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Disruptive selection for alternative life histories in salmon

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Many salmon species include males which mature as much as 50% younger and as small as 30% of the adult body size of other males in the population[1-8]. In the semelparous Pacific salmon *Oncorhynchus* spp., these small males are known as 'jacks', and they compete with larger late-maturing 'hooknose' males for opportunity to spawn on the breeding grounds. The existence of jacks is problematical as it is believed that salmon populations should have a single optimal age or size at maturity[9-11]. I now show, however, that these two alternative life histories are evolutionarily favoured by frequency-dependent disruptive[12] selection on the breeding grounds. In coho salmon (*Oncorhynchus kisutch*), small and large males gain access to females by sneaking and fighting respectively. By contrast, intermediate-sized males are at a competitive disadvantage. Jacks, which are specialized at sneaking, and hooknose males, which are specialized at fighting, have negatively frequency-dependent fitnesses from these alternative breeding tactics. Calculations suggest that the lifetime fitness of jacks is similar to that of hooknose males. Thus, age of maturity in salmon has probably not evolved as a single optimum, but rather as a 'mixed evolutionarily stable strategy[13,14] in which precocious maturity is an evolutionarily viable alternative life history strategy.

In 1981-82 I studied a wild population of coho breeding in Deer Creek Junior, a small stream in Washington State, United States. This species was selected because males mature at only two ages (Fig. 1). Field procedures involved collecting fish at a weir near the mouth of the stream as they migrated upstream to spawn. Before release above the weir to spawn naturally, their sex was determined, and body length measured, and each fish was tagged with colour-coded Petersen disks. Tagging permitted subsequent recognition of individuals by observation from the stream bank without disturbing spawning.

Thirty-seven randomly chosen breeding groups were studied, each of which included a sexually active female and several males. While the female excavated a nest for oviposition, the males competed among themselves for proximity to the nest. Proximity is important in determining male mating success, because successive males fertilize smaller proportions of eggs[15] and nest entry order is strongly correlated with male proximity ($r = 0.73$, $n = 66$ males, $P < 0.001$). Males make use of two tactics

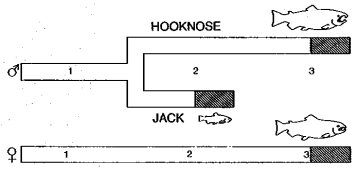

Fig. 1 Two life histories exist in male coho salmon: precocious maturity at age 2 as a small jack, or delayed maturity to age 3 as a large hooknose[26]. The term 'hooknose' is derived from the exaggerated snout and enlarged teeth which develop at maturity and are used in fighting. By contrast, 'jacks' lack secondary sexual characters and are relatively cryptic on the breeding grounds. Both jack and hooknose males die after breeding, as do the females. Coho life history involves autumn-winter spawning (November-January); egg and larval incubation (November-March) in gravel nests excavated by females; 1 yr stream residency as fry before migration to the ocean as smolts; 5-8 months' ocean residency before return as jacks, or 17-20 months before return as mature females and hooknose males. Hatched areas indicate reproductive maturity.

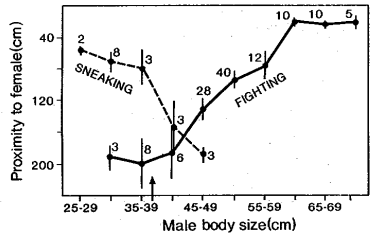

Fig. 2 This plot shows a threshold in male size above which female proximity is best gained by fighting, and below by sneaking. The success of male coho on the breeding ground depends on their body size and behavioural tactic. Proximity to ovipositing females may be obtained through two tactics: sneaking or fighting.
Methods: Behavioural and proximity data are from naturally breeding males of known body size (sample sizes and standard errors are shown). Two techniques were used to measure distance from the nest centre to the mid-region of the male: (1) male position was marked by eye, and immediately after spawning the distance was measured using a tape measure, or (2) the distance was estimated by eye, with estimates having an error of ±6% based on 19 repeated measurements. These two techniques were used randomly for fishes of all sizes and behavioural tactics. The body size range of hooknose males (fork length) was 39-72 cm (mean = 51.7 ± 4.2), that of jack males 25-39 cm (mean = 33.6 ± 4.7). The size distinction between jack and hooknose males is indicated on the size axis with an arrow. The proximity of hooknose males to females achieved through fighting averaged 90 cm ($n = 111$ observations) and through sneaking 170 cm ($n = 6$). By contrast, jack proximity achieved through fighting averaged 197 cm ($n = 11$) and through sneaking 71 cm ($n = 13$). These proximities are statistically different within male type, and between male types (Mann-Whitney U tests, $P < 0.05$ for the four comparisons).

to gain proximity: (1) fighting, where a linear dominance hierarchy is established with the 'alpha' male closest to the female and subordinates more distant; and (2) sneaking, where males use 'refuges' (rocks, debris, or shallow areas in the stream) to escape aggression from larger males while remaining close to the nest site. Male success from fighting and sneaking was size-dependent: larger males were best at fighting; smaller males were best at sneaking. Males of intermediate size could not obtain suitable refuges for sneaking, nor could they fight successfully against the larger males. These males were usually most distant from the female (Fig. 2). During mating, natural selection thus favours large- and small-bodied males at the expense of intermediate-sized males, thereby placing body size under disruptive selection.

The small, early maturing jack males were ideally suited for sneaking (Fig. 1), but poorly suited for fighting. Opportunity to sneak depended on the availability of suitable refuges, which were limited in quantity and could generally be used by only one jack at a time. Since jack density in the stream was too high for all to sneak successfully, some were forced to fight. In 45% of jack matings, jacks had to fight for proximity and obtained positions at the low end of dominance hierarchies (Fig. 2). The average proximity of jacks from the 'mix' of sneaking and fighting observed was 124.6 ± 15.5 cm (mean ± s.e., $n = 24$). By contrast, the average proximity of hooknose males was 93.0 ± 6.1 cm ($n = 117$; Mann-Whitney, $z = 1.96$, two-tailed $P = 0.05$). Because the relationship between proximity and success is approximately 'fertilization success = a constant/male proximity' (ref. 15), relative male proximity provides a means of measuring relative male mating success. Thus, assuming random sperm competition among males, a reasonable assumption because of the nature of this mating system[16], jack success was approximately 66% $(1 - [124.6 - 93.0]/93.0)$ that of hooknose males. Any increase in the proportion of jacks would decrease their average proximity because more jacks would be forced to fight; conversely, any decrease in jack frequency would increase

average proximity because relatively more jacks could sneak matings. Thus, the mating success of jacks relative to hooknose males is negatively frequency-dependent.

Negatively frequency-dependent disruptive selection may, in theory, give rise to stable alternative life history strategies[13,17,18]. If the alternative life histories are a mixed evolutionarily stable strategy (mESS) in salmon, the lifetime fitnesses of jack and hooknose males should be equal at the frequency observed. In the coho population, fitness calculations are relatively simple since the population has discrete generations and, to the best of my knowledge, is stationary[19]. Lifetime fitness can be estimated from the product of probability of survival to maturity, breeding lifespan, and mating success. In calculating survival to maturity, I assume that early freshwater survival of young jacks and hooknose males is equal, and that the critical difference in survivorship is ocean mortality. The study population is part of the Skykomish River coho stock for which the Washington State Department of Fisheries maintains ocean mortality records[20]. In this stock the average ocean survivorship is 13% for jacks and 6% for hooknose males. I have found from following tagged individuals on the breeding grounds that jacks are reproductively active for 8.4 ± 2.3 days ($n = 7$), and the hooknose males for 12.7 ± 1.2 days ($n = 35$). I assume that the number of opportunities for spawning is proportional to length of life on the breeding grounds. Therefore, the relative lifetime fitness of jack (W_j) and hooknose (W_h) life histories is:

$$\frac{W_j}{W_h} = \frac{0.13}{0.06}\,(\text{survivorship to maturity}) \times \frac{8.4}{12.7}\,(\text{breeding lifespan}) \times \frac{0.66}{1}\,(\text{mating success}) = 0.95$$

This calculation suggests that the fitnesses of the alternative life histories approach equality. The estimate may be conservative for jacks as it does not include fishing pressure, which is greater on hooknose males than jacks. How salmon populations of the west coast are responding evolutionarily to fishing pressure is not yet known[21].

The similarity in lifetime fitness estimates combined with evidence for negatively frequency-dependent success suggests that the jack life history exists in a mixed evolutionarily stable strategy with hooknose males. This conclusion is supported by two findings: (1) Those coho males maturing as jacks are not smaller in body size at age 2 (refs 5, 22) and thus are not competitively inferior to males that delay maturity to become hooknoses. A size difference would be expected if jack maturity was a BBS strategy (best of a bad situation)[23] rather than a mESS. (2) Recent breeding studies suggest that jack maturity is heritable[24]. Heritability in a stationary population will probably exist only through equal fitnesses, as genes coding for an inferior life history should be removed from the gene pool by natural selection[18,25].

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