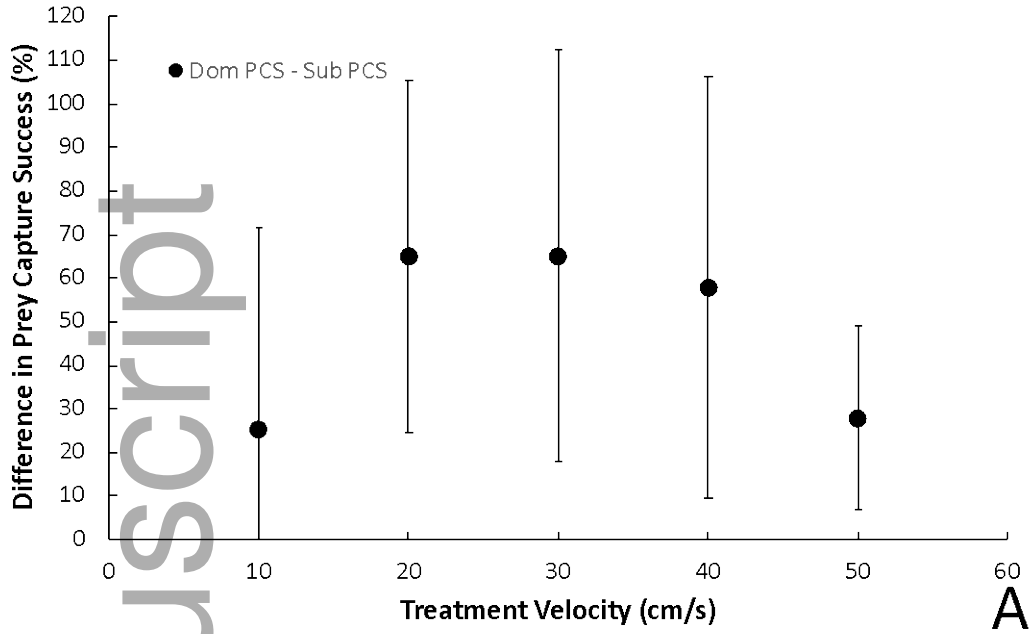
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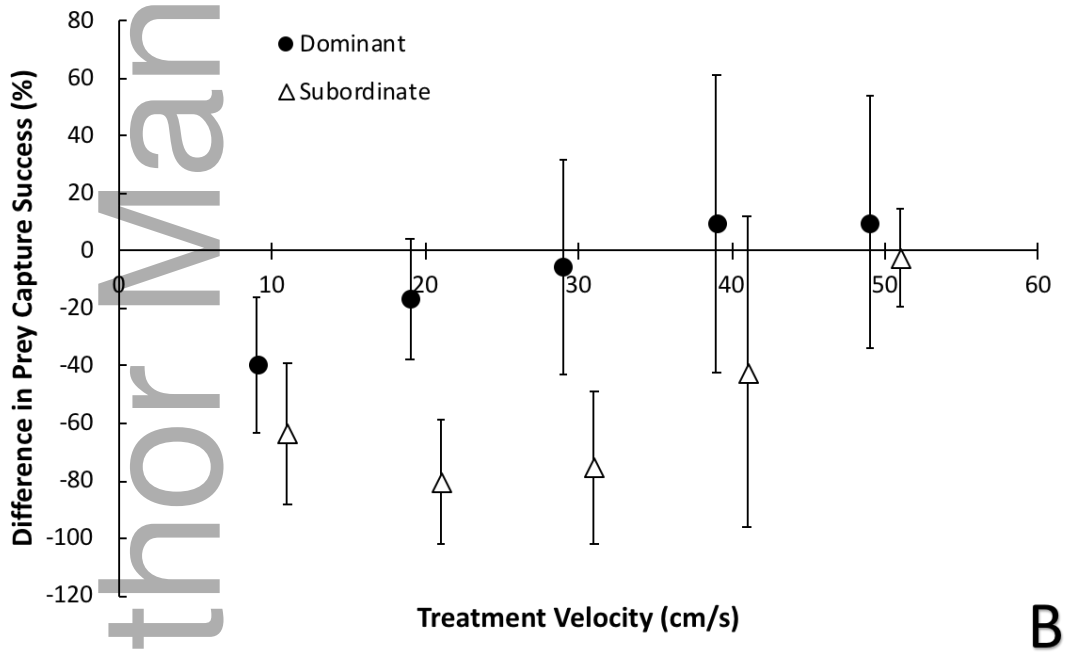
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965 Figure 7



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