



Factors affecting the outcome of territorial contests between hatchery and naturally reared coho salmon parr in the laboratory

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In aquarium experiments using coho salmon as a model species, prior residents dominated intruders of the same size but intruders with a 6% length advantage were equally matched against prior residents. Prior winning experience (distinct from individual recognition) also strongly influenced competitive success and overcame a prior residence effect. Coho salmon reared in a hatchery dominated size-matched fish from the same parental population reared in a stream. Hatchery-reared salmon also dominated naturally spawned salmon, even when the wild salmon were prior residents. Thus the combined effects of greater size and rearing experience of hatchery-produced salmon were sufficient to overcome a wild salmon's advantage of prior residence. Efforts to rehabilitate salmonid populations must consider such behavioural interactions if displacement of wild fish is to be prevented.

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Key words: coho salmon; hatchery; competition; prior residence; experience; size asymmetry.

INTRODUCTION

Intraspecific competition for mating, nesting, and feeding territories occurs in many taxa (e.g. McNicol & Noakes, 1984; Cristol *et al.*, 1990; Baugh & Forester, 1994). Territory quality varies, and often the number of animals exceeds the number of territories. Several factors can influence the outcome of competition between individuals: prior territorial residence (Cristol *et al.*, 1990; Dearborn & Wiley, 1993; Baugh & Forester, 1994), prior winning experience (McDonald *et al.*, 1968; Francis, 1983; Chase *et al.*, 1994), body size (Abbott *et al.*, 1985; Wazlavsek & Figler, 1989; Sabo & Pauley, 1997), sibling recognition (Brown & Brown, 1996), and aggressive behaviour (Magnuson, 1962; Cole & Noakes, 1980; Grant, 1990).

Juvenile stream rearing salmonids have been used as model subjects for studying competitive interactions (Dill *et al.*, 1981; McNicol & Noakes, 1984; Abbott *et al.*, 1985). Low stream flows in the summer may limit the number of feeding territories (Chapman, 1966) and studies reviewed by Dill *et al.* (1981) suggested a direct relationship between ability to hold a territory and fitness. Juveniles develop dominance hierarchies (Chapman, 1962; Nielsen, 1992); individuals higher in rank defend more profitable feeding territories and grow faster (Li & Brocksen, 1977; Fausch, 1984; Nielsen, 1992). Higher growth rates

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increase chances of survival in fresh water (Quinn & Peterson, 1996) and at sea (Holtby *et al.*, 1990).

Size has been positively correlated with dominance in juvenile salmonids (Bachman, 1984; Grant, 1990; Holtby *et al.*, 1993). However, there is some debate as to whether large size is the consequence or the cause of dominance (Abbott & Dill, 1989; Huntingford *et al.*, 1990). Prior winning experience (Abbott *et al.*, 1985; Johnsson, 1997) and aggressive behaviour (Grant, 1990; Holtby *et al.*, 1993) also influence competitive success in salmonids.

Hatcheries have been used widely to enhance salmon populations (Lichatowich & McIntyre, 1987) and there is great debate concerning the impact of hatcheries on natural populations of salmon. One concern is that hatchery-reared salmon released into streams as parr may compete with wild salmon (Nickelson *et al.*, 1986). Without knowing the relative influence of the different factors that affect dominance success (e.g. size, prior residence, prior winning experience, and aggression) it is difficult to predict the outcome of competition between hatchery and wild salmon after hatchery fish are released into streams. For example, wild fish have prior residence but hatchery fish are typically larger and no previous study, to our knowledge, has determined the size advantage an intruder needs to balance a prior residence effect. Likewise, no previous study has attempted to compare the magnitude of the prior residence effect with the influence of prior winning experience.

Hatchery environments appear to produce aggressive juvenile salmonids (Fenderson *et al.*, 1968; Fenderson & Carpenter, 1971; Mesa, 1991). However, the extent to which high levels of aggression in hatchery fish is determined genetically (caused by unintentional selection) or determined environmentally (caused by artificial hatchery conditions) is unresolved (Olla *et al.*, 1994). The goal of the present study was to evaluate the influences of various environmental factors on the competitive ability of juvenile coho salmon *Oncorhynchus kisutch* (Walbaum). In addition to testing the relative influences of prior residence, body size, and prior winning experience on competitive outcome, we compared the competitive ability of hatchery and naturally reared coho salmon matched for size, age, and genetic background, and present a new hypothesis to explain why hatchery-reared fish may be more aggressive than naturally reared fish.

MATERIALS AND METHODS

EXPERIMENTAL SUBJECTS

Experiments were carried out in the spring and summer of 1996 and 1997 when juvenile coho salmon were 50–90 mm long. Four types of coho salmon were used in the experiments: 'Forks hatchery', 'Forks natural', 'Forks wild', and 'UW hatchery'. Each type differed from the others as a result of rearing environment, genetic background or both. Forks hatchery and Forks natural were both progeny of the same parental group of adult coho salmon that returned to the Forks Creek Hatchery, WA, U.S.A. The groups were incubated together as embryos and alevins, then divided arbitrarily as unfed fry. Some fry were placed in Forks Creek above a 16-m fall (Forks natural) to rear naturally at a density of $c. 0.5 \text{ fish m}^{-2}$ until they were captured for experimentation. The falls are impassable to anadromous salmon, so there were no other coho salmon in the reach, but it contained resident resident cutthroat trout *Oncorhynchus clarki clarki* (Richardson) and riffle *Cottus gulosus* (Girard) and torrent *C. rhotheus* (Smith) sculpins. Other fry (designated Forks hatchery) were placed into hatchery ponds (average depth

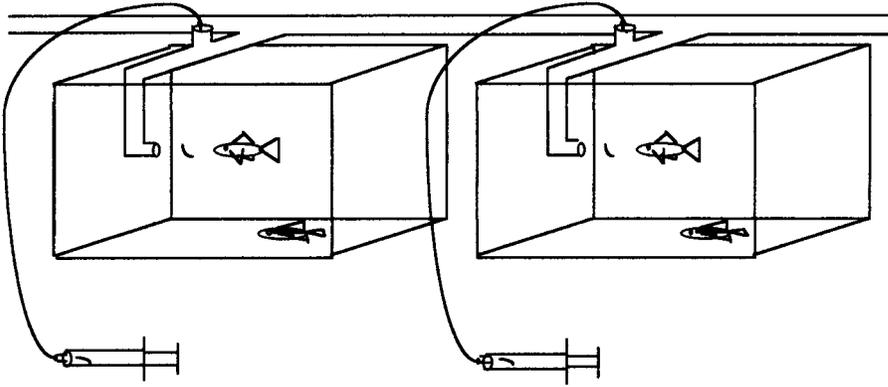


FIG. 1. Diagram of aquaria used to test the outcome of dyadic contests between coho.

1 m) at the Forks Creek Hatchery and were reared by conventional hatchery practices at densities >400 fish m^{-2} (hand fed eight times a day as fry and once a day as parr). Forks wild fish were sampled from Forks Creek below the falls and were naturally reared progeny of naturally spawning parents. Their parents may have been either wild or hatchery fish as the populations are not distinguished in this system. Forks wild fish reared at densities estimated to be <0.5 fish m^{-2} . University of Washington (UW) hatchery coho salmon (genetically dissimilar from the Forks Creek fish) were spawned and reared at the UW hatchery at densities >500 fish m^{-2} , and were hand fed.

GENERAL PROCEDURE

Two parr, identified by left and right ventral fin clips, were placed together in a 20-l aquarium supplied with flowing water and were allowed to compete for access to a feeding station (Fig. 1). Aquaria were screened with opaque plastic on three sides. Approximately 25 mm of gravel was placed on the floor of each tank. Water temperature varied from 12 to 16°C and light was provided from overhead ceiling lamps on a 10 : 14 h light : dark cycle.

All fish used in the experiments were first anaesthetized, measured for weight and length, fin clipped, and placed in their own 20-l aquarium. Fish were size matched based on length (± 1 mm). In experiments involving both Forks hatchery and Forks wild or forks natural fish, Forks hatchery fish were removed from their aquarium and electrofished in a raceway to control for any effects of electrofishing on behaviour (because the other fish were captured by electrofishing). After these procedures, the fish were left to acclimate overnight. In the morning and afternoon of the next day the test fish were fed by injecting up to 10 bloodworms through a tube connected to the tank's inflow (Fig. 1). This feeding regime was repeated for 2 more days. At each feeding period the number of bloodworms eaten by each fish was recorded. On the fourth morning after the fish were introduced to their aquaria the acclimation period ended and fish were paired off in different tanks depending on the specific experiment. In experiments where one fish was given prior residence, that fish was first removed from its tank by dipnet and then returned to its home tank to control for handling stress before the intruder was introduced. In experiments where prior residence was controlled, both fish were moved to a new tank. All experiments were replicated at least 19 times with different fish.

After the fish were paired, the competitive success of each fish was evaluated. Five bloodworms were injected into each tank in the morning, afternoon, and evening of the experiment. The number of bloodworms eaten and the dominance status of each fish were noted at all three experimental feeding periods. The dominant fish swam in the middle of the tank, oriented towards the flow. Its fins were fanned out and periodically it chased, rammed or bit the subordinate fish. Usually the subordinate fish remained

TABLE I. Summary of experiments

Experiment	Population(s) used	Sample size
Prior residence	UW hatchery	43
	Forks hatchery	19
	Forks wild	21
Prior residence and intruder 4% length advantage	Forks hatchery	25
Prior residence and intruder 6% length advantage	Forks hatchery	19
Prior residence and intruder 9% length advantage	Forks hatchery	25
Prior winning experience	UW hatchery	24
Prior winning experience and prior residence	UW hatchery	19
Hatchery reared <i>v.</i> naturally reared	Forks hatchery and naturally reared	62
Hatchery reared <i>v.</i> wild	Forks hatchery and wild	41
Hatchery reared <i>v.</i> wild prior residence	Forks hatchery and wild	19
Naturally reared <i>v.</i> wild	Forks wild and naturally reared	24
Cohorts of hatchery reared	Forks hatchery reared	37

motionless at the bottom of the tank unless it was being chased. Its fins were collapsed and it always displayed a wide, dark, lateral stripe along the middle of the body (Fig. 1).

EXPERIMENTAL DESIGN (TABLE I)

The prior residence effect was examined in experiments using three different types of fish: UW hatchery, Forks hatchery, and Forks wild. In each experiment, one coho salmon in size-matched pairs was given prior residence. The size needed to compensate for a prior residence effect was determined by conducting three additional prior residence experiments using Forks hatchery fish in which the intruding fish was given a 4, 6 or 9% length advantage. Fish in these trials averaged 82 mm, and the length advantages given were 3, 5 or 7 mm.

The influence of prior winning experience was tested in an experiment involving two sequential trials separated by the 3-day acclimation period using UW hatchery fish. First, winners and losers were established by giving one fish in each pair prior residence. Winners were then matched against losers in new pairs with the prior residence factor removed and size controlled. The relative strength of prior winning experience *v.* prior residence in determining dominance was assessed using a similar procedure, also with UW hatchery fish. First, winners and losers were established in a first trial using the prior residence effect. After fish were separated for 3 days, a second trial was conducted pairing the same fish but this time previous prior residents were made the intruders and previous intruders were the prior residents.

The influence of rearing environment on dominance was examined by pairing size-matched Forks hatchery fish with Forks natural fish with neither given prior residence. Forks hatchery fish were also compared to Forks wild fish in two experiments. In the first experiment fish were size-matched and neither had prior residence. In the second experiment fish were size-matched but the forks wild fish were given prior residence. Forks wild fish were also compared to Forks natural fish to determine if parental population, early incubation conditions, and differing stream conditions (Forks wild fish were reared below the falls and Forks natural fish were reared above the falls) influenced competitive ability. The Forks hatchery fish were also compared to another, similarly treated, hatchery cohort produced by other parents to assess any variation within the hatchery population.

DATA ANALYSIS

In all experiments (except the one where prior winning experience was isolated) fish were paired randomly without any prior knowledge of their competitive abilities. Therefore, the null hypothesis was that the probability that a given fish in a pair would be dominant equals 0.5. The alternative was that the variable or variables tested influenced the probability that a fish would become dominant. One- or two-tailed tests (depending on whether the direction of probability bias was predicted a priori) were conducted on binomial distributions with $p, q=0.5$.

In the experiment where prior winning experience was isolated, analysis was more complicated because fish were paired in a second trial based on some knowledge of their inherent competitive ability in the first trial. For example, prior residence influences the probability of success in a contest, i.e. $p>0.5$ (shown in Results). However, prior residents do not always win. Some intruders have enough competitive ability to defeat prior residents. Therefore, when winning intruders are matched against losers, the probability the intruders will win again if prior winning experience has no effect is probably >0.5 , especially if they are matched against losing prior residents (a possibility, given the design). This violates the assumption for the null hypothesis that $p=q=0.5$. A Monte Carlo simulation was conducted to provide an appropriate probability density function to test the hypothesis that prior winning experience had no effect.

A program in Matlab[®] placed integers 1–48 in random order. The values represented inherent dominance rank of individuals. Adjacent numbers were paired and the first number in each pair was given prior residence. Win and lose lists were created. Prior residents were placed on the win list if they were higher in rank than their opponents. If they were lower in rank, then only prior residents with the slightest difference in rank compared to their opponents were placed on the win list until 80% of the win list was composed of prior residents (because in actual trials prior residents won 80% of the time). The remainder of the win list was composed of individuals that were higher in rank than their opponents. Winners were then matched against losers in new pairs. The null distribution was approximated by a histogram of the number of cases where prior winners were lower in rank than their competitors using results from 2000 simulations.

RESULTS

Dominance status was determined easily and was retained almost always (372 out of 378 trials) for all three feeding periods. In the six trials when it was not retained the result at the final feeding period was used to assess dominance status. Dominant fish ate more bloodworms than subordinate fish in a majority of trials (325 out of the 378 trials, normal approximation to the binomial test, $P<0.001$). Some dominant fish refused to eat and others were outmanoeuvred by fast subordinates, probably an artifact of confinement. Thus, the behavioural criteria (see Materials and Methods) rather than the number of bloodworms eaten were used to evaluate dominance.

Prior residence increased the probability of winning a dyadic contest in hatchery fish but not in wild fish. The prior resident won in 14 of 19 pairs (74%, one-tailed, $P<0.05$) when Forks hatchery fish were tested and in 34 of 43 pairs (79%, one-tailed, $P<0.001$) when UW hatchery fish were tested. However, prior residents won in only 12 out of 21 pairs (57%, NS) when Forks wild fish were tested.

A χ^2 test for independence conducted on the win/lose counts of Forks hatchery fish from the four prior residence trials differing with respect to intruder length advantage (0, 4, 6, and 9%) indicated that a size advantage increased the probability that an intruder would defeat a prior resident ($\chi^2=8.7$, d.f.=3,

$P < 0.05$). Twenty-six per cent of intruders with a 0% length advantage won (see above) whereas 48% of intruders with a 4% length advantage (3 mm) won (12 out of 25 pairs). Intruders with a 6% length advantage (5 mm) won in 12 out of 19 pairs (63%), and those with a 9% length advantage (7 mm) won in 17 out of 25 pairs (68%).

The simulated null distribution for the prior winning experience experiment indicated that prior winners from the first trial would lose on average 25% of the time (six out of the 24 pairs) if there were no prior winning experience effects. Experimental results indicated that prior winners lost in only one pair out of 24 which was at the tail end of the null distribution (one-tailed test, $P < 0.01$). Furthermore, prior winning experience probably had a greater effect than prior residence on determining dominance because in the first trial of a similar experiment, prior residents won in 17 of the 19 pairs (89%, one-tailed test, $P < 0.001$), but in the second trial (when prior residence was reversed) the intruders (previous prior residents) won in 16 of the 19 pairs (84%, two-tailed test, $P < 0.01$).

Forks hatchery fish dominated Forks natural fish in 42 out of 62 size matched pairs (68%, two-tailed test, $P < 0.01$) when prior residence was controlled. Forks hatchery fish also won most contests against Forks wild fish (32 out of 41, 78%, two-tailed test, $P < 0.001$), even when the wild fish were given prior residence (15 out of 19, 79%, two-tailed test, $P < 0.05$). Forks natural fish were slightly dominant over Forks wild fish (17 out of 24 pairs, 71%, two-tailed test, $P < 0.1$), therefore incubation environment, stream rearing environment (above or below the falls) or genetic effects may have influenced competitive behaviour. There was no difference in competitive ability between two cohorts of Forks hatchery reared fish (the ratio was 21:16, NS).

DISCUSSION

Prior residence, size, prior winning experience, and rearing environment all influenced competitive outcome in coho salmon parr. The relative importance of some of the factors was revealed in contests between fish that differed in two or more variables with opposing influences. For example, fish with prior winning experience were dominant over prior residents with losing experience, and intruders with a 4–6% size advantage were equally matched against prior residents. Hatchery fish won a majority of territorial contests in aquaria against size-matched naturally reared and wild coho salmon, even when wild coho salmon were prior residents. Thus hatchery-reared fish were more aggressive competitors in aquaria than wild or naturally reared salmon.

When hatchery fish are released into streams they are typically larger than the resident wild fish (Nickelson *et al.*, 1986). For example, coho salmon reared at the Forks Creek Hatchery were 9% longer, on average, than naturally reared coho salmon in June even though both were the same size in February (Rhodes, 1998). Hence, if hatchery-reared fish are more aggressive than naturally reared fish in streams typically they will have the advantages of both size and aggression whereas wild fish will have only prior residence, and the prior residence advantage may be compensated by a 4–6% size advantage. It should be noted, however, that prior residents were removed and returned to their tanks

immediately before intruders were introduced in prior residence experiments. Such handling was a necessary experimental control but would not naturally occur. Thus prior residents in a stream might have more of an advantage than our experiments indicated.

In this study prior residence influenced the outcome of territorial contests between competing hatchery coho salmon in two populations (UW and Forks Creek). Prior residence contributes to dominance rank in a variety of animals including birds (Cristol *et al.*, 1990; Holberton *et al.*, 1990; Dearborn & Wiley, 1993), frogs (Baugh & Forester, 1994), and fish (Wazlavek & Figler, 1989; Huntingford & Garcia de Leaniz, 1997). A resident possesses knowledge about its territory which includes the value of its resources. Consequently, residents should expend more energy defending their territories than naive intruders (Baugh & Forester, 1994).

Theoretically animals should fight or submit after assessing the probable outcome of the contest (Krebs & Davies, 1993). An animal that remembers being beaten by a previous opponent should submit again readily if challenged by the same opponent [e.g. rainbow trout *Oncorhynchus mykiss* (Walbaum), Johnsson, 1997]. Apart from such individual recognition, animals that have experienced losing should submit more readily in subsequent contests than animals that have experienced winning. Dominance experience contributes to subsequent dominance success in a wide variety of vertebrates including birds (Wiley, 1990; Drummond & Osorno, 1992) and fish (Francis, 1983; Bakker *et al.*, 1989; Chase *et al.*, 1994). Winberg & Nilsson (1993) provided a possible mechanism for the feedback between winning experience and aggression. An increase in brain serotonergic activity in subordinate fish inhibited aggression whereas dominant fish showed signs of elevated dopaminergic activity in the telencephalon.

We conducted two experiments to investigate the influence of prior winning experience on dominance. In one experiment we did not separate the effects of individual recognition from prior winning experience. In the experiment where the same fish were re-matched with residence status reversed, the influence of prior residence on dominance was overcome by the prior experience of winning or individual recognition. An additional experiment was conducted to remove the effect of individual recognition and isolate the prior winning experience effect. When winners and losers were matched in new pairs winning experience predicted the outcome of the contests. Thus prior winning experience alone could explain the results of the reversed prior residence trial, even though some individual recognition may have taken place.

The influence of prior winning experience on aggressive behaviour may facilitate the development and stability of dominance hierarchies among juvenile coho salmon in streams. Fish of different ranks may avoid escalated contests because they display levels of aggression consistent with their winning experience and rank (Abbott *et al.*, 1985). This might explain why prior residence did not influence competitive outcome among wild fish. Wild fish were collected from a stream with no information on their rank in dominance hierarchies. Fish were paired and one was given prior residence randomly. Prior winning experience, i.e. rank, may have varied enough among wild fish to overcome the prior residence effect. In contrast, experientially induced ranks may have been

distributed narrowly or absent in hatchery ponds, rendering the influence of prior residence on dominance detectable in hatchery fish.

Hatchery-reared fish dominated naturally reared fish of equal size in 42 of 66 pairs, and wild fish in 32 of 41 trials, suggesting that the hatchery environment produced more aggressive fish than the stream environment, consistent with the findings of Fenderson *et al.* (1968), and Mesa (1991). However, Fenderson & Carpenter (1971) concluded that probably there are interactions between levels of aggression, density and rearing type, such that hatchery-reared fish are more aggressive at moderate densities and naturally reared fish are more aggressive at low densities. We cannot rule out the possibility that the naturally reared fish would have been more aggressive than the hatchery fish in streams. However, in a field experiment with representatives from the same experimental groups as the present study, hatchery-reared coho salmon grew at slightly higher rates than naturally reared salmon in streams, indicating that they competed successfully for the best territories (Rhodes, 1998).

The result that hatchery-reared fish out-competed naturally reared fish is important, and we considered some possible confounding factors. Hatchery-reared fish might have out-competed naturally reared fish in aquaria because they were less stressed. However, the aquarium set up was probably as foreign to hatchery-reared fish as it was to naturally reared fish, and both hatchery and naturally reared fish ate similar numbers of bloodworms during acclimation (1578 : 1512, normal approximation to the binomial test, NS). Fish were size-matched based on length: thus if hatchery-reared fish were heavier, their weight advantage might explain why they dominated wild and naturally reared salmon. However, hatchery-reared fish were actually lighter than their wild or naturally reared competitors of equal length (paired *t*-tests; mean difference = 0.5 g; $P < 0.001$; mean difference = 0.9 g, $P < 0.01$, respectively). Thus the levels of aggression exhibited by hatchery-reared fish was enough to overcome a weight disadvantage.

We believe the hatchery-reared fish were more aggressive than the naturally reared fish in our experiments because they lacked prior losing experience. Losing apparently has a much stronger influence than winning on the outcome of subsequent dominance encounters (Francis, 1983; Bakker *et al.*, 1989; Chase *et al.*, 1994). If coho salmon evolved to adjust levels of aggressive behaviour based on losing experience, presumably they would exhibit high levels if left unchallenged. High densities, high food rations, and absence of habitat structure in hatcheries may prevent hatchery fish from engaging in dyadic contests that are typical in streams, so hatchery fish may exhibit high levels of aggression independent of any genetic effects.

The conclusion that hatchery-reared fish were more aggressive than naturally reared fish says nothing about how aggression evolves in wild and hatchery lines. High levels of aggression may enhance fitness under certain conditions and decrease it under others (Ruzzante, 1994). Forks wild fish were dominated by Forks hatchery fish, even when given prior residence and there was some indication that Forks natural fish dominated forks wild fish. However, the relative influence of genetic *v.* environmental factors on the outcome of these experiments is unknown. In the experiment comparing Forks wild fish and Forks natural fish, any possible genetic differences were confounded by

environmental differences because Forks wild fish incubated in gravel whereas Forks natural fish incubated in the hatchery and the fish reared in different areas of Forks Creek (above and below the falls).

There is evidence that inadvertent selection in hatcheries can increase aggression in coho salmon (e.g. Swain & Riddell, 1990). However, genetic differences between the wild and hatchery coho salmon in Forks Creek are unlikely because the hatchery has been operating for over 100 years, and has made no attempt to prevent hatchery fish from interbreeding with wild fish in either the hatchery or the river. The operation of the weir and hatchery practices make it inevitable that wild salmon will be spawned in the hatchery, and that hatchery-produced salmon will spawn in the river every year.

In summary, several factors affected the outcome of competition between hatchery and wild fish in aquaria: relative size, prior residence, and influences of the hatchery-rearing experience. Genetic differences may also play a role but were not studied systematically. For coho salmon in Forks Creek, if there are no behavioural differences between two competing fish a 6% size advantage may balance a prior residence advantage. However, hatchery fish may be both larger and more aggressive, perhaps because they lack losing experience. Therefore, to balance competitive ability, hatchery-reared fish should be either size matched or given a size disadvantage. The exact size difference between hatchery and wild fish that would render both equal competitors in the field probably varies among hatchery-wild populations depending on genetic differences and site-specific environmental factors such as density and feeding regime.

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