

## Reproductive behavioral interactions between wild and captive reared coho salmon (*Oncorhynchus kisutch*)

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Captive rearing is an evolving strategy for restoring depleted salmon populations; it involves capturing wild juvenile salmon from natural streams, rearing them in captivity to adulthood, and then releasing them as adults back into their natal streams to spawn naturally. The conservation benefit of captive rearing is that it bypasses the typically high smolt-to-adult mortality experienced by wild populations, but its success as a restoration strategy depends upon the ability of captive reared salmon to spawn and reproduce in natural streams. In an experimental channel, wild males dominated captive reared males of similar size in 86% of spawning events. Both wild and captive reared females attacked captive reared males more frequently than wild males, indicating a preference for wild over captive reared males, although the interplay between male dominance and female mate choice was unclear. Wild females established nesting territories earlier and constructed more nests per individual than captive reared females of similar size, suggesting a competitive advantage for wild females. Nevertheless, captive reared coho salmon demonstrated the full range of behaviors shown by wild coho salmon of both sexes and the ability to spawn naturally.

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### Introduction

Captive broodstock programs for Pacific salmon (*Oncorhynchus* spp.) involve capturing wild fish from their native habitats and culturing the populations to maturity in hatcheries, where survival generally far exceeds that in the wild (Flagg *et al.*, 1995a, b). Captive broodstocks are usually established by collecting eggs and sperm from returning adults, although they may also be established by capturing juveniles. Typically, first- or second-generation offspring from captive broodstocks are stocked into ancestral streams at one or more juvenile life-history stages (egg, fry, parr, or smolt). Another strategy, termed captive rearing, involves culturing the fish to adulthood, and then releasing them back into their natal streams to spawn naturally. Its success, however, ultimately depends upon the ability of captive reared salmon to reproduce in natural streams.

Captively reared and naturally produced (wild) adult salmon experience sharply different environmental regimes. Whether cultured in fresh or sea water, captive reared salmon are fed artificially formulated diets, and do not undergo extensive migrations. Fish reared in sea pens differ morphologically from wild fish, and the degree of divergence appears positively related to the duration of confinement (Fleming *et al.*, 1994). In the past, certain morphological features have been linked to the reproductive fitness of male and female salmon (Schroder, 1981; van den Berghe, 1986; van den Berghe and Gross, 1989; Jarvi, 1990; Fleming and Gross, 1994; Quinn and Foote, 1994). Hatchery rearing also affects the development of social behavior of juvenile salmonids and interactions with wild fish (Symons, 1968; Dickson and MacCrimmon, 1982; Berejikian *et al.*, 1996), but the effects of long-term freshwater culture on the reproductive behavior of any of the Pacific salmon species are unknown (but see Fleming *et al.*, 1996).

In this paper we investigate the behavioral interactions of adult wild coho salmon (*O. kisutch*) and coho salmon that were captured as fry from a natural stream and cultured in fresh water to adulthood (i.e. captively reared salmon). In addition to describing behavior before, during, and after spawning, we investigated (1) whether the rearing history of males affected their ability to spawn with females, (2) the amount of intersexual aggression they experienced, and (3) whether wild and captively reared females differed in their ability to acquire and defend spawning territories.

## Materials and methods

Wild adult coho salmon were collected between 28 October 1995 and 11 November 1995 at a permanent weir located on the estuary of Big Beef Creek, a small stream flowing into north-east Hood Canal, WA. All fish used in the experiment were initially determined to be offspring of naturally spawning adults from the absence of the adipose fin, which was clipped from all naturally produced smolts leaving Big Beef Creek in 1994. Scale analysis confirmed that these fish were naturally produced (J. Sneva, Washington Department of Fish and Wildlife, N. Olympia, Washington, USA pers. comm.). Big Beef Creek adults were transported by tank truck for approximately 2 h to the Long Live the Kings Hatchery, located alongside Lilliwaup Creek, which flows into the west side of Hood Canal. Males and females were held separately in fresh water in 2.8 m diameter tanks until they were ready to spawn. The transportation may have created additional stress to the wild fish that was not experienced by captively reared salmon cultured at the Long Live the Kings Hatchery.

Captively reared coho salmon were captured as newly emerged fry by electro-fishing in April 1993 in Stavis Creek, which enters Hood Canal approximately 7 km south from the mouth of Big Beef Creek. The Stavis Creek fry were transported to the Long Live the Kings Hatchery, where they were cultured in 1.2 m diameter tanks. Fish were transferred to 3.0 m diameter tanks at an age of approximately 6 mo (average weight of 4.5 g), and then transferred to 6 m diameter tanks at 14 mo of age (average weight of 500 g). Two months before the experiments began, the fish were returned to 3 m diameter vessels to facilitate future handling. Fish were fed a Bioproducts (reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA) Starter diet until reaching an average weight of 2.0 g; they were then fed a Biodry diet until reaching an average weight of 100 g, after which they were fed Bioproducts Brood formula (high carotenoid levels) until feeding was terminated on 10 November 1995.

Big Beef Creek coho salmon were used as the wild fish in this experiment because we were unable to

capture sufficient wild adults from Stavis Creek in 1995. Nevertheless, a decade of extensive straying of hatchery fish into Stavis Creek, Big Beef Creek, and other northern Hood Canal streams has created a panmictic population of coho salmon in this part of Puget Sound. Consequently, coho salmon returning to Big Beef and Stavis Creeks should have similar genetic properties (Washington Department of Fisheries *et al.*, 1993; Weitkamp *et al.*, 1995).

Behavioral observations were made on wild and captively reared coho salmon (marked with numbered 2.0 cm Peterson disk tags) by placing them into upstream and downstream sections of an unnamed tributary (SW, 19, 23°N, 03°W) to Lilliwaup Creek at the Long Live the Kings Hatchery. The two stream sections measured approximately 40 m long by 2.5 m wide, and were modified by adding clean 2 cm to 8 cm diameter gravel to a depth of 40 to 60 cm. Water flowed through the sections at a minimum rate of approximately  $17.5 \text{ l s}^{-1}$ . Picket-type fences were placed at the upstream and downstream boundaries of each section to retain all introduced salmon. The sections were separated by 2 m in such a manner that the fish in one section could not see those in the other. A grid system was set approximately 15 cm above each stream section, dividing it into 0.5 m by 0.5 m quadrants, so the spatial position of individual fish and redds could be identified. The channel sections were slightly curved; therefore, the grid sections were not perfectly square, but were very close to 0.5 m by 0.5 m.

Five males and five females from each of the two populations (20 fish in total) were placed into the upper channel (section 1) on 15 November 1995. The same number were placed into the lower channel (section 2) on 23 November 1995. Fish were selected for the experiment based on fork length in an attempt to size-match individuals between the two populations, within each sex and within each channel section. The fish were anesthetized (MS-222) and checked for ripeness: when either eggs or milt could be expressed manually, the fish were considered to be ripe. Wild fish were paired with captively reared fish of similar size (fork length  $\pm 1.5$  cm) within a sex, except that females in section 2 could not be so closely matched. The mean length and body weight of males in both channels and females in section 1 did not differ between the populations (two sample t-tests), whereas the fork length (but not body weight) of wild females in section 2 was significantly greater than that of captively reared females (Table 1). All but one fish used in the experiment were sexually mature (section 2 received one captively reared female that did not express eggs at the time of stocking and had not ovulated by the time she was removed 6 d later). This female was largely inactive and was not included or represented in any of the behavioral analyses.

Table 1. Total body weight (g) and fork length (mm) of hatchery and wild males (M) and females (F) used in channel sections 1 and 2. Significance (p) values represent population comparisons based on two-sample t-tests.

	Sex	Captively reared			n	Wild			n	p
		Mean	s.d.	Range		Mean	s.d.	Range		
Section 1										
Weight	F	1812	593.6	1140–2470	5	1661	363.7	1051–1968	5	0.640
Length	F	526	45.9	467–578	5	534	42.4	460–566	5	0.766
Weight	M	1569	595.7	711–2052	5	1467	657.6	590–2102	5	0.802
Length	M	507	68.15	400–560	5	500	76.8	387–564	5	0.886
Section 2										
Weight	F	1942	234.2	1580–2150	4	2253	295.9	1795–2432	5	0.103
Length	F	534	15.8	520–560	4	576	16.0	554–590	5	0.003
Weight	M	1444	419.9	1110–2080	5	1583	350.0	1083–1905	5	0.584
Length	M	497	46.5	454–567	5	515	41.7	458–554	5	0.546

Aggressive and courtship behaviors were recorded from observations of each fish for two 7 min periods daily, between 0730 and 1630 h. Observations continued until no females remained sexually active, except that in section 1 activity surrounding the last active female could not be reliably observed due to heavy precipitation and poor visibility. Aggressive behaviors recorded were lateral displays (LAT), bites, and chases. Lateral displays were defined as parallel body presentations to a competitor, where the anal fin is lowered, the pelvic and pectoral fins are spread, and the dorsal fin is erected. Bites were generally defined as open-mouthed pursuits that ended in contacts, but included instances where fish charged and rammed competitors with their snouts. Chases were defined as instances where the aggressor pursued a subordinate fish beyond the location of the subordinate fish prior to the pursuit.

Female breeding behaviors recorded were nest digs, cover digs, and probes. Nest digs were performed during nest construction by multiple caudal fin flexures. Cover digs were considered as digs that covered eggs in the nest pocket; these digs began immediately following spawning. Probes were defined as the movement made by females when they lowered their anal fins and mid-body into a developing nest depression. Soon after the anal fin contacted the gravel, the female would lift out of the nest pocket.

Male courtship behaviors recorded were crossovers, quivers, and nudges, and were defined as follows. Crossovers occurred when a male swam over the back or caudal peduncle of a female. Quivers were head-to-tail, high frequency undulations performed by a male next to the female, often with the male's body sloped downward towards the head. A nudge was a prod by a male snout against a female midsection.

Aggressive and courtship behaviors were also quantified by continuous observation of spawning aggregations from up to 2.5 h before spawning until approximately 15 min after spawning. The previously

defined behaviors of all fish associated with a sexually active female were described by experienced observers onto audio tapes. As many as three observers recorded behaviors in a channel section at any one time. Behaviors were summed for each 2 min of observation prior to spawning and each 1 min following spawning. These data provided information on mating combinations, male dominance hierarchies, and a continuous description of aggressive and courtship behaviors and nest digging activity. Mating combinations and male dominance hierarchies at the time of spawning were either determined directly by observing spawning events or they were predicted based on three conditions: (1) the presence of a female digging a well-defined nest where, (2) a stable dominance hierarchy had been established at night-fall, and (3) the female was observed guarding the nest area the following morning (cf. Maekawa and Hino, 1990; Fleming and Gross, 1992, 1993). Satellite males were defined as those males maintaining either the first (satellite 1) or second (satellite 2) positions immediately downstream from a courting pair. For females we also recorded to the nearest half day the time to onset of spawning, total time in the channel from introduction to death, duration of sexual activity (i.e. first to last spawning event), post-spawning lifespan, and nest-guarding duration. The number of nests constructed by each female was determined by combining the number of nests each female constructed where spawning was observed with the number of nests that were presumed to have been constructed by the same female. This was based on nest construction locations at night-fall and nest-covering activity by the same female in the same area the following morning. In some cases two covered nests (identified by mounded gravel) were constructed by a single female overnight.

Aggressive and courtship behavior frequencies recorded during observation of individual fish were statistically analyzed in the following manner. The behavioral frequencies for each fish were summed over

Table 2. Analysis of covariance results comparing intrasexual bites, chases, and lateral displays (LAT) by captively reared and wild males and females in both channel sections, and population by channel section interactions. Significant relationships between the covariate (body weight) and behavior were always positive.

Sex and behavior	d.f. <sup>a</sup>	Population		Section		Interaction		Covariate: body weight	
		F <sup>b</sup>	p <sup>c</sup>	F	p	F	p	F	p
Males									
LAT	1,15	0.417	0.528	0.000	0.985	2.200	0.159	1.332	0.266
Bite	1,15	0.376	0.549	2.433	0.140	0.395	0.539	9.158	0.008
Chase	1,15	1.613	0.226	0.077	0.784	2.016	0.176	51.777	0.000
Females									
LAT	1,14	3.861	0.068	4.304	0.056	2.741	0.119	0.298	0.593
Bite	1,14	1.920	0.186	1.120	0.307	0.569	0.462	9.883	0.007
Chase	1,14	1.542	0.233	4.470	0.052	0.067	0.799	11.386	0.004

<sup>a</sup>Degrees of freedom; <sup>b</sup>F-statistic; <sup>c</sup>significance value.

the entire observation period and divided by the number of days the fish were observed in each section. Thus, the dependent variables analyzed were behavior frequencies per 14 min of observation. Intrasexual aggression data ( $\log_{10}+1$  transformed to correct for heteroscedasticity) were analyzed separately for each sex by two-way analysis of covariance (ANCOVA), where population type and channel section were the main effects and body weight was the covariate. Intersexual aggression ( $\log_{10}+1$  transformed) was analyzed by a three-way, full factorial analysis of variance (ANOVA). For male aggression against females, male population (aggressor), female population (receiving aggression), and channel section were the main effects. For female aggression against males, female population (aggressor), male population (receiving aggression), and channel section were the main effects. Male breeding behaviors, female breeding durations, and the number of nests constructed per female were analyzed by ANCOVA, with population and channel section as the main effects and body weight as the covariate. In all cases where there was a significant covariate relationship, the assumption of parallelism was met (i.e. there were no covariate by main effects interactions,  $p>0.10$ ), and comparisons of main effects were made on adjusted means (Kleinbaum and Kupper, 1978). The number of spawnings (i.e. breeding success) by captively reared and wild males were analyzed using a binomial test. All analyses were conducted with an *a priori* significance level of 0.05.

## Results

Levels of aggressive behaviors did not differ significantly between populations or between sections (Table 2). A positive linear relationship between body weight and aggressive behavior was significant for male bites ( $p=0.008$ ) and chases ( $p<0.001$ ) and female bites ( $p=0.007$ ) and chases ( $p<0.001$ ). The relationship

between total aggressive attacks (i.e. bites+chases) is shown in Figure 1.

Females (both populations combined) bit and chased captively reared males more often than they did wild males (significant male population effect for chases,  $p=0.013$ , and bites,  $p=0.017$ , Fig. 2). There was no significant female population effect, section effect, section-by-female population interaction, or section-by-male population interaction for either bites or chases ( $p>0.17$  for all effects). There was a significant section-by-female population interaction for lateral displays ( $p=0.04$ ): captively reared females performed lateral displays more frequently against both male populations in section 2 than in section 1.

Males from both populations expressed similar levels of aggression against females from both populations (i.e. no male population effect or male population-by-female population interaction, Fig. 2). There was, however, a significant female population (receiving aggression) by-section interaction for bites ( $p=0.008$ ) and chases ( $p=0.035$ ). That is, males from both populations attacked captively reared females more frequently than wild females in section 2, but not in section 1.

Observations of spawning aggregations revealed that the proportion of captively reared and wild males that courted spawning captively reared and wild females did not differ ( $\chi^2=2.17$ , 1 df,  $p=0.16$ ), so captively reared and wild female spawnings were combined for an analysis of male dominance and participation in these spawnings. Wild males maintained the dominant position in 85.7% of eventual spawnings compared with 14.3% for captively reared males (binomial test,  $n=21$ ,  $p<0.001$ ). The ratio of dominant wild to captively reared males for observed (9 wild: 2 captively reared) and predicted (9 wild: 1 captively reared) matings were similar, so the data were combined for analysis. The 21 observed and predicted matings included five different dominant wild males and only one dominant captively reared male. In

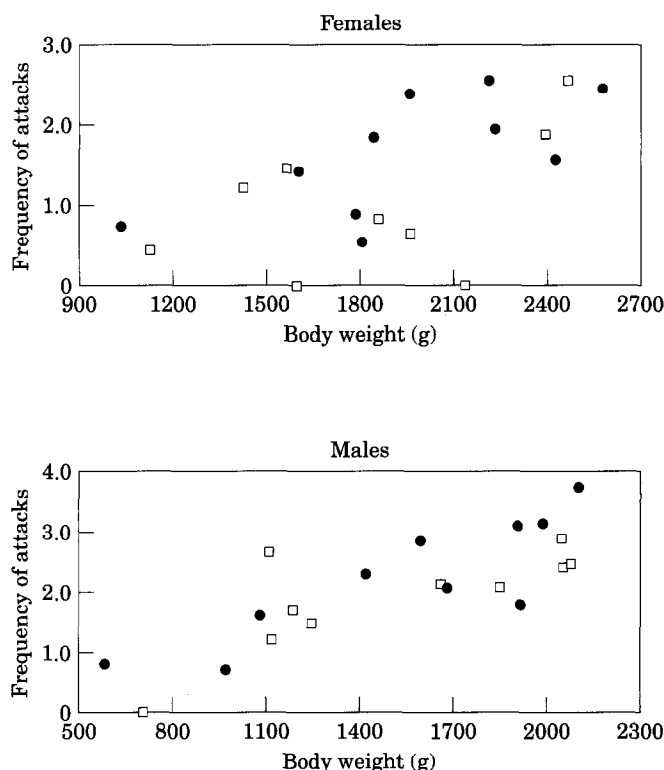


Figure 1. The relationship between body weight and the average frequency of aggressive attacks (bites+chases) per 14 min of observation (i.e. per day) by male ( $p<0.001$ ) and female ( $p=0.006$ ) captively reared (□) and wild (●) coho salmon.

matings that involved at least two males, wild males were also more frequently observed in the satellite 1 position (62.5%) than were captively reared males (37.5%; binomial test,  $n=16$ ,  $p=0.097$ , non-significant), and captively reared males were observed in the satellite 2 position in two out of three matings where a second satellite male was observed. In 9 of 11 observed spawnings, the dominant male entered the nest first and spawned, obtaining a spawning position next to the female. One dominant captively reared male, which had courted a wild female for at least 65 min, left the nest area briefly to chase another male; while he was gone, the female spawned with the satellite captively reared male. In a different situation, the same captively reared male courted a female for 48 min, then volitionally left the female 3 min before she spawned with a wild male.

Observations of individuals twice daily throughout the period of female sexual activity revealed that wild males had significantly higher frequencies of crossovers ( $p=0.012$ ) and quivers ( $p=0.030$ ) than did captively reared males (Fig. 3). Wild males nudged females no more often than did captively reared males ( $p=0.224$ ). There were no significant section or section-by-population interactions for any of the courtship behaviors ( $p>0.10$  in all cases). The effect of body weight

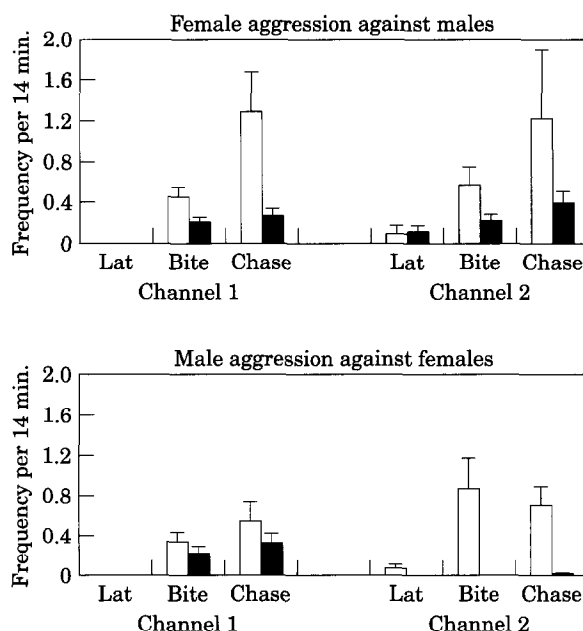


Figure 2. Average frequency ( $\pm$  S.E.) of intersexual aggressive behaviors per 14 min of observation (i.e., per day) in sections 1 and 2. The upper graphs shows aggression by all females against captively reared (□) and wild (■) males, and the lower graph shows aggression by all males against captively reared (□) and wild (■) females.

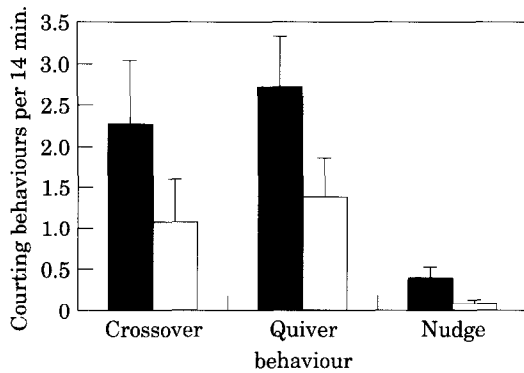


Figure 3. Average frequency ( $\pm$  S.E.) per 14 min of observation (i.e. per day) of courtship behaviors by wild (■) and captive reared (□) males. There was no significant channel effect, or population by channel interaction, so this graph represents combined data from both channel sections.

was non-significant for crossovers ( $p=0.378$ ), quivers ( $p=0.139$ ), and nudges ( $p=0.058$ ).

There were no population-by-section interactions for any of the female breeding and post-spawning durations analyzed (Table 3). Captively reared females delayed spawning in their first nest for an average of twice as long (3.4 d) as wild females (1.7 d;  $p=0.017$ ). Lifespan from the introduction of fish into the sections to death was greater for captive reared females (10.5 d) than wild females (7.7 d;  $p=0.001$ ). There were no significant differences between populations in the length of time it took a female to complete all of the nests (i.e. spawning duration). Individual spawning durations ranged from 0.5 d (i.e. overnight) to 8 d, with the shortest time between successive observed spawnings being 4 h. Neither the duration of nest guarding, nor the time from last spawning to death (post-spawning lifespan) differed significantly between the populations (mean nest guarding: wild=4.1 d, captive reared=5.3 d; mean spawning duration: wild=1.3 d, captive reared=2.0 d). There were significant positive relationships between the covariate body weight and duration of spawning activity ( $p=0.004$ ) and nest guarding duration

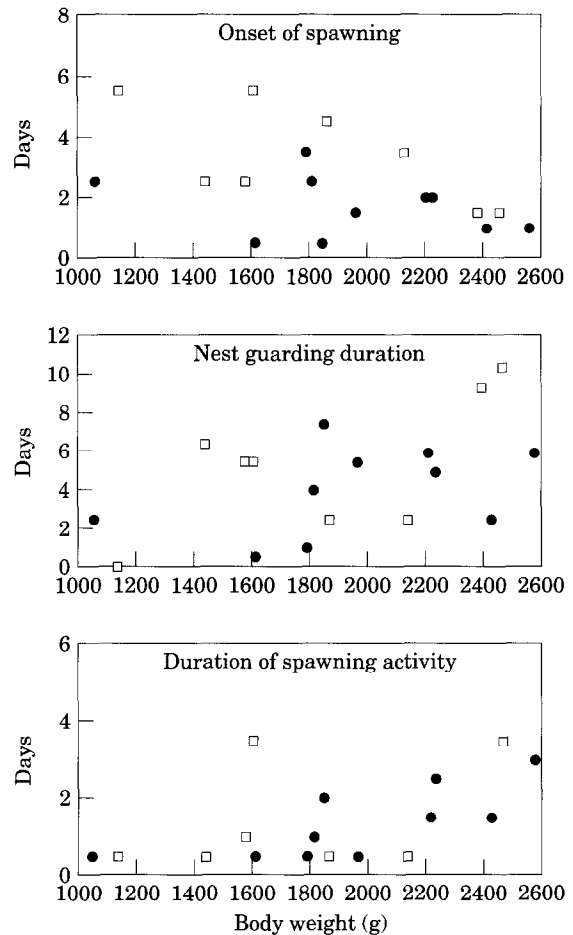


Figure 4. Relationship of the covariate, body weight, to onset of spawning ( $p=0.001$ ), nest guarding duration ( $p=0.004$ ) and time from first to last spawning (i.e. breeding duration,  $p=0.004$ ) in days for captive reared (□) and wild (●) females.

( $p=0.004$ , Fig. 4), and a significant negative relationship between body weight and onset of spawning ( $p=0.007$ ).

The number of nests constructed by individual females ranged from 0 (one captive reared female)

Table 3. Spawning durations for wild and captive reared (CR) females analyzed by ANCOVA with body weight as the covariate. In all cases significant covariance results reflect positive relationships between body weight and the duration variable.

Duration	d.f. <sup>a</sup>	Female type		Section		Interaction		Covariate: body weight	
		CR	Wild	F	p	F	p	F	p
Pre-spawn	1,13	7.40	0.017	3.14	0.100	1.56	0.233	10.08	0.007
Spawning	1,13	1.31	0.273	6.51	0.024	1.56	0.234	12.33	0.004
Post-spawn	1,13	0.46	0.509	1.64	0.222	1.89	0.193	0.36	0.782
Nest-guard	1,13	1.85	0.196	6.47	0.024	0.02	0.881	11.84	0.004
Total lifespan	1,14	21.22	0.001	10.04	0.007	0.48	0.498	0.49	0.497

<sup>a</sup>Degrees of freedom; <sup>b</sup>F-statistic; <sup>c</sup>significance value.

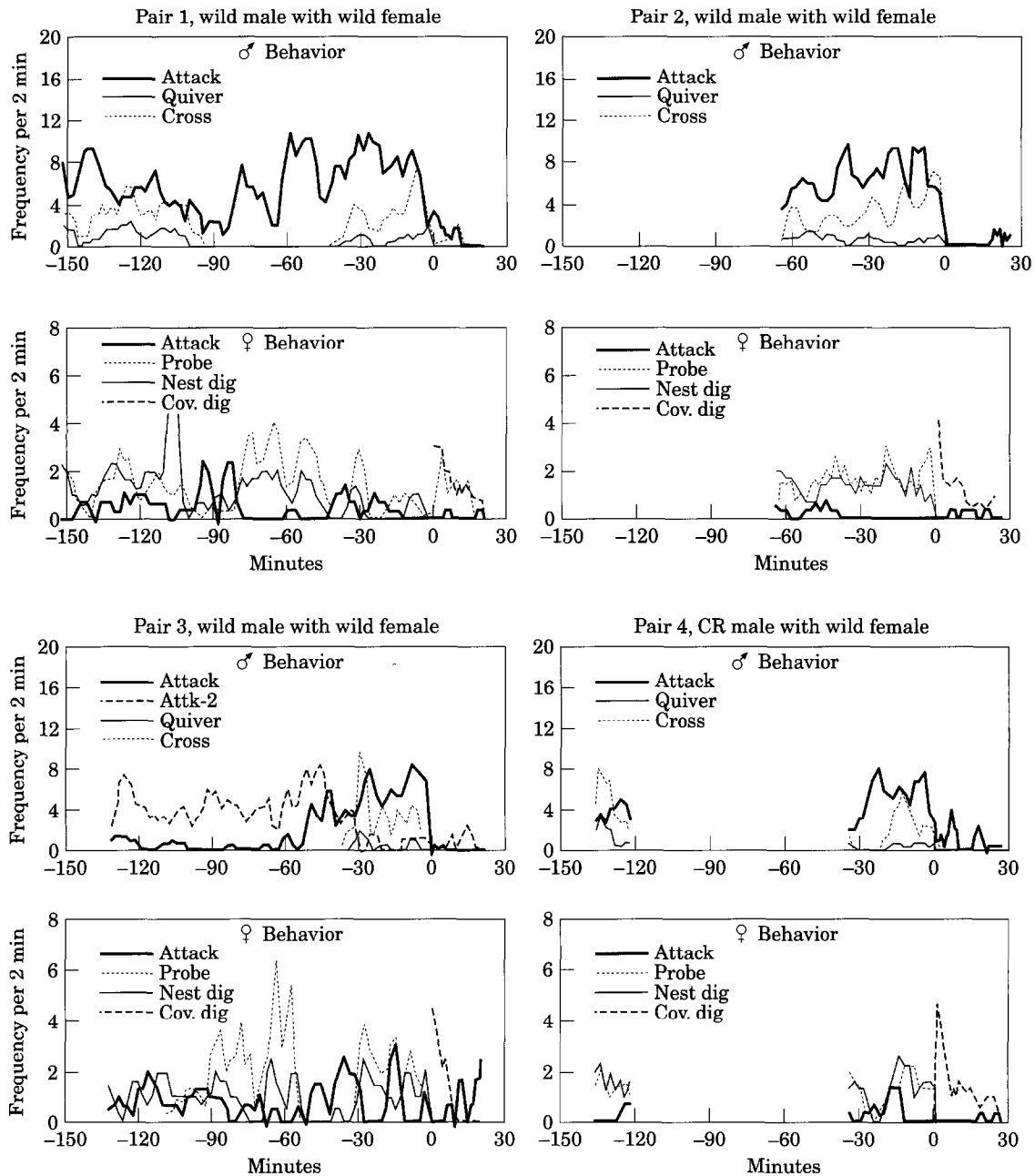


Figure 5.

to 4. A total of 50 nests were identified in both sections combined, of which 32 belonged to wild females and 18 to captive reared females. Wild females averaged 3.0 nests in section 1 and 3.4 nests in section 2, compared with 2.6 nests (section 1) and 1.3 nests (section 2) by captive reared females (population effect:  $p=0.025$ ; section effect:  $p=0.480$ ; interaction:  $p=0.347$ ). There was a significant positive relationship between the number of nests constructed

by each female and the female's body weight ( $p=0.014$ ).

Continuous observations of courtship, aggression, and digging behaviors were obtained for 11 spawnings, six of which provided a substantial temporal profile before, during, and after spawning (Fig. 5). Male competition surrounding sexually active females involved very high levels of attacking behaviors (bites and chases), primarily by the dominant male, and low levels

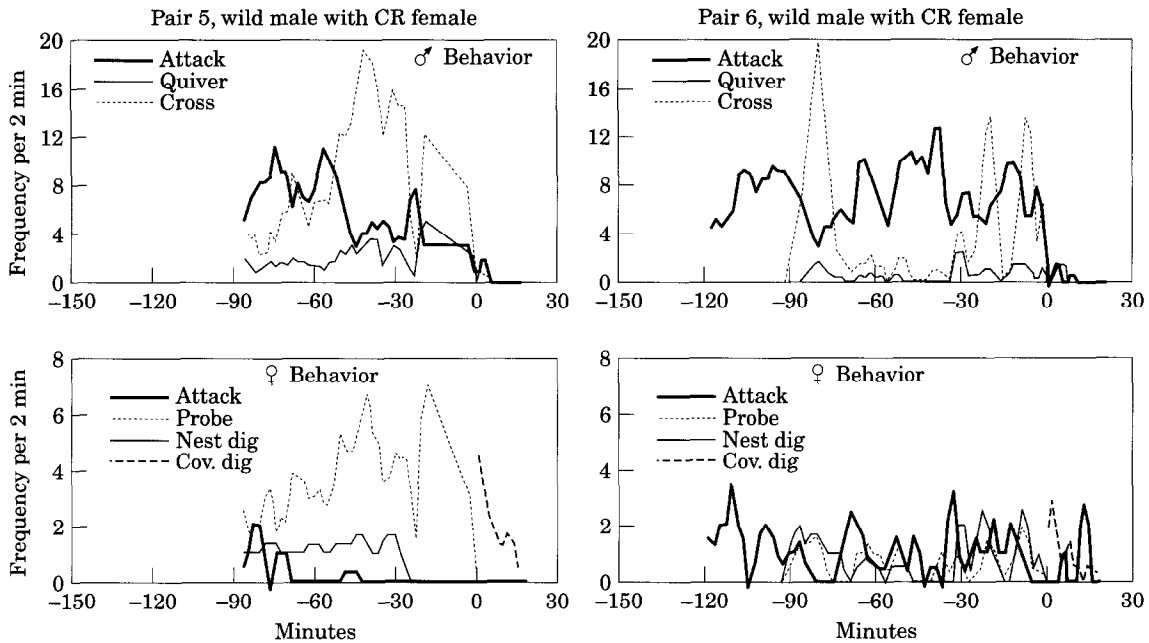
Figure 5. *continued.*

Figure 5. Continuous data from six courting pairs of captively reared and wild coho salmon. Frequencies of dominant male (top panel) and female (bottom panel) behaviors are summarized every 2 min (lines show a 6 min running average) before spawning, and every minute following spawning. Negative numbers represent time prior to spawning, and positive numbers represent time after spawning (spawning occurred at minute 0). Attacks include bites and chases by the dominant male or spawning female, but not lateral displays. The "Attk-2" designation refers to attacks by a second male that courted the female for a period of time but was usurped by the dominant male prior to spawning.

of lateral displays, which appeared to be primarily defensive displays by subordinate males. Male courtship of females generally increased as spawning neared, followed by a dramatic reduction in dominant male courtship activity after spawning, although satellite males would often court a recently spawned female. Aggressive activity by the dominant male temporarily interrupted courtship behaviors. Generally, as dominant male attacks on competitors increased, male crossovers and quivers and female probes decreased (Fig. 5; pairs 1, 2, and 5). Aggressive activity by the dominant males terminated almost completely following spawning, and the dominant male abandoned the female usually within 5 min following spawning.

Female nest digging occurred approximately once every 2 min, and was fairly constant over time. Males responded quickly to female digs and probes by crossing over and quivering alongside the female (note the correlation between female probing and digging and male courtship behavior frequencies in Fig. 5). Females initiated spawning by lowering themselves into the nest and gaping (mouth wide open) and releasing eggs. The dominant male, which on some occasions began gaping prior to the female, followed immediately by releasing sperm. Satellites (if present) followed by darting into the nest, gaping, and releasing milt. The duration of simul-

taneous female and dominant male gaping ranged between 10 and 15 s (mean = 12.3,  $n=9$ ). Sperm was generally visible within 2 to 3 s after both fish began gaping.

Females began covering their nests (using the caudal fin) immediately after spawning. Generally, four to six covering digs were made within the first minute following spawning; these initial digs consisted of only two to three body flexures. The length of a covering dig and the number of body flexures used per dig increased over time. Approximately 15 min after spawning, digging frequency had declined to approximately 1 dig  $\text{min}^{-1}$ , by which time some females resumed nest defense (Fig. 5, pairs 3 and 6). Dominant males would generally abandon the female within 5 to 10 min following spawning to search for another mate.

## Discussion

The results from this study demonstrate that wild Big Beef Creek coho salmon were competitively superior to captively reared Stavis Creek coho salmon, and that this difference in competitive ability between the populations appeared to be greater between males of the two populations than between females. Wild males clearly



dominated access to spawning females in both channel sections, as they were dominant in 86% of observed and predicted spawnings, and held the satellite-1 position in 62% of the spawnings where at least one satellite male was identified. Other studies of salmonids have demonstrated that dominant males fertilize the majority of eggs laid by their mates, and the proximity of satellites to the female largely determines their fertilization success (Schroder, 1981; Chevanov *et al.*, 1984; Maekawa and Onozato, 1986; Hutchings and Meyers, 1988). Wild males in this study showed higher frequencies of courtship behaviors probably resulting from their ability to obtain and defend access to sexually active females. Body size has been identified as a major determinant of dominance success for adult male char (*Salvelinus* sp.) (Kitano *et al.*, 1994), sockeye salmon (Foote, 1990; Quinn and Foote, 1994), chum salmon (Schroder, 1981), and coho salmon (Fleming and Gross, 1992, 1993, 1994). In our study, the aggression data suggest that dominance was positively related to size. The two largest wild males obtained dominance status most often in section 1 of our experimental channel, but in section 2 the males most frequently dominant were the third and fourth largest. Nevertheless, males from both populations were closely size-matched, suggesting that other factors must have been responsible for the strong dominance of wild males over captive reared males.

Recent evidence suggests that certain morphological characters, independent of body size and other variables, can influence male breeding success. Quinn and Foote (1994) found that hump height was correlated with male sockeye salmon breeding success. In another study, coho salmon with longer snouts had greater access to spawning opportunities and greater estimated fertilization success than those with shorter snouts (Fleming and Gross, 1994). The morphology, particularly the expression of secondary sexual characteristics (e.g. hump size and kype development), of wild and captive reared males used in our experiments differed markedly (J. Hard, National Marine Fisheries Service, Seattle, Washington, USA, unpublished data). Although we did not quantify the coloration patterns of the two populations, wild males had striking red and black coloration patterns typical of wild coho salmon (Briggs, 1953) compared to the generally dull, brown color of the captive reared males. Coloration patterns are used as status signals in juvenile salmonids (Keenleyside and Yamamoto, 1962; Abbott *et al.*, 1984) and adult chum salmon (Schroder, 1981), and Hanson and Smith (1967) speculated that these patterns affect behavioral interactions in adult sockeye salmon. Levels of aggression did not differ significantly between the populations, suggesting that contests for mates may have been influenced by more subtle mechanisms, such as status signaling (see Jarvi, 1990), possibly influenced by population differences in morphology or coloration.

Captively reared females constructed, on average, only 62.5% as many nests as wild females, with larger females constructing more nests than smaller ones in both groups. Over half of the counted nests were spawned at night, and we therefore relied on the post-spawning behavior (cover digging and guarding) and position of individual females to assign nests to individual females, which may have introduced some unknown error. Nevertheless, competitively inferior females may not have been able or willing to dig and defend numerous nests, which should make it more profitable for them to spawn more eggs in fewer nests (Fleming and Gross, 1993). In natural streams, females that construct more nests may spread the risks of embryo and alevin death from stream bed scour, suffocation, or entombment (see Peterson and Quinn, 1996) and nest superimposition by later-spawning females (Fleming and Gross, 1992, 1993), although such a tactic carries possible energetic costs associated with nest construction and territory defense.

To be reproductively successful, a female must acquire a territory, construct a series of nests (redd), and defend her developing eggs from mechanical shock caused by neighboring females (Schroder, 1982; Fleming and Gross, 1993). Early onset of spawning and longer nest-guarding duration suggest a competitive advantage, and body size has been positively associated with both factors in coho salmon (van den Berghe, 1986; van den Berghe and Gross, 1989; Fleming and Gross, 1993). In this study, time to onset of spawning was negatively correlated with female body weight, and nest-guarding duration was positively correlated with female body weight (Fig. 4). Independent of size, wild females took only half as long as captive reared females to spawn in their first nest. Before initiating nest construction, many of the later spawning females were largely inactive, held stationary positions near the stream banks, and were repeatedly attacked by territorial females. Hence, smaller females from both populations and captive reared females, more so than wild females, may have been excluded from establishing territories and initiating nest construction, or may have chosen to remain quiescent until competition for nest sites diminished, similar to other indications of female competition in coho salmon (Fleming and Gross, 1993), and as suggested for chum salmon (Schroder, 1981). Although all females placed in the channel sections had ovulated, we cannot rule out the possibility that the timing of female reproductive behaviors may have been affected by undetected variation in maturity levels. Delayed onset of spawning can result in reduced reproductive fitness caused by higher egg retention, or even the possibility that the female will die before spawning at all (Schroder, 1973). Early spawners, on the other hand, risk having their nests superimposed by later-spawning fish (McNeil, 1964; van den Berghe and Gross, 1984; Fleming and

Gross, 1992), although we observed only partial superimposition of a single nest in our study.

The interplay between male dominance and female mate choice has been difficult to determine in salmon reproduction because female choice is restricted by the outcomes of intrasexual male competition. Females do, however, make indirect choices regarding potential mates (Foote, 1990; Quinn and Foote, 1994). Females may exhibit some mate selection by attacking undesirable males or delaying spawning until courted by a desirable male (Schroder, 1981; Foote, 1988; Foote and Larkin, 1988). Although we could not determine whether females delayed spawning or decreased digging frequencies in the presence of captive reared males, females from both populations attacked captive reared males more than twice as often as wild males (Fig. 2), thereby demonstrating one form of intersexual selection favoring wild males. This may have been caused by the marked coloration and morphological differences between males of the two populations. Female aggression against captive reared males may have contributed to the success of wild males in competing for access to females. Alternatively, dominant males may have been more acceptable to females because of the probability that characters associated with male dominance will be inherited by her offspring (Schroder, 1981), in which case, intersexual female aggression against captive reared males might have merely assisted in maintaining wild male dominance previously attained through competition among males.

Fleming and Gross (1993) found that breeding success in two wild populations of coho salmon was higher than that in a hatchery (sea-ranched) population; they speculated that this may have resulted from genetic divergence of the hatchery population from the wild populations over four to five generations. The opportunity for genetic divergence to occur in our study was much less, because the captive reared population was captive for less than one generation (see Reisenbichler, 1996), but environmental influences on reproductive phenotypes were probably greater because they were reared throughout their life-cycle rather than released at the smolt stage (see Fleming *et al.*, 1994). In any case, environmental effects on phenotype would overwhelm any genetic divergence that could occur in this situation. Our results are similar to those of Fleming and Gross (1992, 1993), in that data from both studies suggest that greater differences in breeding success existed between cultured and wild males than between cultured and wild females. Intrasexual selection of Pacific salmon is believed to be more intense for males than for females, because male competition for access to females (primarily) and territories (Foote, 1990), is more intense than female competition for acquisition and defense of nesting territories, and female mate choice (i.e. intersexual selection) exerts further selective pressures on male

reproductive characters (Fleming and Gross, 1994; Quinn and Foote, 1994). Hence, any behavioral and morphological divergence of captive reared coho salmon from the wild state probably had greater consequences for males than females in terms of intrasexual competition.

The results of this study suggest that captive reared coho salmon released as adults into natural streams should exhibit the full range of coho salmon reproductive behaviors and will successfully reproduce if they are able to migrate to suitable spawning areas and have viable gametes. Work by S. Schroder and colleagues at the Washington Department of Fish and Wildlife (unpublished data) indicates that gametes of captive reared Stavis Creek and wild Big Beef Creek coho salmon have similar viability. Captively reared salmon will probably not, however, attain the same level of reproductive success as intermixed wild coho salmon because of diminished competitive ability. Further research is needed to understand the mechanisms behind the disparity in competitive ability and to more fully understand the overall mating patterns of intermixed captive reared and wild coho salmon.

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