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A comparison of aggressive and foraging behaviour between juvenile cutthroat trout, rainbow trout and F1 hybrids

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'Successful' introduced species are often thought to cause declines or extinctions of native species through competitive superiority. In western North America, introduced rainbow trout, *Oncorhynchus mykiss*, have completely replaced many native cutthroat trout, *Oncorhynchus clarkii*, populations; however, few studies have identified the mechanisms that may allow rainbow trout to outcompete cutthroat trout. We raised Yellowstone cutthroat trout, *Oncorhynchus clarkii bouvieri*, rainbow trout, and their first generation hybrids in a common environment and conducted pairwise contests to test for differences in aggression, ability to defend a feeding station, and amount of food captured between these species and their hybrids. We did not detect a difference in number of aggressive acts conducted between cutthroat, rainbow and hybrid trout; however, cutthroat trout had the lowest success in occupying the feeding station and captured a lower proportion of food than rainbow and hybrid trout. Furthermore, hybrid crosses and rainbow trout had highest success at holding the feeding station and capturing food items when competing against cutthroat trout. Our study suggests that juvenile Yellowstone cutthroat trout are less successful at maintaining profitable feeding territories and capturing food items when competing against rainbow trout and first generation hybrids.

Keywords: aggression; foraging ability; hybridization; *Oncorhynchus clarkii bouvieri*; *Oncorhynchus mykiss*; rainbow trout; Yellowstone cutthroat trout

When introduced species become established and proliferate within a new community, they are commonly thought to possess characteristics that allow them to outcompete ecologically similar native species. Several studies on ecology of invasive species have described traits of successful invasive species and ecosystems prone to invasion (Elton 1964; Lodge 1993; Marchetti et al. 2004). Such studies have been important for laying theoretical groundwork for invasive species ecology; however, more detailed information on the interactions between native and invasive species are needed to reach the goals of predicting and preventing invasions or identifying methods to remove non-native species (Kolar & Lodge 2001; Sakai et al. 2001). Despite the recognition that behavioural characteristics may play a large role in the establishment and spread of non-native species (Holway & Suarez 1999), relatively few studies have investigated behavioural mechanisms that may allow introduced species to outcompete ecologically similar native species.

Behavioural differences may play an especially important role in competitive interactions between native and introduced salmonid species and therefore the spread of non-native trout and salmon species within native populations. Stream-dwelling salmonid fish primarily feed on drifting aquatic invertebrates by establishing and defending feeding territories (Quinn 2005). Because of temporal and spatial differences in invertebrate drift availability, the quality of foraging positions is not equal within streams and salmonids use aggressive displays and attacks to establish and defend profitable feeding stations from competitors (Chapman 1962; Keeley & Grant 1995). Aggressive individuals tend to defend larger feeding territories and capture more food than less aggressive competitors (Grant 1990). Given the importance of territorial behaviour to the acquisition of food resources, we hypothesized that differences in aggression and foraging behaviour may influence the displacement of native trout by introduced trout.

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Some of the most severe impacts of introduced species occur when they compete and hybridize with native species (Rhymer & Simberloff 1996). In western North America, competition and introgressive hybridization with introduced rainbow trout, *Oncorhynchus mykiss*, have been especially damaging to native cutthroat trout populations, *Oncorhynchus clarkii*. Despite studies that imply strong competitive displacement of cutthroat trout by rainbow trout and cutthroat–rainbow hybrids (Gresswell 1988; Young 1995), we do not know of any studies that have experimentally identified competitive mechanisms that might allow non-native rainbow and cutthroat–rainbow hybrid trout to outcompete native cutthroat trout.

To test for competitive behavioural differences between native trout, an introduced competitor, and their hybrids, we raised Yellowstone cutthroat trout, *Oncorhynchus clarkii bouvieri*, rainbow trout and their reciprocal hybrids in a common environment and conducted pairwise contests. We conducted contests for access to a foraging station between similar sized pairs of trout across all combinations of genotypes to determine whether Yellowstone cutthroat trout show differences in aggression and foraging behaviour when competing against rainbow and hybrid trout. Given the common pattern of replacement of native cutthroat trout by introduced rainbow trout and cutthroat–rainbow hybrids (Young 1995; Hitt et al. 2003; Weigel et al. 2003), we predicted that Yellowstone cutthroat trout would show lower levels of aggressive behaviour, spend less time defending the most profitable foraging location, and have lower foraging success when competing against rainbow and hybrid trout.

METHODS

Collection and Rearing of Experimental Animals

To control potential environmental effects between different cohorts of trout, we created experimental cohorts from gametes and reared them at equal densities in a common environment. We collected cutthroat trout eggs and sperm from a tributary stream of Henrys Lake, Island Park, Idaho, and rainbow trout eggs and sperm from the Hayspur Hatchery, Hayspur, Idaho, U.S.A. The Idaho Department of Fish and Game creates cutthroat trout, rainbow trout and cutthroat–rainbow hybrids using these source populations to stock throughout waterways in Idaho. We collected eggs and sperm from individual trout and transported them to Idaho State University to create the experimental cohorts.

We created the cohorts for this experiment in 2 consecutive years. The cohorts for the first year were created on 23 April 2004, and the second set was created on 10 February 2005. In both years, we created replicate cohorts of four trout genotypes: Yellowstone cutthroat trout, maternal cutthroat hybrids (cutthroat eggs fertilized with rainbow trout sperm), maternal rainbow hybrids (rainbow trout eggs fertilized with cutthroat trout sperm) and rainbow trout. In 2004, we divided clutches from each female in half, and to minimize the possibility of using an infertile male, we combined sperm from two conspecific males and used half to fertilize a conspecific egg lot and half to fertilize a heterospecific egg lot. In 2005, we followed a similar procedure, however, we used an entire egg clutch and the entire volume of sperm for each cross. Therefore, during 2004, hybrid crosses were maternal or paternal half-siblings to the pure parental crosses; in 2005, hybrid crosses were not directly related to the pure parental crosses. In each year, we created four replicates of each genotype (32 total cohorts, 16 cohorts each year). All cohorts were incubated in egg baskets suspended in recirculating water at 12°C (±1°C). After hatching and development to the exogenously feeding stage, trout from each cohort were transferred to separate compartments of a rearing system. We transferred an equal number of trout to the rearing system in each year, 100 and 330 trout to each rearing compartment during 2004 and 2005, respectively.

The rearing system for the trout cohorts consisted of four channels constructed out of plywood lined with fibreglass and coated with nontoxic aquaculture paint. We divided each channel crosswise with screens to create four rearing compartments measuring 109 cm long × 36 cm wide and maintained water depth at 24 cm with a standpipe drain. We supplied water to each channel from a common reservoir (~3 litres/min) equipped with a water-chilling unit to maintain temperature at 12°C (±1°C). Outflow from all channels was collected in a common reservoir, filtered, and pumped back to the header reservoir. We provided a slow input (~1.5 litres/min) of fresh, dechlorinated water to the header reservoir throughout development. Although we did not expect position within channels to influence development of a cohort, we accounted for any potential effect of position by assigning replicate cohorts of each genotype to one of the 16 compartments such that each genotype appeared only once in a channel and in every possible position across the array of channels. We fed each cohort standard hatchery feed (Biodry 1000, Bio-Oregon Inc., Warrenton, OR, U.S.A.) three times a day until satiation over the first month of development and twice daily thereafter. We removed uneaten food and waste several times a week. After the fish reached 4–5 cm fork length, we began our experimental trials.

Competitive Interactions

To quantify the frequency of aggressive interactions, ability to occupy a feeding location, and success at capturing food items between the four genotypes, we conducted pairwise contests between all combinations of the genotypes (Table 1). We conducted all contests in an aquarium measuring 80 × 25 × 25 cm high, which we subdivided to create an arena measuring 30 cm long × 15 cm wide located along the transparent front wall. The size of the arena was equal to 65.6% of the predicted territory size based on the mean size of trout in our trials (mean ± SD fork length = 4.36 ± 2.46 cm; Grant & Kramer 1990) and was purposely chosen to induce pairs of fish to compete for the single, central feeding station.

Table 1. The number of contests conducted within each pairwise combination of contestants to measure aggressiveness and relative competitive ability between Yellowstone cutthroat trout, rainbow trout and first generation hybrids

	YCT	MCH	MRH	RBT
YCT	40	—	—	—
MCH	40	40	—	—
MRH	40	40	40	—
RBT	40	40	40	40

YCT, Yellowstone cutthroat trout; MCH, maternal cutthroat hybrid; MRH, maternal rainbow hybrid; RBT, rainbow trout.

We maintained temperature and oxygenation of water with a slow input from the incubation and rearing reservoir, and circulated water through the arena using a submersible pump. Water velocity in the central location of the arena was 10 ± 1 cm/s. Over the size range of fish we observed (3.8–5.2 cm fork length), this equated to 1.92–2.63 body lengths per second. This velocity is well below the maximum sustainable swimming velocities for trout of this size (Seiler & Keeley 2007), but was still enough to orient fish to the flow, to transport food items downstream, and to induce trout to compete for the central feeding station.

Because even small differences in mass may affect behavioural and competitive interactions between salmonids (Abbott et al. 1985), we matched the size of competing fish across a gradient of relative mass and used relative size as a covariate in statistical analyses. To pair fish for contests, we randomly chose one genotype and haphazardly selected five trout from across the replicate cohorts. We lightly anaesthetized each trout (buffered Finquel MS-222, Argent Chemical Laboratories, Inc., Redmond, WA, U.S.A.; concentration: 1 g/litre), measured it for fork length (±0.5 mm) and mass (±0.01 g) and then paired one conspecific trout to one of the other four trout with the limitation that they were not from the same rearing population or related as a half-sibling. Next, we randomly chose a genotype from the three remaining genotypes and haphazardly selected five trout from across the replicate cohorts to pair the heterospecific competitor and establish competitors for other pairings. Trout from the remaining two genotypes were likewise sampled and matched with competitors to complete all 10 combinations (Table 1). We paired contestants within each combination of contestant genotypes across a broad range in relative size (range across all genotype combinations = 78–133%). We clipped a small piece of adipose fin from one randomly chosen individual of each pair to identify contestants. To allow recovery from anaesthesia and to equalize feeding status of all the contestants, we placed each trout into a PVC tube measuring 16.5 cm long × 5 cm diameter, covered the ends with mesh screening, and returned them to their rearing channels.

To begin each contest, we simultaneously introduced a pair of trout into the arena and allowed 1 min of acclimation without water flow, followed by 2 min with flow. After acclimation, we introduced food items (same as rearing) to the surface of the water at the front of the arena through a PVC tube (1.2 cm diameter × 60 cm long). Individual food items were added to the arena at a rate of one pellet every 10 s, or as quickly as they were eaten, over a 2-min period. Beginning after the last pellet was eaten, we recorded the amount of time that each fish spent holding the central feeding station and the aggressive behaviours initiated by each fish for a 5-min period. We recorded aggressive behaviours as displays, chases, or nips (Keenleyside & Yamamoto 1962); however, in preliminary trials, displays were the most common aggressive behaviour and nips and chases were rare. We combined all behaviours into one variable summarizing the total number of aggressive acts to avoid individual categories lacking observations and to create a response variable that met the assumptions of parametric statistical analyses. To accurately measure the response variables, we recorded each contest with a VHS camcorder and dictated each food capture, changes in position of contestants, and each aggressive behaviour by direct observation. After each trial, we euthanized contestants by blunt trauma to the head as mandated by our collection and rearing permit and preserved them in 10% formalin. We conducted 40 contests for each combination of contestant genotypes, for a total of 400 contests (110 trials during 2004, 290 trials during 2005).

Statistical Analyses

Although the behaviour of each individual in a contest could be reported as an observation in a statistical analysis, the competitive ability of either contestant is dependent on the success of its competitor. Pairwise contests typically have only two species or treatment groups, thus the response variables are commonly measured from the perspective of one species or treatment group (Abbott et al. 1985; Young 2003), allowing each trial to serve as an independent observation in an analysis of variance (ANOVA) model of relative competitive ability. In our study, we were interested in competitive ability across all combinations of the four genotypes. To provide an estimate of competitive ability of each trout genotype in competition against each other genotype with statistically independent observations, we used a random sampling method to choose one fish from each contest to serve as the individual under observation, hereafter referred to as the focal fish. We randomly assigned one fish from each trial to serve as the focal fish using PROC SURVEYSELECT (SAS Institute 2003). By using the STRATA option (strata = genotype combinations), each genotype was assigned to the focal genotype in one-half of the trials (20 out of 40) between different genotypes.

After the assignment of focal fish within each contest, we compared three response variables across the four genotypes using separate ANOVA models: the number of aggressive acts, proportion of time spent holding the feeding station and proportion of food items captured. We conducted an ANOVA with the genotype of the focal fish, the genotype of the competitor fish, and the interaction between focal genotype and competitor genotype as main effects, and the relative mass of contestants as a covariate. The effect of focal genotype tests for differences in the response variable between the four genotypes by averaging across the competitor genotypes; the effect of focal genotype compares the performance of focal genotypes regardless of the genotype of the competitor. Conversely, the effect of competitor genotype tests for differences in the response variables of the focal fish by averaging across the focal genotypes; the effect of competitor genotype compares the performance of focal fish, regardless of genotype, based on the competitor genotype. We also included a priori pairwise comparisons to compare each response variable between Yellowstone cutthroat trout and each of the other genotypes as both focal fish and competitor. To meet assumptions of homogeneity of variance, we $\log_{10}(x+1)$ transformed the number of aggressive behaviours and arcsine square-root transformed proportional data before conducting statistical analyses.

We used different measures of relative mass for the ANOVA model comparing aggression versus the models testing the proportion of time holding the feeding station and proportion of food captured. As the asymmetry in mass between contestants increases, we expected a size hierarchy to be recognized more quickly, limiting the number of aggressive interactions (Parker 1974). Therefore, regardless of the direction of relative size between the focal trout and its competitor, greater differences in mass would cause a decline in the number of aggressive behaviours by the focal fish. Our calculation for relative mass to compare aggression was: absolute value ((1 − focal genotype's mass (g)/competitor's mass (g)). In contrast, when we compared success at occupying the central feeding station and food captures, we expected increasing differences in relative mass to be positively related to these response variables. If the relative mass of contestants in our experiment had an effect on the ability to defend the feeding station and in capturing food, we expected focal fish that were smaller than their competitor to show lower competitive ability and focal fish that were larger than their competitor to show greater competitive ability. Therefore, we calculated relative mass as: mass of the focal genotype (g)/mass of competitor (g).

To provide a robust estimate of aggression and competitive ability between our four genotypes, we used a resampling procedure (Crowley 1992). After randomly selecting focal fish from each trial and conducting the ANOVAs, we stored the test statistics from each ANOVA model in an output file. We automated this analysis to loop 10 000 times to estimate the treatment effects from a random selection of the large number of possible combinations of focal fish within trials. We determined terms in each ANOVA model to be significant if the test statistic was significant in at least 95% of the models (9500/10 000 models), providing an approximation of a significance level of $\alpha = 0.05$ (for a similar example, see Adams & Anthony 1996). Our main results are the proportion of ANOVA models with significant model terms and pairwise comparisons. To illustrate relative differences in aggression and competitive ability between focal and competitor genotype combinations, we show the distribution of least squares means across 10 000 ANOVA models.

RESULTS

Using our criteria for detecting differences in each response variable between Yellowstone cutthroat trout, rainbow trout and their hybrids, we did not find a difference in the number of aggressive acts conducted by focal fish based on focal or competitor genotype (Table 2). Although aggression tended to be higher within trials involving rainbow trout as the focal or competitor genotype, aggression was not different across the treatment effects of focal or competitor genotype (Fig. 1a). The covariate of relative size indicates that the size of contestants did not explain a significant portion of the variability in aggression (Table 2). Similarly, the interaction term between focal and competitor genotypes indicated that the magnitude of change in aggression between focal and competitor genotypes did not differ across genotypes regardless of competitor genotype (Table 2, Fig. 1a).

In contrast to the number of aggressive acts, we found a difference in the proportion of time spent occupying the feeding station based on focal genotype (Table 2). When averaged across competitor genotypes, Yellowstone cutthroat trout as focal fish spent the least amount of time occupying the feeding station and rainbow trout, as focal fish, spent the highest amount of time occupying the feeding station (Fig. 1b). The pairwise comparisons clarify the differences in performance between Yellowstone cutthroat

Table 2. The percentage of significant model terms from 10 000 ANOVA models testing the effects of focal genotype, competitor genotype, the interaction of focal and competitor genotype, and the relative mass of contestants

		Response variable		
Factor effect	*df* for each model	Number of aggressive acts	Proportion of time occupying the feeding station	Proportion of food items captured
Focal genotype	3	60.3	95.2*	100*
Competitor genotype	3	81.1	94.7	100*
Focal × competitor genotype	9	0.5	15.6	41.8
Relative mass	1	0.1	10.9	0.0

Four hundred contests were conducted between all pairwise combinations of Yellowstone cutthroat trout, rainbow trout and first generation hybrids. One fish from each trial was randomly selected as the focal fish before conducting each ANOVA.
*Indicates significance at $\alpha = 0.05$.

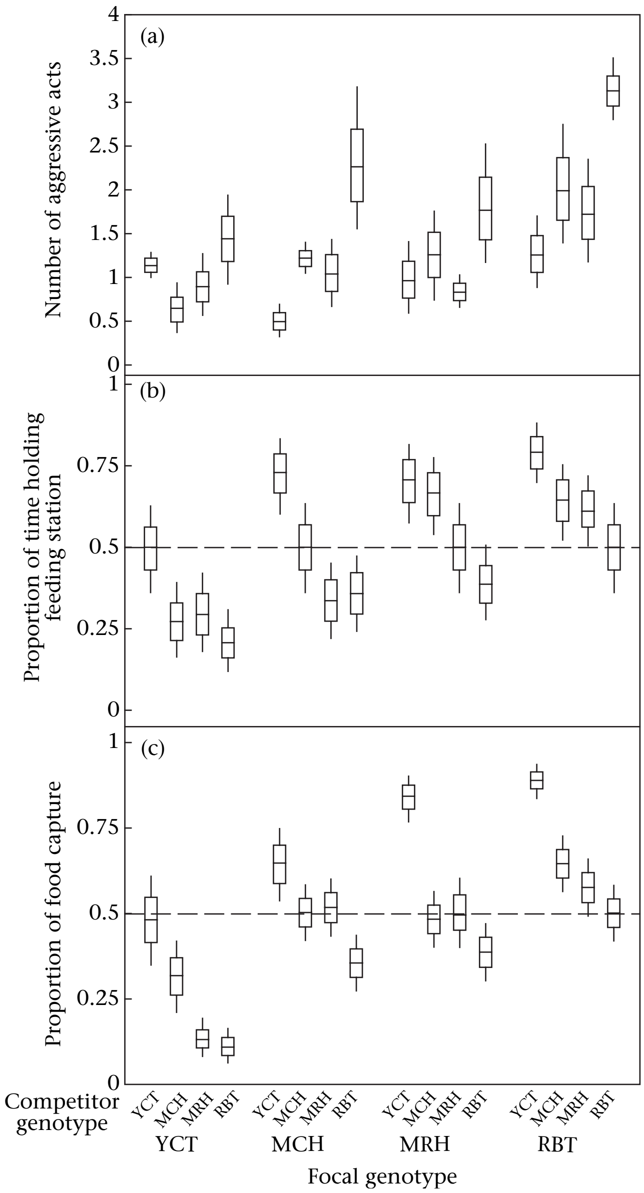

Figure 1. Box and whisker plots illustrating the distribution of least squares means for (a) number of aggressive acts conducted by focal fish, (b) the time focal fish held the central foraging station and (c) the proportion of food items captured by focal fish for all focal and competitor genotype combinations. Box and whisker plots represent the median and interquartile range of the least squares means from 10 000 ANOVA models. Lower and upper whiskers represent 10% and 90% values, respectively. Acronyms are defined as follows: YCT, Yellowstone cutthroat trout; MCH, maternal cutthroat hybrids; MRH, maternal rainbow hybrids; RBT, rainbow trout. The statistical tests were performed on transformed data; for clarity, back-transformed values are presented.

trout, maternal cutthroat hybrids, maternal rainbow hybrids and rainbow trout as the focal genotype: Yellowstone cutthroat trout spent a lower proportion of time in the central feeding station than maternal cutthroat hybrid, maternal rainbow hybrid, and rainbow trout in 41.9%, 89.3% and 99.5% of the ANOVA models, respectively. Based on the least squares means over 10 000 ANOVA models, maternal cutthroat hybrids, maternal rainbow hybrids and rainbow trout spent 53.3%, 78.9% and 104.5% more time occupying the feeding station than Yellowstone cutthroat trout, respectively. Although we found a significant difference in the proportion of time spent occupying the foraging station based on competitor genotype in 94.7% of the ANOVA models (Table 2) this was not enough to conclude significance by our criteria. The covariate of relative mass did not explain a significant proportion of the variability in the time focal fish occupied the feeding station (Table 2). Similarly, the interaction between focal and competitor genotypes indicates that the magnitude of change in the time focal fish occupied the feeding station was not different across focal genotypes; within each focal genotype, we found a consistent decline in time spent occupying the feeding station from Yellowstone cutthroat trout to rainbow trout (Table 2, Fig. 1b).

In addition to differences in monopolizing the central feeding station, we found strong differences in the amount of food captured across focal and competitor genotypes (Table 2). When averaged across competitor genotypes, Yellowstone cutthroat trout as focal fish captured the lowest proportion of food items and rainbow trout as focal fish captured the highest proportion of food items (Fig. 1c). The pairwise comparisons clarify the differences in food capture between Yellowstone cutthroat trout, maternal cutthroat hybrids, maternal rainbow hybrids and rainbow trout as focal and competitor genotypes. Averaged across competitor genotypes, Yellowstone cutthroat trout captured a lower proportion of food items than maternal cutthroat hybrids, maternal rainbow hybrids and rainbow trout in 99.9%, 99.9% and 100% of the ANOVA models, respectively. Based on the least squares means over 10 000 ANOVA models, maternal cutthroat hybrids, maternal rainbow hybrids and rainbow trout captured 106%, 129% and 171% more food items than Yellowstone cutthroat trout, respectively. When averaged across focal genotypes, focal fish captured significantly more food against Yellowstone cutthroat trout than maternal cutthroat hybrids, maternal rainbow hybrids and rainbow trout in 99.5%, 99.9%, and 100% of the ANOVA models, respectively. Based on the least squares means over the 10 000 ANOVA models, focal fish captured 50%, 43% and 61% less food when the competitor genotype was a maternal cutthroat hybrid, a maternal rainbow hybrid, and a rainbow trout, respectively, than when the competitor was a Yellowstone cutthroat trout. The covariate of relative mass between contestants did not explain a significant proportion of the variability in the proportion of food items captured (Table 2). Similarly, the interaction term between focal and competitor genotypes indicates that the magnitude of change in the proportion of food items captured did not differ across focal genotypes regardless of the competitor genotype. Within each focal genotype, the order of success at food captured by competitor genotypes indicates a consistent decline from Yellowstone cutthroat trout to rainbow trout (Table 2, Fig. 1c).

Two features from our plot of the least squares means indicate that our analyses provide an accurate assessment of relative aggression and competitive ability between Yellowstone cutthroat trout, rainbow trout, and their hybrids. First, based on the distribution of least squares means from 10 000 ANOVA models, we found a pattern of increasing number of aggressive acts from Yellowstone cutthroat trout to rainbow trout within each focal genotype (Fig. 1a). We also found a pattern of decreasing proportion of time holding the feeding station and a decreasing proportion of food items captured from Yellowstone cutthroat trout to rainbow trout within each focal genotype (Fig. 1b, c). Had we detected a high proportion of models with a significant interaction term with any response variable, we would expect deviations from these patterns. Second, the distribution of least squares means from 10 000 ANOVAs for the proportion of time holding the feeding station and the proportion of food captured between conspecific genotypes was centred around 50% indicating, as expected, equal competitive ability within contests between individuals of the same genotype (Fig. 1b, c).

DISCUSSION

Our study provides evidence of poor competitive ability by juvenile Yellowstone cutthroat trout when competing for a foraging location against rainbow trout and first generation cutthroat–rainbow hybrid trout. We did not detect differences in the number of aggressive acts used by Yellowstone cutthroat trout, rainbow trout, and first generation hybrids; however, Yellowstone cutthroat trout as the focal genotype spent a lower proportion of time occupying the feeding station and had the lowest foraging success. Rainbow trout and hybrid genotypes had the highest success at holding the feeding station and captured the highest proportion of food items when Yellowstone cutthroat trout were the competitors. Cutthroat trout and rainbow trout are closely related species and, along with their hybrids, are thought to have similar ecological roles in stream environments. Given that we controlled for rearing environment and the relative size of contestants, and that we simultaneously introduced contestants to the competition arena, we assume that no gross differences exist between the genotypes in acclimation to the test conditions or in foraging behaviour; therefore, we interpret the differences in ability to occupy the central feeding station and food capture as consequences of intergenotypic competitive ability.

The levels of aggressive behaviour between our genotypes did not fit our prediction that Yellowstone cutthroat trout would be less aggressive than rainbow trout and hybrid genotypes. The lack of differences in aggression used by focal or competitor genotypes provide indirect evidence that genotypic differences may have been a consequence of assessment of opponents at early stages of a contest. In another study (Seiler & Keeley 2007), we investigated morphological differences from a subset of trout created during the first set of crosses of this experiment and found that Yellowstone cutthroat trout have shallower bodies and smaller pelvic fins than rainbow trout and hybrid crosses. Contestants may have visually assessed differences in resource holding potential (RHP; Parker 1974) during the initial stages of a contest rather than using aggressive attacks to settle the contest. Unlike intraspecific contests with highly ritualized behaviour patterns (e.g. cichlid sp.; Myrberg 1965; Enquist et al. 1990), RHP assessment between our trout may occur on shape differences during the early portions of a contest that could limit the escalation of aggressive acts, even within interspecific contests between trout of very similar mass.

Although we did not detect differences in aggression, aggression may still play a role in success of non-native rainbow trout and cutthroat–rainbow hybrids at displacing Yellowstone cutthroat trout in the wild. Aggressiveness is recognized as an important characteristic in many successful invading species (amphipods: Dick et al. 1995; ants: Holway 1999; crayfish: Bovbjerg 1970; Gambadt et al. 1997; Usio et al. 2001; fish: Moyle 1986; Marchetti 1999). Across many species of salmonid fish, rearing in hatcheries is associated with elevated aggression relative to wild populations (Fenderson et al. 1968; Swain & Riddell 1990; see review by Weber & Fausch 2003). Most, if not all, rainbow trout and cutthroat–rainbow hybrids present within the native range of Yellowstone cutthroat trout are from hatcheries or are the wild offspring of rainbow trout with extensive hatchery ancestry. Aggressiveness and other phenotypic differences expressed by hatchery salmonids are known to have a genetic basis (Swain & Riddell 1990; Riddell & Swain 1991; Berejikian et al. 1996). Hence, rainbow trout and hybrid trout may retain elevated aggressiveness and its potential competitive advantages for generations after release into the wild. Field observations of the aggressive foraging behaviours used between juvenile Yellowstone cutthroat trout, rainbow trout and hybrids could address this issue; however, positive identification of these genotypes would prove difficult because phenotypic differences between them are difficult to discern by eye (Seiler & Keeley 2007).

The differences we found in the abilities of Yellowstone cutthroat trout, rainbow trout and hybrid trout to occupy a feeding station and capture food items indicate that our results may be important to the competitive interactions between these species in the wild. Competition for foraging locations, and presumably food resources, between juvenile salmonid fish is thought to be intense and individuals that cannot acquire a feeding territory are forced to emigrate from stream reaches or die (Chapman 1962; Elliott 1986; Keeley 2001). Therefore, if native Yellowstone cutthroat trout are less successful at defending feeding territories and capturing food items when competing against rainbow and hybrid trout, they may be displaced from streams through lower growth rates, higher emigration rates and higher mortality rates.

Size asymmetry between juvenile Yellowstone cutthroat trout, rainbow trout and hybrids in the wild may indicate another concern for native cutthroat trout populations. Across many species, size asymmetry is known to influence competitive ability (Parker 1974; Archer 1988). In controlled contests between rainbow trout pairs, size differences as small as 6% were enough to predict the outcome of competition for food resources (Abbott et al. 1985). Although size did not explain a significant portion of the variation in aggression or foraging ability in our experiment, the relative size between Yellowstone cutthroat trout, rainbow trout and hybrid fish in the wild is probably greater. We do not know any studies that have measured size differences between sympatric Yellowstone cutthroat trout, rainbow trout and hybrids during their first summer of growth; however, Henderson et al. (2000) found that rainbow trout and cutthroat–rainbow hybrids spawn earlier than Yellowstone cutthroat trout. Earlier spawning may allow young-of-the-year to emerge earlier, providing an initial size and competitive advantage that could be difficult for native Yellowstone cutthroat trout to overcome. If young-of-the-year Yellowstone cutthroat trout are consistently smaller than rainbow trout and hybrids in the wild, they may experience a persistent competitive disadvantage that is even greater than what we observed.

Despite the severe impacts that often occur when native species hybridize with introduced species (Rhymer & Simberloff 1996), few studies have tested the competitive mechanisms that may allow introduced species and hybrids to displace native species (but see Rosenfield et al. 2004; Seiler & Keeley 2007). Our study adds to a growing body of evidence indicating that behavioural interactions play an important role in the displacement of native species by introduced species (cf. Gherardi & Cioni 2004; Gherardi & Daniels 2004). The differences we identified in foraging behaviour between Yellowstone cutthroat trout, rainbow trout and their hybrids could explain, in part, the rapid decline of native cutthroat trout after the introduction of rainbow trout. Future studies should address whether such differences translate into differences in growth, mortality, or emigration rates between native cutthroat trout, introduced rainbow trout and their hybrids.

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