Interbreeding with Domestic Strain Increases Foraging under Threat of Predation in Juvenile Steelhead Trout (*Oncorhynchus mykiss*): An Experimental Study

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The foraging behaviour of laboratory-reared juvenile steelhead trout (*Oncorhynchus mykiss*) and steelhead/domesticated rainbow trout hybrids were compared. In 10 replicate experiments, 10 fish from each strain were allowed to choose between foraging in a safe area or an area containing a predator. The hybrid trout were significantly more willing to risk exposure to the predator than were the steelhead. It was possible that differences in the relative willingness to risk exposure may have reflected differences in their susceptibility to predation. A second experiment measured the susceptibility of these two strains to the predator by simulating standardized encounters between predator and prey. Both strains suffered identical mortality rates and therefore were considered to be equally susceptible to the predator. This experiment confirmed that the hybrid trout were significantly more willing to take risks than the wild steelhead. These results indicate that interbreeding between escaped hatchery and wild fish may have a potentially damaging effect on the wild population.

On a comparé le comportement de recherche de nourriture de la truite arc-en-ciel anadrome (*Oncorhynchus mykiss*) et d'hybrides de cette truite avec la truite arc-en-ciel d'élevage. Dans le cadre de 10 sous-expériences, 10 poissons de chaque souche ont pu choisir entre la recherche de nourriture dans une zone sécuritaire ou une zone abritant un prédateur. Les truites hybrides étaient nettement plus portées à s'exposer au prédateur que les truites arc-en-ciel anadromes. Il se peut que les écarts d'exposition traduisent des différences de prédisposition à la prédation. On a tenté au moyen d'une deuxième expérience de quantifier la prédisposition de ces deux souches à la prédation en simulant des rencontres normalisées entre prédateur et proie. Comme les deux souches ont fait l'objet de taux identiques de mortalité, on les a considérées également sujettes à la prédation. Cette expérience a confirmé l'hypothèse selon laquelle les truites hybrides sont nettement plus prédisposées à prendre des risques que les truites arc-en-ciel anadromes sauvages. Les résultats révèlent que le croisement de poissons d'élevage en liberté et de poissons sauvages pourrait nuire aux populations sauvages.

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Recent research in behavioural ecology has demonstrated that foraging behaviour is significantly altered by risk of predation (see Lima and Dill 1990 for a recent review). Responses to predator intimidation include alteration of the prey's diet (Dill and Fraser 1984), of foraging mode (Valone and Lima 1987), and of the time (Lima 1988) and location of foraging (Kotler 1984; Abrahams and Dill 1989). Furthermore, the behavioural modifications generated by predator intimidation can amplify inter- and intraspecific competition. Indeed, risk of predation is now considered to be a major ecological force.

A concern of salmon biologists is that selection in hatcheries may be against phenotypes which are adaptive in the wild, ultimately resulting in reduced returns of hatchery fish. Some evolutionary responses to hatchery environments have already been detected. For example, domesticated brook trout (*Salvelinus fontinalis*) are less sensitive to human-caused disturbance, are more oriented to the water surface (Vincent 1960; Moyle 1969), and are also more aggressive than wild trout (Moyle 1969). Swain and Riddell (1990) have also observed increased aggressiveness in hatchery-reared coho salmon (*Oncorhynchus kisutch*).

Here, we compare the foraging behaviour of a wild strain and a hybrid wild/domesticated strain of juvenile rainbow trout (*Oncorhynchus mykiss*). In freshwater, juvenile trout are territorial, opportunistic feeders (Hartman 1965; Antonelli et al. 1972) that are exposed to a variety of predators. In the wild, these trout must continuously make trade-offs between feeding and risking exposure to predators. However, in a hatchery, fish are raised in an environment containing no predators and must compete for food thrown on the water surface. Cautious fish tend to remain lower in the water column (Vincent 1960) where they are less able to compete for food. Selection for high growth rate by hatcheries (Gall and Huang 1988; Johnsson and Clarke 1988; Gjerde and Schaeffer 1989) may therefore select against predator avoidance. Consequently, our hypothesis is that domestication increases foraging under threat of predation in trout.

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We tested this hypothesis by comparing the relative willingness of wild and hybrid wild/domesticated trout to risk exposure to a predator in order to gain access to additional food. To determine whether the fish from the two strains were taking equivalent risk when exposed to the predator, their susceptibility to the predator in this apparatus was also compared.

Methods

Experimental Strains

Wild steelhead trout were obtained from the winter run population in the Big Qualicum river (1 male, 7 females) and the summer run population in the Puntledge river (10 males, 4 females). Both rivers are situated on the east coast of Vancouver Island, approximately 50 km apart. Eleven rainbow trout males were obtained at HyWave Sea Farm in Prince Rupert from a stock that had been domesticated for more than 20 yr. Half of the eggs from each wild steelhead female were fertilized by a wild male and the other half by a domesticated male. Each male was used only once. Of the resulting 22 half-sib families, 11 were pooled within each male parent type creating the two strains. The proportional contribution of offspring from each female was similar between the strains.

The strains were held in separate 200-L freshwater flowtanks maintained at ambient temperature, decreasing from 17°C (25 August) to 12°C at the end of the experiments (24 October). The fish were fed commercial dry crumbles (White Crest) at a rate of 2–2.5% body weight per day and received a simulated natural photoperiod.

Experiment 1: Foraging and Predation Risk

The influence of predation risk on patch choice was studied in 10 replicate experiments using a procedure developed by M. V. Abrahams and M. C. Healy (unpubl. data). Steelhead ($n = 100$) and hybrids ($n = 100$) of similar fork length (7.1 to 8.7 cm depending on the replicate) were used for this purpose (Table 1). Prior to each experiment, 10 fish from each strain were allowed 3 to 6 d to acclimate to the experimental food, Murex Medium freeze-dried plankton (*Euphausia pacifica*), which was provided once per day at maintenance rations. One day before the experiment, the acclimated fish were anaesthetized in 2-phenoxyethanol and one strain received a freeze brand on the dorsal surface between the head and dorsal fin. Weight and fork length were measured for each individual and the fish were allowed 1 d to recover from the treatment in a 200-L tank. No food was provided during the recovery.

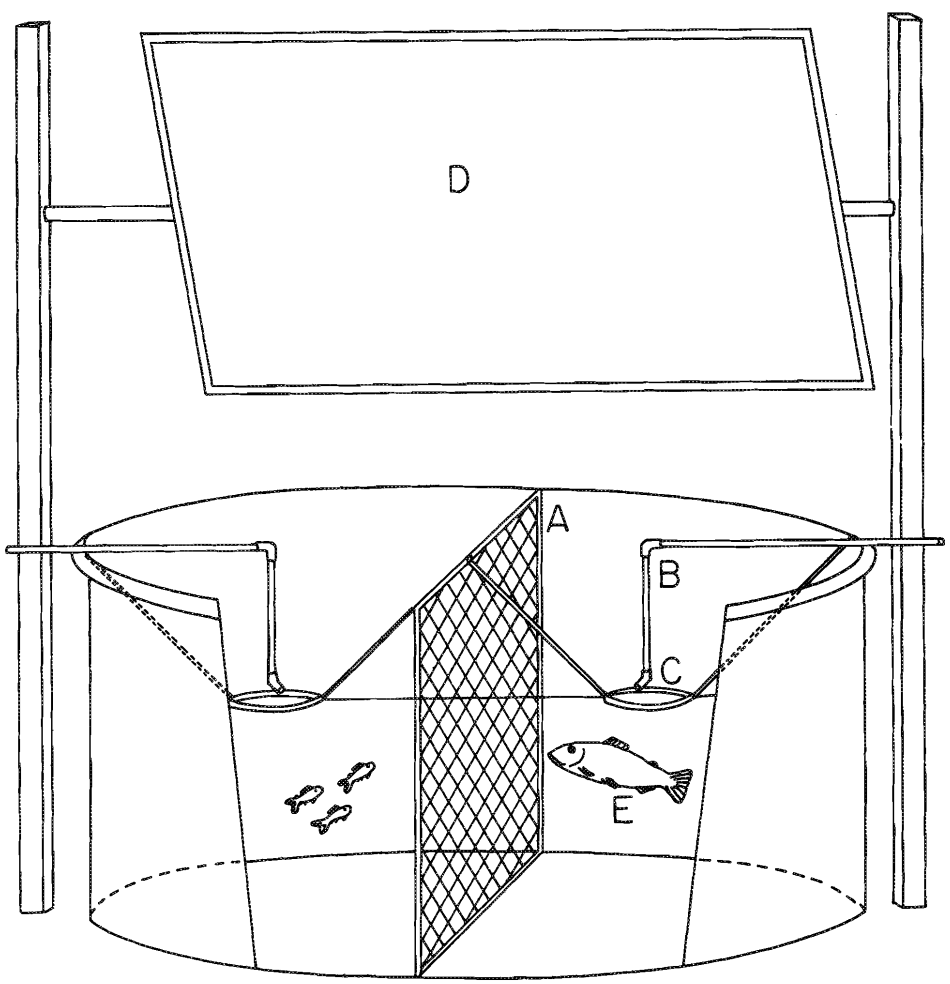

FIG. 1. Experimental tank in the foraging risk experiment. A, dividing net screen; B, tube containing food which could be blown into floating rings (C) on each side using compressed air; D, mirror through which the fishes were observed; E, predator.

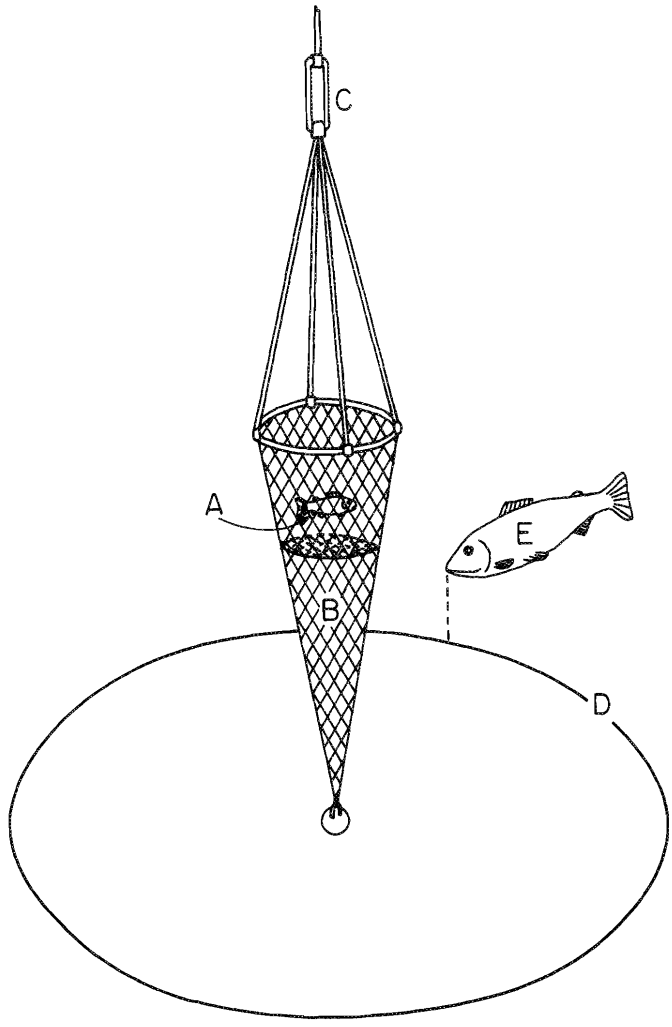

FIG. 2. Predation susceptibility experiment. The juvenile (A) was enclosed in a net (B) which instantly sank to the bottom when the line (C) was released. D, painted circled at bottom of tank to standardize the attack distance of the predator (E).

The following morning the hybrid and steelhead trout were transferred simultaneously to a 2500-L circular experimental tank (Fig. 1). The tank was divided in two by a net screen (mesh size 2.1 cm), through which the juveniles could pass freely, while the predator (an adult rainbow trout) was constrained to one side of the tank. The juveniles were allowed 30 min to investigate the tank before food was presented. Equal amounts of food (0.4 g) were added remotely to both sides of the tank by forcing compressed air through feeding tubes (Fig. 1). No observations were made on the first day to allow the fish to acclimate to the apparatus.

Food was provided at 0900 on the second day. A mirror placed over the tank (Fig. 1) allowed us to record the positions of the fish at 30-s intervals for 25 min. The freeze brand allowed the two strains to be distinguished in the apparatus. These recordings were repeated in four trials per day, separated by 2 h. However, food was only provided in the first trial. After the final trial, all prey fish were removed from the apparatus. Mean frequencies were calculated within each strain and trial by dividing the total number of juveniles recorded in the risky area by the number of observations (= 50). Ten replicate experiments, each with 10 fish from each strain, were conducted between 13 September and 1 October 1989.

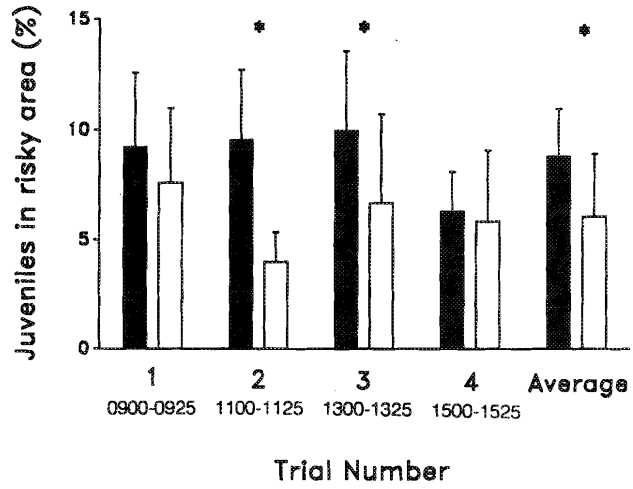

FIG. 3. Mean percent steelhead (open bars) and hybrid trout (solid bars) juveniles present in the risky area (with predator) at four trials in 10 replicate food patch choice experiments. Food was provided at the start of trial 1. Error bars denote standard errors of mean frequencies. Differences among strains were tested using the one-tailed Wilcoxon matched-pairs signed-ranks test ($P < 0.05$).

Experiment 2: Susceptibility to Predation

To determine whether the steelhead and hybrid trout were equally susceptible to the predator, we exposed both strains to a standardized encounter with the predator and estimated their probability of escape. Experiments were conducted in a 2500-L circular tank, 2 m in diameter, which contained a predator (an 850-g rainbow trout).

Figure 2 illustrates the conical enclosure developed by M. V. Abrahams and M. C. Healey (unpubl. data) to constrain the prey in the centre of the tank. A circle was drawn on the bottom of the tank, 46 cm from the enclosure. When the predator placed its nose on the line, the prey was released. If the prey survived for 10 s, it was considered to have escaped.

Experiments were conducted between 10 and 24 October 1989. Six juveniles were tested each day. One day prior to each experiment, similar-sized hybrid and steelhead trout were removed from the holding tanks and anaesthetized in 2-phenoxyethanol to obtain their weight and fork length. After handling, the two strains were kept in separate 200-L tanks without being fed. Experiments were conducted between 1300 and 1400 the next day. Steelhead and hybrid trout were presented in alternating order to the predator and the relative order was alternated each day to minimize effects of variations in predatory motivation.

Results

Experiment 1: Foraging and Predation Risk

During these experiments, three steelhead trout and one hybrid were killed by the predator. On average over all trials, the hybrids were more frequently observed on the risky side (one-tailed Wilcoxon matched-pairs signed-ranks test, $n = 10$,

$P<0.05$). Within trials, the hybrids were significantly more risk prone during trials 2 and 3 (one-tailed Wilcoxon matched-pairs signed rank test, $P<0.04$ for both trials), but not during trials 1 and 4 ($P>0.1$ for both trials, Fig. 3). On average, 9% of the hybrids occupied the risky side compared with 6% of the juvenile steelheads. No significant effect of trials on the frequency of juveniles in the risky area was found when all four observation periods were compared for each strain separately (Friedman two-way analysis of variance by ranks, $n=10$, $P>0.3$ for both strains). Size was not significantly different among strains in any replicate (Table 1, Mann-Whitney U-test, $P>0.1$ for all groups). Freeze branding had no effect on the relative willingness of individuals within a strain to risk exposure to the predator (Mann-Whitney U-test, $P>0.2$ for all tests).

Experiment 2: Susceptibility to Predation

The mean weight of the hybrid and steelhead juveniles used in the trials was 12.4 g (SE 0.4) and 12.3 g (SE 0.4), respectively. Of 45 individuals tested from each strain, 29 hybrids and 29 steelheads (or 64%) escaped. Thus, no difference existed in susceptibility to the predator between the strains.

Discussion

This study demonstrated that a hybrid wild/domesticated strain of trout was significantly more willing to risk exposure to a predator than a wild strain of trout. Furthermore, since both the wild trout and the hybrid trout were reared under identical conditions and were half-sib progeny from wild steelhead females, the behavioural difference is inherited from the male parental strain. We tested an alternative hypothesis that the hybrid trout were less vulnerable to the predator and thus inhabited the risky area with a lower cost than the steelhead. This hypothesis was rejected, as both strains were equally vulnerable to predator attacks. Increased risk proneness without a simultaneous improvement in predator avoidance ability is likely to reduce the survival of hybrid fish in natural habitats. Size differences can influence predation risk and behavioural responses in fish (Werner et al. 1983; Hargreaves and LeBrasseur 1986) but were minimized in this study, since both strains were the same size.

Since the first encounter with a predator may be lethal, it is essential that the young animal behaves appropriately without experience of the situation (Slater 1983). This view is supported by the high survival of inexperienced juveniles in our predation susceptibility experiment and the observation that virtually all juveniles in the foraging experiments occupied the safe area in the tank after 30 min of exposure to the predator. However, predator avoidance in salmon is enhanced by learning. Olla and Davis (1989) demonstrated that hatchery-reared coho salmon avoid predation from lingcod (*Ophiodon elongatus*) better after conditioning to live predators and predation-associated stimuli. In our foraging experiments the juveniles were exposed to the experimental conditions for 24 h before observations were made. We do not know how behavioural differences caused by domestication are influenced by the time of exposure to predators, an important consideration to predict the fitness of hybrid salmonids in natural habitats.

It is possible that the observed differences among the strains were caused by life history differences unrelated to domestication. Interpopulation differences in aggressive behaviour have been described for coho salmon (Rosenau and McPhail 1987; Swain and Holtby 1989). However, our results are consistent with those of Swain and Riddell (1990) who observed higher aggression in hatchery stocks compared with wild coho salmon. Both aggressive behaviour and foraging in the presence of a predator increase susceptibility to predation under natural conditions, but are not disadvantageous in domesticated environments and may even be selected for indirectly if they enhance growth through improved competitive ability (Moyle 1969; Kinghorn 1983). Hence, the direction of behavioural differences found between wild and hatchery populations is in agreement with adaptive arguments.

Our results are of interest in light of the increasing numbers of escaped farm salmon, which may affect the gene pools of natural salmon populations if interbreeding occurs. Increased willingness to risk exposure to predators will ultimately reduce survival of the offspring from such crosses, which would decrease natural production. Possible effects of behavioural changes should also be considered when hatchery juveniles are used to rebuild natural populations (see Nickelson et al. 1986). Reisenbichler and McIntyre (1977) found lower survival in a stream by the offspring of hatchery-reared steelhead trout and hatchery/wild trout hybrids than by wild offspring after only

TABLE 1. Mean weight (SE), fork length (SE), and average frequency in risky area (with predator) in juvenile steelhead trout (S) and steelhead/domesticated rainbow trout hybrids (H) in 10 food patch choice experiments. Ten fish from each strain were pooled in each replicate. The identity of the freeze-branded strain is indicated for each experiment.

Replicate No.	Weight (g)		Length (cm)		Branded strain	Frequency (%) in risky area	
	H	S	H	S		H	S
1	4.4 (0.3)	4.3 (0.2)	7.1 (0.2)	7.3 (0.1)	H	10.9	3.6
2	4.5 (0.2)	4.5 (0.2)	7.2 (0.1)	7.4 (0.1)	S	22.6	12.2
3	4.5 (0.3)	4.5 (0.4)	7.1 (0.1)	7.3 (0.2)	H	2.5	2.4
4	4.9 (0.3)	4.8 (0.5)	7.3 (0.2)	7.4 (0.2)	S	1.5	1.0
5	6.6 (0.4)	6.6 (0.4)	7.9 (0.1)	8.1 (0.2)	H	7.2	1.8
6	5.9 (0.5)	5.7 (0.4)	7.7 (0.2)	7.8 (0.2)	S	1.2	0
7	6.8 (0.5)	7.3 (0.6)	8.1 (0.2)	8.4 (0.2)	H	16.8	29.8
8	6.2 (0.5)	6.1 (0.4)	7.9 (0.2)	8.0 (0.2)	S	10.4	4.5
9	8.0 (0.7)	7.9 (0.6)	8.6 (0.2)	8.7 (0.2)	H	6.5	2.4
10	7.4 (0.5)	7.6 (0.4)	8.3 (0.2)	8.6 (0.1)	S	8.1	2.6

two generations of hatchery rearing. Further, in a study by Chilcote et al. (1986), the success of hatchery steelhead in producing smolt offspring was only 28% of that for wild fish. Future studies should examine the extent of behaviour changes caused by domestication and how such changes affect production in natural and artificial aquatic systems.

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