



between arrival and territory establishment). Longevity is likely very important to female reproductive success. McPhee and Quinn (1998) and Hendry et al. (1999) note that early-arriving female sockeye salmon likely suffer a higher probability of dig-up and suggest that this explains why they live longer (and thus defend their territories for more days) than do late-arriving females. A seasonal de-

shows that

Table 1: Parameters and variables used in the longevity and waiting models

Parameter or variable	Value
Maximum number of eggs, $E$	500 <sup>a</sup>
Reduction in eggs for each additional day of longevity, $C_e$	10, 20, or 30
Increase in longevity for each additional day of waiting, $B_w$	.25 or .75 d
Number of females, $N_f$	10,000
Number of nesting sites, $N_s$	10,000, 15,000, or 20,000
Daily probability of predation, $p_f$	.01, .10, or .15
Probability of egg mortality if nest reused, $p_e$	.25, .30, or .50

<sup>a</sup> A fecundity of 500 eggs is arbitrary and does not affect the model output so long as  $C_e$  is adjusted accordingly. The fecundity of Meadow Creek kokanee in 1998 and 1999 was  $220 \pm 46$  eggs (Morbey 2002a).

dry et al. 1999) spanning a 15-d season. Each female was also assigned a longevity drawn randomly from a uniform distribution spanning 2–14 d. We assumed females required a minimum of 2 d to spawn all their eggs successfully. Arrival times and longevities were rounded to the nearest day to yield 195 (15 arrival days  $\times$  13 longevities) combinations with starting values  $p(l(t))$ .

We quantified dig-up on the basis of a method used by Maunder (1997). A female was assumed to settle on a territory immediately on arrival, with no waiting phase. The total number of eggs laid depended on her assigned longevity, with each additional day of longevity reducing the number of eggs by  $C_e$  from the maximum egg number  $E$  (cf. Hendry et al. 1999; the interpretation of the model results should not differ substantially if the cost was a reduction in egg size instead). In order of their unique arrival times, females settled on territories selected randomly from those unoccupied at the time of arrival. There were always sufficient territories available. We introduced some error in arrival time by subjecting females to a random delay in arrival of up to 1 d.

The state of every female (alive or dead, number of eggs still alive in her redd) and territory (occupied or not) was updated as each new female settled on a territory. Females died (and their territories became available) when their longevity expired or when they were depredated. As predation on the spawning grounds can be important in some populations (e.g., Ruggerone et al. 2000), females were subjected to random daily predation mortality at a rate of  $\mu$ . When a territory was reused, a proportion of previously laid eggs suffered mortality ( $\mu_r$ ). The reproductive success of each female was the number of eggs she spawned minus the number of eggs lost because of dig-up. The fitness (expected number of surviving eggs) of females,  $w(l(t))$ , was the average reproductive success of all females arriving on day  $t$  with longevity  $l$ .

For the next iteration of the model,  $p(l(t))$  was replicated in direct proportion to  $w(l(t))$ . To add new variation, the updated probability distribution  $p(l(t))$  was adjusted at each generation by adding 0.0001 to any zero category and rescaling so that  $p(l(t))$  summed to 1.0. Iterations continued for 500 generations until  $p(l(t))$  converged on a stable solution and  $w(l(t))$  approximated a constant on each arrival day  $t$ . For each arrival day, the solution is represented in our results as the mean  $\pm$  SD.

We explored the sensitivity of the model by varying parameters one at a time. We varied female density by setting the number of available territories ( $N_s$ ) to 10,000, 15,000, or 20,000. The daily mortality rate for females ( $\mu$ ) was set to 0.01, 0.10, or 0.15; the probability of egg mortality given territory reuse ( $\mu_r$ ) was set to 0.25, 0.30, or 0.50; and the cost of an additional day of longevity was set to 10, 20, or 30 eggs. These parameter values were

chosen to produce a wide range of solutions. The model was robust to variations in starting conditions.

### *Evolutionarily Stable Waiting*

We next determined what conditions would allow a strategy of waiting before territory settlement to invade a population with evolutionarily stable longevities. The benefit of waiting ( $B_w$ ) was assumed to be an increase in longevity

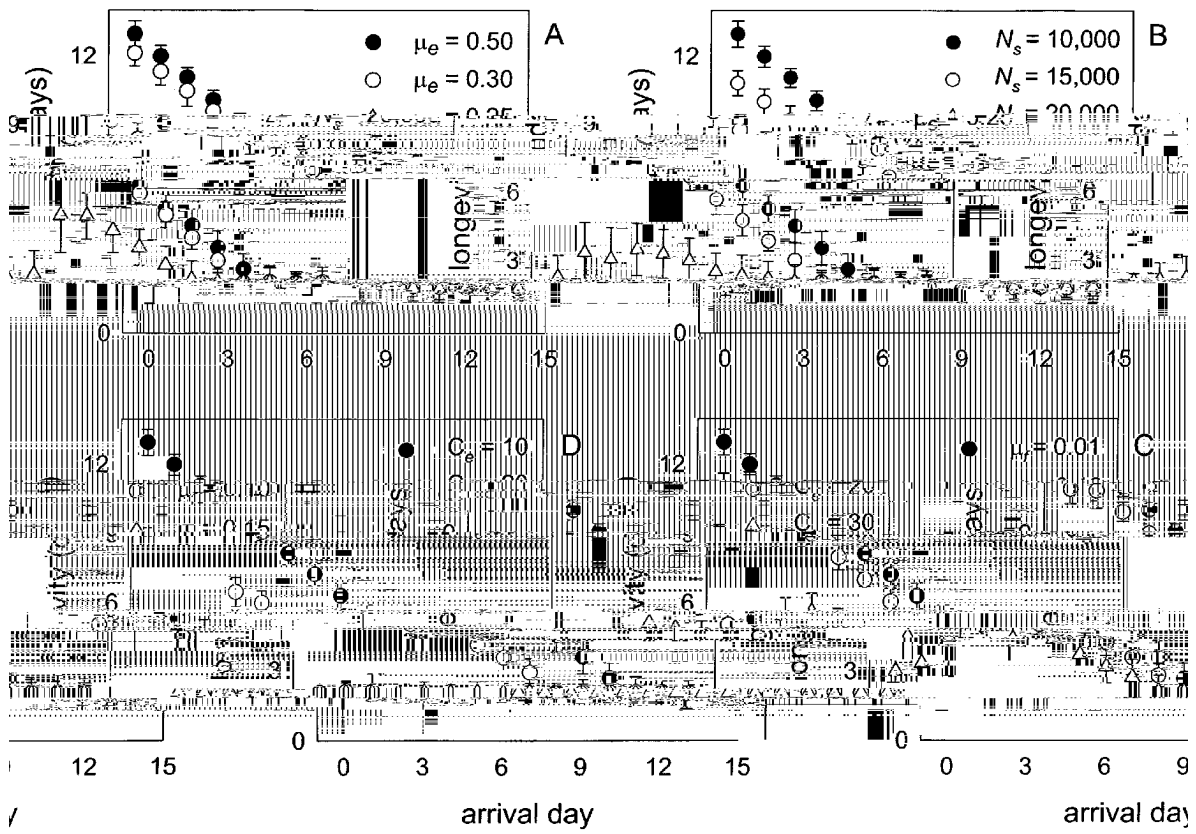


Figure 1: Output from the longevity model with different levels of egg mortality due to territory reuse (A), territory availability (B), daily mortality rate (C), and fecundity cost (D)

C should not defend because she is the last to arrive. If female B does not defend because it is too costly ( $x < sy$ ), neither should female A ( $sx < s^2y$ , or  $x < sy$ ). Female A would defend when female B defends ( $x > sy$ ) if  $sx > sy$  or  $x > y$ . However, because by definition  $y > x$ , female A should not defend when female B does. This simplified argument demonstrates how an earlier-arriving female could take advantage of the nest defense performed by a later-arriving female.

Note that it is not the case that all females die on the last day of the spawning period. If the ESS solution were "die on the last day of the spawning period," the calculated longevity for females arriving on day  $t$  would be  $14 - t$ . But females arriving on day 0 have ESS longevitys ranging from 2 to 13 d (depending on the set of parameter values used; see fig. 1) and would die (if not depredated) from 12 to 1 d before the last female arrived. The results confirm that it can be evolutionarily stable for death to precede the arrival of the last females. According to the model, this is because females invest in eggs instead of longevity when the probability of dig-up is low.

Figure 2 shows the phenological consequences when the option of waiting is introduced into a situation with prolonged longevity ( $N_f = 10,000$ ,  $N_s = 10,000$ ,  $r = 0.01$ ,  $e = 0.50$ , and  $C_e = 10$  eggs; solid circles in all three panels of fig. 1). Waiting does not evolve when it is as expensive as spawning and territory defense because it subjects females to pre-spawning mortality without any longevity benefit (results not shown). Waiting readily invades when it is less energetically expensive than breeding (fig. 2A). When waiting is inexpensive, females wait longer and even reduce investment in longevity to increase their fecundity (fig. 2B). When waiting is relatively expensive, females increase their waiting capacity by allocating more to longevity and reducing fecundity.

The restriction of breeding activity to days 0–20 limits the benefits of waiting among late-arriving females. With a later seasonal time constraint, selection would favor even greater waiting and longevity among all females. Thus, depending on the benefits of waiting and the range of allowable breeding days, all females may do better or worse than they do in the nonwaiting situation.

The benefits of completing defense relatively late and the benefits of breeding before the end of the season in-

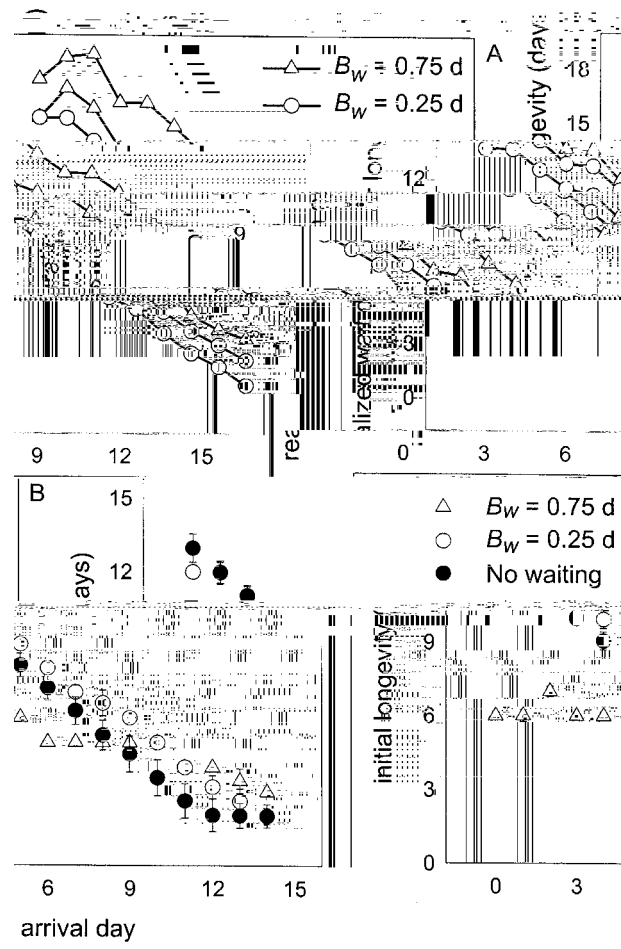


Figure 2: Output from the model that allows waiting and longevity to coevolve. The upper graph (A) shows the realized wait durations and longevitys when the benefit of waiting,  $B_w$ , equals 0.75 d (open triangles and solid lines) or 0.25 d (open circles and solid lines). The longevity line lies above the corresponding waiting line. Females invest more in waiting and longevity earlier in the year and when waiting is less energetically expensive. The lower graph (B) shows the initial allocation to longevity ( $\pm$ SD) when the benefit of waiting,  $B_w$ , equals 0.75 d (open triangles) or 0.25 d (open circles) in relation to a situation with no waiting (filled circles). As the benefits of waiting increase, females may allocate less to longevity (maintenance) and more to eggs. Breeding is restricted to days 0–20.

(50°15.4'N, 116°59.8')

Table 2: Numbers of female kokanee used in the experiments and analyses and their spawning success

Year and experiment	Number of females	Number in analyses of longevity <sup>a</sup>	Number in analyses of waiting <sup>b</sup>	Number spawning/ number dying naturally (proportion)
1998:				
Low density	15	14	8	8/14 (.57)
Medium density	15	7	8	6/7 (.86)
High density	13	8	6	5/8 (.63)
Natural variation	47	45	32	32/45 (.71)
1999:				
Low density	14	12	13	12/12 (1.00)
Low density	15	11	14	11/11 (1.00)
High density	14	13	14	13/13 (1.00)
High density	15	15	14	15/15 (1.00)
Maturity	15	9	13	7/9 (.78)
Maturity	15	6	11	5/6 (.83)
Natural variation	48	43	46	41/43 (.95)

<sup>a</sup> Includes all females who died naturally.

<sup>b</sup> Includes all females who settled and spawned.

five individuals per category). The sample sizes in the 1998 density experiment were too small to test for an effect of density.

The prediction of decreased longevity and wait duration for later-arriving females was tested on females in the 1998 and 1999 natural variation experiments using general linear models. The full statistical models included year, arrival day, and the interaction between year and arrival day. An effect of spawning density on longevity and wait duration was tested in the 1998 and 1999 density experiments. For each analysis, the full statistical model included density (low, medium, or high) in 1998 and density (low or high) and pen (nested within density) in 1999.

A separate set of analyses was conducted to examine the proximate factors affecting longevity and waiting. Water temperature (Heggberget 1988), female maturation status (Groot and Margolis 1991), spawning density (van den Berghe and Gross 1986), and fork length (Foote 1990; Fleming and Gross 1994) are all proximate factors that may affect the longevity of female salmonids. Nesting success (spawned or not) also may affect longevity if the completion of spawning triggers senescence. If these factors vary seasonally, they may explain any seasonal pattern in waiting and longevity observed in the natural variation experiment. The full statistical model included year, arrival day, fork length, maturation status, water temperature on arrival, nesting success (for the longevity analyses only), and all interactions with year, maturation status, and nesting success (for the longevity analyses only). An effect of maturation status on longevity and waiting also was tested in the 1999 maturity experiment. The full statistical model

included maturation status, pen (nested within maturation status), and all interactions.

We determined the benefit of waiting by examining the effect of wait duration on the duration of territory defense (i.e., reproductive life span) in the 1998 and 1999 natural variation experiments. The analysis examined  $\beta_{05.1}(\text{exam}i7g-0.0003\text{oduc}$







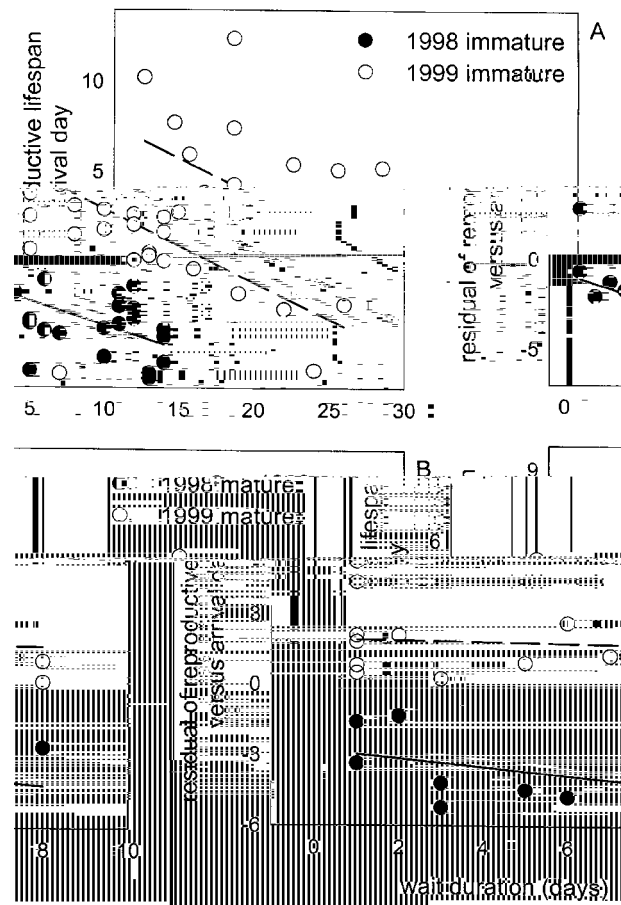


Figure 5: Effect of wait duration on the reproductive life span of female kokanee who arrived immature (A)

embryos to mechanical shock and displacement. Second, the probability of dig-up seems to be high. Sockeye salmon (including kokanee) typically spawn at high densities (Burgner 1991), and the Meadow Creek spawning channel was filled to capacity in both 1998 and 1999. When territory reuse was defined as territory placement within 0.5 m of an existing, undefended redd, approximately one-third of all territories were reused. Furthermore, spawning densities in the experiment were equal to or lower than those observed in the channel. Third, predation risk in the channel was likely low. Fourth, although the fecundity cost was not measured for females with similar arrival days, early- and late-arriving females had similar fecundities (Y. E. Morbey, unpublished data). Because early-arriving females also lived for more days, this suggests a low fecundity cost of prolonging longevity. Finally, waiting is an effective strategy for prolonging longevity in Meadow Creek. Pre-spawning mortality is unlikely, and kokanee minimize energy expenditure when waiting by schooling in cooler (shadowed) regions or areas of lower water velocity (cf. Foote 1990). Females who waited 1 d prolonged their longevity by about 0.65 d. We are cautious about generating quantitative predictions of longevity and waiting for Meadow Creek kokanee because we lack good estimates for  $N_s$ ,  $\rho_e$ , and  $C_e$ . However, by using realistic guesses for the set of parameters ( $N =$  , ,

Greater ectoparasite load may have also contributed to the greater prespawning mortality of females in 1998 than in 1999. Water temperature could not account for the seasonal decline in longevity because it did not decline over the 21-d period.

Fork length was unimportant in affecting wait duration and longevity (cf. Quinn and Foote 1994; McPhee and Quinn 1998). Detecting an effect of fork length is made difficult because Meadow Creek kokanee comprise a single age class (Vernon 1957), and fork length may not accurately reflect energy reserves because it includes the tail fin (body weight and post-orbital-hypural length are better measures). These results contrast with previous studies in which larger body size allowed females increased access to breeding territories (Foote 1990; Fleming and Gross 1994). Foote (1990) also studied Meadow Creek kokanee, but he selected large and small females and probably had greater power to detect a size difference in settlement timing.

Finally, breeding competition, viewed as a proximate factor, could not account for the seasonal decline in longevity or wait duration. This is consistent with previous studies that did not observe any effect of breeding competition on the settlement timing or longevity of female sockeye salmon (McPhee and Quinn 1998; Quinn and McPhee 1998). At high enough densities, forced delays due to overcrowding are known to occur (Foote 1990; Parnskiy 1990; Fleming and Gross 1994). For example, female-female competition prevented females from establishing breeding territories under experimentally high densities in coho salmon (Fleming and Gross 1994). Furthermore, mature female kokanee, taken from schools in the Meadow Creek spawning channel, delayed territory settlement when reintroduced into the crowded spawning channel (Foote 1990). Even if females are forced to delay territory settlement, this cannot account for the seasonal decline in wait duration because competition from established females would cause later-arriving females to delay territory settlement.

#### *Alternative Hypotheses*

There are other explanations for the seasonal patterns in longevity and waiting predicted here, and they are not mutually exclusive. First, early-arriving females may invest more in longevity to allow greater searching time for high-quality territories. Later in the year, greater competition for limited territories would presumably favor quicker territory settlement (cf. Kokko 1999). This hypothesis has little support because female salmon do not appear to search actively while waiting (Y. E. Morbey, personal observation) and because females find and defend high-quality territories quickly (Foote 1990; Quinn and Foote 1994; Hendry et al. 1995). A second related hypothesis is

that delayed settlement allows a female to avoid displacement by better competitors and to improve her chances of acquiring a high-quality territory by queuing (cf. Kokko and Sutherland 1998). The lower risk of displacement later in the season would favor less waiting.

Third, females may be selected to spawn synchronously so that earlier-arriving females delay territory settlement and later-arriving females hurry settlement. Synchrony may be advantageous if there is an optimal time to avoid scouring, freezing, or siltation of nests. Other advantages of synchronous spawning include dig-up avoidance, predator swamping, and synchronous fry emergence. The relative importance of these factors in explaining ex ex21-



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