Breeding games and dimorphism in male salmon

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In certain species of salmon, male phenotypes occur in two distinct morphs: the large 'hooknose' or the small 'jack'. Hooknoses fight each other for access to females, while jacks occupy refuges near spawning beds to sneak fertilizations. Jacks also fight each other over opportunities for sneaking without immediate gains. To explore whether the jack behavioural strategy is equally adaptive to that of the hooknose, we built a game-theoretic model similar to the classic hawk–dove game, with and without conditions of density dependence. Our model demonstrates that fitness of the jack strategy increases with the frequency of the hooknose strategy, because jacks can steal the benefits otherwise accrued by hooknoses. The coexistence of strategies is much more easily achieved in this game than in the hawk–dove game. When negative density effects on benefits are introduced to the model, coexistence conditions are further relaxed. Hence, the jack and hooknose strategies can be viewed as equally adaptive, resulting in a stable mixed evolutionarily stable strategy (ESS).
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In many animal species, competition among males for mating privileges is prevalent (Krebs & Davies 1987). Such rivalries may favour selection for male dimorphism, alternative mating strategies, or both. The hawk–dove game was developed as a means of understanding the theoretical basis of animal conflict (Maynard Smith & Price 1973), and the evolutionary game of animal fighting in particular (Bulmer 1994). However, it has only rarely been applied to the evolutionary ecology of mating systems.

In a number of salmonid fishes, males are distinctly dimorphic in body size, external morphology and life history (Gross 1984, 1985). Large breeding males, called 'hooknoses', undergo full development, having spent 2–3 years at sea before returning to their natal rivers to spawn with females. Hooknoses display courtship coloration and a hooked nose with sharp teeth for

fighting. By contrast, small males, called 'jacks', undergo limited development and resemble immature fish. As juveniles, precocious males become jacks and return to spawning beds at least 1 year before hooknoses (Gross 1991). Hooknose males battle other hooknoses for access to females. Jacks, however, seek refuges near the breeding grounds of paired fish, from which they sneak to release sperm immediately following female spawning.

Hooknoses and jacks are considered alternative mating strategies (Gross 1982; Thornhill & Alcock 1983) or conditional mating strategies (Gross 1996). Gross (1996) found that the lifetime fitnesses of hooknoses and jacks in coho salmon, *Oncorhynchus kisutch*, are about equal at their switchpoint, indicating that the mixed strategy of both hooknoses and jacks is an evolutionarily stable strategy (ESS) (Maynard Smith 1982; Gross 1985). Thus, Gross (1984, 1985) suggested that the dimorphism in male salmon might have evolved through an evolutionary game. However, as far as we know, its explicit payoff matrices, with the conditions for coexistence of alternative strategies, have not been examined in the context of a hawk–dove game.

A recent version of the hawk–dove game has been developed to further our understanding of dimorphic male strategies in male

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orang-utans (Tainaka et al. 2007). However, life history considerations for evolutionary games differ substantially between the orang-utan and salmon. In the orang-utan, subordinate adult males can switch conditionally to a dominant phenotype, whereas dominant morphs cannot switch back to the subordinate phenotype. In salmon, the choice between developing into a hooknose or a jack reflects early developmental differences in individual life history and is absolutely irreversible (Gross 1985, 1991). Gross (1991) further suggested that juvenile body size, a strong predictor of mating strategy, is a function of population density. Published estimates of additive genetic variance indicate heritability for the choice of strategy, at least as a contributing factor highlighting the potential genetic basis of alternative phenotypes (Silverstein & Hershberger 1992; Repka & Gross 1995; Gross 1996; Gross & Repka 1998a, b). Any underlying genetic mechanisms regulating salmon dimorphism may be similar to genetic polymorphisms in the fruit fly (Fitzpatrick et al. 2007) or scale-eating cichlid fish (Hori 1993; Takahashi & Hori 1994).

Here we show that male dimorphism in salmon can be explained by a breeding game similar to the hawk–dove game. We build a payoff matrix for two mating strategies of male salmon: hooknose and jack. We analyse the ESS conditions according to the benefits and costs of winning and losing, including an explicit examination of the effects of population density. We also discuss the utility and generality of hawk–dove-like games in male dimorphisms and alternative mating strategies.

HOOKNOSE–JACK MODEL

Our game model resembles that of the hawk–dove game (Maynard Smith & Price 1973). For our purposes, 'hawk versus dove' is equivalent to 'dominant versus subordinate' or, more generally, 'honest contestant versus cheater'. The payoff matrix for a male salmon is given in Table 1. A hooknose (H) fights with others. The winning hooknose gets the benefit V (mating value), while the loser suffers the fighting cost C. Hence the average payoff for a hooknose is $(V - C)/2$. A hooknose can defeat a jack (J) easily, but a jack can sneak in and spawn surreptitiously. By sneaking fertilizations from hooknoses, a jack obtains the benefit G (on the average), while the hooknose loses G, yielding the payoff $V - G$. Unlike the well-known 'dove,' which does not fight, a jack battles other jacks over positions advantageous for sneaking. The losing jack suffers cost L. On the other hand, the winning jack gains control of the refuge from which he can sneak, but without immediate benefits. For now, we simply assume that the winning jack gains nothing. Therefore, the average cost to jacks of fighting is $L/2$, since one will lose. Because of the great disparity in body size between hooknose and jack, we assume that $V > G > 0$ and $C > L > 0$. In reality, both benefits and costs of fighting between hooknoses should be very large and those of jacks should be relatively small, so that $V \gg G$, and $C \gg L$.

The payoffs in Table 1 differ from those of the classic hawk–dove game in all values except that of hooknoses versus hooknoses. Without considering the population size of male salmon, the fitness values of both hooknoses and jacks can be evaluated by the traditional ESS analysis (that implicitly assumes an infinite population size) (see Riley 1979; Fogel et al. 1998; Taylor et al. 2004). Let p be the proportion of hooknoses in the population. Then the fitness of a hooknose, $W_H(p)$, is represented by equation (1) (Table 2). On the other hand, the fitness of a jack, $W_J(p)$, is represented by equation (2) (Table 2).

Note that $W_J(p)$ is an increasing function of the hooknose proportion p. This is because jacks that steal the benefits from hooknoses fight other jacks. We now examine $W_H(p)$ and $W_J(p)$ for $0 \leq p \leq 1$ (Fig. 1). At $p = 0$, $W_H = V - G > W_J = -L/2$. At $p = 1$, the condition for coexistence, with $W_H < W_J$, is given in equation (3) (Table 2). When fighting between hooknoses is severe, that is, $V < C$, condition (3) is always true (Fig. 1a). This is the same result as coexistence of evolutionary strategies in the hawk–dove game. On the other hand, when fighting between hooknoses is not severe (i.e. is mild), that is, $V > C$, condition (3) is not always true (Fig. 1b). When $V > C$, the condition (3) incurring cost C can be expressed as equation (4) (Table 2). Therefore, the fighting cost C of hooknoses should be close to V and/or the benefit of jack G should be rather small. From condition (4), if $2G > V$, condition (3) automatically holds (see Fig. 1b).

In either case, the ESS mixed frequency p^* is solved by $W_H(p) = W_J(p)$, and we get equation (5) (Table 2). However, the ESS becomes a pure hooknose strategy (i.e. $p^* = 1$), if equation (6) (Table 2) holds. This equation implies that, if the benefit to jacks of sneaking (G) is less than half the benefit when hooknoses wins, then the ESS is a pure hooknose strategy.

When $V > C$, the slope of W_H ($= G - (V + C)/2$) can be positive, if equation (7) (Table 2) holds. This means that the fitness W_H of a hooknose is a decreasing function of the frequency of p. Even under this condition, the ESS frequency p^* becomes the mixed strategy given by equation (5), since condition (4) holds; that is,

Table 1
Payoff matrix of hooknose–jack game in salmon males

Player	Opponent	
	Hooknose	Jack
Hooknose	$(V-C)/2$	$V-G$
Jack	G	$-L/2$

V: the benefit of winning a female; C: the fighting cost of a loser; G: the benefit of sneaking; L: the fighting cost of a losing jack. We assume that $V > G > 0$ and $C > L > 0$.

Table 2
Equations for hooknose–jack games in male salmon

$$W_H(p) = p\frac{V-C}{2} + (1-p)(V-G) = (V-G) - p\left(\frac{V+C}{2} - G\right) \qquad (1)$$

$$W_J(p) = pG + (1-p)\frac{-L}{2} = \left(\frac{-L}{2}\right) + p\left(G + \frac{L}{2}\right) \qquad (2)$$

$$G > \frac{V-C}{2} \qquad (3)$$

$$V > C > V - 2G \qquad (4)$$

$$p^* = \frac{2(V-G)+L}{V+C+L} \qquad (5)$$

$$G < \frac{V-C}{2} \qquad (6)$$

$$2G - C > V \qquad (7)$$

$$V_N = V\frac{B}{B+N} \qquad (8a)$$

$$G_N = G\frac{B}{B+N} \qquad (8b)$$

$$W_H(p,N) = p\frac{V_N-C}{2} + (1-p)(V_N - G_N) \qquad (9)$$

$$W_J(p,N) = pG_N + (1-p)\frac{-L}{2} \qquad (10)$$

$$G_N > \frac{V_N-C}{2} \qquad (11)$$

$$V > C > (V-2G)\frac{B}{B+N} \qquad (12)$$

$$V - 2G > C > (V-2G)\frac{B}{B+N} \qquad (13)$$