



The cost of peripheral males in a brook trout mating system

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A focus on the reproductive contributions of males displaying alternative life histories has neglected the role of size-dependent peripheral males in salmonine mating systems. We documented mating behaviour of brook trout, *Salvelinus fontinalis*, including observations of spawning, over two breeding seasons to determine the mating costs of peripheral males to dominant males (kleptogamy) and females (egg cannibalism). For males and females, the mating costs of peripheral males were substantial because more than half (56%) of all observed brook trout spawnings involved peripheral males. Males that paired with large females experienced a greater incidence of kleptogamy due to increased numbers of peripheral males present. Large males face a conflict when mating in that they prefer to spawn with large females; however, these same females attract numerous males against which the dominant male cannot defend. From paternity studies, we estimated that males that had peripheral males participate in spawning may fertilize, on average, equal numbers of eggs compared to males spawning solely with a smaller female. Females that paired with relatively smaller males had significantly more eggs eaten by peripheral males than females that paired with relatively larger males. Latency to spawn by females increased when paired with a relatively small male, and resulted in females obtaining a larger spawning partner. The observed patterns of size-assortative mating, kleptogamy and cannibalism are discussed in relation to mate choice for this population of brook trout.

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Competition among males for mates generally results in males that occupy a 'satellite' or 'peripheral' position relative to that of dominant individuals (Magnhagen 1992; Gross 1996). Males relegated to peripheral positions (from here on termed 'peripheral males') can impose a number of fitness costs on dominant males and females that include parasitizing the effort of larger males by stealing fertilizations (kleptogamy: e.g. mammals, Clutton-Brock et al. 1979; amphibians, Perill et al. 1978; insects, Crespi 1986; fish, Taborsky 1998), reducing mating opportunities (van den Berghe et al. 1989), and cannibalizing eggs deposited by females (Dominey & Blumer 1984; Katano 1990).

The mating systems of salmonine fish (salmon, trout and char) include various reproductive strategies that have received considerable attention with respect to kleptogamy (Gross 1984, 1985; Taborsky 1994). In this group of fish, males compete for access to females, which they guard intensely prior to spawning in an attempt to

be the sole spawning male (e.g. Keenleyside & Dupuis 1988). Paternity analyses have shown that males closest to the female at the time of spawning fertilize most of the eggs (Schroder 1981; Chebanov et al. 1983; Mjølnerød et al. 1998). Males compete for close proximity to females on the basis of body size, as well as other traits such as hooked snout length (kype) and hump height, independent of body size (Fleming & Gross 1994; Quinn & Foote 1994). The fitness costs within these mating systems have therefore been formulated around the loss of paternity through kleptogamy, largely based on the question of reproductive contributions from precocial males following an alternative life history strategy (parr in Atlantic salmon, *Salmo salar*, and jacks in Pacific salmon, *Oncorhynchus* sp.: Jones & King 1952; Hutchings & Myers 1988; Groot & Margolis 1991; Foote et al. 1997). The fitness costs associated with peripheral males following a conditional strategy, where body size determines the position of individuals relative to a spawning female, has received considerably less attention. The cost of peripheral males for females, based on either alternative or conditional strategies, appears to be egg cannibalism (Greeley 1932; Maekawa & Hino 1987, 1990; Thomaz

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et al. 1997) but has generally remained undetected in this group of fish (Foote 1989).

The objective of this study was to determine the costs of peripheral males to spawning males and females in the mating system of brook trout, *Salvelinus fontinalis*. In this study we linked the cost of peripheral males to male and female choice of mates. Experimental studies (Foote 1988a; Foote & Larkin 1988) have revealed that mate choice in salmonines is based on relative, not absolute, body size, such that males prefer mates that are equal to or larger than themselves. Male preference for females of equal or greater size corresponds to 'threshold' models of mate choice (Janetos 1980; Gibson & Langen 1996) and for salmonines this threshold level varies depending on male size (Foote 1988a). Similar size-based experiments have not been performed with female salmonines, so there is no indication whether female preference is based on absolute male body size. However, field or enclosure studies demonstrate that females delay spawning when paired with relatively small males (Schroder 1981; Foote & Larkin 1988; Foote 1989). Where a size discrepancy occurs between a male and a larger female, delaying tactics by the female appear to result in a more equitable size-based pairing between spawning fish (Schroder 1981; Foote & Larkin 1988). This process of displacement of small males by larger males presumably accounts for the widespread observation of spawning pairs being roughly equal in size (e.g. sockeye salmon, *Oncorhynchus nerka*: Hanson & Smith 1967; dolly varden, *Salvelinus malma*: Maekawa et al. 1993; Japanese char, *Salvelinus leucomaenis*: Maekawa et al. 1994). However, this process of female choice under natural conditions has yet to be documented.

In salmonine mating systems, larger females also tend to be accompanied by greater numbers of males when spawning (e.g. Sargent et al. 1986). The cost to males that prefer to spawn with large females is the attraction of many other males to these same females. Thus males pairing with large females have greater potential for loss of paternity to peripheral males. In addition to these mating costs of peripheral males, field observations suggest that egg cannibalism is also a cost associated with the presence of peripheral males (Maekawa & Hino 1987). Female Miyabe char, *Salvelinus malma miyabei*, deposit more eggs during their first spawning in a nest, relative to later spawnings, in an apparent attempt to reduce egg cannibalism by peripheral males (Maekawa & Hino 1990).

We link our predictions regarding the fitness costs associated with peripheral males to the patterns of mate choice prevalent in mating systems of salmonine fish. For males paired with large females, we predict an increased incidence of kleptogamy by peripheral males. This is based on the prediction that a positive relationship between female size and the number of peripheral males will exist because large females are attractive to a greater number of males based on relative body size. We predicted that females that paired with large males would have a lower incidence of egg cannibalism by peripheral males, and that females would actively choose larger mates by increasing latency to spawn when accompanied by relatively small males.

METHODS

Field Observations

We individually marked and followed the reproductive behaviour of most individuals in a population of brook trout at Scott Lake, Algonquin Provincial Park, Ontario (45°29'N, 78°43'W) on a daily basis over two breeding seasons (for complete details of the study site and tagging procedure see Blanchfield & Ridgway 1997). Fork lengths (FL) of all fish were measured to the nearest millimetre. We conducted a census of the entire spawning area four times daily (weather permitting) once spawning activity commenced (10 October 1994 and 1995) until fish were no longer present on the spawning grounds (6 December 1994) or the lake surface was frozen (24 November 1995). During each census, the position and activity of all fish were recorded on underwater slates by swimmers using drysuits, mask and snorkel. For each census, we calculated the operational sex ratio (OSR) as the mean number of males around active females (this measure excludes males on the spawning grounds that were not associated with active females even though all males were sexually active or ripe; Blanchfield 1998).

In total, 45 spawning events (involving 39 females and 30 males) were observed by swimmers or recorded on videotape (Sony® Hi-8 videocamera with Amphibico® underwater housing). To determine a female's latency to spawn, we recorded the time from the first observation of female activity at a site until the actual time of spawning at that site. If females were not observed at the spawning site prior to spawning, then we assumed a time of 1.5 h, because census swims were roughly every 2 h. Similarly, females that took greater than one day to spawn were allotted a time of 10 h because little activity occurs at night (Blanchfield & Ridgway 1997).

We considered only instances in which peripheral males were observed to gape and quiver (i.e. orgasm behaviour associated with the release of sperm; Jones & Ball 1954) in the nest of the female during the spawning event as spawnings in which there was a potential for loss of paternity. A cloud of milt expelled by peripheral males was also distinguishable to the observer (or noticeable on video). Often males were seen diving into the nest at the moment of spawning; however, unless gaping and quivering or sperm release were observed, these males were not considered as potential spawners. Similarly, we labelled spawnings as cannibalistic only when peripheral males were observed eating eggs. Our observations may underestimate cannibalism because it occurred in the video recordings up to 30 min after spawning.

Video Analyses

We analysed video records of spawnings ($N=25$) for the frequency and duration of aggressive interactions by the dominant male 5 min immediately prior to spawning using The Observer® (version 3.0; Noldus Information Technology, Wageningen, The Netherlands). For males, we recorded the following behaviour: (1) cross-over: male remains in close proximity to the female (≤ 30 cm) and

Table 1. Comparison of mean (\pm SE) per capita aggression by the dominant male 5 min prior to spawning in relation to the number of peripheral males present

	Peripheral males		
	1	2	>2
<i>N</i>	5	6	7
Per capita aggression			
Chase	10.6 ^a (4.2)	11.0 ^a (3.0)	2.2 ^b (0.7)
Threat	8.0 (2.3)	6.2 (1.7)	2.8 (1.4)

Means with different superscript letters are significantly different (ANOVA and Tukey post hoc tests).

prevents access to female by other males; (2) nonguard: male moves away from female (>30 cm) and does not prevent access to female by other males; (3) chase: male aggressively charges another male (including bites); and (4) threat: male performs lateral displays at or attempts to charge other males. We divided the duration and frequency of aggressive behaviour by the number of peripheral males to determine per capita aggression.

We transformed (\log_e) all body size and frequency of aggression data prior to parametric analyses to conform to assumptions of homogeneity of variance. Proportion data were arcsine transformed. Means (\pm SE) are presented.

RESULTS

The time dominant males spent in aggressive interactions was strongly influenced by the number of peripheral males, such that significantly more per capita chases occurred when one or two males were present than with increasing numbers of peripheral males (ANOVA: $F_{2,15}=7.1$, $P<0.01$; Table 1). There were no differences in per capita threat displays by the dominant male with the number of peripheral males present around the spawning pair.

The number of peripheral males releasing sperm during spawnings increased with the number of peripheral males around active females (Spearman rank correlation: $r_s=0.61$, $N=32$, $P<0.00001$; Fig. 1a). Peripheral males participated in 49% of all spawnings when less than four peripheral males were present, and in 100% of all spawnings when five or more peripheral males were present. The proportion of peripheral males spawning did not vary in relation to the number of peripheral males present ($r_s=0.0085$, $N=32$, NS; Fig. 1b). For spawnings in which we observed males releasing sperm at the moment of spawning (21/32), approximately half (55%) of the peripheral males present participated. However, peripheral males did not release sperm during one-third (11/32) of the observed spawnings in which they were present, and overall 37% of peripheral males present attempted to steal fertilizations.

More than half (56%) of all observed spawnings involved kleptogamy or egg predation by peripheral males. The relative body size of a spawning pair appeared

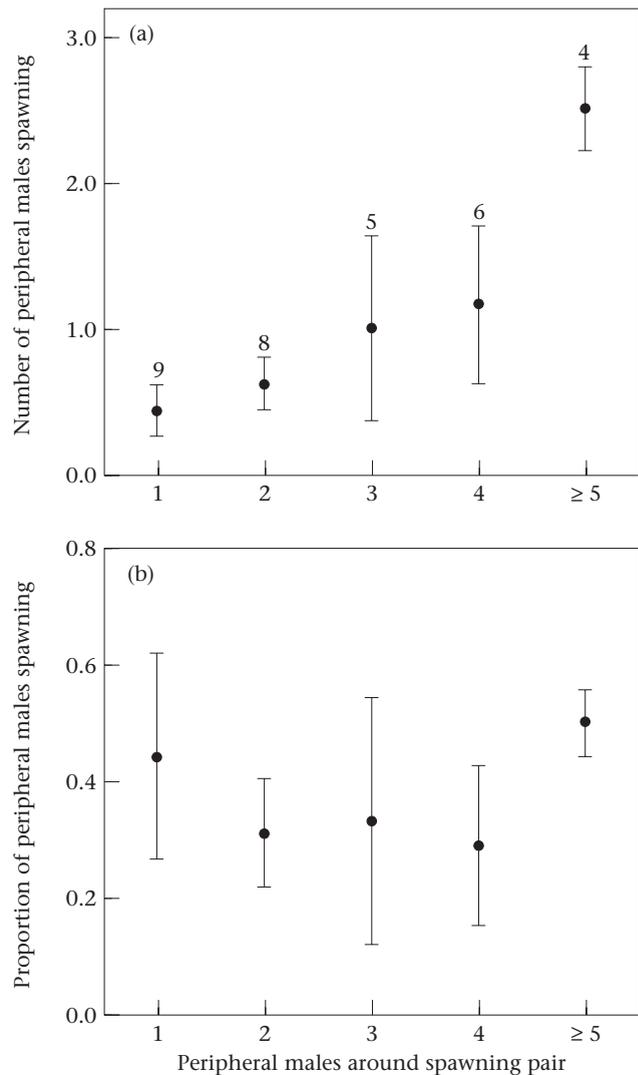


Figure 1. The (a) number, and (b) proportion of peripheral males ($\bar{X}\pm$ SE) releasing sperm during spawning in relation to the number of peripheral males present.

to influence whether peripheral males participated in spawning events. Males were significantly larger than their mates (5.0 ± 1.3 cm; Wilcoxon signed-ranks test: $Z=3.1$, $P<0.01$) only for spawnings in which peripheral males did not participate in kleptogamy or egg predation (Fig. 2). Peripheral males were observed to release sperm in 47% (21/45) of the witnessed spawning events, with one-third of these spawnings (7/21) involving both sperm release and egg predation by peripheral males (Fig. 2). Kleptogamy did not depend on the body size of the dominant male or relative pair size. Instead, the size of the female to which a male was paired and number of peripheral males present determined a male's likelihood of stolen fertilizations. Males that paired with large females had greater numbers of peripheral males present and incurred a significantly greater incidence of kleptogamy compared with males that paired with smaller females, which attracted fewer peripheral males (Table 2). The size of male aggregations in which peripheral males

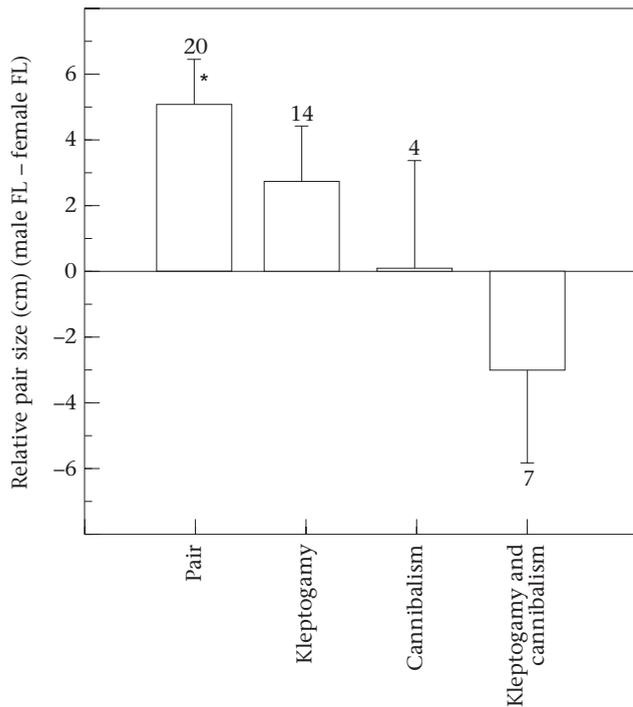


Figure 2. Relative pair size ($\bar{X} \pm \text{SE}$ fork length (FL); male FL–female FL) was compared for spawnings that involved only the spawning pair versus those that involved peripheral male participation (sperm release only, egg predation only and both sperm release and egg predation). Categories for which differences in pair size were significant are marked (* $P < 0.05$; Wilcoxon signed-ranks test).

participated during spawning (4.1 ± 0.4) was greater than the average size of male aggregations in the spawning area on that day (i.e. OSR; 3.1 ± 0.2 ; paired t test: $t_{20} = -3.1$, $P < 0.01$). In contrast, the size of male aggregations in which none of the peripheral males released sperm during spawning (2.0 ± 0.3) was less than the average size of male aggregations in the spawning area on that day (3.0 ± 0.2 ; paired t test: $t_{23} = 3.6$, $P < 0.01$).

Egg predation by peripheral males occurred in almost one-quarter (24%) of witnessed spawning events. The extent to which egg cannibalism occurred did not vary with female body size or the number of peripheral males

present. Instead, the size of the male to which a female was paired determined her potential for egg cannibalism. Females paired with smaller males had significantly more eggs eaten than those paired with larger males (Table 2). This difference in male body size also resulted in a significantly greater incidence of egg cannibalism for females paired with relatively smaller males than for those paired with relatively larger males (Table 2).

Assortative mating was apparent ($R^2 = 0.28$, $F_{1,43} = 16.1$, $P < 0.001$; Fig. 3a) although males were larger than their mates (paired t test: $t_{44} = 2.51$, $P < 0.05$). The number of males around active female brook trout increased with female body size ($R^2 = 0.26$, $F_{1,43} = 15.0$, $P < 0.001$; Fig. 3b). For spawnings in which peripheral males were absent, females were significantly smaller (34.4 ± 1.2 cm; $t = -3.1$, $N = 13$; $P < 0.01$) than females with peripheral males present (40.3 ± 1.1 cm; $N = 32$). The number of peripheral males present around active females did not change during the hours leading up to spawning ($r_s = -0.14$, $N = 57$, NS).

The time from start of nest construction to actual spawning was significantly longer (7.2 ± 0.9 h) for females that paired with a relatively small male prior to spawning than for females that always paired with males of equal or greater size (2.7 ± 0.7 h; $t_{43} = 3.9$, $P < 0.001$). Females that paired with males smaller than themselves were also larger (41.0 ± 1.5 cm) than females that paired with males of equal or greater size (36.5 ± 1.1 cm; $t_{43} = 2.4$, $P < 0.05$). We examined to what extent latency to spawn by females was a result of absolute female size or relative size of the spawning pair (i.e. mate choice). A female's latency to spawn did not depend on her body size (forward stepwise multiple regression partial correlation: $t = 0.4$, NS), but on the difference between her body size and the body size of her original mate ($t = -2.7$, $P < 0.01$).

We compared the size of the dominant male present during census swims prior to spawning with the size of the dominant male present during spawning. The dominant male present 4–6 h prior to spawning was, on average, 5.8 ± 3.5 cm smaller than the dominant male at spawning (Fig. 4). The difference in size between early males observed as dominant during census swims and the dominant male at spawning decreased as the time to spawning came closer ($r_s = -0.29$, $N = 58$, $P < 0.05$; Fig. 4),

Table 2. The extent to which kleptogamy and egg cannibalism were influenced by the body size of each member of the mating pair and number of peripheral males present, as determined by logistic regression analysis

	Kleptogamy				Cannibalism			
	No	Yes	χ^2	P	No	Yes	χ^2	P
Body size (cm)								
Male	40.7 ± 1.6	41.8 ± 1.5	0.4	NS	42.4 ± 1.2	37.5 ± 2.0	3.9	<0.05
Female	36.5 ± 1.2	41.1 ± 1.3	6.6	<0.05	38.3 ± 1.1	39.4 ± 2.0	0.3	NS
Relative pair size*	4.2 ± 1.2	0.8 ± 1.5	3.1	NS	4.1 ± 1.0	-1.9 ± 2.1	6.9	<0.01
Number of peripheral males	1.0 ± 0.3	3.1 ± 0.4	17.4	<0.0001	1.8 ± 0.4	2.4 ± 0.4	0.7	NS
<i>N</i>	24	21			34	11		

Mean ($\pm \text{SE}$) body sizes and number of peripheral males are shown for spawnings that involved peripheral males releasing sperm and those in which peripheral males ate eggs.

*Relative pair size = (fork length of spawning male – fork length of spawning female).

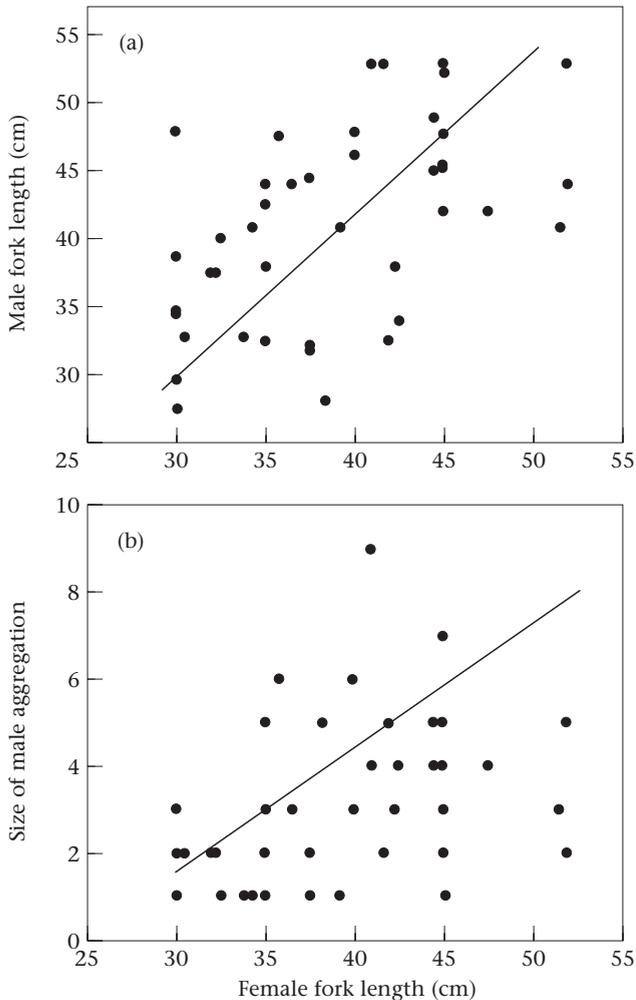


Figure 3. The relationship between female body size and (a) the size of dominant male present, and (b) the number of males around females at the time of spawning for 45 observed spawnings. The lines represent the best fit obtained with Model II regression (size of dominant male: $Y=1.13X-2.58$; size of male aggregation: $Y=0.26X-7.07$).

thus the size of the dominant male increased as spawning time approached. Most females (80%) that were paired with a relatively small male during the first observation of spawning activity eventually spawned with a male that was larger than their original male.

DISCUSSION

Male and female brook trout incurred mating costs through kleptogamy and egg cannibalism, respectively, in the presence of peripheral males. For males, the potential for kleptogamy by peripheral males was great, with peripheral males releasing sperm in nearly half (47%) of all spawnings. Kleptogamy was a result of males pairing with large females, which attracted a relatively large aggregation of peripheral males. Female brook trout delayed spawning when paired with relatively small males, and in doing so obtained larger mates. It appears that the choice of relatively large males by females is

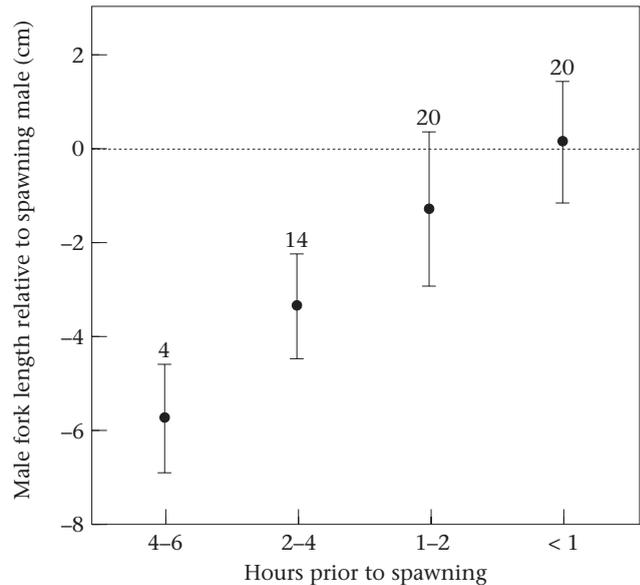


Figure 4. The difference between the mean (\pm SE) body size of dominant males present during transect swims prior to spawning and the dominant male present at spawning (represented as the dashed line passing through zero).

related to a reduced incidence of egg cannibalism. Although we were not able to quantify the exact proportion of eggs eaten by peripheral males, brood cannibalism was commonly observed in this population, and is probably the cost driving female choice for larger males.

Natural selection favours large body size for egg production in female salmonines (van den Berghe & Gross 1989; Fleming & Gross 1994). Because female quality (fecundity and egg biomass) increases with body size, males mating with large females have the potential to sire many offspring. Thus, large male brook trout face a conflict when mating; they prefer to spawn with similar-sized (i.e. large) females. However, large females attract many males, against which dominant males are unable to defend (Quinn et al. 1996), thereby increasing the opportunity for loss of fertilization. Chases by dominant males, which are the most effective way to keep peripheral males away from the spawning female, decreased with increasing numbers of peripheral males.

We further explored the conflict of loss of paternity that males face when spawning with large females by examining male mating success with respect to the number of eggs fertilized. From fecundity estimates of wild brook trout (Vladykov 1956), we calculated the mean number of eggs available to males during spawnings in which peripheral males released sperm, based on the size of females to which these males were paired (2194 eggs; Fig. 5, line A). We then calculated the mean number of eggs available to males during spawnings in which peripheral males did not release sperm based on the size of females to which these males were paired (1415 eggs; Fig. 5, line B). While we do not know the exact proportion of eggs fertilized by peripheral males, a review of salmonine paternity studies revealed that dominant

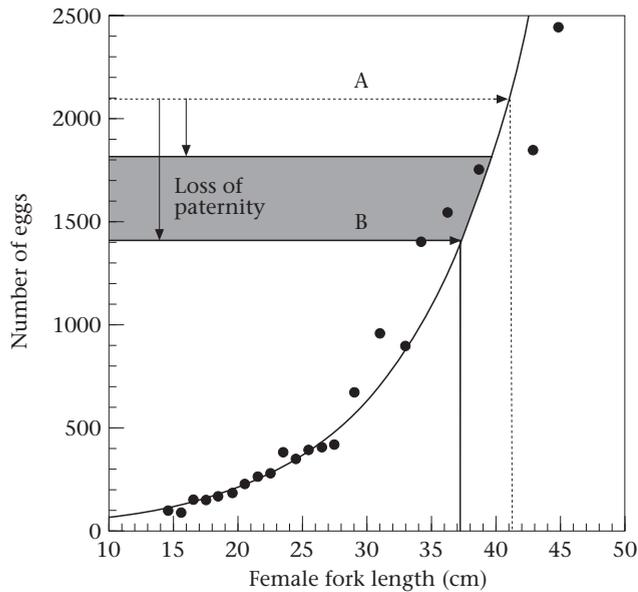


Figure 5. Fecundity (i.e. number of eggs) of female brook trout increases exponentially with body size (from Vladykov 1956). The potential fertilization success of dominant males that did (line A) or did not (line B) have peripheral males participate in spawning, based on the size of females with which males were paired (see Table 2). Males that paired with larger females (line A) suffered a 17–36% loss of paternity (arrows) to peripheral males. These dominant males could potentially fertilize, on average, an equal number of eggs as males that pair with a smaller female (line B), which attract fewer peripheral males during spawning. Loss of paternity (grey area) was calculated as the 95% confidence intervals from paternity studies (success of the dominant male; Schroder 1981: 71.7%; Chebanov et al. 1983: 71.2%; Maekawa & Onozato 1986: 83.1%; Hutchings & Myers 1988: 77.0%; Jordan & Youngson 1992: 89.2%; Foote et al. 1997: 57.8%; M. R. Gross, B. D. Neff & I. A. Fleming, unpublished data: 65.0%).

males, on average, fertilize roughly three-quarters (74%) of a given female's eggs during a spawning event in which peripheral males participate. Assuming a 17–36% loss of paternity (\pm 95% confidence intervals from published studies; see arrows on Fig. 5), then males in this study that had the potential to lose paternity may have fertilized, on average, an equivalent number of eggs (1404–1821 eggs) if they had solely fertilized the eggs of a smaller female (Fig. 5). Therefore, males paired with large females have the opportunity to sire many offspring, although peripheral males may reduce this measure of success due to an increased incidence of kleptogamy. It is important to note, however, that male mating success ought not to be considered solely in terms of the number of eggs fertilized. Other studies have shown that over and above greater fecundity, male salmonines mating with large females enjoy greater reproductive success by producing larger young (Ferguson et al. 1995; Hayashizaki et al. 1995) and having a greater proportion of these young survive (see van den Berghe & Gross 1989; Fleming & Gross 1994). Therefore benefits accrued by males spawning with large females may be greater than realized, even if the absolute number of eggs fertilized is reduced through kleptogamy by peripheral males.

Large body size and/or other secondary sexual characters used in mating competition among male salmonines leads to greater access to females (Fleming & Gross 1994; Quinn & Foote 1994; Kitano 1996). Male body size in brook trout corresponds to greater mating opportunity in this system. The patterns of competitive mate searching and pair formation we observed agree with observations of Pacific salmon which show that male mate choice is dependent on female readiness to spawn and female size (Schroder 1981; Quinn et al. 1996). We agree that an association between female size and male aggregation size is not, in itself, direct evidence of male mate choice (Foote 1988b). However, the fact that male aggregation size remained constant over the course of spawning suggests that large females always attract more males than small females, and that aggregation size is not a product of passive accumulation of males around females.

Female mate choice plays an important role in determining the observed patterns of egg predation in this population of brook trout. Experimental studies have shown that females prefer mates equal to or greater in body size than themselves (Foote 1989). For females, which remain site-attached, this choice is expressed through aggression towards the dominant male (Kitano 1996), a delay in site preparation (Schroder 1981; Foote & Larkin 1988), or the deposition of fewer eggs (Foote 1989) when paired with a relatively small male. By delaying site preparation, females paired with relatively small males increase their likelihood of attracting a larger male with which to spawn (Foote & Larkin 1988). Our results from free-ranging fish are the first to confirm that female delaying tactics in salmonines do indeed result in females gaining a larger mate. In addition, these findings come from observing reproduction under natural conditions and therefore lend strong support to the role of female mate choice in promoting size-assortative mating that results in spawning females and males of equivalent size. This pattern of spawning pairs of equivalent size is commonly observed among salmonines (Hanson & Smith 1967; Schroder 1981; Foote & Larkin 1988; Maekawa et al. 1993, 1994; this study).

There is a growing body of evidence linking female preference for large males with greater survival of eggs in fish where males make a significant parental investment. In these cases male parental care leads to a greater hatching success of eggs due to the ability of large males to defend eggs from predators (Downhower & Brown 1980; Bisazza & Marconato 1988; Côté & Hunte 1989). Unlike Pacific salmon, which cease feeding during the breeding season, this brook trout mating system is characterized by a high degree of egg predation by peripheral males (24% of spawnings). Although males in this group of fish are generally not known to provide extended parental care, female preference for relatively large males appears to play a role in determining which spawnings will incur egg predation. Overall, females paired with relatively larger males had significantly fewer eggs eaten than those paired with relatively smaller males. Thus, for this population of brook trout, one proximate mechanism for female choice of relatively larger males may be the apparent reduction in the incidence of brood

cannibalism. Presently, there is no evidence for female preference of absolutely versus relatively larger mates in salmonines; however, female Japanese char have been observed to actively select against relatively large males by discontinuing spawning activities when paired with males that are much larger (>10 cm) than themselves (Maekawa et al. 1994). We did not observe this upper size limit for female preference during our study, in which several spawnings involved females paired with much larger males (male > female by 10 cm FL; $N=5$). In Pacific salmon, female choice of relatively large males is accounted for by a good genes argument and is based on evidence of faster growth rates and greater size at maturity by progeny of large male pink salmon, *Oncorhynchus gorbuscha* (Beacham & Murray 1988).

Within our comparisons of spawnings with peripheral male participation (sperm release and egg cannibalism) versus those with no peripheral male participation, we included spawnings in which no peripheral males were present (13/45). We argue that spawnings that occurred when no peripheral males were present represent an active choice by males to avoid certain spawning pairs, and thus should be included in our analysis of the behaviour of peripheral males. Because male brook trout move and choose among females on the spawning grounds (Blanchfield 1998), female body size and the number and size of male competitors will most likely be important deciding factors for male choice of females. Evidence that female body size is an important factor in male mate choice comes from the finding that females were significantly smaller at spawnings where peripheral males were absent.

In summary, we have shown that peripheral males exert mating costs to males and females, and that these costs are linked to mate choice for this population of brook trout. A low proportion of individual peripheral male participation in spawnings (37%), in addition to an estimated low gain of paternity by these males (17–36%), suggests that male mating success could be more greatly skewed towards large males than previously realized. Female choice may be a strong determinant of male mating success in salmonine mating systems and could well determine the distribution of condition-dependent mating behaviour among males (Henson & Warner 1997). If females spawn more readily in the presence of relatively large males, as we have shown, then the potential reproductive rate of males may vary widely (Clutton-Brock & Parker 1992). Observations of mate searching would provide much needed data on the choice of females by males of varying size.

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