The effects of hatchery domestication on competitive dominance of juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: We tested the null hypotheses that competitive dominance among juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in contest and scramble experiments would not be affected by domestication selection after one generation of state-of-the-art hatchery culture. Dyadic challenges of size-matched juvenile fish were conducted after a 6-day acclimation in 113.4 L aquaria. Differences in dominance and frequency of different types of agonistic interactions used were not significantly different in contest (n = 505) or scramble (n = 363) competition experiments ($P > 0.05$). However, wild origin fish were more aggressive than hatchery origin fish in both types of experiments ($P \le 0.05$). Furthermore, wild origin fish gained more weight than hatchery origin fish during contest experiments, and hatchery origin fish lost less weight than wild origin fish in scramble experiments ($P \le 0.05$). Dominant fish, regardless of origin, grew more than subordinate fish in both contest and scramble experiments ($P \le 0.05$). Our results indicate that aggression, and growth mediated by competition, can be affected by domestication after only one generation of state-of-the-art hatchery culture; however, impacts to competitive dominance appear to be small.

Résumé : Nous testons les hypothèses nulles qui veulent que la dominance de compétition chez de jeunes saumons chinook (*Oncorhynchus tshawytscha*) dans des expériences de compétition de combat et de mêlée ne soit pas affectée par la sélection due à la domestication après une génération d'élevage dans une pisciculture de pointe. Nous avons organisé des confrontations dyadiques de jeunes poissons appariés en fonction de la taille après 6 jours d'acclimatation dans des aquariums de 113,4 L. Les différences dans la dominance et dans la fréquence des diverses interactions agonistes ne sont pas significativement ($P > 0,05$) distinctes dans les expériences de compétition de combat (n = 505) et de mêlée (n = 363). Cependant, les poissons d'origine sauvage sont plus agressifs ($P \le 0,05$) que les poissons d'élevage dans les deux types d'expériences. De plus, les poissons d'origine sauvage accumulent plus de masse que les poissons d'élevage au cours des expériences de combat et les poissons d'élevage perdent moins de masse que les poissons sauvages dans les expériences de mêlée ($P \le 0,05$). Les poissons dominants, quelle que soit leur origine, croissent plus rapidement que les poissons subordonnés, tant dans les expériences de combat que de mêlée ($P \le 0,05$). Nos résultats indiquent que l'agressivité et la croissance sous le contrôle de la compétition peuvent être affectées après une seule génération d'élevage dans une pisciculture de pointe; les effets sur la dominance de compétition semblent, cependant, être limités.

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Introduction

Despite our best efforts, raising fish in hatcheries may cause unintended behavioral changes in salmonids because of domestication selection, but no studies have evaluated whether our best efforts reduce behavioral changes. Domestication is defined as natural selection in artificial environments (Campton 1995). Selection in artificial environments could be due to intentional or artificial selection, biased sampling during some stage of culture, or unintentional selection (Busack and Currens 1995). The goal of supplementation or conservation hatcheries is to produce fish that will integrate well into natural populations (Mobrand et al. 2005). Managers of conservation hatcheries attempt to minimize intentional or biased sampling so that the hatchery fish are genetically similar to naturally produced fish. However, the selective pressures in hatcheries are dramatically different than in the natural environment, which can result in genetic differences between hatchery and wild fish (Reisenbichler and McIntyre 1977; Einum and Fleming 2001; Weber and Fausch 2003) and subsequently differences in behavior (Berejikian et al. 1996; Metcalfe et al. 2003; Wessel et al. 2006). The selective pressures may be particularly prominent during the freshwater rearing stage where substantial mortality of wild fish occurs (Groot and Margolis 1991).

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During freshwater rearing, salmonids in hatcheries and rivers use very different methods to acquire food. River environments are heterogenous with respect to food and habitat quality. Salmonids rearing in streams primarily feed on drifting invertebrates as they maintain energetically profitable stream locations (Fausch 1984). Dominant fish secure the most food and often grow the fastest (Metcalfe 1986). These fish use a variety of agonistic interactions, such as nips, butts, chases, and threats to defend territories that have predictably high levels of food (Chapman 1962; Grant and Kramer 1990; McMichael et al. 1999). This type of interaction is referred to as contest or interference competition (Birch 1957). Salmonids in hatchery raceways live in homogenous environments and at high densities where defending distinct territories may not be advantageous or even possible (Maynard et al. 1995). Fish in hatcheries frequently use shoaling or schooling behaviors and acquire food from the water surface (Weber and Fausch 2003). Thus, agonistic interactions prior to feeding may waste energy, but result in few immediate negative consequences (e.g., reduced growth, reduced survival) in hatchery environments, where food is plentiful and predators absent (Maynard et al. 1995; Einum and Fleming 2001). Fish that are in the right place at the right time and that swim rapidly towards the food are the most successful. This type of interaction is referred to as scramble or exploitative competition (Birch 1957). Exploitative competition may also occur in natural environments, particularly when space is not limited but fish densities are sufficiently high, fish densities are so high that territorial behavior is unprofitable, aggression levels are low, or locally abundant sources of food are unpredictable (Rodriguez 1995; Grant and Imre 2005).

Domestication selection has been shown to alter the aggressiveness and dominance of hatchery fish. For example, domestication has been implicated as causing either an increase, no change, or decrease in aggressive and schooling behavior in fish (Ruzzante 1994; Einum and Fleming 2001). Berejikian et al. (1996) found that offspring of wild steelhead trout (sea-run *Oncorhynchus mykiss*) were initially more aggressive and dominant than size-matched offspring of parents that had been in hatchery culture for four to seven generations. However, when hatchery fry had a 3.0%–4.5% size advantage, they dominated wild fish in 68% of encounters. Swain and Riddell (1990) found that domesticated coho salmon (*Oncorhynchus kisutch*) were more aggressive than those of natural origin from nearby streams. Three domesticated stocks of Atlantic salmon (*Salmo salar*) were generally dominant over wild origin juveniles when both had been raised in a common hatchery environment; however, when wild origin fish were given a 2-day period of prior residence, the asymmetry in dominance was reversed (Metcalfe et al. 2003). Petersson and Jarvi (2000) suggested that both contest and scramble competition affected the growth of brown trout (*Salmo trutta*) parr of natural and sea-ranched origins. Farrell (2003) found that wild spring Chinook salmon (*Oncorhynchus tshawytscha*) from the Yakima Basin were competitively dominant to descendents of first generation, local origin hatchery fish in a contest competition experiment during 2002.

The goals of this study were to determine if there are differences in dominance between offspring of wild and first generation hatchery spring Chinook salmon from the upper Yakima Basin under (*i*) contest and (*ii*) scramble competition. If domestication has not occurred, we would expect offspring of hatchery and wild fish to have equivalent levels of aggression and dominance. If domestication has occurred, we would expect offspring of hatchery fish to be dominant in scramble competition and offspring of wild fish to be dominant in contest competition. We also conducted a separate growth experiment to determine if differences in growth in the competition trials could be attributed to inherent capabilities to grow caused by domestication.

Materials and methods

Fish used in this experiment were juvenile offspring of either wild spring Chinook salmon or offspring of fish that were spawned artificially in the hatchery, reared to smolt, and released. As such, these fish were neither truly hatchery nor wild fish because they were not produced in the natural environment or with conventional hatchery practices (e.g., reared in circular tanks, not concrete raceways). However, for the ease of communication we refer to offspring of wild spring Chinook salmon as wild, and the offspring of fish that were spawned artificially in the hatchery, reared, and released as smolts are referred to as hatchery. The fish that spent one generation in the hatchery were offspring of wild spring Chinook salmon that were collected at Roza Dam, located in central Washington, as part of the Yakima/Klickitat Fisheries Project Supplementation Program. The only difference between the two types of fish was that the hatchery fish spent a portion of one generation in the hatchery. The hatchery fish were treated using state-of-the-art fish culture practices. For example, natural origin adult fish were collected in proportion to their abundance and timing at Roza Adult Monitoring Facility, located at Roza Dam, and a factorial mating design (e.g., 2 × 2 or 3 × 3) was used to increase the genetic diversity of the offspring. Adult fish that were taken to the hatchery were held in ponds, spawned, their eggs incubated, and juveniles reared in raceways (30.5 m long × 3.0 m wide × 1.1 m water deep) containing densities of approximately 40 000 fish per raceway.

Parental fish used for this experiment were collected, held, and spawned in the same way as previously described for the hatchery. Naturally produced fish were spawned with naturally produced fish to produce wild fish, and hatchery fish were spawned with hatchery fish to produce hatchery fish. After spawning, fertilized eggs were disinfected and placed in small cylindrical containers (isolettes; 10.2 cm in diameter and 5 cm tall), within incubation trays as a means to identify individual families. Isolettes were selected in a way that ensured nearly all adult broodstock used for the experimental isolette crosses were represented in our sample at least once (wild females: 33 (2003), 18 (2004); wild males: 25 (2003), 18 (2004); hatchery females: 32 (2003), 20 (2004); hatchery males: 15 (2003), 20 (2004); wild families: 58 (2003), 54 (2004); hatchery families: 59 (2003), 58 (2004)). Hatchery and wild fish were transferred to two identical 1710 L polyethylene, conical-bottomed circular tanks on 17 April 2003 and 19 April 2004 and then fed starter feed until large enough to feed on Bio-Oregon moist pellets. Circular tanks were exposed to natural light and were supplied with water from the same source as the hatchery (i.e., mostly Yakima River water).

Experiments were conducted in eighty 113.4 L glass aquaria (91.4 cm long, 30.5 cm wide, 40.6 cm deep inside dimensions) at the Cle Elum Supplementation and Research Facility, located in the upper Yakima Basin near the town of Cle Elum, Washington. Experiments were initiated when fish were large enough to be clearly identified by a fin clip during behavioral observations (approximately early July) and concluded when interaction rates declined substantially (e.g., likely due to cold water temperatures in mid-October). Two types of dominance experiments were conducted. The first experiment was designed to assess dominance under contest competition, and the second experiment was designed to assess dominance under scramble competition. In both experiments, fish were anesthetized with MS-222 (tricaine methanesulphonate), fork length (FL, mm) and weight (mg) were recorded, the fish were size-matched to the nearest 1 mm (FL), and the adipose fin was either completely excised or slit so that the fin remained intact. The presence or absence of the fin clip allowed us to differentiate the fish during observations. The slit fin was intended to put the unmarked fish under similar handling procedures as the marked fish. Marks were alternated between aquaria and origin to eliminate any behavioral difference due to marking stress. Fish were allowed to recover from the anesthetic and then stocked in aquaria. One hatchery and one wild spring Chinook salmon were placed in each aquarium. Both fish were introduced at the same time to prevent any prior residence advantage (e.g., Metcalfe et al. 2003).

Fish were acclimated in aquaria for 6 days. This acclimation period was determined by comparing behavioral responses and dominance from pairs of fish that were held for different lengths of time during previous experiments (Pearsons et al. 2001). After 6 days, the behavioral responses and dominance did not generally change. In addition, it was possible to measure differences in growth over this length of time. Fish were fed a total of 10 pellets during each acclimation day, except for the first day stocked and the sixth day when fish were not fed so that they would be hungry and interact on the observation day. During 2003, we increased the size of the pellets that were fed to the fish as fish length increased. During 2004, we used small pellets throughout the duration of the experiment to ensure that fish would not become satiated and cease interacting during the experiments. During the acclimation period, fish interacted with one another, and it is likely that dominance was established prior to the seventh day.

After the 6-day acclimation, food acquisition, agonistic interaction, and habitat location was assessed on day 7. An observer recorded observations from behind a blind constructed out of camouflage netting to prevent fish from seeing the observer. The observer distinguished fish origin based on the presence or absence of a fin clip, but the observer did not know which origin had each clip. The number of food items acquired by each fish was recorded. Agonistic interactions were recorded throughout the duration of the observations. We recorded which fish initiated an interaction and whether they dominated. Dominance of an interaction was assigned to the fish that defended a position or removed another fish from a preferred position. Type of interaction was recorded as follows: nip (contact with mouth open), butt (contact with mouth closed), chase (no contact, swimming after another fish for at least one body length), threat (no contact; for example fin flares, opercle flares, swimming side by side), and crowd (no clear threat but physical presence moved the other fish away) (McMichael et al. 1999). After observations were completed, fish were removed from aquaria, anesthetized with MS-222, and FL (mm), weight (mg), and presence or absence of adipose fin was recorded. Growth was calculated by subtracting the length or weight of each fish at the end of the experiment by the length or weight at the beginning of the experiment.

Contest competition

The aquaria were configured to provide one location that was close to a source of underwater food, water flow, and cover. Food pellets, ground into a slurry, were introduced through a tube with running water to alert fish that food was available. Once both fish had keyed into the food source, one food pellet was added at approximately 1 min intervals. The location of each fish was recorded at least once every minute. The location was expressed as which fish, if any, was in an area that was closest to the source of food, flow, and cover. This was generally in the middle of the tank, from 2.5 to 25 cm off the bottom and from the end of the pipe to 30 cm downflow of the pipe. If both fish were in this zone, then the fish closest to the pipe was assessed to be in the most desirable location. The cover was made out of thick wire, black plastic sheeting on the top, and window screen on the side furthest from the observer and was 20 cm long, 16 cm tall, and 16 cm wide. Total observation time for each replicate was approximately 20–25 min (not including the time that the food slurry was introduced). Dominance was attributed to the fish that won at least two of three categories: acquired the most food, dominated the most behavioral contests, and occupied the location closest to the outlet of the pipe the most. If fish did not consume at least 10 pellets together or if fish did not interact with each other, then they were not included in the analysis because dominance could not be reasonably assessed. All fish were size-matched to the same length (mm FL) except in 2003, when 15 replicates differed in size by 1 mm (nine of the wild fish and six of the hatchery fish were bigger, and this difference was less than 2% of the body length of the smaller fish). This size difference is not thought to be influential in behavioral dominance (Abbott et al. 1985).

Scramble competition

Methods for scramble competition were the same as those for contest competition except for the following differences. The configuration of aquaria was the same except that the cover was removed. In addition, food was introduced onto the surface of the water from behind the blind into one of five locations every minute. The locations were the four corners and the center of the aquaria. The order of food presentation into these locations was rotated. Dominance was assigned to the fish that ate the most pellets. In 2003, the fish were the same length in all but 21 of the replicates, and of these 21 replicates they were 1 mm FL different (12 of the wild fish and 9 of the hatchery fish were bigger, and this difference was less than 2% of the body length of the smaller fish). All of the fish were the same size at stocking during 2004.

Growth experiment

To determine if there were inherent differences in hatchery and wild fish to grow and thereby influence our assessment of growth in competition trials, we performed a separate growth experiment during 2004. The protocols and aquaria for this experiment were exactly the same as those used in the contest competition experiment except that only one fish was placed into each aquarium. Equal numbers of replicates were completed for both origins of fish. The same number of pellets (10 during acclimation and 20 on day 7) was added to the tank so that growth in the contest competition experiments could be compared with growth without competition. Measurement of growth was done in the same way as described for contest competition experiments.

Analysis

A variety of parametric and nonparametric tests were used to test for differences among comparisons (Sokal and Rohlf 1981). Paired comparisons between total dominance of hatchery and wild fish were made for each replicate using a two-tailed Wilcoxon matched pairs test. This test was a matched comparison of the sums of the percentages of the food acquisition, habitat used, and interactions dominated in contest experiments and percentage of food eaten in scramble experiments. Comparisons of types (e.g., chase, butt, nip) and frequencies of interactions were made with a *G* test. Aggressiveness (average interactions initiated per minute for all tanks) was compared with a Mann–Whitney *U* test for hatchery versus wild fish. To determine sources of aggressive differences and to standardize comparisons, (*i*) dominant hatchery versus dominant wild fish and (*ii*) subordinate hatchery versus subordinate wild fish were compared using the same test. Aggressiveness of dominant fish (regardless of origin) was compared with subordinate fish using a Mann–Whitney *U* test. Paired comparisons of growth in the competition experiments were compared using a two-tailed paired Student's *t* test. A paired sign test was used to compare whether fish in each replicate that grew the most were also classified as dominant. Comparisons of growth in the single fish growth experiment were made with a two-tailed Student's *t* test. With the exception of growth and interaction rate data in scramble experiments, data collected during 2003 and 2004 were pooled because differences between years were not significantly different ($P > 0.05$), and increased sample size contributes to increased statistical power. Differences were considered statistically significant if $P \leq 0.05$. Student's *t* tests and *G* tests were calculated using Microsoft Excel, and the remainder of tests was calculated using the software program STATISTICA (StatSoft, Inc. 2001).

Results

Contest competition

Dominance was assessed in 229 out of 255 replicates during 2003 and in 276 out of 314 replicates during 2004. A total of 26 replicates in 2003 were eliminated because fish died or were missing (2: 1 hatchery and 1 both hatchery and wild fish), neither fish ate (14), no interactions were observed (7), or at least one fish behaved abnormally (3: all hatchery; e.g., swimming up and down against the side of the aquarium). Thirty-eight replicates in 2004 were eliminated because fish jumped out of tanks (4: all hatchery), fish died or were missing (5: 1 hatchery, 3 wild, 1 unknown), neither fish ate (12), no interactions were observed (5), or at least one fish behaved abnormally (12: 9 hatchery and 3 wild; e.g., swimming up and down against the side of the aquarium). Most of the failed replicates were caused by both fish in the aquarium exhibiting behavior that would not allow us to assess dominance (22 out of 26 in 2003 and 17 out of 38 in 2004). However, hatchery fish were most often the cause of failed replicates when one fish could be identified as the cause of failure.

Overall dominance scores were not significantly different between hatchery (mean ± 1 standard deviation, SD; 141 ± 124) and wild (mean ± 1 SD; 159 ± 124) fish ($P = 0.058$). Food, habitat, and agonism dominance were consistently higher for wild fish (Fig. 1), and 53% of the replicates were dominated by wild fish (Fig. 1). Of the replicates where fish differed by 1 mm, hatchery fish dominated 1 of 5 replicates when it was bigger, and wild fish dominated 5 of 10 replicates when it was bigger. These results indicate that the small differences in size did not influence dominance. The frequencies of different types of interactions used by hatchery and wild fish were not significantly different (*G* test, $P = 1.000$; Fig. 2). Wild fish initiated a total of 7865 interactions, and hatchery fish initiated a total of 7245 interactions. Wild fish were 8.1% more aggressive than hatchery fish ($P = 0.05$; Fig. 3), and this difference was likely caused by higher aggressiveness of subordinate wild fish (Fig. 3). Significant differences in aggressiveness were not detected between dominant fish of the two origins (Fig. 3). However, dominant fish (regardless of origin) were more aggressive than subordinate fish ($P < 0.0001$; Fig. 3).

Wild fish gained more weight than hatchery fish (2003 and 2004 combined), and this finding was largely due to differences detected in 2004 (Table 1). Significant difference in length growth of hatchery and wild fish were not detected (Table 1). However, dominant fish, regardless of origin, grew significantly more than subordinate fish in both length and weight (Table 1). Both origins of fish gained weight in 2003 and lost weight in 2004 (Table 1).

Scramble competition

Dominance was assessed in 97 out of 112 replicates during 2003 and in 266 out of 296 replicates during 2004. Fifteen replicates in 2003 were eliminated because fish died or were missing (7: 1 hatchery and 6 wild), neither fish ate (4), no interactions were observed (1), or at least one fish behaved abnormally (3: all wild). Thirty replicates in 2004 were eliminated because fish died or were missing (7: 4 hatchery, 2 wild, and 1 both), neither fish ate (17), no interactions were observed (5), or at least one fish behaved abnormally (1 hatchery). Most of the failed replicates were caused by both fish in the aquarium exhibiting behavior that would not allow us to assess dominance (5 out of 15 in 2003 and 23 out of 30 in 2004). However, wild fish were most of-

Fig. 1. Comparisons of mean (±1 standard deviation) of the food acquisition, habitat occupation, agonism dominance (agonism), and replicates dominated by wild (open bars) and hatchery (solid bars) fish in contest competition experiments.

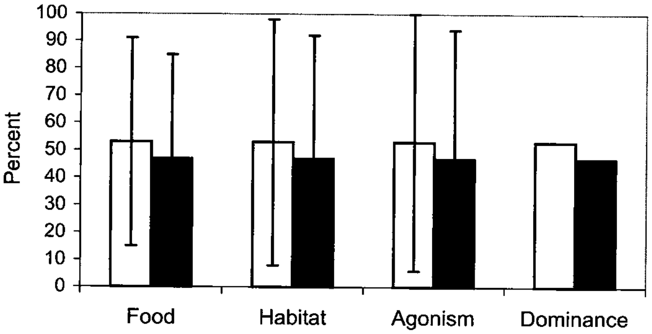


Fig. 2. Comparisons of frequencies of interaction types initiated (mean interaction per fish in each tank ±1 standard deviation) by wild (open bars) and hatchery (solid bars) fish in contest competition experiments.

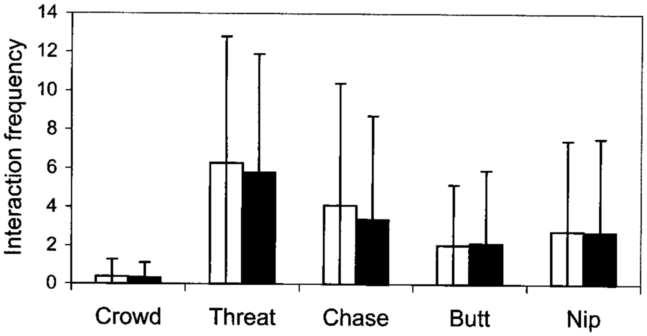
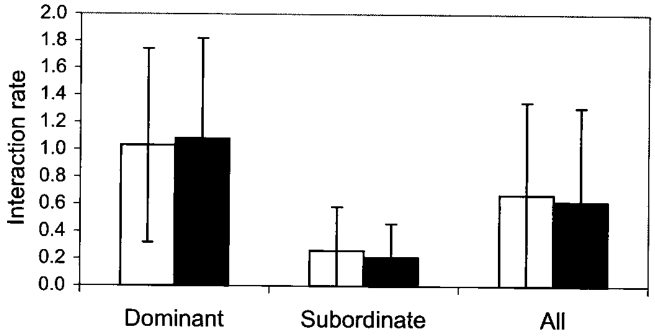


Fig. 3. Interaction rates (mean interaction per fish per minute ±1 standard deviation) of agonistic interactions initiated by wild (open bars) and hatchery (solid bars) fish in contest experiments.



ten the cause of failed replicates when one fish could be identified as the cause of failure.

Overall dominance was not significantly different between hatchery and wild fish ($P = 0.74$); hatchery fish were dominant for 47% of replicates, and dominance was equal in 5% of the replicates (Fig. 4). If the percentage of replicates that were tied for dominance were equally apportioned to origin (e.g., 2.5%), then 49.5% of replicates were dominated by hatchery fish. Food and agonism dominance were slightly higher for wild fish (Fig. 4). Of the replicates where fish differed by 1 mm, hatchery fish dominated 5 of 11 replicates when it was bigger, and wild fish dominated 6 of 10 replicates when it was bigger. These results indicate that the small differences in size did not influence dominance. The frequencies of different types of interactions that hatchery and wild fish used were not significantly different ($P = 1.000$; Fig. 5). Wild fish initiated a total of 6222 interactions, and hatchery fish initiated a total of 5717 interactions. Wild fish were 10.1% more aggressive than hatchery fish (Table 2), and this difference was likely caused by higher aggressiveness of subordinate wild fish than subordinate hatchery fish in 2003 (Table 2). Significant differences in aggressiveness were not detected between dominant fish of the two origins (Table 2). However, dominant fish were more aggressive than subordinate fish ($P < 0.0001$; Table 2).

Hatchery fish lost less weight and grew longer than wild fish (2003 and 2004 combined), and this finding was largely due to differences detected in 2003 (Table 3). Dominant fish, regardless of origin, grew significantly more than subordinate fish in both length and weight (Table 3). Both origins of fish gained weight in 2003 and lost weight in 2004 (Table 3).

Growth experiment

Growth of single fish was assessed in 125 wild and 125 hatchery origin replicates out of 320. Seventy replicates were eliminated because three fish jumped out of tanks (2 hatchery and 1 wild), and 67 fish ate fewer than 10 pellets on the seventh day (33 hatchery and 34 wild). The same number of hatchery and wild origin fish were responsible for failed replicates (35). There was no detectable difference in growth between wild and hatchery fish ($P = 0.95$; Fig. 6). Mean growth of hatchery and wild fish was considerably higher in single fish replicates than growth of individual fish of the same origin in paired contest experiments during 2004 ($P < 0.0001$).

Discussion

If we had the resources to perform a higher number of replicates in contest competition trials, it is possible that the increased statistical power would have resulted in a significant probability of rejecting the total dominance null hypothesis ($P \leq 0.05$), but the magnitude of difference would still be small. As it was, we had a 5.8% chance of rejecting the null hypothesis of no difference between fish origins in contest competition dominance when it was actually true. Approximately 29 additional replicates would be necessary to detect a significant difference in dominance ($P = 0.050$) if we extrapolate the results we observed for the 505 replicates. That being said, the number of replicates that we conducted is the highest that we are aware of for this type of study. Our study demonstrates that large numbers of replicates are necessary to detect statistically significant differences when differences in competitive dominance are small.

It is not uncommon for replicates in these kinds of studies to be discarded because some behaviors make it difficult to assess dominance (e.g., Metcalfe et al. 2003). We discarded about 5% of the replicates in our study, because we could not assess dominance when fish jumped out of tanks or when fish expressed behavior indicative of wanting to leave an aquarium. However, it is possible that 24 of the replicates

Table 1. Comparisons of mean (±1 standard deviation in parentheses) wild and hatchery fish growth and percentage of replicates that the dominant fish grew more than the subordinate in contest competition experiments.

		Growth		% of dominant fish that grew more	
Origin	n[a]	Length (mm)	Weight (mg)	Length	Weight
2003					
Wild	227	0.44 (1.24)	94.70 (279.32)	75	80
Hatchery	227	0.59 (1.33)	57.72 (290.37)	82	80
P[b]		0.133	0.223	<<0.001	<<0.001
2004					
Wild	276	0.31 (0.96)	-52.55 (216.57)	69	87
Hatchery	276	0.34 (0.93)	−102.53 (256.63)	75	84
P[b]		0.698	0.026	<<0.001	<<0.001
Total					
Wild	503	0.37 (1.09)	14.22 (257.43)	72	84
Hatchery	503	0.46 (1.14)	−30.21 (283.56)	78	82
P[b]		0.156	0.017	<<0.001	<<0.001

[a] Number of replicates.
[b] P values for statistical tests.

Fig. 4. Comparisons of mean (±1 standard deviation) food acquisition, agonism dominance, and replicates dominated by wild (open bars) and hatchery (solid bars) fish in scramble competition experiments.

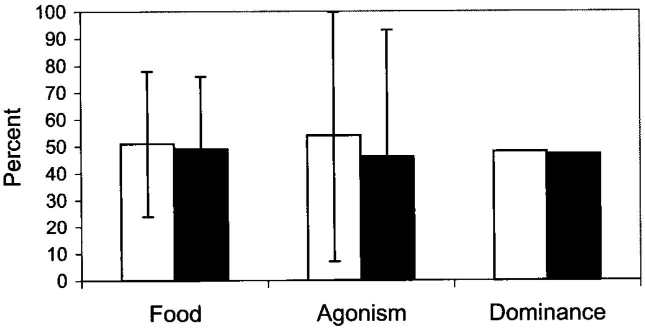
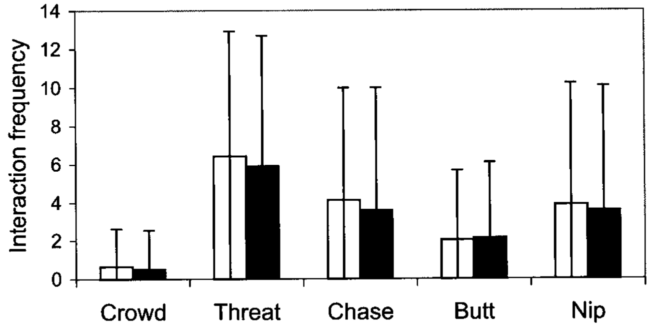


Fig. 5. Comparisons of frequencies of interaction types initiated (mean interaction per fish in each tank ±1 standard deviation) by wild (open bars) and hatchery (solid bars) fish in scramble competition experiments.



that were discarded may have been extreme responses to aggression (e.g., one fish was so aggressive that the other fish tried to leave the aquarium), and in 18 of those, wild fish may have been dominant. If discarded replicates were biased towards wild fish dominance, as is suggested by the data, then it is likely that a significant result would have been observed if dominance could have been quantified. If we assume an average dominance score for these discarded replicates, then a significant difference would be detected (P = 0.041). A significant difference would be consistent with a comparable study conducted during 2002 that used similar fish and facilities in the upper Yakima River Watershed. In that study, wild fish were more dominant than hatchery fish in contest competition experiments (Farrell 2003).

The most important finding of this study is that state-of-the-art fish culture practices, which are intended to minimize domestication selection on competitive dominance, produced effects that were small or undetectable after one generation of hatchery exposure. Although no comparisons were significantly different, wild fish were 6% more dominant in contest experiments and were nearly identical in scramble experiments. In addition, the types and frequencies of agonistic behaviors that were observed between hatchery and wild fish were not significantly different in either contest or scramble experiments. These findings suggest that hatchery fish behaved in a similar manner as wild fish.

It is possible that the behaviors of the two test groups that we observed in our experiments were influenced by selective survival or previous experience, as they were held in circular tanks prior to experimentation. These issues are common to almost all common garden experiments, because test subjects are held or tested in similar environments that may not be identical to natural environments. Selective survival was unlikely in our study because the mortality rates in our tanks were low and represented a small proportion of the experimental population (e.g., <2%). Previous experience is more difficult to rule out. However, there are a number of issues that suggest that it was not a major factor influencing our conclusions. For instance, there was no noticeable differ-

Table 2. Interaction rates (mean interaction per fish per minute ±1 standard deviation) of agonistic interactions initiated by hatchery and wild fish in scramble experiments.

Origin	n^a	Interaction rate	P^b
2003			
Wild	97	0.60 (0.65)	0.02
Hatchery	97	0.46 (0.66)	
Wild dominant	44	0.61 (0.46)	0.43
Hatchery dominant	46	0.60 (0.68)	
Wild subordinate	46	0.57 (0.72)	0.01
Hatchery subordinate	44	0.27 (0.56)	
2004			
Wild	266	0.82 (0.83)	0.13
Hatchery	266	0.78 (0.91)	
Wild dominant	132	1.17 (0.83)	0.40
Hatchery dominant	123	1.16 (1.01)	
Wild subordinate	123	0.43 (0.61)	0.21
Hatchery subordinate	132	0.35 (0.50)	
Total			
Wild	363	0.76 (0.79)	0.01
Hatchery	363	0.69 (0.87)	
Wild dominant	176	1.03 (0.79)	0.23
Hatchery dominant	169	1.01 (0.96)	
Wild subordinate	169	0.47 (0.65)	0.01
Hatchery subordinate	176	0.33 (0.51)	

[a] Number of replicates.

[b] P values from Mann–Whitney U tests are for comparisons between hatchery and wild fish regardless of dominance, when they were dominant, and when they were subordinate.

Table 3. Comparisons of mean (±1 standard deviation in parentheses) wild and hatchery fish growth and percentage of replicates that the dominant fish grew more than the subordinate in scramble competition experiments.

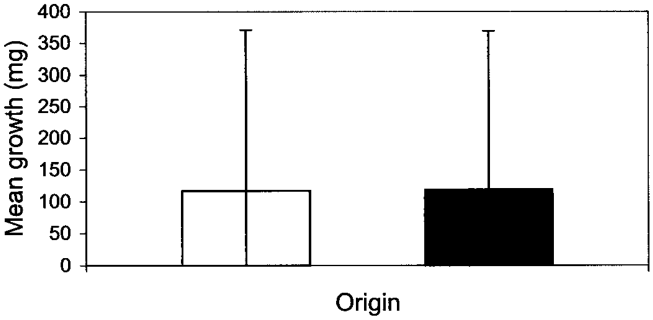
		Growth		% of dominant fish that grew more	
Origin	n^a	Length (mm)	Weight (mg)	Length	Weight
2003					
Wild	97	0.37 (0.86)	48.85 (513.12)	39%	48%
Hatchery	97	0.77 (0.80)	285.35 (456.74)	80%	78%
P^b		0.0008	0.0009	0.049	0.015
2004					
Wild	266	0.24 (1.27)	−133.54 (303.66)	68%	80%
Hatchery	266	0.27 (1.11)	−131.06 (294.81)	66%	79%
P^b		0.647	0.937	<<0.001	<<0.001
Total					
Wild	363	0.27 (1.18)	-84.53 (379.64)	61%	72%
Hatchery	363	0.41 (1.06)	−19.79 (391.14)	70%	79%
P^b		0.048	0.015	<<0.001	<<0.001

[a] Number of replicates.

[b] P values for statistical tests.

ences in behavior between hatchery and wild fish in circular tanks throughout their rearing or during the months that experimental trials were conducted in aquaria (similar to Salonen and Peuhkuri 2004); behaviors that were exhibited during trials were similar to what we observe among wild fish in the Yakima River (T.N. Pearsons, unpublished data); behaviors used by older, wild fish collected from the river were similar to ones we observed in this study (T.N. Pearsons, unpublished data); and we tested fish under different conditions than how they were reared.

Fig. 6. Comparisons of mean weekly growth (±1 standard deviation) between wild (open bars) and hatchery (solid bars) fish that were reared in isolation.



The behaviors that we observed on the seventh day of our experiment may have been more related to dominance maintenance than establishment of dominance. Fish had the opportunity to interact with each other during the 6 days prior to our observations on the seventh day. Indeed, we saw fish interacting with each other during the days of acclimation as they were being fed. Even though we observed thousands of interactions on the seventh day, the interaction rate and frequency of physical contact behaviors may have been higher during some of the earlier days as fish were trying to establish dominance. In short, the observations that we observed on the seventh day were likely influenced by interactions that had occurred during the previous 6 days and thus were probably better indicators of sustained dominance than if we had used a shorter acclimation time.

Even though our dominance results were not significantly different, wild fish grew (weight) more than hatchery fish in contest experiments, and hatchery fish grew more than wild fish in scramble experiments. This finding supported our original hypothesis that previous rearing environments and selective pressures would influence dominance and produce opposite outcomes. It is possible that our measures of competitive dominance were not as sensitive as our measures of growth. For example, growth was measured during 7 days, but our measure of dominance was measured during approximately 20 min on the seventh day. Ultimately, competitive dominance is probably best measured as a fitness-related trait such as growth than through other habitat and behavioral measures. However, if domestication affects inherent growth rates (Weber and Fausch 2003), then differences in growth rates may not indicate a difference in competitive dominance. For this reason, we have relied primarily on behavioral measures to assess dominance. However, we did not find any difference in growth between the wild and hatchery fish in 2004 when they were reared for 1 week in isolation using the same aquaria and feeding methods as were used in the contest competition experiments. Thus, the differences in growth that we observed were likely due to domesticating effects of competitive dominance.

Fish gained weight in 2003 but lost weight in 2004 during contest and scramble competition experiments. The weight loss in 2004 was likely due to feeding the fish the same weight of food throughout the duration of the experiment. At the same time, the size of fish used in the experiment increased and the water temperature increased. Both of these factors contribute to an increased metabolic demand. In contrast, in 2003 we increased the pellet size (greater mass of food) fed to the fish as fish size and the metabolic demand increased.

Wild fish were significantly more aggressive than hatchery fish in both the contest and scramble experiments. This was largely due to a difference in the aggressiveness of subordinate fish of each origin (i.e., the fish that were dominated). We did not detect significant differences in aggression between dominant fish in either experiment. In other words, wild fish were more likely than hatchery fish to be aggressive towards dominant fish. It is possible that wild fish are more likely to fight for a habitat than hatchery fish, even if a wild fish is not dominant. This may be because energetically profitable locations in natural environments are so heterogeneous compared with hatchery environments and thus worth fighting for (e.g., places are important). In another study, prior residence was found to be more important to wild origin Atlantic salmon than to domesticated Atlantic salmon in determining dominance (Metcalfe et al. 2003). Alternatively, the hatchery origin fish that we tested may not have been very aggressive, because the juvenile life stage of the parents were reared at relatively low densities in the hatchery and had high access to food (Ruzzante 1994). Berejikian et al. (1996) also found that size-matched fry of wild steelhead were initially more aggressive and dominant than those that had been domesticated.

The differences in growth and aggression that we observed were likely due to genetic changes that occurred from one generation of fish culture. However, we cannot exclude the possibility that changes were caused by a maternal rearing environment effect (e.g., not a genetic effect). This might occur if hatchery rearing caused phenotypic differences in females that were passed on to progeny. We believe that this was unlikely to have had much of an effect on our experiments because (*i*) egg sizes of hatchery and wild fish were not significantly different (Knudsen 2005), and (*ii*) fish were tested approximately 4 months after hatching. Most studies that have reported maternal effects in fish have documented relationships between female size and progeny size (Heath and Blouw 1998). We attempted to control for size effects by size-matching our fish. Maternal effects are more likely to occur when fish are very young. In a review of maternal effects in fish, Heath and Blouw (1998) concluded that "maternal effects in fishes are usually negligible beyond the early juvenile life stages".

In comparison with our observations, juvenile coho salmon (Swain and Riddell 1990; Berejikian et al. 1999) and juvenile Chinook salmon (Wessel et al. 2006) reared in hatcheries have been documented to be more aggressive than wild fish, or for steelhead fry, less aggressive (Berejikian et al. 1996). Furthermore, Einum and Fleming's (2001) meta-analysis of aggression revealed that hatchery fish were more aggressive than wild fish. We suspect that the differences in findings are caused by (*i*) the duration and type of hatchery practices and (*ii*) differences in the rearing environment or stock of the fish tested. Most, if not all, of the studies that have previously been conducted have used hatchery fish that have been under culture for more than one generation, and frequently these are of nonlocal origin. If genetic changes or maternal effects are additive, then it is likely that larger differences in aggression will be detected with each additional generation of fish culture. Furthermore, fish that are collected from natural environments and compared with fish reared in hatchery environments are likely to produce differences because of the differences in rearing conditions. For example, in another contest competition study, we found that spring Chinook smolts reared in the hatchery dominated salmon smolts that were reared in the Yakima River. Larger fish generally dominated smaller fish, but the size difference did not have to be as great for hatchery fish to dominate as for wild fish (T.N. Pearsons, unpublished data). In short, hatchery fish were dominant over wild fish in contest competition experiments unless wild fish were sufficiently larger than hatchery fish. In a study of coho salmon, Rhodes and Quinn (1998) reported similar findings. It is important to note that competitive dominance does not always result in improved survival. For example, hatchery fish could be competitively dominant at one life stage and still suffer higher rates of mortality because of increased susceptibility to predators, inefficient use of resources, or subordination during another life stage (Bachman 1984; McMichael et al. 1999; Weber and Fausch 2003).

The little (or no) difference in domesticating effects on competitive dominance that was observed in this study was also observed in a sister study examining domesticating effects on vulnerability to predators. Fritts et al. (2007) documented that offspring of hatchery parents were eaten by rainbow trout (*Oncorhynchus mykiss*) and torrent sculpin (*Cottus rhotheus*) predators at a 2% greater rate than offspring of wild parents. The fish used in these predation experiments were from the same matings and same rearing procedures used in this study. Although this difference was significantly different, the size of the difference was very small.

This study and Fritts et al. (2007) support the concept that conservation hatcheries have the potential to produce small domesticating effects after one generation of fish culture. Our results are also consistent with a recent study showing that steelhead from a supplementation hatchery (local origin and single generation hatchery exposure) had reproductive success (adult to adult survival) in natural environments indistinguishable from that of wild steelhead (Araki et al. 2007). There are still considerable scientific uncertainties about the domesticating influence of hatcheries on fish. For example, we do not know whether multiple generations of hatchery culture will produce additive effects or whether cycling through the natural environment will remove any behavioral deficits if they exist. The Yakima/Klickitat Fisheries Project is attempting to answer these questions through a long-term field and laboratory study of domestication. Other field studies will also be necessary before the domesticating influences of behavioral changes can be evaluated within the context of productivity and long-term fitness.

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