Condition-dependent reproductive tactics by large and small anadromous male sockeye salmon

*Oncorhynchus nerka*

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Reproductive tactics, aggression and courtship by large and small (jack) male sockeye salmon *Oncorhynchus nerka* with ripe females in temporary enclosures depended on the size and behaviour of the competitor, not the size of the focal male. When paired with other jacks or with large but less aggressive males, jacks fought for access to ripe females rather than sneaking, but used sneaking tactics when paired with large, aggressive males. Dominant males of both size groups courted actively and females spawned readily with all combinations of males.

Key words: aggression; alternate reproductive tactics; jacks; sockeye salmon.

In many fishes, intense competition for mates can lead to the evolution of alternate male life-history strategies and divergent reproductive tactics (Gross, 1996) as shown for bluegill *Lepomis macrochirus* Rafinesque by Dominey (1980) and Gross & Charnov (1980). One important question is whether the alternative male types are non-sequential, developmentally fixed, and fundamentally different (*e.g.* plainfin midshipman *Porichthys notatus* Girard; Bass et al., 1996), sequential (*i.e.* males change types as they grow) or plastic responses to local conditions. In Salmonidae females compete for breeding sites and males compete for access to females (Fleming & Reynolds, 2004; Quinn, 2005). These pressures have led to sexual dimorphism and variation in age at maturity, body size and alternate reproductive tactics in males. The family includes many anadromous species but often a fraction of the males do not migrate to sea, instead maturing in fresh water at a very small size (Quinn & Myers, 2004). There are also males (jacks) that spend fewer years at sea (hence are much smaller) than females and most males of the population. As density and competition increase on the spawning grounds, the ability of a dominant

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male to defend a female decreases, while the opportunities for small males to sneak access to ovipositing females increase. The resulting disruptive selection on male body size may play a role in the evolution of alternative male life-history patterns and tactics (Gross, 1985). In anadromous Pacific salmon *Oncorhynchus* spp. consistent variation in the proportion of jacks among populations (Young, 1999; Healey et al., 2000; Quinn et al., 2001), and controlled breeding studies (Iwamoto et al., 1984; Heath et al., 1994) indicate a genetic influence on whether males mature as jacks or not, though the trait is also linked to juvenile body size or juvenile growth rate (Hutchings, 2004; Vøllestad et al., 2004).

Gross (1985) reported that sneaking was the primary tactic of jacks in coho salmon *Oncorhynchus kisutch* (Walbaum) but that they would fight if refuges were scarce: ‘Since jack density in the stream was too high for all to sneak successfully, some were forced to fight’. This has contributed to the view that these life-history alternatives are linked to reproductive tactics (Yamamoto & Edo, 2002), and the genetic influence on early male maturity might extend to reproductive behaviour as well. On the other hand, behavioural tactics might be entirely contingent on the number and size of males competing for access to the female. The purpose of the present study was to test the hypothesis that the frequency of courtship and aggression by jacks is similar to that of larger males, indicating that these behaviour patterns are context-dependent, against the alternative hypothesis that jacks are less aggressive and court less frequently, even when competing with other jacks. Jacks are rare (<5% of males) in most sockeye salmon *Oncorhynchus nerka* (Walbaum) populations (Healey et al., 2000; Quinn et al., 2001) but in 2005 an unusually large proportion (33-8%, T. P. Quinn & H. B. Rich, unpubl. data) of the males in Hansen Creek, a small tributary of Lake Aleknagik, AK, U.S.A. (59°19′42″ N; 158°41′48″ W) (Carlson et al., 2004), were jacks. This provided an unusual opportunity to study alternative life-history patterns in this species.

Hansen Creek drains a large beaver pond and a series of spring-fed ponds, flowing 2 km to Lake Aleknagik. The creek’s small size (average width = 3-9 m, average depth = 10 cm), clear water and consistent flow rate make it ideal for behaviour observations. Sockeye salmon spawn in Hansen Creek from late July to mid-late August at average densities of >7400 ha⁻¹ in recent years (Quinn et al., 2003), indicating that it is very suitable habitat.

During the breeding period in 2005, a reach of stream was selected for the study based on the high density of sockeye salmon (consistent with observations in previous years), greater than average width, and absence of obstructions that would hinder observations. A temporary 2 × 4 m mesh enclosure was erected around a ripe female and her redd (nest site). Two male sockeye salmon from the stream were caught by hand and transferred into the enclosure with the female. After a 10 min acclimation period the fish were observed for 15 min, during which time acts of aggression and courtship were recorded. The fish were distinguished by differences in size or by features such as scars, torn fins and wounds, and colour variation so there was no need for them to be tagged.

Aggression was quantified as the sum of all aggressive acts (chasing, ramming, biting the competitor and actively guarding the female by blocking).
Quivering was used as the index of courtship, as this behaviour is readily and unambiguously discernable and it is an important part of the courtship sequence (Berejikian et al., 2000; de Gaudemar et al., 2000; Esteve, 2005). At the end of the trial, one male was replaced with another male and 5 min were allowed for acclimation before the next 15 min observation period. The male that had been in the enclosure for two trials was then replaced with a new individual, and so on for the day. Analysis of length at age indicated that 350 mm (mid-eye to hypural plate) is a reliable cutoff for separating jacks (males that spent 1 year at sea) from older males that spent 2 or 3 years at sea in the Hansen Creek population (Carlson et al., 2004). The sizes of the males being tested were alternated so that each male was tested twice with the same female, once with a male of comparable size and once with a male of different size. To ensure against repeated trials of the previously sampled individuals a new section of creek was selected for each day of the experiment.

A total of 54 large and 49 jack sockeye salmon were observed in 95 trials with eight females. Successful spawning events, when both eggs and milt were released, occurred in 11 different trials, and the proportion of trials in which spawning took place did not differ with respect to the males being observed: one of 29 trials involving two large males, seven of 36 trials with males of mixed sizes and three of 30 trials with only jacks ($\chi^2$, $P > 0.05$). Notwithstanding the occurrence of spawning with both jacks and large males, females were more aggressive towards jacks. Females attacked large males in only 14% of the trials (average = 0.16 attacks per male per trial) whereas jacks were attacked in 49% of the trials (average = 2.05 attacks per fish per trial). The non-normal distribution of the data (many zero values) precluded parametric analysis but a Mann–Whitney rank sum test indicated that jacks were more often attacked than large males ($P < 0.001$).

Jacks were more aggressive when paired with other jacks than when paired with larger males (mean values: jack to jack = 6.28 v. jack to large = 2.81; paired t-test, $P < 0.05$). Large males were as aggressive with jacks as they were with other large males (mean values: large to jack = 7.2 v. large to large = 6.6, paired t-test, $P > 0.05$). When jacks were paired with jacks their aggression was similar to that of large males paired with other large males (unpaired t-test, $P > 0.05$). To evaluate courtship behaviour, acts of quivering were summed for each fish. Quivering was strongly associated with dominance (determined by sustained proximity to the female and greater level of aggression). In 84 of the 95 trials one male could be classified as dominant based on overall interactions, and in 63 cases the dominant male quivered more often than the subdominant male, in 14 trials neither male quivered, and in only seven trials did the subdominant male quiver more than the dominant male (means: 7.34 v. 0.40, $P < 0.001$). Large males quivered more often when paired with jacks than when paired with other large males (large to jack = 5.5 v. large to large = 2.2, t-test, $P < 0.05$), reflecting the fact that large males generally dominated jacks and dominant males quivered more than their competitors. The number of quivering displayed by jacks tended to be higher when they were paired with other jacks than with large males, again reflecting the fact that jacks seldom dominated large males, though the difference was not significant (jack to jack = 4.3 v. jack to large = 2.4; paired t-test, $P > 0.05$).
Several experiments have found that females discriminated against smaller males as mates, by attacks (Svedäng, 1992; Maekawa et al., 1993) and by delaying spawning (Schroder, 1982; Foote, 1989; Maekawa et al., 1993; de Gaudemar et al., 2000). For example, Berejikian et al. (2000) reported that female Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) spawned as readily with small males (c. 46% of the female’s mass) as with large males (c. 112% of the female’s mass) when spawning their first nest. The latency increased, however, for subsequent spawning events and was longer for small males (16·2 h) than large males (12·6 h). This evidence that females delayed spawning when courted by small males was inconsistent with the results of the present study; females spawned readily whether courted by jacks, large males or mixed pairs. Spawning frequency and duration of latency were not the focus of this study but half of the females (four of eight) spawned more than once and the average period between the spawning events was only 67 min (range: 3 h to 16 min). Thus the sockeye salmon in the enclosures seemed to spawn much more readily than those observed by Berejikian et al. (2000). Unconstrained females in Hansen Creek completed spawning quickly as well (McPhee & Quinn, 1998). Rapid spawning may be more important in this population than mate choice, perhaps because there is intense bear predation (Quinn et al., 2001, 2003). The bears tend to kill newly arrived females (Gende et al., 2004) so any delay significantly increases the risk of prespawning mortality.

Analysis of quivering behaviour suggested that this courtship display reflects the relative status of the males. Overall, both large and jack males tended to quiver more when their competitor was a jack, and the difference was most marked between large males and jacks. Thus the weaker the competitor, the more frequent the quivering display. When their competitor was similar in size (*i.e.* jack to jack and large to large), rates of quivering by jacks were comparable to those of large males, providing further evidence of the generally similar behaviour patterns of the two groups of males.

The present data indicated that aggression was also a conditional trait in these male sockeye salmon. When jacks were paired with jacks they were as aggressive as large males but when jacks were paired with large males their aggression rate was much lower. Thus there was no evidence of linkage between age at maturity and aggression *per se*, only the probability that jacks will encounter larger males and therefore show reduced aggression. The effect of competition on aggression is consistent with the observation that the operational sex ratio (OSR) influences the frequency of aggression in male sockeye salmon (Quinn et al., 1996). Aggression was most frequent in groups of intermediate size (two to four males per female) but declined when male aggregations were large (greater than four) and when one male dominated access to a female. Finally, the study design (sequential replacement of one of the two males) allowed the role of prior residence in the arenas on the outcome of the next contest to be examined. The prior resident dominated the newcomer in 16 of 25 contests between two jacks, and 17 of 21 contests between two large males, indicating a clear advantage to the prior resident in cases where sizes were similar ($\chi^2$, $P < 0.001$). Taken together, these results indicate that aggression in male sockeye salmon is highly dependent on conditions (size and density of competitors) and recent experience rather than the absolute size, age or other attributes of the fish.
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References


