Behavioural and heart rate responses to predation risk in wild and domesticated Atlantic salmon

Jörgen I. Johnsson, Johan Höjesjö, and Ian A. Fleming

Abstract: Artificial culture may relax the selective pressures from predators, thereby altering behavioural and heart rate responses to predation risk. Culture may also impose new selection that adapts fish to confinement. Predictions from these hypotheses were tested by comparing seventh-generation farm Atlantic salmon (Salmo salar) with wild Atlantic salmon from the principal founder population of the farm strain. Wild age 1+ salmon had higher standard heart rates and showed a more pronounced flight and heart rate response to a simulated predator attack than did farmed salmon. However, wild fish were closer to the model predator at attack, which may have accentuated these differences. Both strains habituated to the threat, showing less response to the second attack than to the first. In contrast with age 1+ fish, wild age 2+ salmon had lower standard heart rates than farmed fish. Moreover, in age 2+ salmon, domestication effects were less clear and the response to predation threat considerably weaker, suggesting that environmental effects of culture override genetic effects as time in captivity increases. Domestication selection may thus alter reaction norms of farmed animals over environmental gradients and time. This should be considered when attempting to predict the consequences of release or escape of domesticated animals in the wild.

Résumé: L’élevage en milieu artificiel diminue les pressions des prédateurs et change ainsi les réactions comportementales et physiologiques (rythme cardiaque) aux risques de prédation. L’élevage peut aussi imposer un nouveau type de sélection qui favorise l’adaptation des poissons à la restriction d’espace. La comparaison de Saumons de l’Atlantique (Salmo salar) élevés depuis 7 générations en pisciculture et de saumons sauvages provenant de la population souche principale de la pisciculture a permis de vérifier certaines prédictions générées à partir de ces hypothèses. Les saumons sauvages d’âge 1+ ont des rythmes cardiaques standard plus élevés et exhibent des réactions plus fortes de fuite et de modification du rythme cardiaque à l’attaque simulée d’un prédateur que les saumons de pisciculture. Cependant, les poissons sauvages étaient plus près du modèle de prédateur lors de l’attaque, ce qui peut avoir accentué ces différences. Les deux groupes développent une habitation aux attaques et réagissent moins fortement à une seconde attaque qu’à la première. Contrairement aux poissons d’âge 1+, les saumons sauvages d’âge 2+ ont des rythmes cardiaques standard plus bas que les saumons de pisciculture. De plus, chez les saumons d’âge 2+, les effets de la domestication sont moins apparents et les réactions à la menace de prédation sont considérablement diminuées, ce qui laisse croire que les effets environnementaux de l’élevage masquent les effets génétiques à mesure que la durée de la captivité augmente. La sélection opérée par la domestication peut ainsi modifier les normes des réactions des animaux élevés en milieu artificiel sur une gamme de gradients environnementaux et temporels. Ce sont des facteurs dont on doit tenir compte lorsqu’on cherche à évaluer l’impact de la libération ou de la fuite d’animaux domestiqués dans la nature.

Introduction

When animal populations are domesticated, their environment changes dramatically. Predictability and homogeneity replace spatial and temporal unpredictability and variation, and the selective pressure from natural predators is removed. (Kohane and Parsons 1989). A straightforward prediction from this scenario is that domestication should reduce behavioural responses to predation risk. This prediction has been supported by various experimental studies on salmonids including rainbow/steelhead trout (Oncorhynchus mykiss) (Johnsson and Abrahams 1991; Berejikian 1995), brown trout (Salmo trutta) (Johnsson et al. 1996), and Atlantic salmon (Salmo salar) (Einum and Fleming 1997; Fleming and Einum 1997).

Predation risk can induce cardioventilatory responses. In threatened mammals, bradycardia (decreasing heart rate) is generally associated with freezing or hiding and tachycardia (increasing heart rate) with flight or defence (Moen et al. 1978; Smith et al. 1981; Espmark and Langvatn 1985). There is, however, little information on heart rate effects of threat in aquatic animals and even less on integrated behavioural and heart rate responses. Metcalfe et al. (1987) found that exposure to a model trout predator increased opercular beat rate (which is positively correlated with heart rate) in juvenile Atlantic salmon. In rainbow trout, simulated attacks
by a heron model induced both tachycardia and flight (Höjesjö et al. 1999).

The aim of this study was to investigate how artificial selection affects behavioural and heart rate responses to predation threat in salmon. Such knowledge may help to predict the performance and impact of released and escaped farm fish in the wild (Jonsson 1997). Using a method where biopotentials are recorded from the water by external electrodes (Goodman and Weinberger 1971), we simultaneously measured heart rate and behaviour of free-swimming farm and wild Atlantic salmon. Furthermore, by comparing seventh-generation farm salmon with wild fish reared under similar environmental conditions and derived from the principal founder population of the farm strain, we studied the effects of domestication selection on heart rate and behaviour. Two experiments were conducted on age 1+ fish (1997) and age 2+ fish (1998), respectively, addressing two specific questions. (i) Has domestication selection reduced the behavioural and heart rate response to predation risk in salmon? (ii) Has domestication selection in the confined hatchery environment reduced the standard heart rate of farm salmon?

**Methods**

**Experimental fish**

The farm salmon originated in Norway’s national breeding programme at Sunndalsøra (AquaGen) and were taken as eyed eggs in 1996 to the Norwegian Institute for Nature Research Station at Ims, southwest Norway. These fish constituted the seventh generation of the first brood line (“population 1” sensu Gjedrem et al. 1991) that has undergone intentional selection since it is now derived principally, if not solely, from the river Namsen, mid-Norway (Gjedrem et al. 1991; Fleming and Einum 1997). Simultaneously, eyed eggs of wild salmon from the River Namsen were taken to the Norwegian Institute for Nature Research Station. The juveniles were initially reared in separate 1-m² tanks, two tanks per population, with rotation among the tanks approximately once a month. After 3 months, the juveniles were transferred to 2-m² tanks (approximately 2000 fish per tank), two tanks per population, with each tank containing equal numbers of fish from the 1-m² duplicate tanks. Rotation among tanks occurred after 2 months, and 2 months subsequent, 100 parr from each 2-m² tank were anaesthetised using chlorobutanol, tagged with passive integrated transponders, and placed into a single, common 7-m² tank. Thus, by rearing the juveniles under similar environmental conditions, including common densities and rotation among tanks, we attempted to reduce possible rearing tank effects (Fleming and Einum 1997). Age 1+ and 2+ fish were subsequently used in the experiments.

**Heart rate monitoring**

We monitored action potentials generated by the heart musculature using stainless steel electrodes, a method first introduced by Goodman and Weinberger (1971) and later used in various studies (e.g., Borate et al. 1993). A bar-shaped electrode was placed on the bottom of an aquarium and another electrode, constructed as a cage to match the aquarium dimensions, was positioned over the bar, thus enclosing the fish. The signals were amplified using a Grass EEG amplifier (model 7p511). In experiment I (age 1+ fish, 1997), the signals were filtered with a Rockland series 2000 filter used as a bandpass filter, allowing the electrocardiogram signal to be separated from the total muscular activity. The resulting electrocardiogram complex was simultaneously observed on an oscilloscope (Siemens, Sieskop 4M) and recorded on a Teac tape recorder (model R-70). In experiment II (age 2+ fish, 1998), the signals were filtered and analysed electronically using LabView 5.0 software (National Instruments). The use of external electrodes avoided the stress caused by surgery and handling (Laitinen and Valtonen 1994).

**Experimental procedure**

Eight to 10 experimental fish, half from the Namsen strain and half from the AquaGen strain, were transferred from holding tanks to experimental aquaria: 31 L for age 1+ fish and 50 L for age 2+ fish. The aquarium sizes were chosen to allow the fish maximal swimming space while ensuring stable water chemistry reduced the standard heart rate of farm salmon? environment. Reduced the standard heart rate of farm salmon? The aquarium sizes were chosen to allow the fish maximal swimming space while ensuring stable water chemistry. The aquarium sizes were chosen to allow the fish maximal swimming space while ensuring stable water chemistry. Reduced the standard heart rate of farm salmon? environment? Reduced the standard heart rate of farm salmon? The aquarium sizes were chosen to allow the fish maximal swimming space while ensuring stable water chemistry. Reduced the standard heart rate of farm salmon? environment? Reduced the standard heart rate of farm salmon? Reduced the standard heart rate of farm salmon? environment? Reduced the standard heart rate of farm salmon? environment? Reduced the standard heart rate of farm salmon? environment? Reduced the standard heart rate of farm salmon? environment? Reduced the standard heart rate of farm salmon? environment? Reduced the standard heart rate of farm salmon? environment? Reduced the standard heart rate of farm salmon? environment? Reduced the standard heart rate of farm salmon? environment? Reduced

Heart rate Data analysis

The activity level of each fish was measured and transformed to an activity index where “0” represents a fish that is motionless, “1” a fish that is moving fins or body without moving forward, and “2” a fish that is swimming. Vertical position was determined by relating the position (i.e., lateral line) of the fish to two horizontal bars dividing the aquarium into three parts where “1” represents the lower third of the aquarium, “2” the middle third of the aquarium, and “3” the upper third of the aquarium. The behavioural and heart rate data were divided into 10 time periods for each 15-min trial, where period 1 = 180–0 s before food/predator attack, 2 = 0–15 s after food/predator attack, and 3 = 15–30 s, 4 = 30–45 s, 5 = 45–60 s, 6 = 60–120 s, 7 = 120–180 s, 8 = 180–360 s, 9 = 360–540 s, and 10 = 540–720 s after the attack. Thus, the data for periods 2–5 that immediately followed the predator attack were integrated over the shortest time (15 s) to provide more detail. An initial analysis where period 1 was broken into 1-min intervals revealed no significant variation in heart rate with time prior to food/predator attack, indicating that it was relatively stable. The average of these first time periods from each of the four trials, when the fish were considered to be undisturbed, was used for analysing standard activity, vertical position, and heart rate.
The time elapsed from the moment (video frame) before the bill of the heron hit the water surface until the fish started to flee (burst swimming) was used to estimate the reaction time to the predator attack. The time elapsed from the start of this escape reaction until the fish coasted (ceased active swimming) was used to estimate the duration of the flight reaction. The number (proportion) of fish showing a flight reaction was also calculated. The distance from the eye of the fish to the place where the heron bill hit the water surface, measured immediately before the heron attack, was used to estimate the proximity to the predator at attack. The difference in performance between period 1 (before attack) and period 2 (0–15 s after attack, for activity) or period 5 (45–60 s after attack, for vertical position) was used to measure the response to the predator. In order to avoid any observational bias, all behavioural analyses were carried out without knowing the origin of the fish.

The normally distributed heart rate data were analysed using a t test to examine mean differences in standard heart rate between strains. Strain effects were also analysed using analysis of variance for repeated measurements to include variation among the 10 time periods. The behavioural data did not conform to a normal distribution and were therefore analysed using nonparametric statistical methods. To simplify presentation, figures only present data from the most interesting trials (trial II (first predator attack) and trial III (second predator attack)), and detailed statistics are only presented for P < 0.05. The alpha value was set to 0.05 for all tests.

Results

Preliminary analyses revealed no significant effects of size (Table 1), sex, or maturation.

Experiment I on age 1+ salmon

Activity and position

Standard swimming activity was higher in wild than in farm salmon (Mann–Whitney U test; U = 92; P = 0.03). Moreover, both predator attacks induced a significant increase in activity (Wilcoxon signed rank test; first attack: z = –3.82, P < 0.001; second attack: z = –2.19, P = 0.03) (Figs. 1c and 1d), but the response of wild and farm salmon did not differ in this respect.

Fish generally occupied the lower third of the water column. The first predator attack induced a lower vertical position (Wilcoxon signed rank test; z = –2.52, P = 0.01) independent of strain. No other treatment effects were found.

Escape reaction

More wild fish (100%) than farm fish (72%) reacted with a flight to the first simulated heron attack (Fishers exact test; P = 0.04) but not to the second attack (67% fled in both strains). There was no significant difference in reaction time between wild and farm fish either for the first attack (mean ± SE = 0.16 ± 0.11 versus 0.62 ± 0.56 s, respectively) or for the second attack (0.40 ± 0.23 versus 0.81 ± 0.52 s, respectively). Flight duration was significantly longer in wild fish in response to the first attack but not to the second where flight duration was reduced independent of strain (Fig. 2). Flight duration was negatively correlated with the distance to the predator at attack (first attack: r = –0.41, P = 0.02; second attack: r = –0.42, P = 0.01). Wild fish were closer to the predator than farm fish at the first attack (Mann–Whitney U test; U = 94.5, P = 0.03) but not at the second attack.

Heart rate

Standard heart rate was higher in wild fish than in farm fish (t = –2.18, P = 0.04) (Figs. 1c and 1d). Following the first predator attack, heart rate varied significantly with time (F9,288 = 4.50, P < 0.0001). Moreover, a significant interaction between strain and time period (F9,288 = 2.18, P = 0.02) indicated that wild salmon responded stronger than farm fish to the first predator attack. The heart rate of the wild fish first decreased (bradycardia) and then increased (tachycardia), remaining high until the end of the observation period. Farm fish had a weaker response, with heart rate returning to preattack levels by the end of the last observation period (Fig. 1c). There was no significant variation in heart rate following the second predator attack (Fig. 1d).

In both strains, heart rate measured 540–720 s after the first attack was positively correlated with flight duration (r = 0.35, P = 0.04), suggesting that heart rate and escape responses were linked.

Experiment II on age 2+ salmon

Activity and position

Neither standard swimming activity nor the predator-induced increase in swimming activity (Wilcoxon signed rank test; first attack: z = –3.21, P = 0.001; second attack: z = –2.18, P = 0.03) differed significantly between wild and farm salmon (Figs. 1e and 1f).

Fish generally occupied the lower two thirds of the water column (mean position index = 1.7 ± 0.1), and the first predator attack induced a lower vertical position (Wilcoxon signed rank test; z = –3.20, P = 0.001) independent of strain. No other significant treatment effects were found.

Table 1. Mean weights and lengths (±SE) of wild Namsen and farm AquaGen Atlantic salmon used in the two experiments.

<table>
<thead>
<tr>
<th></th>
<th>Wild Males</th>
<th>Wild Females</th>
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<tr>
<td><strong>Age 1+ salmon</strong></td>
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<tr>
<td>n</td>
<td>13</td>
<td>5</td>
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<td>3</td>
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<tr>
<td>Weight (g)</td>
<td>83.7 (3.7)</td>
<td>84.1 (6.0)</td>
<td>81.8 (3.3)</td>
<td>87.9 (22.4)</td>
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<tr>
<td>Length (cm)</td>
<td>18.0 (0.2)</td>
<td>18.2 (0.3)</td>
<td>18.5 (0.2)</td>
<td>18.9 (2.0)</td>
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<td><strong>Age 2+ salmon</strong></td>
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<tr>
<td>n</td>
<td>12</td>
<td>7</td>
<td>11</td>
<td>6</td>
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<tr>
<td>Weight (g)</td>
<td>283.9 (10.2)</td>
<td>313.3 (28.1)</td>
<td>337.6 (20.9)</td>
<td>326.9 (29.3)</td>
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<tr>
<td>Length (cm)</td>
<td>30.5 (0.4)</td>
<td>31.3 (0.9)</td>
<td>32.3 (0.8)</td>
<td>32.2 (1.1)</td>
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Escape reaction

Less than half of the wild (42%) and farm fish (44%) reacted with a flight to the first simulated heron attack. The second attack induced fewer flight responses both by the wild (26%) and the farm fish (22%). Neither reaction time (first attack: 0.09 ± 0.02 versus 0.11 ± 0.03 s; second attack: 0.16 ± 0.06 versus 0.24 ± 0.11 s, respectively) nor flight duration (Fig. 2) differed significantly between wild and farm.
Comparing performance of 1+ and 2+ age-classes

Table 2 compares the performance of the two age-classes. The flight response to the predator was much more pronounced in age 1+ than in age 2+ fish. Moreover, heart rate 9–12 min after the attack was positively correlated with flight duration, and, in contrast with age 1+ salmon, the heart rate of farm fish did not quickly return to pre-attack levels. Typically, individuals are often initially cautious of all approaching large animals (or models) and then gradually learn which are really dangerous (see review by Smith 1997). Our results suggest that this ability has not been lost in AquaGen farm salmon after seven generations of domestication. In agreement with previous studies on rainbow trout (Jönsson et al. 1996), both farm and wild salmon lowered their position in the water column following the first model heron attack. This should increase survival probabilities in the wild, as the capture success of live herons declines with increasing water depth (Kramer et al. 1983).

The stronger behavioural response to the first predation threat in age 1+ wild salmon was accompanied by a more pronounced heart rate response. Moreover, heart rate 9–12 min after the attack was positively correlated with flight duration, and, in contrast with the farm fish, the heart rate of wild fish did not quickly return to pre-attack levels. Clearly, behavioural and heart rate fright responses were closely linked. Thus, it seems that the wild salmon were more “stressed” by the predator attack. This may be adaptive if a high heart rate supplies the body with oxygen to prepare for flight, should the predator appear again (Höjesjö et al. 1999). The farm salmon in the present study showed a reduced flight reaction to the first aerial predation threat compared with wild fish from the progenitor population. We compared cultured fish with wild fish derived from the principal founding population of the cultured strain and reared from eggs under similar environmental conditions (also see Fleming and Einum 1997). Thus, the differences observed are likely attributable directly to the effects of domestication. While maternal influences (e.g., differences in egg size) are possible, these are likely to be confined to the earliest life stages (i.e., the first few months following hatching; Swain and Lindsey 1986; Einum and Fleming 2000) and are unlikely to have played an important role in the results. Theoretically, the decision whether to flee from a predator or not should be guided by the trade-off between the risk of capture if remaining and the loss of foraging opportunities if fleeing (Ydenberg and Dill 1986; Endler 1991). Selection in the predator-free culture environment may have altered this trade-off decision, with farm salmon being less inclined to flee for a given level of threat. Alternatively, the ability of farm salmon to detect or evaluate a predator threat may be diminished. Either way, this will likely reduce their probability of surviving an encounter with a real predator (Webb 1984; Berejikian 1995).

It should be pointed out, however, that the stronger anti-predator response in wild salmon could be due partly to the fact that they were closer to the predator model at attack than farmed fish. The flight reaction of both strains was stronger the closer the predator was at attack, supporting the economic model proposed by Ydenberg and Dill (1986) that predicts an inverse relationship between flight probability and the distance of the predator. Both strains habituated rapidly to the model heron, being less likely to flee and reducing their flight duration during the second attack, indicating that they could rapidly discount the danger from the repeated, simulated predation threat. The cost of being killed by a predator is considerably greater than that of lost foraging opportunities (the death versus dinner dilemma). Consistently, individuals are often initially cautious of all approaching large animals (or models) and then gradually learn which are really dangerous (see review by Smith 1997). Our results suggest that this ability has not been lost in AquaGen farm salmon after seven generations of domestication. In agreement with previous studies on rainbow trout (Jönsson et al. 1996), both farm and wild salmon lowered their position in the water column following the first model heron attack. This should increase survival probabilities in the wild, as the capture success of live herons declines with increasing water depth (Kramer et al. 1983).

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Discussion

The behaviour of age 1+ wild and farm salmon in this study supports previous findings that cultured fish show a reduced behavioural response towards predators (Johnsson and Abrahams 1991; Johnsson et al. 1996; Einum and Fleming 1997). The farm salmon in the present study showed a reduced flight reaction to the first aerial predation threat compared with wild fish from the progenitor population. We compared cultured fish with wild fish derived from the principal founding population of the cultured strain and reared from eggs under similar environmental conditions (also see Fleming and Einum 1997). Thus, the differences observed are likely attributable directly to the effects of domestication. While maternal influences (e.g., differences in egg size) are possible, these are likely to be confined to the earliest life stages (i.e., the first few months following hatching; Swain and Lindsey 1986; Einum and Fleming 2000) and are unlikely to have played an important role in the results. Theoretically, the decision whether to flee from a predator or not should be guided by the trade-off between the risk of capture if remaining and the loss of foraging opportunities if fleeing (Ydenberg and Dill 1986; Endler 1991). Selection in the predator-free culture environment may have altered this trade-off decision, with farm salmon being less inclined to flee for a given level of threat. Alternatively, the ability of farm salmon to detect or evaluate a predator threat may be diminished. Either way, this will likely reduce their probability of surviving an encounter with a real predator (Webb 1984; Berejikian 1995).

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Domestication had no significant effect on antipredator...
behaviour in age 2+ fish. It is unlikely that the difference in water temperature between the experiments was responsible for this discrepancy. A clear difference in antipredator behaviour occurred with age 0+ fish from the same two populations at around 15°C (Fleming and Einum 1997). Instead, environmental effects of culture could override genetic effects as time in captivity increases. For example, sensitivity to disturbances such as overhead movements and netting may decrease with time spent in captivity, reducing general vigilance as well as masking genetic differences in behaviour. The general reduction in antipredator response in age 2+ salmon may also be due to their larger size and older age, as larger prey are more likely to survive a predator attack (Godin 1997). Given the linkage between heart rate and behaviour in age 1+ fish, it is perhaps not surprising that wild and farm age 2+ salmon showed a much less pronounced heart rate response to the predator attack in association with the reduced behavioural response.

The prediction that fish confined under farm conditions for multiple generations would adapt physiologically and would show lower standard heart rates than wild salmon was supported in age 1+ fish. The increased heart rate in the wild salmon may have resulted from their higher general activity, suggesting higher energy expenditure. Thus, if these differences occur in the hatchery as well, they may help explain the faster hatchery growth in domesticated salmon compared with wild-type salmon (Einum and Fleming 1997; Fleming and Einum 1997). The prediction was not supported in age 2+ fish because farm salmon had higher standard heart rates than the wild salmon. As activity levels did not differ between age 2+ farm and wild salmon, the domesticated strain seemed to maintain a higher heart rate for a given activity level. We have no good explanation for this discrepancy between age 1+ and 2+ fish. Clearly, more controlled studies are needed to elucidate how domestication and the culture environment alter basic physiological adaptations in fish.

In summary, age 1+ salmon showed behavioural and heart rate responses to predation risk that were integrated and reduced by artificial culture. Given that the strains had a common origin seven generations back, the differences found in age 1+ fish likely reflect evolutionary changes due to domestication selection. In age 2+ salmon, antipredator responses were considerably reduced and genetic domestication effects were less clear, suggesting that environmental effects of artificial rearing override genetic effects as time in captivity increases. This should be taken into account when wild-type stocks are maintained in hatcheries or when attempting to predict the consequences of release or escape of domesticated animals in the wild (Snyder et al. 1996; Jonsson 1997; Fleming et al. 2000).

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