

Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance

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By using newly hatched (approximately 2 weeks old) brown trout (*Salmo trutta*) from six families of wild and six families of sea-ranched origin (seventh generation), we tested the hypotheses that (1) the hatchery environment selects for increased boldness, and (2) boldness predicts dominance status. Sea-ranched trout spend their first 2 years in the hatchery before being released into the wild at the onset of seaward migration. Trout were presented with a novel object (tack) and with food (brine shrimp), and their responses were measured and scored in terms of boldness. Siblings with increasing difference in boldness were then paired in dyadic contests. Fish of sea-ranched origin were on average bolder than were fish of wild origin, and bolder individuals were more likely to become dominant regardless of origin. Boldness was not related to RNA levels, indicating that bold behavior was not a consequence of higher metabolism or growth rate. Neither was size a predictor of bold behavior or the outcome of dyadic contests. These results are consistent with studies on older life stages showing increased boldness toward predators in hatchery-selected fish, which suggests that behavioral consequences of hatchery selection are manifested very early in life. The concordance between boldness and dominance may suggest that these behaviors are linked in a risk prone-aggressive phenotype, which may be promoted by hatchery selection. However, we also found significant variation in behavioral and growth-related traits among families, suggesting that heritable variation has not been exhausted by sea-ranching procedures. *Key words*: boldness, dominance, family variation, sea-ranched, selection, wild. [*Behav Ecol* 15:192–198 (2004)]

In a variable environment, or when the fitness consequences of a behavioral strategy depend on the behavior of other individuals, different strategies may coexist, and frequency-dependent selection can promote different behaviors (see Bradbury and Vehrencamp, 1998; Maynard-Smith, 1982).

The shy-bold continuum describes how an individual reacts when confronted with a challenging situation or facing a novel object (Wilson, 1998; Wilson et al., 1994). Boldness may be context specific, that is, an individual that is bold in one situation will probably react the same way if the same situation arises again, but in another situation the same individual may become shy (Coleman and Wilson, 1998). Furthermore, responses seem to depend on a variety of environmental factors such as the extent of contrast between the object and the environment. In a familiar environment, the animal may avoid a novel object, whereas the same object is less avoided when the animal is unfamiliar with the environment (Misslin and Ropartz, 1981).

Venturing into new situations or approaching unknown objects incurs a certain degree of unpredicted risk. The animal faces a trade-off situation in which it must weigh the benefits of exploring versus the costs. If a novel object becomes associated with a reward, which thus increases the benefit of exploration, it is more likely that the animal will return to the object again (Menzel and Juno, 1982). Furthermore, when large body size reduces the risk of

predation (Godin, 1997), larger animals can appear bolder than do small ones because the predation risk associated with exploratory behavior decreases (see Jones et al., 1997).

Environmental conditions during the early part of the animal's life are crucial for the development of individual characteristics (cf. Futuyma, 1998). Monkeys (*Macaca fascicularis*) reared with natural mothers more often approached a novel object, whereas most of those reared with a surrogate mother avoided it (Timmermans et al., 1994). Effects of the rearing condition were still present in some individuals after 2 years, and surrogate-reared monkeys also avoided other large novel objects, indicating that the early experience had effects later in life. Domestic chicks (*Gallus gallus domesticus*) reared in an enriched environment became less fearful toward a range of stimuli compared with chicks reared in an impoverished environment (Jones and Waddington, 1992).

Less is known of the genetic aspects of bold behavior. Piglets (*Sus scrofa*) appear to have an innate mechanism to promote behaviors of exploration and examination (Wood-Gush and Vestergaard, 1991), indicating selective advantages associated with boldness. Godin and Dugatkin (1996) found that female guppies (*Poecilia reticulata*) prefer to mate with bold males. Moreover, bolder bighorn ewes (*Ovis canadensis*) start to reproduce earlier and have higher weaning success than do shy ewes (Reale et al., 2000), indicating that the reproductive success may be higher for the bolder individuals.

If a bold individual is rewarded in its exploratory behavior, it may grow large and strong and consequently become successful in social disputes. Alternatively, socially dominant individuals can displace subordinates and thereby exclude them from beneficial exploration. Thus, the expression of boldness may be closely linked with social status.

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Received 30 January 2002; revised 10 February 2003; accepted 25 March 2003.

Table 1
Body measurements (SE) for newly hatched brown trout
(*Salmo trutta*) studied over four sessions

Family	Session	N	Weight (mg)	Length (mm)	Condition factor
S1	2	20	137 (3.5)	21.2 (0.2)	1.5 (0.05)
S2	4	20	181 (9.6)	21.6 (0.2)	1.8 (0.06)
S3	3	16	164 (7.3)	20.2 (0.2)	2.0 (0.06)
S4	3	20	160 (7.1)	20.5 (0.2)	1.8 (0.05)
S5	1	18	140 (2.4)	21.5 (0.2)	1.5 (0.03)
S6	1	20	140 (4.0)	21.3 (0.2)	1.4 (0.03)
W1	2	20	127 (2.6)	19.7 (0.1)	1.7 (0.03)
W2	2	20	138 (2.9)	20.0 (0.2)	1.7 (0.04)
W3	3	20	164 (5.6)	21.2 (0.2)	1.7 (0.05)
W4	4	20	134 (7.0)	20.8 (0.2)	1.5 (0.07)
W5	4	20	149 (10.3)	20.7 (0.3)	1.6 (0.06)
W6	1	20	143 (3.5)	20.5 (0.2)	1.7 (0.04)

S in the family name indicates fish of sea-ranched origin; W, fish of wild origin.

Metcalfe et al. (1995) found a positive correlation between standard metabolic rate and dominance in Atlantic salmon (*Salmo salar*). In a situation with limited resources, this increased energetic demand may require an increased tendency to try new routes to obtain enough food. A curious or bold individual would therefore benefit as long as the predation pressure does not outweigh the advantage of the exploratory behavior. Then, boldness would be an indication of an individual's social status, and we would expect to find a strong correlation between boldness and social dominance (Huntingford, 1976). However, if a dominant individual is able to monopolize the resources (Alanåra and Brännas, 1996), it may instead be the subordinate individual that is forced to be innovative and bold (Gotceitas and Godin, 1991; Laland and Reader, 1999; Lima and Dill, 1990). Thus, environmental variation may affect the relation between boldness and dominance, but it cannot a priori be concluded which individual should adopt a certain strategy.

The hatchery environment of salmonid fishes presents little variation, and there are few opportunities for alternative behavioral strategies. Several common garden experiments show that selection in the predator-free hatchery environment reduces behavioral responses to predation risk (Berejikian, 1995; Einum and Fleming, 1997; Fernö and Järvi, 1998; Johnsson and Abrahams, 1991; Johnsson et al., 1996). However, studies on domestication effects on the behavior of newly hatched fish are few even though behavioral variation at early life stages can have dramatic fitness consequences (Elliott, 1986). For example, only the few percentages of hatched brown trout (*Salmo trutta*) that are able to obtain a feeding territory may survive the first month after emergence (Elliott, 1994).

In the present study, we tested two hypotheses: (1) because previous work confirmed that hatchery selection increases boldness toward predators, we hypothesized that newly hatched fish originating from sea-ranched parents are bolder and thus show more exploratory behavior than do offspring from wild parents. From this, we predicted that the young hatchery fish should be bolder toward a novel object and a novel food item than are the wild-type fish of the same age. (2) By staging the fish, previously scored for boldness, in dyadic contests against siblings, we also tested the prediction that bolder individuals are more likely to become dominant. By using six families of wild and sea-ranched trout, respectively, we were also able to estimate variation in boldness among families.

METHODS

The study was conducted from 20 May–5 June 1999 at the Älvkarleby salmon hatchery in Sweden. Fertilized eggs, originating from six wild and six sea-ranched females of brown trout in River Dalälven, were incubated in the hatchery at Älvkarleby. Each family was produced from one unique male and one unique female so that within families all fish were full siblings and neither family shared a parent. The sea-ranched fish were reared in the hatchery during the freshwater stage and then released into River Dalälven upon smoltification and the onset of seaward migration. The tip of the left pectoral fin was cut on released fish so that they can be used to produce progeny when they return to spawn a few years later. The sea-ranched fish used in this study originate from a breeding program that started in 1970. The average generation time for females is 4.35 years and males 4.03 years in River Dalälven, which means that our fish have been sea-ranched for approximately seven generations. Wild fish originate from trout that live naturally in the stream where the sea-ranched fish are released. Because they are free to interbreed, the wild stock is of more or less mixed origin (Palm et al., 2003). Petersson et al. (1996) provide more details on the stocks.

Novel object trials

Fish were collected from the rearing tanks 8–15 days after yolk sac absorption, and special care was taken to mix the fish (stirring the water with the net) before netting to avoid sampling only individuals near the surface or in the front of the rearing tank, which could possibly bias for bolder specimens. In each of four sessions, 20 fish from three families, making a total of 240 trout from 12 families (six of sea-ranched origin and six of wild origin), were put singly in 1-l aquaria with an approximate flow rate of 1 l/min (Table 1). The aquaria were flow-through with a mix of ground water and river water similar to what the eggs were incubated in. The bottom was covered with fine gravel (3–5 mm), and all sides except the front were screened with black plastic. Horizontal and vertical positions of the fish were determined visually from a grid, counting 5 × 3 (width × height), drawn on the front of each aquarium. Position in the visual depth was determined as either front, middle, or back.

Fish were transferred to their experimental aquaria in the evening, and their positions and activity were noted during the first minute. Activity was categorized as freezing (remaining motionless on the bottom), holding position (maintaining position in the water column with no net movement), or swimming (movement in any direction by active swimming). After the initial observation, fish were left over night. The following morning, fish were again observed for 1 min, after which half of the fish were fed brine shrimp (*Artemia salina*) nauplii ad libitum, and the other half was presented a novel object (25-mm tack) that was slowly lowered into the aquarium. We counted the number of brine shrimps consumed and the number of approaches and bites toward the nail as well as any flight responses. We also noted the time of each act. If an approach ended with a bite, it was recorded as a bite only. Thus, a fish could be recorded for a bite but not necessarily for an approach. The same procedure was reversed the next morning, so that a fish fed at day 1 was presented the nail on day 2 and vice versa.

Dyadic contests

Based on the results obtained from the novel object trials, fish were assigned a boldness rank (ranging from 1–20, with 20 being the boldest) within its family. Fish with the highest number of bites were given the highest score. If two or more

fish were equal, the number of approaches was counted to separate them. If still required, we assigned the higher score to the fish that bit first. This was enough to separate any fish that bit or approached the nail. Fish that did not bite or approach were ranked according to the number of brine shrimps consumed and then to general activity (swimming, holding, freezing), in which swimming was given a higher score and freezing a lower. Fish that remained motionless throughout both nail presentation and feeding were randomly assigned the lower ranks after the active fish had been scored. The lowest ranks were given to fish that showed a flight response.

In the afternoon, we paired the fish with increasing rank differences (rank 10 versus rank 11 and so on until rank 1 was paired with rank 20) before they were put together in a new aquarium, unfamiliar to both fish, to avoid owner effects (Johnsson et al., 2000). In the first session, fish were distinguished by injecting Alcian blue in the caudal peduncle in one fish and sham-injecting the other fish in the pair. However, this marking was sometimes difficult to see by eye, so the identity of some individuals was confirmed by using a stereo microscope after the trial. In sessions 2–4, a white or red thread of sewing cotton was knitted around the caudal fin of each fish, which allowed for easy identification. Marking did not significantly affect the outcome of dominance dyads (session 1; Alcian blue versus sham injection: $\chi^2_{2,58} = 4.500$, $p = .105$, sessions 2–4; red versus white thread: $\chi^2_{2,176} = 3.275$, $p = .194$).

Fish were paired only with members from their own family to avoid genetic and size differences between families that could influence dyadic contests (Johnsson et al., 1999). Each pair was observed for 2 min in the evening and 1 min the following morning, after which they were fed brine shrimp ad libitum and then observed for another 2 min. If dominance could not be clearly established based on one fish being more aggressive than the other (giving more attacks than receiving), fish position and color was used (Keenleyside and Yamamoto, 1962; O'Connor et al., 1999). A lightly colored fish positioned in the center of the aquarium was regarded as dominant if the other fish was dark and positioned in the perimeter. If neither fish appeared dominant, we noted if either fish fed. If only one fish fed, it was removed and the remaining fish was again fed. If the remaining fish now fed, we regarded the removed as dominant and the remaining as subordinate. If dominance could still not be determined, fish were referred to as of undetermined status.

After the final observation, fish were killed with an overdose of MS-222. Weight and length were measured before fish were sent for RNA sampling. The RNA level provides an estimate of the instantaneous growth, as opposed to specific growth rate that yields the growth over a longer period.

Data treatment

Differences in the number of brine shrimps consumed, number of bites and approaches, initial activity, RNA levels, response to the nail, movements, weight, length, and condition factor (cf) (calculated as $cf = 100 \times \text{weight} \times \text{length}^{-3}$) between genetic origins and among families were tested with nested general linear model ANOVAs: response variable = origin + family (origin). The above variables, except RNA, movement, weight, length, and condition factor, were log-transformed to approach normal distribution. In tests with time as a factor, inactive fish were assigned a dummy value. An experimental error rate of 0.2 was used in nonparametric multiple comparison tests (Kruskal-Wallis χ^2 approximated), and Dunn's multiple comparisons test (statistic Q) was used to differentiate between groups (Lehner,

1996). Categorical data modeling was used to test whether differences in boldness or body length had any effect on status. In tests of boldness, origin was nested within the difference in rank. Whether wild and sea-ranched fish differed in this respect was tested with the Kolmogorov-Smirnov two-sample test.

RESULTS

A total of 234 fish were studied in the novel object trial because six fish escaped during acclimation. Body measurements differed both between families and origins (Tables 1 and 2). Of all fish, 129 (55%) approached and 114 (49%) bit the nail, whereas 162 (69%) fed on brine shrimp. Of those that fed, 107 also approached and 95 bit the nail. Of the 129 that approached the nail, 104 also bit. The remaining 47 (20%) showed none of the three behaviors.

There were no significant correlations between the number of bites, approaches, and consumed brine shrimp ($p > .1$ in all cases) in the 114 fish that bit at least once. Nor was there any significant correlations between weight and the number of approaches, bites, or consumed brine shrimp ($p > .1$ in all cases).

Origin and family effects

Both genetic background and family had effects on behavior (Table 2 and Figure 1). Sea-ranched fish were faster to initiate feeding than were wild fish, but not faster to approach or bite the nail. Families varied in both the time to first feeding and first bite but not in the time to first approach. Sea-ranched individuals bit more but did not approach or feed more than did wild individuals. Families differed in the number of bites and the number of consumed brine shrimps, but not in the number of approaches. There were no differences among families or origins in initial activity. Neither did the activity change after object presentation, but wild fish tended to move closer to the central area of the aquarium after the object had been presented. RNA levels differed between families but not between wild and sea-ranched fish.

The number of individuals that approached ($\chi^2_{11,234} = 22.3$, $p = .02$), bit ($\chi^2_{11,234} = 40.4$, $p < .001$), and consumed brine shrimp ($\chi^2_{11,234} = 32.1$, $p = .001$) differed among families but not between wild and sea-ranched fish ($p > .1$ in all cases).

Social status

A total of 117 pairs were tested for social status in dyadic contests. Status could be determined in 90 pairs, and the status of fish in 27 pairs remained undetermined. Thus, fish were categorized as being dominant, subordinate, or of undetermined status. The status of an individual was independent of the relative (to the other fish in the pair) body length ($\chi^2_3 = 1.3$, $p = .73$), meaning that the larger fish in the pair was not more likely to become dominant than was the smaller.

The categories differed in the time to feed ($\chi^2_2 = 6.9$, $p = .03$); dominant fish were faster than were subordinates to feed ($Q = 2.6$, $p < .05$). There were no significant differences among categories on the time to first bite ($\chi^2_2 = 5.2$, $p = .07$) or approach ($\chi^2_2 = 0.65$, $p = .72$).

The categorical data modeling showed that there was a positive relation between status and the difference in boldness rank ($\chi^2_{18} = 28.9$, $p = .0496$). Thus, the larger the difference in boldness, the higher probability for the bolder fish to become dominant (Figure 2). Wild and sea-ranched fish did not differ in this respect ($D_{\max} = 0.05$, $p > .05$).

Table 2
Family and domestication effects on the behavior of newly hatched brown trout (*Salmo trutta*)

Variable	Family effect ^a	Domestication effect ^b
Overall effect ^c	$F_{70,1266} = 1.77, p < .001$	$F_{7,216} = 2.20, p = .04$
*Feeding ^d	$F = 2.64, p = .004$	$F = 2.64, p = .11$
*Bites ^e	$F = 3.83, p < .001$	$F = 5.60, p = .02$
*Approaches ^e	$F = 1.10, p = .37$	$F = 2.07, p = .15$
*Initial activity	$F = 1.20, p = .29$	$F = 1.29, p = .26$
*RNA-level	$F = 3.28, p < .001$	$F = 3.20, p = .08$
*Distance to central area ^f	$F = 0.57, p = .84$	$F = 3.53, p = .06$
*Activity level ^f	$F = 0.96, p = .48$	$F = 0.45, p = .50$
Weight (mg)	$F = 6.05, p < .001$	$F = 12.9, p < .001$
Length (mm)	$F = 7.28, p < .001$	$F = 22.6, p < .001$
Condition factor	$F = 7.27, p < .001$	$F = 8.98, p = .003$
Time to first feeding	$\chi^2_{11} = 30.8, p = .001$	$\chi^2_1 = 4.45, p = .035$
Time to first approach	$\chi^2_{11} = 17.4, p = .10$	$\chi^2_1 = 0.73, p = .39$
Time to first bite	$\chi^2_{11} = 38.8, p < .001$	$\chi^2_1 = 0.87, p = .35$

^a df = 10,233 unless otherwise stated.

^b df = 1,233 unless otherwise stated.

^c Results from MANOVA (response variable = origin + family [origin]) are given as Wilks' lambda. Response variable included are marked with asterisk.

^d Number of brine shrimp consumed.

^e Number of behaviors directed toward the novel object.

^f Before and after presentation of the novel object.

DISCUSSION

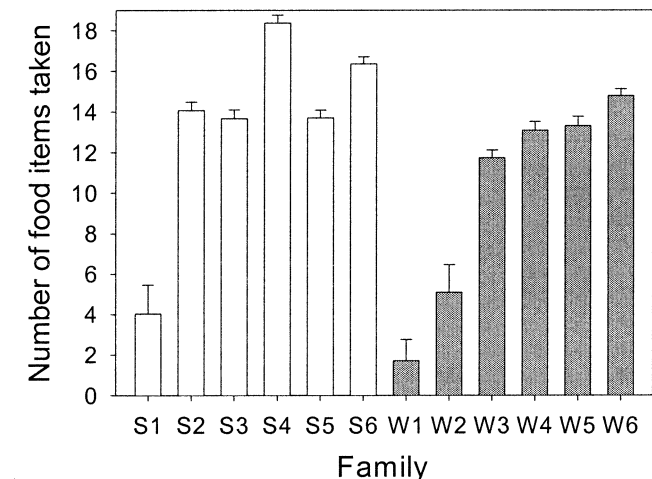
Although our results suggest that hatchery selection promotes boldness in young trout, it cannot be excluded that this effect is a correlated response to selection on other traits rather than direct selection for boldness itself. For example, if the hatchery environment selects for higher aggression and aggressive behavior is genetically linked to boldness, this could explain why sea-ranched fish were bolder than were wild. However, the effects of domestication on aggressive behavior are unclear, with different studies showing inconsistent results (Einum and Fleming, 2001; Hedenskog et al., 2002; Ruzzante, 1994). Rather, we suggest that boldness is linked to the willingness to take risks, which is one component of the decision whether to approach an unknown object or enter a novel situation (Greenberg, 1995; Wilson et al., 1994). As the hatchery-environment lacks predators, selection on antipredator behavior is relaxed, and consequently, fish bred in the hatchery for several generations have become more willing to take risks (see Einum and Fleming, 1997; Fernö and Järvi, 1998; Johnsson et al., 1996). A reduced need for predator vigilance may thus promote exploratory behavior (Krause and Godin, 1996). Because sea-ranched fish spend half of their lives in the wild, bold individuals may run a higher risk of predation once released into the wild and, consequently, may leave less offspring to take part in our experiment. Thus, there may be stronger promotion for boldness than was actually shown in this experiment. Furthermore, although sea-ranched fish truly originate from fish that have been sea-ranched for seven generations, the ancestry of wild fish is not completely known although their parental fish are reared in the wild (Pettersson et al., 1996).

We have shown that innately bold individuals are more likely to become dominant than are their shyer conspecifics. Bold behavior may be advantageous when searching for new feeding territories, but because new and unknown habitats may be associated with higher risk, exploring should usually be avoided if equivalent resources are readily available in known and less risky habitats (Abrahams and Dill, 1989). However, when competition in the safe habitat increases,

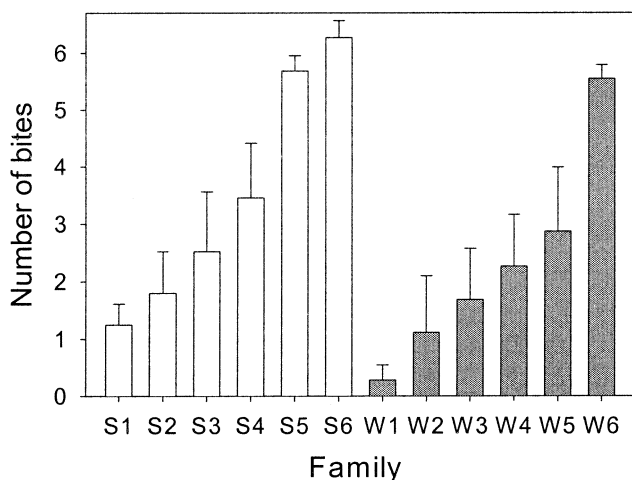
bolder individuals may venture into riskier areas and benefit from the lower competition. In juvenile pumpkinseed sunfish (*Lepomis gibbosus*), bold individuals fed sooner in the laboratory than did shy ones and they also had more food in their stomach upon capture in the wild (Wilson et al., 1993).

Because salmonids appear to monitor the behavior of other individuals (see Höjesjö et al., 1998; Johnsson and Åkerman, 1998; Sundström and Johnsson, 2001) a bold individual that ventures into unknown areas may be followed by others once the explorer has proven to survive in that new area. If boldness in this context is to be maintained, the bold individual must be able to successfully defend its new territory because it had to pay the costs of exploring, such as increased risk taking and time lost for other activities. If bold trout were not dominant, they would soon be displaced by other individuals, and the explorer would only pay the costs of being bold but never obtain the reward, and the behavior would be selected against. Consistent with these arguments, there is a positive correlation between territorial aggression and boldness toward a predator in the three-spined stickleback (*Gasterosteus aculeatus*; Huntingford, 1976). Furthermore, it was recently shown that bold individuals of the cichlid, *Nannacara anomala*, are more willing to display and escalate than are their shyer conspecifics, both in the presence and absence of a predator model (Brick and Jakobsson, 2002). The bold individual is therefore also more likely to win against a shyer individual in a dyadic contest.

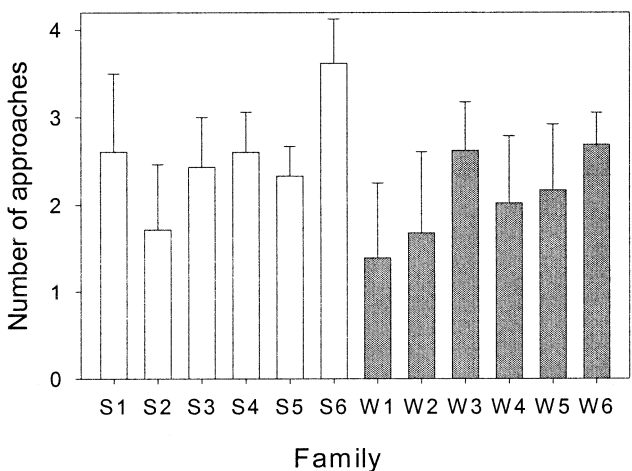
The bold-dominance link does not mean, however, that shy and socially subordinate fish have no prospect. Even if social dominance may lead to better foraging opportunities, especially if the food source is localized and populations are at lower densities (Huntingford and de Leaniz, 1997), dominance does not always result in relatively higher reproductive success (see Pusey and Packer, 1997). For example, if food supply is unpredictable in time or space, it may be too costly to defend a feeding territory (Grant, 1997). Alternative strategies such as sneaking or intercepting females attracted to a dominant individual may be another option for competitively inferior males (Andersson, 1994). Furthermore,



a



b



c

Figure 1
The number of brine shrimp consumed (a), bites on the novel object (b), and approaches toward the novel object (c) by newly hatched brown trout (*Salmo trutta*) from different families of sea-ranched origin (open bars) and wild origin (closed bars). Families were arbitrarily ordered after their number of bites. Error bars denote standard errors of mean. S in the family name indicates fish of sea-ranched origin; W, fish of wild origin.

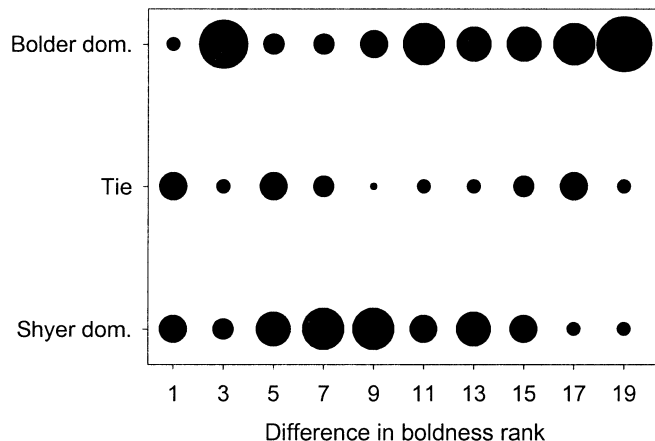


Figure 2

The number of fish that became dominant depending on the difference in boldness rank between the two fish in the pair. Size of the dots indicates the number of individuals that became dominant of a total of 117 pairs of brown trout (*Salmo trutta*). The smallest dot represents one fish; the largest, seven fish.

if predation risk is high, bolder individuals may suffer high mortality, whereas shy individuals will benefit by avoiding exposure. Dearstyne and Wilson (Wilson, 1998: 202) often observed pairs of pumpkinseed sunfish in which one individual invariably swam closer to the diver than the other. Dearstyne and Wilson were able to capture the bolder of the two but never the shy individual.

Body size and energetic demand may influence the propensity to be bold. Individuals with an elevated energetic demand are usually more willing to take risks (Abrahams and Sutterlin, 1999; Höjesjö et al., 1999; Jönsson et al., 1996) and thus may appear bolder. In Atlantic salmon, the exploratory behavior was directly proportional to the size of the fish (Armstrong et al., 1997), and large guppies were more exploratory than were small (Laland and Reader, 1999). Jones et al. (1997) reported that Japanese quail (*Coturnix coturnix japonica*) selected for small body weight showed more avoidance behavior than did those selected for large body weight (about four to five times heavier) when encountering a novel object, whereas a control group showed an intermediate response. However, they could not rule out the possibility that body size rather than the selection for body weight was the determining factor.

In the present study, which was conducted on newly hatched inexperienced fish, there was no correlation between size and boldness despite sea-ranched fish being significantly larger. Similarly, and in agreement with the findings of Huntingford et al. (1990), we found no effect of relative size on the outcome of dyadic contests among inexperienced fish. These results may suggest that large size is a consequence of bold behavior and social dominance rather than vice versa (Huntingford et al., 1990; Jönsson, 1993), an interpretation that is further supported by the correlation between boldness and dominance found in the present study.

Although there were significant domestication effects on some behavioral traits, these were relatively small in comparison to the variation seen among families. Although familial variation is little studied, individual differences in behavior are common in many species of fish (Magurran, 1993). Apparently, selection in the hatchery has not been strong enough to narrow down the variation in the sea-ranched stock. Although the hatchery environment may select for bolder and more active individuals (Einum and Fleming,

1997; Fleming and Einum, 1997; Johnsson and Abrahams, 1991; Johnsson et al., 1996), the sea-ranched fish must also survive a large part of their lives in the sea, where natural selection may counteract the traits favored in the hatchery.

To summarize, we have shown that hatchery selection promotes bold behavior in newly hatched brown trout and that boldness is associated with social dominance. Thus, released hatchery-selected fish may have the potential to displace wild fish through exploratory competition. However, at high predation pressures, risk prone hatchery fish may incur greater mortality than do the wild-type (Jonsson, 1997). These potential effects should be considered when hatchery fish are released to supplement wild populations.

We thank Anna-Carin Löf and Henrik Ohlsson for assistance during the experiment and Thomas Persson and Annika Vinnersten for housing the first author during part of the writing process. Three referees provided useful comments. The work was carried out with financial support from the Commission of the European Communities, Agriculture and Fisheries (FAIR) specific RTD program, CT-97-3498, "Performance and Ecological Impacts of Introduced and Escaped Fish: Physiological and Behavioural Mechanisms." It does not necessarily reflect its views and in no way anticipates the commission's future policy in this area. J.I.J. was financed by the Swedish council for Forestry and Agricultural Research.

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