



## Can the alternative male tactics 'fighter' and 'sneaker' be considered 'coercer' and 'cooperator' in coho salmon?

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(Received 29 June 2004; initial acceptance 13 September 2004;  
final acceptance 31 January 2005; published online 3 October 2005; MS. number: A9922R)

Females often prefer to mate with males with certain traits. Preferred males might cooperate with females to reduce the direct costs of reproduction. However, unpreferred males use alternative tactics that attempt to alter female choice in their favour, such as coercion. When this occurs, females have to choose whether to pay the costs of coercion and mate with preferred males or avoid the costs of coercion by mating with unpreferred males. The decisions females make are expected to depend on the relative costs and benefits of mating with preferred and unpreferred males and the frequencies of the two male types. Here I present a study of simultaneous coercion and cooperation among wild coho salmon, *Oncorhynchus kisutch*. This species is well known for its alternative male types, sneakers and fighters. I found evidence that females prefer to mate with, and cooperate with, small sneaker males, but regularly mate with large fighting males to avoid the costs of coercion. Large males were more aggressive towards females than were small males. In addition, females spent more time preparing their nests when they were alone with small males than when they were accompanied by large males, and they oviposited for longer durations when small males were part of the spawning group.

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Sexual conflict occurs as a result of divergence in the evolutionary interests of males and females (Parker 1979; Partridge & Hurst 1998; Chapman et al. 2003). These conflicts can cause mating to be costly for females (e.g. Blanckenhorn et al. 2002). Mating costs for females may take many forms, such as lost opportunities to forage, increased predation risk, harassment by males, or injury (Martin & Hosken 2004). Thus, females may evolve phenotypes that avoid the costs imposed by males either during mating (Mesnick & Leboeuf 1991; Rowe et al. 1994; Rice 1996; Hosken et al. 2001; Moore et al. 2001; Arnqvist & Rowe 2002b) or while resisting mating (Clutton-Brock & Parker 1995b; Jormalainen et al. 2000). Male phenotypes might then be expected to evolve as effective coercers that can overcome female resistance with force or threats of force (Smuts & Smuts 1993; Clutton-Brock & Parker 1995a; Johnstone & Keller 2000; Arnqvist & Rowe 2002a; Jaeger et al. 2002) or as sneaks that circumvent female choice (Shuster & Wade 2003; Luttbeg 2004). In species with sneaker and fighter male types, the general assumption has been that females prefer the stronger

fighter males. However, recent work in other species has shown that females do not always prefer males that are the best fighters (Ophir & Galef 2003; Wong 2004).

In contrast to sexual coercion, cooperation during sexual interactions is expected to occur when the evolutionary interests of mates coincide (Andersson et al. 2000). In a simplified view, when a female meets a preferred male, cooperation between male and female works to limit the direct costs of mating. In most populations though, the mating value of males varies and females are likely to meet unpreferred males (of low perceived mating value) as well as preferred males (of high perceived mating value). When females concurrently encounter both unpreferred and preferred males, mating dynamics might involve a simultaneous mix of coercion and cooperation.

Coercion and cooperation in mating, although often documented separately, occur in many species. One behaviour described as coercion is a male's use of force to overcome female resistance to mating. For example, male orang-utans, *Pongo pygmaeus*, will often violently restrain females during copulation (Mitani 1985), and low-ranking male elephant seals, *Mirounga angustirostris*, attempt to force copulations when higher-ranking males are away from their harems (Leboeuf & Mesnick 1991). Such behaviour is not limited to vertebrates. Male water striders, *Aquarius remigis*, wrestle with females in an

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attempt to subdue them for mating (Lauer et al. 1996). Larger, more active males are most successful at these attempts (Sih et al. 2002). Cooperation also occurs in mating systems. Male spotted hyaenas, *Crocuta crocuta*, apparently require female cooperation to copulate, and coercion is an unsuccessful mating strategy (East et al. 2003). In the butterfly *Pieris napi*, the mating system is characterized by concurrent conflict and cooperation (Wiklund et al. 2001). In this species, males harass females but they also transfer a chemical to females during mating that frees the female from costly harassment by other males (Andersson et al. 2000). It is possible then, that the simultaneous occurrence of coercion and cooperation occurs in many mating systems.

When females simultaneously encounter both preferred and unpreferred males, preferred males are expected to provide females information indicating their high mating value. These males might cooperate with females to facilitate reproduction. In contrast, unpreferred males may develop phenotypes that can impose precopulatory costs on females who would otherwise avoid mating with them. To maximize fitness, females are expected to choose mates based on the costs and benefits for each male. In this scenario, females are predicted to practise 'cost-avoidance' and make mate choices that reduce the direct costs of mating. When both preferred and unpreferred males simultaneously vie for females, the result is that sometimes females choose preferred males because cooperating with these males to achieve a mutual benefit reduces the direct costs of reproduction. At other times, females choose unpreferred males to avoid the direct costs of coercion. Although simultaneous coercion and cooperation may be widespread, documentation and analysis of the phenomenon is likely to be more feasible in some systems than others. Systems with genetically based alternative mating phenotypes (Iwamoto et al. 1984; Shuster 1989; Radwan 1995; Sinervo & Lively 1996) could be good candidates for the study of coercion and cooperation. In many such species, different male types show different life histories. Males that develop along alternative life histories typically vary in their survival. Often males that develop small, 'sneaker' phenotypes have higher survival (Gross 1985; Tsubaki et al. 1997). Thus, females may use the phenotypic differences of males to pick the mate that will provide the most viable offspring (Andersson 1994). If a female preference for highly viable males exists, 'sneaky' behaviour by preferred males may be a means of reducing the direct costs of mating.

Here I examined sexual coercion and cooperation in wild spawning coho salmon, *Oncorhynchus kisutch*. In this species there are two distinctive male phenotypes, 'jacks' and 'hooknoses'. Small and cryptically coloured jacks are considered sneakers that gain mates surreptitiously, whereas hooknoses are large and gain access to females by fighting (Gross 1985). Jacks, however, have a higher survival rate because they grow faster as juveniles and mature earlier (Hager & Noble 1976). Given that these alternative male types are heritable (Iwamoto et al. 1984; Heath et al. 1994), based on survival value per se (Gross 1996), females might prefer jacks (Andersson 1994). To persist then, hooknoses must offset the survival advantage

of jacks by gaining a mating advantage by coercing females.

I tested the predictions of the cost-avoidance hypothesis. If females prefer to mate with jacks, they might cooperate with them. Simultaneously, unpreferred hooknoses are expected to coerce mates. That is, hooknoses should perform costly behaviours (in terms of female fitness) at higher rates than jacks. I evaluated these predictions by documenting the types of interactions between females and different males, the behaviours performed by males leading up to females' decisions to mate, and the duration of oviposition for females mating with groups composed of different types of males.

## METHODS

### The Study System

In California, coho salmon grow in freshwater for a year before migrating to the ocean as smolts to mature. At maturity, adult coho return to their natal stream to spawn and die (Sandercock 1991). While it is thought that all females of Californian stocks return to spawn at around 2.5 years of age, there is variation in age at maturity for males. Some males mature as 2.5-year-old hooknoses, after 17–20 months in the ocean, while others return to the spawning grounds as 1.5-year-old jacks, after only 5–8 months at sea (Shapovolov & Taft 1954; Gross 1985). Whether a male coho becomes a jack or a hooknose is apparently based on a threshold juvenile size: juveniles larger than the threshold become jacks and those smaller than the threshold become hooknoses (Hager & Noble 1976; Gross 1991).

### Coho Salmon Spawning Behaviour

Upon returning to the natal stream, female coho salmon dig nests in which they will bury their eggs. Females dig in the presence and absence of males. However, once a female starts digging, she is usually joined by a male (or males) and is rarely left alone on the nest site until after spawning (personal observation). Females do not lay all of their eggs in a single nest. Over the course of a week or more, females lay eggs in several closely adjacent nests, which are collectively referred to as a redd (Shapovolov & Taft 1954). As a result, a female may mate with several males or groups of males. Females defend their nest site from use by other females and remain on the redd from the end of egg laying until death.

Male coho salmon play no role in nest preparation or defence. Males fight among themselves for access to females. When more than one hooknose is vying for a female, a linear hierarchy is easily observed, with the primary male taking the position nearest the female. Other hooknoses 'line-up' behind the female, with males queued according to their rank order. The primary male interacts with other males and with the female. Lower-ranked males rarely interact with the female. They tend to hold their position until chased by the primary male, until the primary male is away on another foray, or until the female moves into the nest depression for oviposition.

Jacks do not easily fit into the dominance order of hooknoses. Often, even when there are multiple hooknoses, a jack will be the second-closest male to the female after the primary hooknose. Jacks gain proximity to the female either by hiding near some structure in the creek (rocks, snags, etc.) or by staying just off the redd in the darker area of undisturbed substrate. Jacks spend a good deal of their time avoiding attacks by the primary hooknose, who will bite and kill them if possible. When jacks compete for the same location, they may fight vigorously. Observing a linear dominance hierarchy among jacks is difficult because they interact far less frequently than do hooknoses, and they spend much of their time hiding. Indeed, in spawning situations, jacks interact more with hooknoses than with other jacks. Jacks move onto the redd and interact with females when opportunities arise (e.g. when the primary hooknose is off the redd or on the opposite side of the female). Through these behaviours, the jack appears apparent to the female, and ensures that he is in close proximity to her when spawning occurs.

Spawning occurs quickly. Fertilization is external and commonly more than one male fertilizes a single clutch of eggs (Foote et al. 1997). The female drops into the depression in the nest, males rush alongside her, and all mates express their gametes simultaneously. Gamete expression in all participants is marked by an open-mouth gape. Streamside observers can easily see a cloud of milt, although eggs are difficult to see because they sink into the nest depression. Following oviposition, the female breaks from her position, moves forward, and begins to bury her eggs. This burial digging indicates that the female has oviposited.

## Observations and Analyses

I observed wild coho spawning in Lagunitas Creek, Marin County, California during two spawning seasons, 1999–2000 and 2000–2001. I recorded male–female interactions with video to monitor the behaviours described in

**Table 1.** Videos were made from the bank above the surface of the water. Records began when I located a new female preparing a redd. I observed one to four males present at any one time with each female. Supplemental data were recorded in a notebook. I described the physical markings of all fish present and assigned each a number. At 5-min intervals, I recorded the location of each fish present. I also recorded the identities of males taking part in any oviposition. Occasionally the video camera failed, in which case observations were recorded solely in the field notebook. Observations ended when an oviposition ended, when the redd was vacant for 30 min, or when visibility degraded due to rainfall.

The array of males present at the spawning site determines the males available for mate choice by females. In all, I observed 17 (14 videotaped) females interacting with a total of 59 males, 43 hooknoses and 16 jacks. Of these 17 females, I observed 15 oviposit (12 videotaped). Compositions of male groups that these 15 females were observed to spawn with are shown in **Table 2**. Although females lay more than one clutch of eggs, to avoid pseudoreplication, no data were collected for more than one spawn per female. Males were considered potential mates if they were present and clearly vying for a position near the female for two or more consecutive 5-min intervals before spawning. On average, females were attended at any one time by three potential mates (range 1–4). Group composition, however, changed regularly, with males leaving and returning frequently. Thus, over the course of one prespawning bout, females might be attended by as many as six different males. Behaviours described in **Table 1** were observed for the primary male. Data were gathered from 1233 min of videotape and from field notebooks. For this time, hooknoses were the primary actor for 1089 min. While present for 773 min, jacks were the primary actor for only 98 min. Females were alone for 46 min.

I measured oviposition duration from video as the interval from the female's initial spawning gape to the moment she moved forward to bury the fertilized eggs. I

**Table 1.** Behaviours observed in wild spawning coho salmon

Behaviour	Description	Possible objective or outcome
<b>Male behaviours</b>		
Vibrate	Approach side of the female closely ( $\leq 3$ cm) and quiver (Shapovolov & Taft 1954; Berejikian et al. 2000)	Advertisement: demonstration of condition; usually no contact is made
Nudge	Bump the belly or side of the female with the snout or body (Shapovolov & Taft 1954)	Direct contact is made (energetic/physical cost)
Crossover	Swim over the female, from one side to the other and back again (Berejikian et al. 2000); often includes brushes against the female during crossover, and the female is sometimes pushed into the substrate	Direct contact is made (energetic/physical cost) Potential for increased predation risk via increased conspicuousness (predation cost) Exclude other males' access to female (Shapovolov & Taft 1954)
Chase	Pursue conspecific	Attack (energetic/physical cost)
<b>Female behaviours</b>		
Dig	Turn to one side and use caudal fin to excavate gravel	Nest preparation (Berejikian et al. 2000) High digging frequencies in the presence of males of a particular phenotype may reflect a female preference for that phenotype (Berejikian et al. 2000; de Gaudemar et al. 2000a)
Leave	Swim away from the nest (redd)	Avoid potential harm
Return	Re-enter the nest area	Spawn

**Table 2.** Number of male coho salmon of each phenotype (hooknoses, jacks) observed in spawning groups, number of females observed spawning with males of each phenotype and oviposition duration

Social classification	Male group composition		Number of females observed spawning	Total number of males observed spawning		Oviposition duration (s)*
	Hooknoses	Jacks		Hooknoses	Jacks	
Hooknose alone	1	0	3	3	0	9.5, n/a, n/a
Hooknose alone	2	0	1	2	0	13.2
Hooknose alone	4	0	2	8	0	8, 10.4
Jack alone	0	1	1	0	1	n/a
Hooknose and jack	1	1	4	4	4	13.2, 16.9, 14.5, 16.2
Hooknose and jack	2	1	1	2	1	15.8
Hooknose and jack	2	2	3	6	6	12, 10, 15
Total			15†	25	12	

\*Oviposition durations are reported for spawns captured on videotape. 'n/a' indicates that oviposition was not videotaped and duration data were not available.

†Of the 17 females observed, 15 were observed to oviposit.

recorded all other behaviours (Table 1) according to their frequencies (occurrences/min) and the social situations (numbers of the two types of males) in which they occurred. Data presented in figures represent mean values  $\pm$  standard error.

I compared how alternative male types interacted with females and with each other. Males rarely chased or bit females. Thus, I classified males as to whether they chased or bit females (yes/no) and used a *G* test to compare the occurrence of these two behaviours between male types. For other behaviours, behaviour frequencies when jacks versus hooknoses were primary actors were compared with Mann–Whitney tests. Jacks were never primary actors in the presence of hooknoses. I examined how the behaviour of hooknoses as primary actor changed with male group composition using a standard least-squares multiple regression model. The model determined whether the independent variables 'number of other hooknoses' and 'number of jacks' at the nest site predicted the behaviour of the primary acting hooknose. I ran separate models for each male behaviour.

I analysed whether female behaviour differed when hooknoses versus jacks were the primary actor. Five females were observed both alone with a jack and in situations where the primary actor was a hooknose. I used a matched-pairs analysis (repeated measures *t* test) to compare the frequencies of digging and leaving behaviours performed by these five females when they were alone with a jack and when a hooknose was the primary actor. I employed a Student's *t* test to determine whether these females, observed with both jacks and hooknoses as primary actors, behaved differently when with a hooknose than the 12 females that were observed only with hooknoses as primary actors. I also analysed female behaviour in response to changes in the social group. Here I employed a standard least-squares multiple regression model that used the independent variables 'number of hooknoses' and 'number of jacks' and the dependent variable 'frequency of female behaviour'. Separate models were run for the behaviours digging and leaving. I used logistic regression to establish whether any male behaviour

predicted spawning. The categorical response was whether or not a female spawned, and the effect variable was the frequency of the given behaviour.

To determine whether spawning groups with jacks and without jacks differed in size, the total number of males in each group was compared with a Mann–Whitney test. Foote et al. (1997) found no significant difference in the reproductive success of different male types in sockeye salmon, *Oncorhynchus nerka*. These workers found that proximity to the female and the number of males involved in a spawn did not predict a male's spawning success. I was unable to collect eggs or perform paternity analyses, so I considered a male to be a successful mate if he was involved in an oviposition. I determined whether mating success differed for males of the two phenotypes using a Pearson chi-square test. Regression analysis was used to determine whether the independent variables 'number of males' and 'presence of jack' influenced the duration of oviposition.

## RESULTS

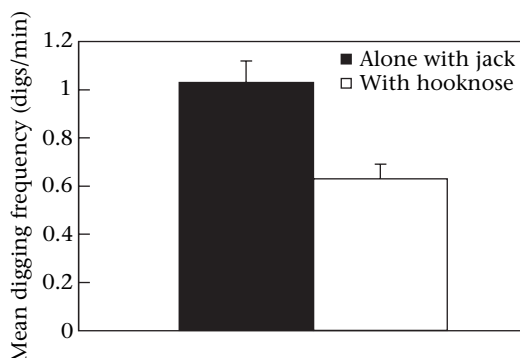
Hooknoses directed more apparently aggressive behaviour (Table 1) towards females than did jacks. Only hooknoses chased or bit females. Eight of 43 hooknoses chased females while zero of 16 jacks did ( $G_1^2 = 5.51$ ,  $P = 0.02$ ) and six of 43 hooknoses bit females ( $G_1^2 = 4.04$ ,  $P = 0.04$ ). Compared to jacks, hooknoses crossed over females (Mann–Whitney *U* test:  $U = 61.00$ ,  $N_{\text{jack}} = 5$ ,  $N_{\text{hook}} = 16$ ,  $P = 0.04$ ) and nudged females at higher frequencies ( $U = 72.00$ ,  $N_{\text{jack}} = 5$ ,  $N_{\text{hook}} = 15$ ,  $P = 0.003$ ). There was no significant difference in the frequency of vibratory movement performed by the two male types ( $U = 44.00$ ,  $N_{\text{jack}} = 5$ ,  $N_{\text{hook}} = 15$ ,  $P = 0.57$ ).

Primary acting hooknoses changed their behaviour towards both males and females depending on the male group composition. As expected, increases in the number of either male type at the spawning site resulted in an increased frequency of attacks by the primary hooknose upon that type (standard least-squares multiple regression:

hooknoses:  $R^2 = 0.65$ ,  $P < 0.0001$ ; jacks:  $R^2 = 0.46$ ,  $P = 0.0009$ ). In addition, hooknoses made fewer vibratory movements towards females as group composition of hooknoses increased ( $R^2 = 0.28$ ,  $P = 0.02$ ).

Female behaviour varied depending on whether the primary actor was a hooknose or a jack. Females worked on their nests (dug) more when the primary actor was a jack than when he was a hooknose (matched-pairs repeated measures  $t$  test:  $t_4$  ratio =  $-4.07$ ,  $N = 5$ ,  $P = 0.015$ ) (Fig. 1). Females that were observed with both jack and hooknose primaries did not behave differently towards hooknoses than females that were observed only with hooknose primaries ( $t_{12}$  ratio =  $-0.09$ ,  $N = 5$  females observed with jack and hooknose primaries,  $N = 9$  females observed with hooknose primary,  $P = 0.93$ ). Among all females, the frequency of digging varied significantly with composition of the social group (standard least-squares multiple regression with number of hooknoses and number of jacks as independent variables: whole model  $R^2 = 0.30$ ,  $P = 0.0031$ ). Tests of the relative importance of the individual effects in this model indicated that, while the presence of more than one jack had no effect on the digging behaviour of females, digging decreased as the number of hooknoses increased ( $P_{\text{hook}} = 0.0009$ ,  $P_{\text{jack}} = 0.32$ ). The phenotype of the primary male actor did not affect the rate at which females left their nest site (repeated measures  $t$  test:  $t_4$  ratio =  $-0.11$ ,  $N = 5$ ,  $P = 0.92$ ;  $t_8$  ratio =  $0.24$ ,  $N_{\text{jack}} = 5$ ,  $N_{\text{hook}} = 8$ ,  $P = 0.81$ ). While the identity of the primary acting male did not affect the frequency with which females left the redd, they were more likely to leave as the number of hooknoses increased ( $R^2 = 0.16$ ,  $P = 0.02$ ). Conversely, the number of jacks present did not influence females' leaving ( $R^2 = 0.014$ ,  $P = 0.51$ ).

Logistic regression revealed that the probability of a female spawning increased with the frequencies of three male behaviours: crossing over ( $\chi^2_1 = 4.24$ ,  $P = 0.039$ ), nudging ( $\chi^2_1 = 7.28$ ,  $P = 0.007$ ) and chasing of jacks by hooknoses ( $\chi^2_1 = 14.34$ ,  $P = 0.0002$ ). In these cases, when a jack was chased prior to spawning, the jack returned quickly and spawning ensued after his return. Thus, following chases, the jack and the hooknose returned and both became part of the spawning group. The frequency with which the primary acting hooknose



**Figure 1.** Mean  $\pm$  SE digging frequency for five female coho salmon in the presence of males of each phenotype (jack or hooknose).

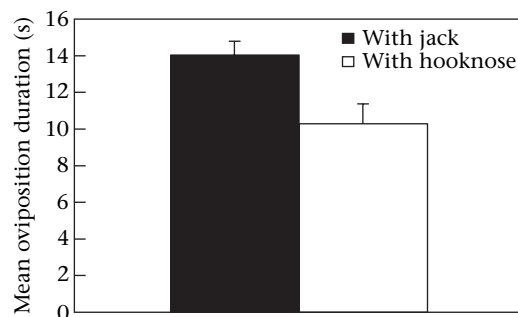
chased other hooknoses did not predict spawning ( $\chi^2_1 = 0.306$ ,  $P = 0.58$ ).

There was no difference in the percentage of males observed to spawn between the two male types; 12 of 16 (75%) jacks and 25 of 43 (58%) hooknoses mated (Pearson chi-square:  $\chi^2_{58} = 1.418$ ,  $P = 0.23$ ). There was no difference in the number of males that spawned between groups with and without jacks (Mann-Whitney  $U$  test:  $Z = -0.87$ ,  $P = 0.39$ ). While there was no significant difference in the proportion of hooknose and jack males that spawned, females oviposited for longer durations when there was a jack in the spawning group (least squares regression: whole model:  $P = 0.02$ ; effect tests: number of males:  $P = 0.13$ ; presence of jack:  $P = 0.012$ ; Fig. 2).

## DISCUSSION

While increased interest in sexual conflict has placed much attention on the costs of sexual coercion (Rowe et al. 1994; Rice 1996; Gowaty & Buschhaus 1998; Crudginton & Siva-Jothy 2000; Blanckenhorn et al. 2002; Martin & Hosken 2004), fewer recent studies have investigated cooperation between potential mates (Andersson et al. 2000; East et al. 2003). Because the expected fitness payoff for different mates varies, it is possible that some pairings represent mutually beneficial payoffs for both mates, while for others the payoff is one sided. In this case, mating systems might be marked by simultaneous coercion of, and cooperation with, females by mates of different mating values. Aspects of this study suggest that the mating system of coho salmon is marked by simultaneous coercion and cooperation.

Some results of this study suggest that females prefer jacks. Although females regularly mated with hooknoses, one female readily mated when alone with a jack (Table 2). This suggests that jacks do not have to rely upon sneaking to mate with females. Females also performed digging behaviour more frequently when accompanied by a jack than when accompanied by a hooknose (Fig. 1). High frequency of digging may demonstrate either a female's mating preference (Berejikian et al. 2000; de Gaudemar et al. 2000a) or freedom from coercion that prevents digging.



**Figure 2.** Mean  $\pm$  SE oviposition duration of female coho salmon as a function of the phenotypic composition of males (jack or hooknose) in the spawning group. 'With jack' indicates that a jack was involved in the spawn, as was a hooknose (or hooknoses) ( $N = 8$ ). 'With hooknose' indicates that the female was alone with one or more hooknoses ( $N = 4$ ).

Either explanation for the increased frequency of digging in the presence of jacks is consistent with the predictions of the cost-avoidance hypothesis. Females of many species invest more in offspring with higher expected fitness than in others (Sheldon 2000; Kolm 2001). In this study, females spent more time preparing their nests when accompanied solely by jacks than when in the company of hooknoses. Coho salmon die shortly after spawning and cannot care for their young after they hatch. Extra care spent in preparing the nest may improve offspring hatching success. Because females do not feed when on the spawning grounds, they are limited regarding how much energy they can expend on nest construction. Female salmon, limited in the amount of care they can invest in young, may make differential investments in the offspring of preferred and unpreferred mates. In chinook salmon, *Oncorhynchus tshawytscha*, digging frequencies of females paired with large and small males of the same life history type do not differ (Berejikian et al. 2000). This observation suggests female chinook salmon show no mate preference for different males of this type. In Atlantic salmon, *Salmo salar*, females dig more when paired with males that are two times their own size (de Gaudemar et al. 2000a). The life history of Atlantic salmon is more variable than that of coho salmon, and large adult male size in the former species probably indicates prior successes, as small size does in the coho jack.

In the current study, females held the oviposition posture longer when jacks were part of the spawning group than when the spawning group comprised only hooknoses. Thus, females may have expelled more eggs when there was opportunity for them to be fertilized by jacks rather than solely by hooknoses (Fig. 2). de Gaudemar et al. (2000b) showed that individual female Atlantic salmon lay varying numbers of eggs in different spawnings. Although females tend to lay fewer eggs in later spawnings, no work has addressed whether females can vary the number of eggs deposited at a given mating. If females can vary the number of eggs laid when in the presence of different males, then they can express their mate preferences by releasing more eggs in the presence of the preferred male. In the Banggai cardinalfish, *Pterapogon kauderi*, females manipulate the mass of the clutch of eggs such that larger clutches are laid with more preferred males (Kolm 2001, 2002; Kolm & Olsson 2003). While female coho salmon may be able to manipulate the quantity of eggs expressed for various mates, most often more than one mate is present when oviposition occurs. Thus, the fitness benefit that females obtain in mating with jacks may be offset by the fact that mating groups with jacks typically also contain hooknoses. In such situations, although females may gain more offspring sired by jacks, hooknoses also benefit by fertilizing some proportion of the clutch.

If jacks are indeed preferred by females, then according to the cost-avoidance hypothesis, hooknoses might coerce females to mate by increasing their precopulatory costs. When these direct costs become too high for the female, she is expected to mate with hooknoses to end the coercion. Several behaviours performed by hooknoses in this study appear to be costly for females, particularly biting and chasing, and in one case, a female was dragged

back to the redd in the jaws of a hooknose after she had left the spawning site. Other behaviours such as crossing over and nudging are subtler and may cause females to accrue costs in smaller increments or serve as threats of potential harm (after Smuts & Smuts 1993). The observation that hooknoses perform these behaviours at higher rates than jacks supports the notion that hooknoses coerce females to mate. Additionally, because males usually leave the female after spawning, spawning is a way for females to prevent further costs.

Male behaviours directed at other males do not appear to represent direct costs to females. The cost-avoidance hypothesis predicts that if hooknose attacks on other hooknoses produce direct costs for females, then higher attack rates by primary hooknoses on other hooknoses should result in rapid spawning by females to avoid these costs. Alternatively, high attack rates by primary hooknoses on other hooknoses might indicate aggressiveness or vigour of the primary hooknose. Again, if females prefer vigorous, aggressive males, then higher attack rates should induce females to spawn. Here, contrary to both predictions, hooknose–hooknose interaction rates did not predict spawning. In contrast, a high rate of chases by the primary hooknose towards jacks was a good predictor of spawning.

While a chase directed by a hooknose towards a jack is clearly a form of intrasexual competition for mates, attacks by unpreferred males on preferred males may also represent indirect coercion of females, because a female's reproductive prospects degrade if the preferred male becomes less likely to mate with her. That females spawn when there are increased attacks on jacks is consistent with the suggestion that females and preferred males cooperate to facilitate reproduction. In this case, the female's action may serve to assure the jack's presence when oviposition occurs. Otherwise, the jack may leave as a result of the high costs imposed by aggressive hooknoses. The data suggesting a female preference for jacks also support this interpretation. If mating with jacks is unacceptable for females and they are more likely to spawn following an attack on a jack, then the expectation would be that oviposition duration would be short when a jack is present. But the opposite was the case. Females oviposited longer when jacks were part of the spawning group, suggesting that females give jacks every opportunity to fertilize their eggs.

In many mating systems, females simultaneously evaluate many males as potential mates and there is great demand on males to be chosen for mating. Females must then weigh the perceived costs and benefits of alternative mate choices when they choose mates. The results of this study indicate that coho salmon jacks appear to have solved the problem of mating by developing a phenotype that not only indicates mating value, but also is not costly to females. Many species show alternative male types that differ in viability, with high viability males expressing a 'sneaker' phenotype (Gross 1985; Tsubaki et al. 1997). These males may be preferred by females and their behaviour and morphology may assist them in reducing the costs of reproduction. This interpretation of the behaviour of sneaky males suggests that these preferred males act to

reduce the direct costs of mating for females because of a shared interest in the successful outcome of mating. Dominant, aggressive males, in contrast, act with a one-sided interest, the acquisition of mates who would otherwise prefer not to mate with them. Understanding the processes that give rise to phenotypic variation in males and the relative viabilities of different male types may lead to new interpretations of female choice.

### Acknowledgments

Thanks to Hugh Dingle, Ann Hedrick, Marc Mangel, Peter Moyle, Andy Sih and Judy Stamps for guidance and suggestions. Scott Carroll and Barney Luttbeg commented on a previous draft. Louise Conrad and Bob Chamberlain helped in the field. Paul Siri helped obtain funding and access to the study site. The Sonoma County Water Agency, the Marin Rod and Gun Club, a University of California (UC) Davis Humanities Fellowship, UC Davis Block Grants, and UC Davis Jastro-Shields Fellowships funded this work. Additional support came from Gabrielle Nevitt.

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