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Social versus genetic measures of reproductive success in sockeye salmon, *Oncorhynchus nerka*

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ABSTRACT

In this paper, we assess the relationship between behavioural (social) and genetic mating success in sockeye salmon (*Oncorhynchus nerka*) and the frequency of multiple genetic partnering in both sexes. We introduced groups of 13 ripe adults (7 males, 6 females) into four spawning arenas in the Weaver Creek spawning channel, British Columbia, and monitored their behaviour until spawning was complete. Genetic fingerprints of adults and offspring were determined with microsatellites. Both males and females spawned with up to four different partners. Only 4 of 24 females mated predominantly with a single male. Behavioural measures of reproductive success in males (social dominance, time as consort, number of female partners) were strongly correlated with genetic reproductive success (proportion of offspring sired and number of females mated with) but explained only 33–40% of the variance in reproductive success. Only longevity (spawning life index) was correlated with indices of female reproductive success. Behaviour provides a practical means to assess reproductive success in males but will underestimate the reproductive success of some subordinate males. Female reproductive success is more difficult to assess, because most females spawn all their eggs and there are no obvious behavioural or genetic attributes that can be used as indices of success.

Keywords: consort, dominance, genetic mating success, life span, partners, sockeye salmon, social mating success.

INTRODUCTION

Many conclusions concerning reproductive strategies and mate choice in animals are based on inferences about paternity and maternity derived from behavioural observations (Clutton-Brock, 1988). Females are frequently considered to be the limiting sex, creating an intense struggle among the males for access to them (Darwin, 1871). Because fighting for access to females is costly, the victor of male–male competition is often superior in quality and one which females may prefer (Cox and Leboeuf, 1977; Berglund *et al.*, 1996). On the other hand, females may seek to mate with multiple partners for a variety of social and

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genetic reasons, including enhanced parental care and genetic risk spreading (Krebs and Davies, 1993; Barlaup *et al.*, 1994; Fleming, 1996). The variation in reproductive success that results from this struggle is critical to understanding the evolution of reproductive traits and the processes of selection in natural populations.

Pacific salmon (genus *Oncorhynchus*) are ideal species for the study of breeding competition and the resulting genetic mating success. They spawn in predictable, accessible freshwater locations where they can easily be observed. Males allocate some of their limited reproductive energy to develop an exaggerated sexual dimorphism. Salmon have also been studied extensively and are among the species for which reproductive success has been inferred from behavioural observations made in the natural environment (Hughes, 1998). The dominant male in a spawning group (assessed by his aggressive and consort position near the receptive female) is believed to fertilize the majority of eggs in salmonids (Schroder, 1982; Chebanov *et al.*, 1983; Quinn and Foote, 1994). Genetic mating success among individuals within groups of spawning Pacific salmon has not been measured, although it has been examined in Atlantic salmon (*Salmo salar*: Garant *et al.*, 2001; Taggart *et al.*, 2001). There has been considerable progress in the study of mating systems with the use of molecular markers at the individual level and these studies have shown that behavioural observations alone are not always an accurate measure of mating success (Hughes, 1998; Coltman *et al.*, 1999; Lebas, 2001). In mammals, Amos *et al.* (1993) and Coltman *et al.* (1999) found that a high proportion of offspring were not sired by the observed social partner. By contrast, other studies have found a high association between behavioural and genetic measures of mating success (Altmann *et al.*, 1996; Abell, 1997; Gullberg *et al.*, 1997). For many species, including salmon, we do not know the quantitative or qualitative relationship between the social and genetic mating success of individuals.

In this paper, we assess the relationship between behavioural (social) and genetic mating success in sockeye salmon (*Oncorhynchus nerka*) and the frequency of multiple genetic partnering in both sexes. Our general hypothesis is that behavioural and genetic measures of reproductive success will be highly correlated. In particular, we predict that behaviourally dominant males will sire a high proportion of offspring. We also examine the concordance between multiple mating as measured by genetic and behavioural methods. We further hypothesize that success in both sexes is related to body energy reserves at the start of spawning and that male mating success is positively correlated with the size of hump and kype, prominent secondary sexual characteristics in males. Finally, we examine whether the fish show assortative mate preference in terms of morphology.

METHODS

Our basic study design was to establish artificial spawning groups with known morphology, energy reserves and genetic fingerprints, monitor spawning behaviour to assess behavioural mate choice and dominance relationships among spawners, and assess genetic mating success by DNA analysis of the embryos produced.

We made all measurements at Weaver Creek spawning channel, located approximately 100 km upstream from the mouth of the Fraser River in southwestern British Columbia, during the 2000 spawning season. Weaver Creek spawning channel was constructed in 1965 to augment the natural run of sockeye to the creek. To create spawning arenas, we installed four 10×3 m wood frame and vexar mesh (5 cm) enclosures near the middle reach of the channel. As the channel has uniform depth and flow and uniform gravel substrate for

spawning, there were no differences in the spawning environment among the enclosures. Six female and seven male mature sockeye salmon in good physical condition were released into each arena. Before release we tagged each fish with a colour-coded Peterson Disk, and measured its body morphology. To estimate the energy density, we removed a piece of muscle tissue weighing approximately 1 g from the dorsal hump of each fish. Hendry *et al.* (2001) have shown this to be a safe technique for non-lethal tissue sampling in large salmonids, and that these samples provide a reasonable measure of mass-specific energy content as estimated by bomb calorimetry. We estimated the fat content of these samples from their moisture content and the relationship between tissue moisture content and fat content in sockeye salmon (Brett, 1995).

We recorded the behaviour of each once a day for 5–10 min. Aggressive behaviours of males included chasing, charging, biting, lateral display and posture display as described by Healey *et al.* (2003). Courtship behaviour of males was confined to quivering beside the female. Female aggression included only chasing, charging and biting, as females do not perform lateral or posture displays (Healey *et al.*, 2003). Female behaviour also included nest construction by digging. Both sexes performed spawning behaviour but only a small fraction of spawnings were actually observed during the short period of observation for each fish. During frequent visits to the arenas each day, we also noted the positions of individual fish and which males were associated with which females. Observations continued until all the females had spawned. The frequency of different behaviours per 10 min of observation was used to determine social status and aggressiveness scores. We also recorded the total number of days each fish survived within the spawning arenas. As soon as each fish died, we collected a tissue sample and stored it in 95% ethanol for DNA analysis.

One month after the last female had spawned, we excavated the redds to collect the developing embryos. We removed the gravel and stones manually until the egg pockets were exposed, collected the eggs using a turkey baster, and placed them in perforated metal cylinders that we stored in the channel. We excavated 4–6 nests per redd, and collected approximately 12 eggs from each nest. When all the eggs were collected, we transported them to the laboratory, and incubated them in Heath trays at 9–11°C for one month after which we preserved the surviving embryos in 95% ethanol for DNA analysis. Dead (or cloudy) eggs were removed each week (mortality ranged from 0 to 10% of eggs per sample).

We analysed tissue from all adult sockeye and 2–4 embryos per nest pocket (60–64 embryos per enclosure). We extracted DNA by standard proteinase K digestion/salt-based purification using the Gentra Systems (Minneapolis, MN) Puregene DNA isolation kit. The DNA was resuspended in 50 μl of TE solution (10 mM Tris, 1 mM EDTA in H_2O; pH 8.0) and stored at −20°C until used. DNA concentrations were determined using spectroscopy, and working stocks of 50 ng $\cdot$ μl^{-1} were made for each sample.

We scored 19 microsatellite loci for all the parents. From these, we chose six loci that showed a high degree of polymorphism. Initially, we examined the tetranucleotide loci *Ots103*, *One108*, *One109*, *One110* and *RT212* and the dinucleotide locus *Ssa85* in half of the offspring samples. *Ots103*, *One108*, *One110* and *RT212* were found to be sufficiently polymorphic for reliable paternity assignment, so that the remaining individuals were amplified with these microsatellites and only the results from these four microsatellites were used to assess paternity. Initial PCR amplification for each primer was carried out in 10 μl volumes [50 ng of DNA template, 0.2 mM each dNTP, 1.0 pmol each primer, 1.5 mM $MgCl_2$, 1.0 U *Taq* DNA polymerase (GibcoBRL), 10 × reaction buffer (20 mM Tris-HCl pH 8.4, 50 mM KCl), and 1.0 pmol of M13-29 primer] using a Robocycler Gradient 96 (Stratagene).

The forward primer for each of *Ots103* and *RT212* and the reverse primer for each of *One108* and *One110* were synthesized with an additional modified 19- or 20-bp (forward labelled and reverse labelled, respectively) M13 tail added to the 5′ end of the oligonucleotide. An M13 primer, with an identical sequence, was directly labelled to the infrared fluorophore, IRD41, which was then used as the labelled primer for detecting the microsatellites (Oetting *et al.*, 1995).

To assign parentage, we size fractionated the products using gel electrophoresis and performed pattern visualization by a LI-COR automated fluorescent DNA sequencer (Middendorf *et al.*, 1992) (LI-COR, Inc., Lincoln, NE). Raw electrophoretic data were stored in TIFF format using the image manipulation subprogram of the Base ImagIR software package (LI-COR, Inc.). Band size analysis was performed using the RFLPScan software (Scanalytics, Billerican, MA). We conducted genotype identification by hand after the initial RFLPScan size determination to ensure consistent and accurate band sizing. Parental assignment was performed by the simulation software CERVUS version 2.0 (Marshall *et al.*, 1998) using the following parameters: 10,000 cycles, 13 candidate parents (the female parent was known for each offspring), 100% of candidate parents sampled, 96–98% of loci typed, and 1% of loci typing error. We assigned parentage at a relaxed confidence level of 90% and a strict confidence level of 95%. Parental assignment was confirmed by the process of exclusion, where the genotypes of candidate parents were compared against the offspring's genotype (taking the mother's genotype into account). Candidate parents were excluded if a mismatch occurred at one or more loci.

We analysed four indices of social reproductive success for males: (1) a social dominance index, (2) a consort index, (3) a spawning life index and (4) a social partners index. For the first two indices, males within an enclosure were given a rank score from 1 (least success) to 7 (greatest success). The social dominance index for each male within an enclosure was based on aggressiveness and dominance displays. Aggressiveness was scored as the difference between aggressive acts (chases, charges and bites) performed by or directed at the focal male. Dominance displays were scored as the frequency of lateral displays and posture displays performed by the focal male. The scores for aggressiveness and dominance display were each normalized on a 1–7 scale, averaged for each male and then rescaled from 1 to 7.

The consort index was derived from daily observations of mating associations between the focal male and one or more of the females. A male seen courting a female all day was given a score of 1, and a male that did not court at all during the day was given a score of 0. Other amounts of courting were given intermediate scores between 0 and 1. Daily consort scores for each male were averaged over the period of observation and used to rank the males from 1 to 7 for this index. The spawning life index was the length of time (days) a male was alive in the spawning arena (males are sexually active until just before death, so that this measure captures the period of sexual activity in males). The social partners index was the proportion of females to whom the male played consort during the study.

We analysed three indices of social reproductive success for females: (1) a social dominance index, ranked 1–7; (2) a spawning life index; and (3) a social partners index. The social dominance index for each female was based only on aggressive behaviours and was the difference between aggressive acts performed by or directed towards the focal female. Female to female and female to male aggression were both included in the index. The spawning life index and social partners index were calculated in the same way as for males.

Spawning life in females includes both the sexually active period during which a female deposits her eggs and the period of redd-guarding, post spawning, when the female prevents other females from appropriating her redd and possibly digging up her eggs. The full length of the spawning life in females is fitness related.

We analysed two indices of male genetic reproductive success: (1) the proportion of offspring sired by each male and (2) the proportion of females with which each male mated. The genetic success of females was more difficult to assess. All females spawned 100% of their eggs, so variation in fertility could not be used. We therefore analysed three indirect indices of female success: (1) the proportion of available males with which the female spawned (as a measure of bet hedging); (2) success as a function of the genetic success of her partners; and (3) success as a function of the social success of her partners. Female success as a function of her partners' genetic success was calculated as:

$$\sum_{i=1}^{7} (\text{total number of female } j\text{'s eggs sired by male } i \times \text{proportion of all eggs sired by male } i \text{ within the enclosure})$$

Female success as a function of her male partners' social mating success was calculated as:

$$\sum_{i=1}^{7} (\text{dominance rank of male } i \times \text{total number of female } j\text{'s eggs sired by male } i)$$

These latter two indices of success were standardized to account for the different numbers of eggs that were analysed per female.

Statistical analyses

One male and four females died within 2 days after the start of the study. These fish were not included in any analyses. Body size, secondary sexual characteristics and pre-spawning body fat estimates were compared among enclosures by analysis of variance (ANOVA) (SAS version 8.2). No significant differences were found among these variables, indicating that the spawning groups were comparable among enclosures.

We used Spearman rank correlations to compare among the social mating success indices and among the genetic reproductive success measures within sexes. We used linear regression to assess the ability of the social mating success measures to predict genetic mating success. Within the males, we also regressed residuals from the relationships between spawning life index and social dominance index, and between spawning life index and consort index, on the genetic measures of mating success to determine whether spawning life index, independent of social dominance (or consort index), was related to the genetic reproductive success. All the variables (raw or transformed) used in the regression analyses were normally distributed according to the Kolmogorov-Smirnov test statistic (at the 0.05 α level). Where appropriate, we adjusted significance tests for multiple comparisons using sequential Bonferroni corrections.

RESULTS

The total number of alleles per locus ranged from 17 at locus *Ots103* to 33 at locus *RT212*. Observed per-locus heterozygosities in the adult and offspring samples ranged from 0.966

(*RT212*) to 0.821 (*One110*), only slightly higher than the expected heterozygosities, which ranged from 0.908 (*RT212*) to 0.775 (*One110*). There was no evidence of null alleles segregating or departures from Hardy-Weinberg equilibrium. The combined exclusion probability (total exclusionary power) across all loci was very high (0.993). Paternity was assigned for 243 of the 247 offspring with 95% confidence. The remaining offspring were assigned to a male with 90% confidence. As all other potential male parents had a mismatching allele(s) with the offspring in question, the male with 90% confidence was considered to be the true father.

The proportion of offspring sired by each male ranged from 0 to 0.52, with a mean of 0.15 (variance = 0.11) (Fig. 1). The number of mates acquired by each male ranged from 0 to 4, with a mean of 1.85 and a variance of 1.06. The proportion of mates acquired by each male ranged from 0 to 0.80, with a mean of 0.38 and a variance of 0.22 (Fig. 1). These results indicate a high variability in mating success among individual males. The number of males that sired offspring from each female ranged from 1 to 4, with a mean of 2.5 and a variance of 1.10 (Table 1). The proportion of potential mates that sired offspring from each female ranged from 0.14 to 0.67, with a mean of 0.37 and a variance of 0.17

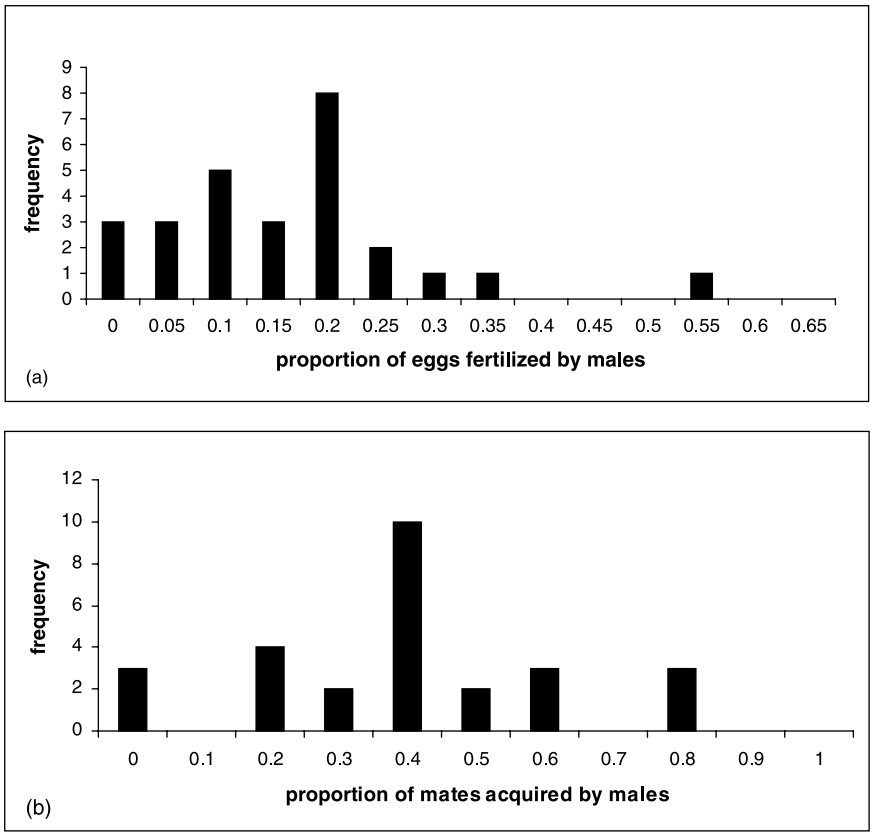

Fig. 1. Frequency distributions of the proportion of eggs fertilized (a) and the proportion of mates acquired (b) by males among all spawning arenas.

Table 1. The genetic mating patterns in each arena

	# Mates	Male 1	Male 2	Male 3	Male 4	Male 5	Male 6	Male 7	Total
Arena 1									
Female 1	2	0	0	4	4	4	0	4	16
Female 2	1	0	0	16	0	0	0	0	16
Female 3	2	0	0	0	6	0	10	0	16
Female 4	3	1	0	13	0	2	0	0	16
Female 5	N/A	0	0	0	0	0	0	0	0
Female 6	N/A	0	0	0	0	0	0	0	0
Total		1	0	33	10	6	10	4	64
Arena 2									
Female 1	2	0	6	0	6	0	0	0	12
Female 2	2	0	6	0	2	4	0	0	12
Female 3	2	0	2	1	4	5	0	0	12
Female 4	1	0	0	2	4	3	0	3	12
Female 5	1	3	0	0	0	0	0	9	12
Female 6	N/A	0	0	0	0	0	3	0	3
Total		3	14	3	16	12	3	12	63
Arena 3									
Female 1	1	0	0	0	0	0	10	0	10
Female 2	2	0	0	0	0	0	10	0	10
Female 3	2	0	3	0	0	0	0	7	10
Female 4	1	0	10	0	0	0	0	0	10
Female 5	2	0	0	0	8	0	0	2	10
Female 6	2	0	0	6	4	0	0	0	10
Total		0	13	6	12	0	20	9	60
Arena 4									
Female 1	1	4	0	4	0	4	0	0	12
Female 2	2	1	0	0	3	5	0	3	12
Female 3	2	0	0	0	4	0	0	8	12
Female 4	1	1	6	3	2	0	0	0	12
Female 5	2	0	4	0	2	0	6	0	12
Female 6	N/A	0	0	0	0	0	0	0	0
Total		6	10	7	11	9	6	11	60

Note: The number in each box is the number of eggs sired by each male for the female in question. Column 2 (# mates) is the number of social mates acquired by each female. Male 1 and Females 5 & 6 from Arena 1, Female 6 from Arena 2, and Female 6 from Arena 4 were eliminated from the analyses (see text for details).

(Fig. 2). Thus, females also showed a high variance in number of genetically successful mates.

As the fish did not differ in size or pre-spawning fat content among enclosures, data from the four spawning arenas were pooled to test for assortative mating. Neither males nor

females showed any statistical preference for mates of similar size or energy content, suggesting that mating was not assortative in these spawning groups.

The male social dominance, consort, spawning life and social partners indices for each enclosure are shown in Table 2. The dominance index, consort index and social partners

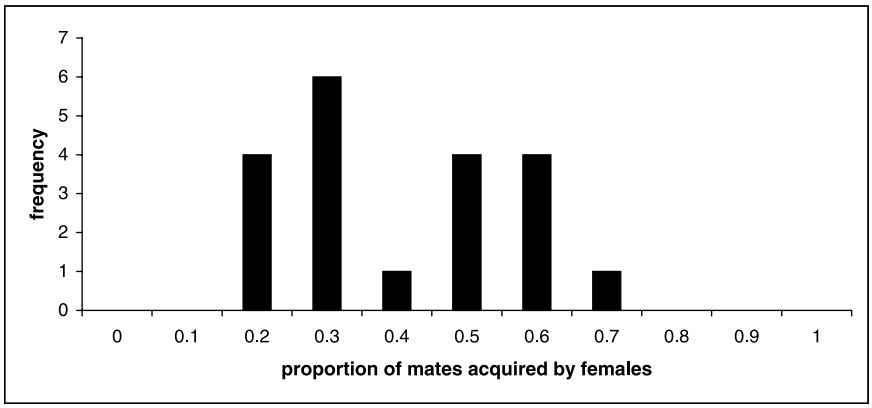

Fig. 2. Frequency distribution of the proportion of mates acquired by females among all spawning arenas.

Table 2. The behavioural mating indices of males in each arena

	Male 1	Male 2	Male 3	Male 4	Male 5	Male 6	Male 7
Arena 1							
Consort score	N/A	2	5.5	3	1	4	5.5
Dominance index	N/A	1	6	2	3	4	5
Longevity (days)	N/A	8	8	6	7	5	10
No. of social mates	N/A	0	3	3	0	2	2
Arena 2							
Consort score	1	4	2.5	7	5	2.5	6
Dominance index	1	5	2	7	6	3	4
Longevity (days)	6	10	8	9	9	9	5
No. of social mates	0	2	1	3	1	1	1
Arena 3							
Consort score	2	6	3.5	3.5	1	6	6
Dominance index	2	5	3	4	1	6	7
Longevity (days)	10	14	9	7	4	12	12
No. of social mates	1	2	2	1	0	2	1
Arena 4							
Consort score	4	6.5	2	2	6.5	2	5
Dominance index	4	7	2	1	5	3	6
Longevity (days)	8	6	5	9	5	9	11
No. of social mates	1	2	0	0	1	1	2

index were all intercorrelated (dominance × consort, $n = 27$, $r = 0.885$, $P < 0.0001$; dominance × social partners, $n = 27$, $r = 0.610$, $P = 0.0007$; and consort × social partners, $n = 27$, $r = 0.649$, $P = 0.0003$). The correlations between the spawning life index and the other social mating success measures were non-significant, although positive. The two indices of genetic reproductive success in males were highly correlated ($n = 27$, $r = 0.667$, $P = 0.0001$). For the females, there were no correlations among the behavioural indices of mating success. Two measures of genetic mating success in females (i.e. success as a function of the genetic success of her partners and success as a function of the social success of her partners) were, however, highly correlated ($n = 20$, $r = 0.736$, $P = 0.0002$).

Male social dominance was a reasonable predictor of both genetic measures of reproductive success (dominance × proportion of offspring: $r^2 = 0.396$, d.f. = 25, $P = 0.0004$; dominance × proportion of mates: $r^2 = 0.176$, d.f. = 25, $P = 0.0296$) (Fig. 3). Consort score was also a reasonable predictor of both genetic measures (consort score × proportion of offspring: $r^2 = 0.368$, d.f. = 25, $P = 0.0008$; consort score × proportion of mates: $r^2 = 0.147$, d.f. = 25, $P = 0.0480$) (Fig. 4). However, after sequential Bonferroni correction, only the proportion of offspring sired can be predicted by the two measures of social mating success. The social partners index was a good predictor of the proportion of offspring sired ($r^2 = 0.328$, d.f. = 25, $P = 0.0018$), but not the proportion of mates acquired (Fig. 5). The spawning life index was positively but not significantly correlated with genetic reproductive success. The residuals from the regressions of the spawning life index on the dominance and consort indices were not correlated with either measure of genetic mating success.

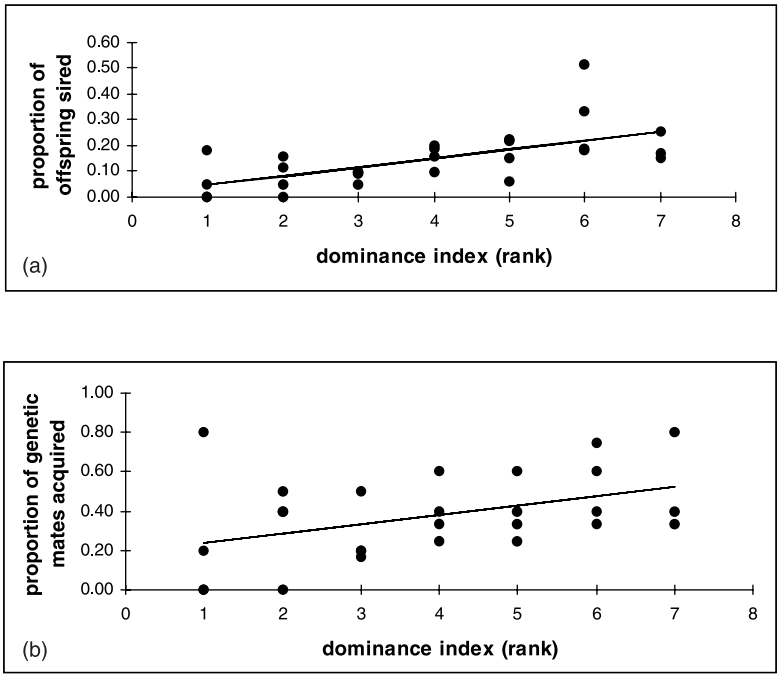

Fig. 3. The relationships between proportion of offspring sired (a) and proportion of mates acquired (b) and male dominance index among all spawning arenas. Proportion offspring sired on dominance, $r^2 = 0.396$, $P < 0.001$; proportion mates acquired on dominance, $r^2 = 0.176$, $P < 0.05$.

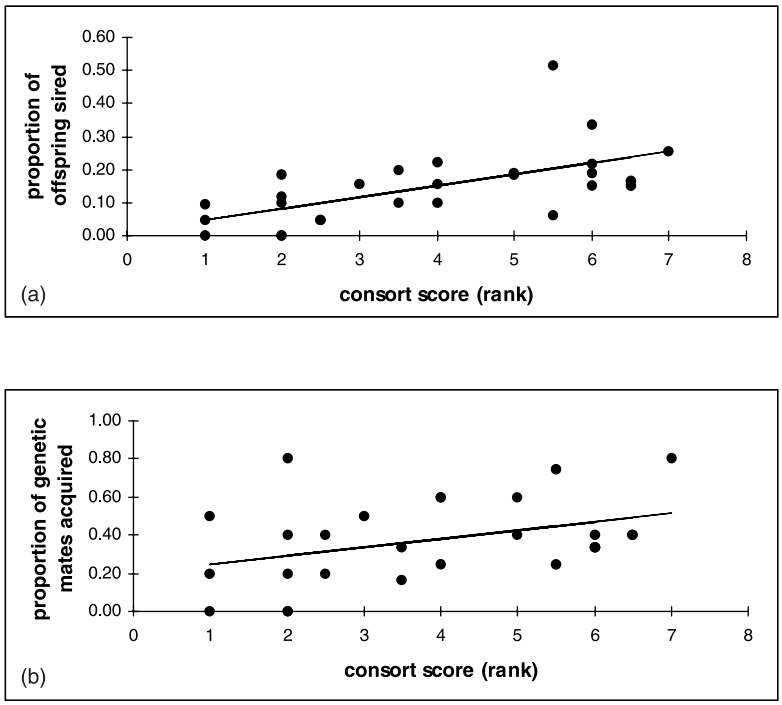

Fig. 4. The relationships between proportion of offspring sired (a) and proportion of mates acquired (b) and male consort score among all spawning arenas. Proportion offspring sired on consort score, $r^2 = 0.368$, $P < 0.001$; proportion mates acquired on consort score, $r^2 = 0.147$, $P < 0.05$.

For females, none of the social mating success measures was a good predictor of the genetic reproductive success measures (all $P > 0.05$). The spawning life index was a reasonable predictor of female success as a function of the social success of her partner ($r^2 = 0.201$, d.f. = 18, $P = 0.0477$); however, with the Bonferroni correction, it was not statistically significant.

DISCUSSION

The primary objectives of this study were to estimate individual reproductive success in groups of sockeye salmon in open competition and to compare genetic reproductive success with behavioural indices of mating success. Microsatellite analysis provided an efficient means to establish parent–offspring relationships. Using four polymorphic microsatellite loci in combination with a maximum-likelihood method (Marshall *et al.*, 1998), and knowing the mother of each offspring, we were able to assign 98.4% of the offspring to a particular sire with a confidence level of 95%, and the remainder with 90% confidence.

Our results show that individual males mated successfully (i.e. sired offspring) with between zero and four females in each arena and that most males spawned with more than one female. Twenty-seven of 28 males in our spawning groups sired some offspring, but the variation in success among males was high, ranging from 0 to 52% of offspring sampled.

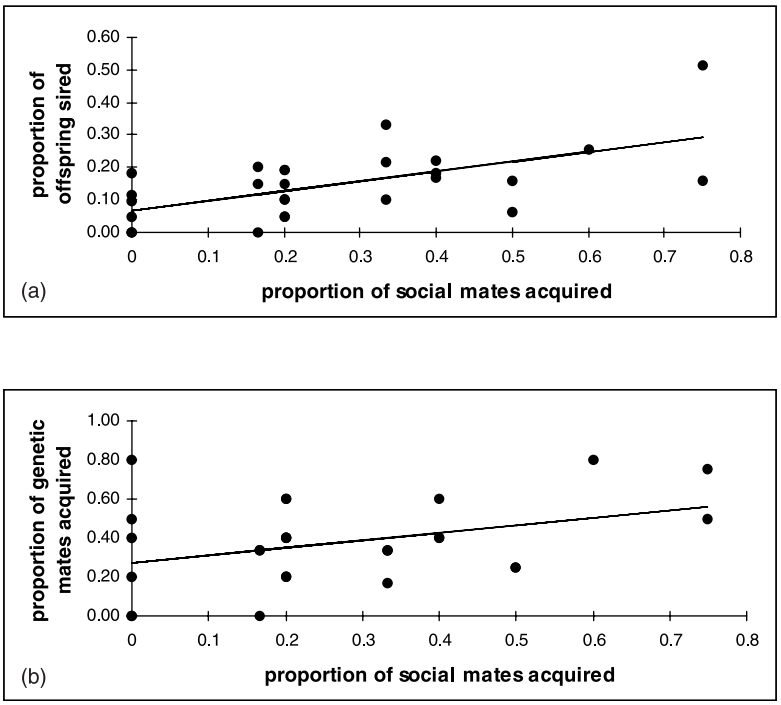

Fig. 5. The relationships between proportion of offspring sired (a) and proportion of genetic mates acquired (b) and the proportion of social mates acquired by males among all spawning arenas. Proportion of offspring sired on social mates, $r^2 = 0.328$, $P < 0.005$; proportion of genetic mates acquired on social mates, $r^2 = 0.131$, $P = 0.06$.

High variance in genetic reproductive success of males appears common in fish. Gross and Kapuscinski (1997) found that 5.4% of all spawning males produced 54.7% of the offspring in smallmouth bass. Garant *et al.* (2001) reported that the variance to mean ratio of assigned offspring among Atlantic salmon males was 8.6. Neff (2001) found that the paternity success of 38 bluegill sunfish males ranged from 26 to 100%.

The mating behaviour in Pacific salmon, in which dominant males monopolize access to females, suggests that a few males are likely to have primary access to most receptive females (Schroder, 1982; Foote *et al.*, 1997; Hamon *et al.*, 1999). Ours, however, are the first actual measures of variance in genetic reproductive success among males in open competition. Females also typically had multiple mates. Between one and four males mated with each female, with two being the most common number (7 of 20 females). The occurrence of multiple partners spawning with female Pacific salmon is also consistent with observed mating behaviour. During oviposition, subordinate males typically rush into the nest and release milt along with the dominant male. Numerous studies have shown that these subordinate males frequently fertilize some offspring (Chebanov *et al.*, 1983; Foote *et al.*, 1997; Garant *et al.*, 2001). We tried to determine whether different male partners dominated separate spawning events in females by sampling sequential egg pockets in each redd. Unfortunately, we found that we could not rule out movement of eggs between nests both from natural causes and during egg collection. For the offspring of about half the females,

however, paternity was distributed rather evenly among two or three sires, suggesting that the dominant male changed between spawning events.

Seeking multiple partners makes evolutionary sense for males, who try to sire as many offspring as possible. The benefits of multiple partners are not so obvious for females. Because of the opportunistic behaviour of sneaker males in salmon, some degree of multiple paternity for a female's offspring may be unavoidable, even if both the female and the consort work hard to exclude all other partners. In many cases, however, the proportion of offspring sired by different males was more consistent with a switch in dominant partner between spawning events than with opportunistic fertilizations by sneaker males. Only four of the females in our experiments mated repeatedly with the same male. The remaining 16 all had multiple partners and, for at least 9 of these, paternity was well distributed between two or more males. Female sockeye do exert some control over whom they mate with and previous studies on Pacific salmon have suggested that females prefer large, well-developed and aggressive males (Schroder, 1982; Foote, 1989). Since females do not spawn simultaneously, we expected that the dominant male would sire a disproportionate fraction of offspring in our spawning arenas. Although dominance and consort behaviour were strongly associated with paternity, less dominant males did much better than we expected. Perhaps having multiple partners conveys a form of fertilization insurance. A dominant male, regardless of his morphological or behavioural quality, may be sterile or have low fertility. Furthermore, male genetic quality may be weakly associated with dominance behaviour and secondary sexual characteristics. Mating with multiple males may be a result of bet-hedging. It may also be a tactic to generate greater genetic diversity among progeny, which may have a selective advantage (Avise, 1994; Barlaup *et al.*, 1994; Fleming, 1996). Finally, multiple mating may reduce inbreeding or reduce the competition among genetically dissimilar siblings (Reynolds, 1996).

Size assortative mating has been observed in Pacific salmon (Hanson and Smith, 1967; Foote, 1988), although Taggart *et al.* (2001) did not find it in Atlantic salmon. In our study, there was no clear pattern of mate choice based on body size, body shape or pre-spawning energy content. Foote (1988) demonstrated that males of all sizes discriminate against females smaller than themselves. The variation in body size and other variables in our study may have been too small for the fish to display assortative mating, or the limited mating opportunities present in our spawning arenas may have precluded such choices. Furthermore, all the females in our study were smaller than the smallest male in the same enclosure, so that males could not afford to discriminate against females smaller than themselves.

Studies of mating success in Pacific salmon have focused on behavioural measures, assuming that large, aggressive or consort males fertilize most of the eggs laid by the female (Schroder, 1982; Chebanov *et al.*, 1983; Quinn and Foote, 1994). Behavioural indices of mating success were highly correlated with the realized genetic reproductive success in male sockeye salmon. However, these indices explained only 33–40% of the variation in male reproductive success. This is much lower than in mammals and lizards, in which as much as 90% of the variance in male reproductive success can be predicted from behavioural data (Pemberton *et al.*, 1992; Gullberg *et al.*, 1997). Field observations provide only a limited view of mating success in salmon because only a fraction of spawnings are observed. Although more intensive observations might lead to more certain predictions about paternity, measures of behaviour alone can sometimes be misleading. In our study, dominance, consort score, or the number of social mates appeared to underestimate the success of some sneaker males. For example, male 4 in arena 4 ranked 1/7 on the dominance scale,

2/7 on the consort scale, had no social mates and was the smallest male in the whole study (body length = 62.3 cm). Nevertheless, this male sired offspring with four of the five females in the spawning group and also sired the most offspring (co-equal with male 7). Particularly successful subordinate males like this one cannot be accounted for by the traditional behavioural measures of mating success.

The two measures of male genetic reproductive success (proportion of offspring sired and proportion of mates acquired) were highly correlated. However, neither measure alone may be sufficient. The proportion of offspring sired provides a measure of fertilization success, but may misrepresent potential fry production. Most salmon embryos die before emergence (>70%), and whole redds are often destroyed. In these circumstances, spreading your offspring among a lot of redds may be just as important to fitness as fertilizing a lot of eggs in one redd. On the other hand, the proportion of mates acquired may provide an inflated measure of mating success for sneaker males, who may fertilize only a few eggs of many females. Thus, the trade-off that distinguishes sneaker males from dominant males may be that the dominant males try to fertilize a lot of eggs, whereas the sneaker males try to get a lot of mates (Healey and Prince, 1998). Ideally, one would assess both these measures.

We examined behavioural and genetic indices of female reproductive success. However, defining measures of genetic success for females that go beyond fecundity is problematic when actual contribution to future generations cannot be measured. Our approach assumed that fitness consequences for the female flow, in part, from the quality of the males who fertilize her eggs. Only female spawning longevity was correlated with female genetic success as indexed by the dominance ranking of her genetic partners. Spawning longevity may have positive fitness consequences, as the longer a female defends her nest the lower the probability it will be dug up by a later spawning female (Quinn and Foote, 1994). This correlation may, therefore, be reflective of male choice, as factors associated with longevity may be used by males to assess female quality.

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