Timing Games in the Reproductive Phenology of Female Pacific Salmon (*Oncorhynchus* spp.)

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ABSTRACT: We use a game-theoretic framework to investigate the reproductive phenology of female kokanee (*Oncorhynchus nerka*). As in the other semelparous species of Pacific salmon, females construct nests in gravel, spawn with males, bury their fertilized eggs, and defend their nest sites until they die several days later. Later-breeding females may reuse previous nest sites, and their digging behavior is thought to subject previously buried eggs to mortality. Using game-theoretic models, we show that females can reduce this risk by allocating resources to longevity (the period between arrival and death) as opposed to eggs. Waiting before territory settlement is also expected if it allows females to conserve energy and delay senescence. The models demonstrate how these costs and benefits interact to select for a seasonal decline in longevity, a well-known phenomenon in the salmonid literature, and a seasonal decline in wait duration. Both of these predictions were supported in a field study of kokanee. Female state of reproductive maturity was the most important proximate factor causing variation in longevity and wait duration. With more than 30% of territories being reused, dig-up is likely an important selective force in this population.

Keywords: reproductive tactics, nest defense, longevity, reproductive phenology, salmon.

Intraspecific competition often plays an important role in the timing of life-history transitions. When entering a new life-history stage, individuals face a new set of ecological pressures that affect their survival, growth, or reproduction. Given such conflicting selective regimes, life-history models can predict the optimal time or age to undergo a life-history transition. When intraspecific competition affects growth or reproduction in the new life-history stage, however, entry timing becomes a game because the success of entering at a certain time depends on how many others enter at that time. Game-theoretic reasoning has proven to be useful for explaining the breeding timing of individuals living in seasonal environments (e.g., Iwasa et al. 1983; Iwasa and Levin 1995; Kokko 1999; Broom et al. 2000; Morbey 2002*b*). Here we use a strategic framework to investigate the reproductive phenology of female kokanee (*Oncorhynchus nerka*).

Pacific salmon (*Oncorhynchus* spp.), particularly the semelparous species, are an excellent group for investigating how intraspecific competition creates opportunities for strategic timing and hence affects breeding phenology. The reproductive behavior of females has been well described, and intraspecific competition features prominently (Groot and Margolis 1991). After arrival at the freshwater breeding area, a female selects and digs nests (collectively a "redd") in suitable gravel and often competes with other females for high-quality territories. She spawns over several days with one or more males and buries successive batches of eggs with gravel from new nesting depressions dug just upstream. After spawning is complete until her death perhaps a week later, she defends her redd against later-arriving females, who may attempt to dig their own nests at the same location (e.g., van den Berghe and Gross 1989; Foote 1990). Although it has not been well quantified, "nest dig-up" is widely accepted as a significant source of egg mortality in salmonids (McNeil 1964; Hayes 1987; van den Berghe and Gross 1989; Essington et al. 1998; Fukushima et al. 1998) and has been shown to be an important selective force on female size (e.g., coho salmon *Oncorhynchus kisutch*: van den Berghe and Gross 1989; sockeye salmon *O. nerka*: Steen and Quinn 1999).

We expect nest dig-up to place potent selection on reproductive phenology because the reproductive success of early-arriving females is affected by later arrivals. The two phenological traits we investigate are longevity (the period between arrival and death) and wait duration (the period

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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 decline in longevity has been widely documented in female Pacific salmon (Neilson and Banford 1983; Perrin and Irvine 1990; McPhee and Quinn 1998; Hendry et al. 1999; but see van den Berghe and Gross 1986; Fukushima and Smoker 1997). Similarly, the delayed breeding of small female brook trout *Salvelinus fontinalis* has been explained as a tactic for avoiding nest dig-up by large females (Blanchfield 1998). Game-theoretic reasoning is implicit in both of these verbal hypotheses.

In some salmon populations, some individuals do not settle on spawning sites immediately on arrival (e.g., pink salmon *Oncorhynchus gorbuscha*: Mattson and Rowland 1963; sockeye salmon: Hoopes 1972; Brett 1995; chinook salmon *Oncorhynchus tshawytscha*: Quinn et al. 2000). Instead, some individuals of both sexes school in sites such as deep pools (e.g., pink salmon: Mattson and Rowland 1963) or shadowed areas (e.g., kokanee or nonanadromous sockeye salmon: Y. E. Morbey, personal observation) and wait several days or even weeks before establishing territories. In some sockeye populations, this waiting period occurs before arrival in lakes near the breeding streams (e.g., Hendry 1998). Prespawning waiting is a well-known phenomenon to salmon biologists, but its adaptive significance is obscure.

We develop a game model of reproductive phenology to investigate whether prolonged longevity and waiting could evolve as dig-up avoidance tactics in female salmon. Under the assumption that fecundity and longevity necessarily trade off, we derive the evolutionarily stable strategy (ESS) for the distribution of longevities under a given arrival distribution in a situation with no waiting. We next allow longevity and waiting to coevolve and derive the joint ESS. We assume these traits are adjusted either evolutionarily (i.e., by selection) or behaviorally (i.e., facultatively by individual females). Analyses on the reproductive phenology of female kokanee, based on data collected at Meadow Creek, British Columbia, are presented to assess the hypothesis' assumptions and predictions. We also investigate some proximate factors thought to affect longevity and waiting, including water temperature, fork length, female density, and state of reproductive maturity. Alternative hypotheses for the observed seasonal patterns in longevity and waiting are also discussed.

Models

Evolutionarily Stable Longevity

We assume that selection acts on longevity through its contrasting effects on reproductive success. Salmon are capital breeders (Jönsson 1997) and do not feed after starting their upstream migration. Females allocate their stored resources to somatic tissue (for sustaining longevity), secondary sexual characteristics, or gonads (Calow 1985); thus, we assume that investment in structures or mechanisms to extend longevity and the nest-defense phase necessitates reduced allocation to other functions. Hendry et al. (1999) provide evidence for a trade-off between longevity and egg production in female sockeye salmon. The presumed benefit of increased longevity is a lower probability of nest dig-up due to prolonged territory defense.

As the probability of dig-up depends not only on a female's reproductive phenology but also on the timing of other females, an explicit game-theoretic approach is necessary (Maynard Smith 1982). Our game model has $N_f = 10,000$ players, each assigned a longevity as a function of arrival day. The model solves for the probability distribution of longevities (l) for each arrival day (t), $p(l(t))$. At the ESS, the fitnesses of all longevities are equal for females with the same arrival day. This approach effectively assumes no selection on arrival day, with spawning success independent of calendar date. The ESS was determined by simulating within-season territory settlement by iterating a model programmed in C (cf. Parker and Courtney 1983). Simulation was chosen over an analytical approach because of the complexity of describing dig-up probabilities. The variables and parameter values used are shown in table 1.

At the start of a model run, each female was assigned a unique arrival time from a beta distribution ($\alpha = \beta = 1.5$; based on analysis of sockeye salmon data in Hen-

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

Parameter or variable	Value
Maximum number of eggs, E	500[a]
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, μ_f	.01, .10, or .15
Probability of egg mortality if nest reused, μ_e	.25, .30, or .50

[a] 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 ± 46 eggs (Morbey 2002*a*).

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 × 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 μ_f. When a territory was reused, a proportion of previously laid eggs suffered mortality (μ_e). 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 $\Sigma p(l(t))$ 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 ± 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 (μ_f) was set to 0.01, 0.10, or 0.15; the probability of egg mortality given territory reuse (μ_e) 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 without any effect on egg number or egg size. During the prespawning waiting phase, females were subject to predation mortality. We assumed that waiting occurs on the spawning grounds after arrival (the model could be modified to simulate waiting in a nearby lake before arrival), and we limited reproduction to a defined period with suitable spawning conditions by assuming zero hatching success for eggs spawned beyond a threshold date (day 20).

We investigated the invasion of waiting in a population with prolonged longevities ($N_f = 10,000$, $N_s = 10,000$, $\mu_f = 0.01$, $\mu_e = 0.50$, and $C_e = 10$ eggs). Because waiting may affect the longevity ESS and vice versa, we alternated selection on longevity and waiting in each of the 500 iterations until a joint ESS was reached. After calculating the longevity ESS without waiting, we used the method described above to calculate the waiting ESS. A population of $N_f = 10,000$ females was assigned unique arrival times from a beta distribution ($\alpha = \beta = 1.5$). Each female was randomly assigned a waiting value between 0 and 14 from a uniform distribution. The waiting value divided by 14 is the proportion of a female's maximum wait duration, and the latter depended on her initial longevity and the benefit of waiting ($B_w = 0.25$ or 0.75 d). A female was assumed to defend a territory immediately on completion of the waiting phase. Egg number depended on a female's initial allocation to longevity, but actual longevity was increased by B_w for each additional day of waiting. We imposed a minimum 2-d period of spawning and nest defense. To calculate expected reproductive success during the simulation, we first sorted females according to their settlement time (arrival time plus wait duration).

Model Results

The model predicts a strong seasonal decline in the longevity of females when the risks associated with dig-up are high or when the probability of nest reuse is high (fig. 1). For example, females invest more in longevity when egg mortality due to dig-up is higher (fig. 1A). The probability of nest reuse is greater when nesting territories are limited, and consequently, females invest more in longevity (fig. 1B). Lower predation risk not only makes it possible for a female's potential longevity to be reached, but it may also increase the probability of nest reuse because of the
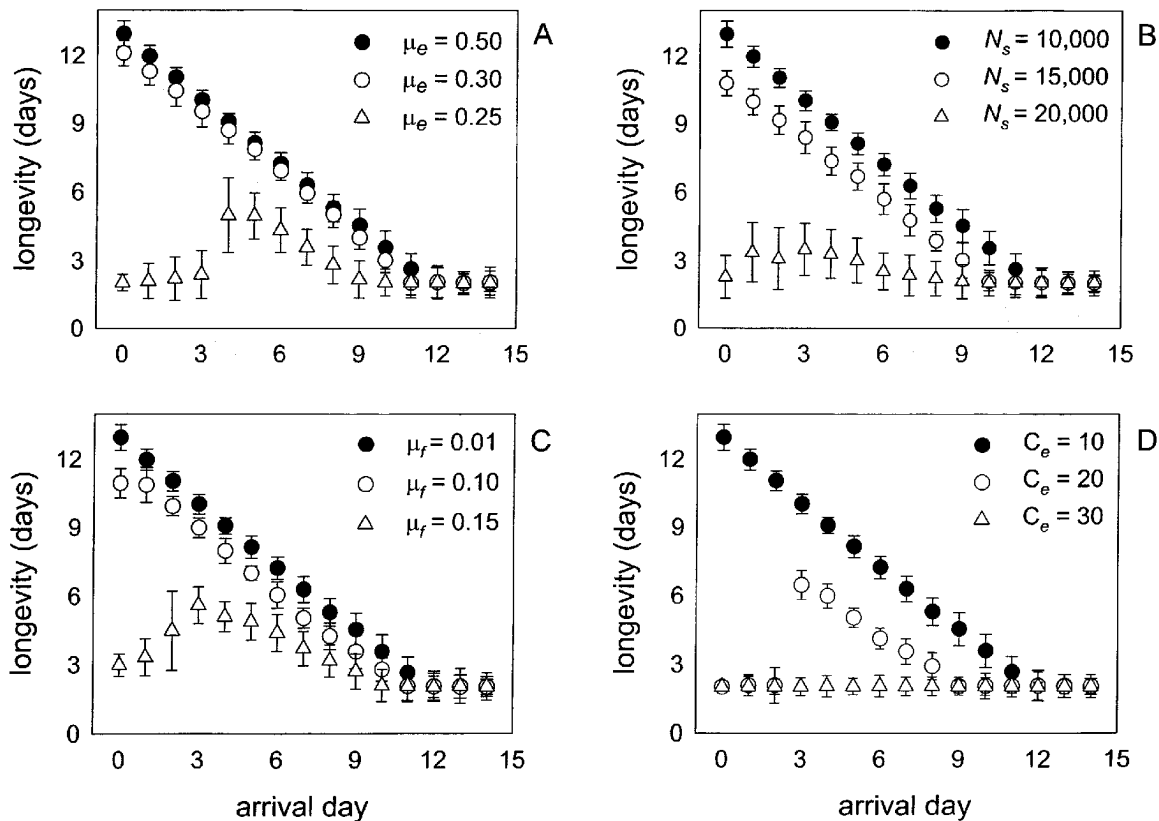
Figure 1: Output from the longevity model with different levels of egg mortality due to territory reuse (*A*), territory availability (*B*), daily mortality rate (*C*), and fecundity cost (*D*). Expected longevity (±SD), calculated from the probability distribution of longevities after 500 generations, is shown for each arrival day. Females are expected to invest more in longevity when egg mortality due to dig-up is higher (*A*), when fewer nesting sites are available (*B*), when daily mortality rate is lower (*C*), and when there is a lower fecundity cost (*D*). Early-arriving females are expected to live for more days than do later-arriving females when the probability of dig-up is low and when dig-up avoidance costs are low. Otherwise, early-arriving females may invest little in their own defense and instead take advantage of the inadvertent defense of later-arriving females. The filled circles in each graph represent the model output when $N_s = 10,000$, $\mu_f = 0.01$, $\mu_e = 0.5$, and $C_e = 10$ eggs.

reduced availability of territories (fig. 1*C*). Finally, females invest more in longevity as the fecundity cost of increasing longevity decreases (fig. 1*D*). In contrast, females invest most of their resources in fecundity when egg mortality due to dig-up is low ($\mu_e < 0.25$), when dig-up is unlikely ($N_s > 20,000$), when predation risk is high ($\mu_f > 0.15$), and when there is a large fecundity cost of increasing longevity ($C_e \geq 30$).

Over the range of arrival days showing declines in longevity, the different parameters affect longevity in a straightforward manner. Females invest more in longevity and have a more pronounced seasonal decline in longevity when egg mortality due to dig-up is higher, when fewer nesting sites are available, when predation risk is lower, and when increasing longevity has a lower fecundity cost. However, between the two extremes (e.g., low vs. high probability of dig-up), an interesting pattern emerges. The earliest-arriving females invest disproportionately less in territory defense. These females may benefit from the defense of later-arriving, longer-lived females who settle on their territories. There is no indication of alternative non-adjacent evolutionarily stable longevities among females arriving on the same day (e.g., 2 and 6 d), and it is unclear whether such an abrupt seasonal switch from little defense to prolonged defense would be observed in nature. Nevertheless, this result suggests that an alternative reproductive tactic might be used by early-arriving females under intermediate conditions.

This result can be explained by a simple model of nest defense with three players. Consider the sequential arrival of three competitor females: A, B, and C. Each female can either invest in *x* eggs and defend against the next arrival or invest in *y* eggs without any nest defense ($y > x$). A proportion (*s*) of eggs survives each competitor. Female

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 longevities 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 ($N_f = 10{,}000$, $N_s = 10{,}000$, $\mu_f = 0.01$, $\mu_e = 0.50$, 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 prespawning 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 interact to produce the seasonal declines in wait duration and longevity (fig. 2A). Late-arriving females are approaching the seasonal time constraint and must invest less in longevity to realize any reproductive success. However, early-arriving females invest more in longevity to avoid dig-up by later-breeding females. The optimal wait duration strongly depends on a female's initial allocation to longevity. All else being equal, longer-lived females have a greater waiting capacity. Thus, the seasonal decline in
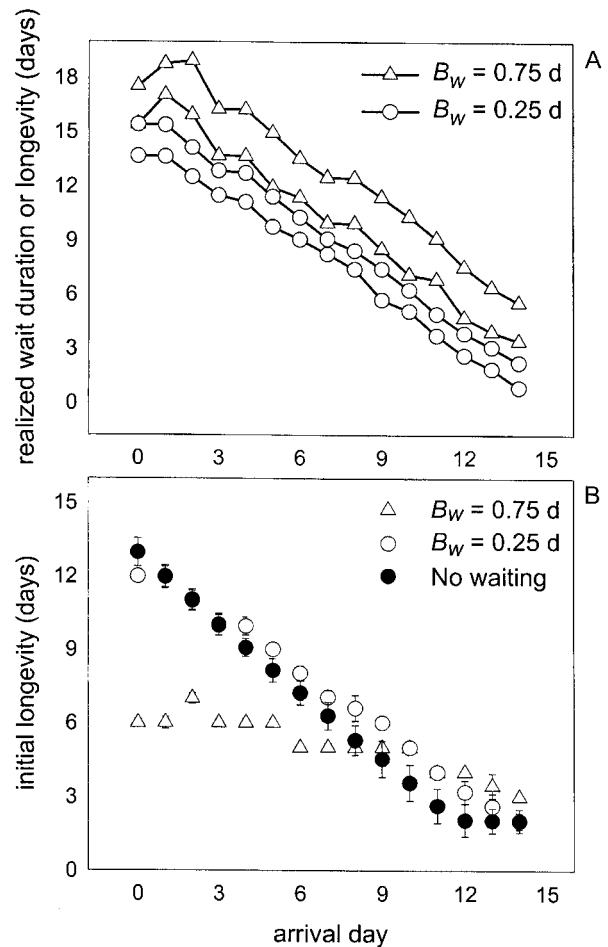
Figure 2: Output from the model that allows waiting and longevity to coevolve. The upper graph (*A*) shows the realized wait durations and longevities when the benefit of waiting, B_w, equals 0.75 d (*open triangles* and *solid lines*) or 0.25 d (*open circles* and *solid lines*). The longevity line 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.

wait duration reflects the seasonal decline in longevity. Females spend most of their time waiting while leaving sufficient time for spawning.

Methods

Study Site

We studied the reproductive phenology of female kokanee at the Meadow Creek spawning channel, British Columbia

(50°15.4′N, 116°59.8′W). With uniform water flow and gravel distribution, this 3.4-km channel provides good spawning habitat for kokanee. Further description of the channel can be found elsewhere (cf. Foote 1990; Morbey 2002*a*). Several predators (bears *Ursus americanus* and *Ursus arctos* and ravens *Corvus corax*) frequent the area and forage most intensively on kokanee at fences that block upstream migration or at shallow bottlenecks downstream of the channel. Predation in the open channel is likely minimal.

Experimental Setup

The reproductive phenology of female kokanee was monitored in three types of experimental setups using pens (the 1998 and 1999 natural variation experiments, the 1998 and 1999 density experiments, and the 1999 maturity experiment). The natural variation experiment simulated natural conditions in the channel and allowed us to investigate how arrival day influenced the reproductive phenology of females. Into a large three-walled pen, we added 48 randomly selected, newly arriving individuals of each sex over a 21-d period. All dates are presented relative to day 0 (August 25, 1998, and September 1, 1999). Other details of the experimental setup can be found elsewhere (Morbey 2002*a*). Over the 21-d arrival period in 1998, the daily average water temperature fluctuated between 9.9° and 11.4°C and showed no significant seasonal decline. Daily average water temperatures were cooler in 1999, varying between 7.8° and 10.0°C over the 21-d arrival period, and showed no significant seasonal decline.

In the 1998 and 1999 density experiments, males and females were stocked into different-sized pens at the beginning of the season to determine whether initial density influenced the reproductive phenology of females as predicted by the models. In 1998, three closed, adjoining pens of different sizes (large = 14.5 m², medium = 11.3 m², small = 7.7 m²) were constructed approximately 1.5 m from the bank. Fifteen randomly selected, newly arriving kokanee of each sex were stocked into each pen on day 2 or 3 (the small pen ended up with 13 females because two males were wrongly identified as females). The 1999 density experiment consisted of two small pens (high density; 7.6 and 7.2 m²) and two large pens (low density; 14.7 and 14.2 m²). Fifteen randomly selected, newly arriving kokanee of each sex were stocked into each pen on the same day (day 2 or 3). Morbey (2002*a*) used the large pens in a study of male mate-guarding behavior and described how the pens are set up in more detail.

A "maturity" experiment was conducted in 1999 to assess whether female state of maturity was a proximate mechanism of waiting. In Meadow Creek, a small proportion of females arrives at the spawning grounds still showing significant silver coloration and blackish backs. These very immature females can be distinguished easily and on dissection invariably have unovulated eggs within intact skeins. Into each of two large pens (14.8 and 14.7 m²), 15 very immature females and 15 randomly selected males were added on the same day (day 2 or 3). The two large, low-density pens were used as comparisons.

Data Collection

At the start of each of the three experiments, we measured the fork length of each female, assessed her maturation status, and tagged her with a unique combination of two color-coded Peterson disk tags. We determined when females initiated spawning activities (i.e., settled on territories) from daily observations of position and behavior (Morbey 2002*a*, 2003). Territorial females exhibited spawning behavior (digging or close association with a male) and aggression toward other females. Females generally defended their territories until the point of exhaustion, and takeovers were rare. Most females died without intervention, but some were killed to end the experiment (table 2). Egg retention (the number of remaining eggs) was measured in all dead females, and all females who defended territories likely spawned on the basis of their low egg retention at death. For each female, longevity (day of death minus arrival day), wait duration (settlement day minus arrival day), and reproductive life span (day of death minus settlement day) were calculated. A female's territory was considered reused if any subsequent territory was within 0.5 m (the choice of 0.5 m was arbitrary).

We also monitored the maturity of arriving kokanee over the duration of the arrival period to the channel in 1999 (days 0–36). Every second day, a random sample of at least 100 kokanee was collected downstream of the enumeration fence with a dipnet to determine daily sex ratio (Morbey 2003). We also assessed the maturation status of the females. Females were considered mature if they released eggs when gently squeezing their abdomen and immature if they did not. We did not distinguish the very immature females with the darker coloration (they comprised a small proportion of immature females).

Statistical Analyses

Annual and seasonal variation in the probability of territory reuse was assessed in the natural variation experiment using logistic regression. The full statistical model included year, arrival day, and the interaction between year and arrival day. Territory reuse was also compared among the high- and low-density pens in the 1999 density experiment using χ^2 analyses (the two pens representing each density were pooled to ensure a minimum frequency of

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[a]	Number in analyses of waiting[b]	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)

[a] Includes all females who died naturally.
[b] 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 how reproductive life span depended on year, maturation status, wait duration, arrival day, fork length, and all interactions with year and maturation status. The benefit of waiting (B_w) is 1 minus the reduction in reproductive life span with each additional day of waiting. We tried to control for any effect of female quality on reproductive life span by including fork length as a covariate. Because wait duration was not experimentally manipulated, any correlation between wait duration and reproductive life span may be confounded by quality differences between females.

All analyses were done using SAS statistical software (version 8). The α level for assessing significance was set at 0.05 for main effects and 0.15 for interactions. F statistics (based on Type III sum of squares) are presented for class variables and interactions, t statistics are presented for continuous variables, and χ^2 statistics are presented for the effects in the logistic regression analysis. In all analyses, nonsignificant interaction effects were sequentially removed before assessing the main effects. In "Results," nonsignificant interactions are not discussed, and effects with P values ranging from .05 to .10 are discussed as nonsignificant trends. Females who had to be killed to end the experiment were excluded from the analyses of longevity, and females who did not defend territories were excluded from the analyses of wait duration (table 2).
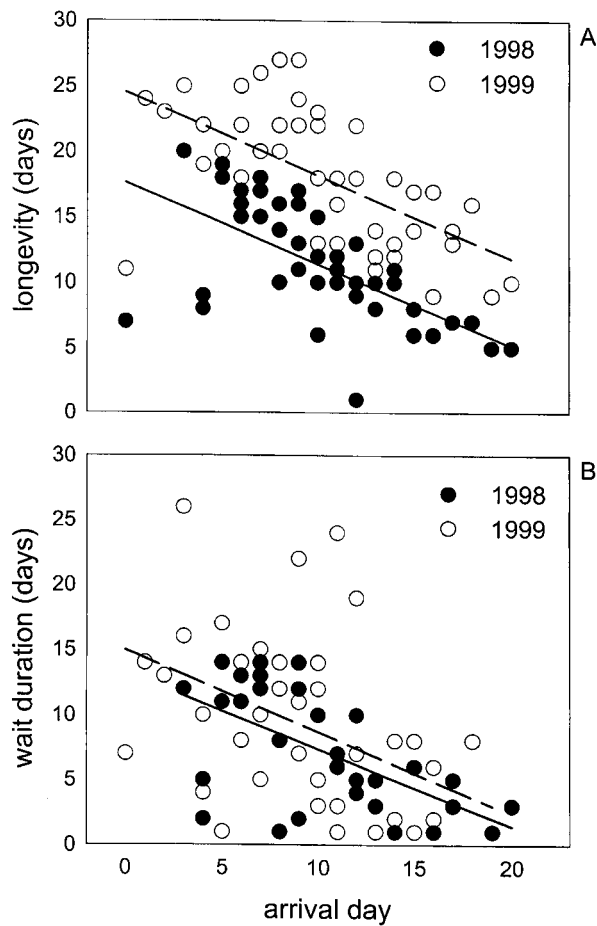
Figure 3: Seasonal declines in the longevity (*A*) and wait duration (*B*) of female kokanee in the 1998 (*solid circles, solid lines*) and 1999 (*open circles, dashed lines*) natural variation experiments. The lines represent the best-fitting linear regressions for each year. For each successive arrival day, longevity declined about 0.63 d, and wait duration declined about 0.61 d. Females lived about 7 d longer in 1999, but wait duration did not differ between years. Females who had to be killed are excluded from the longevity plot, and females who did not defend territories are excluded from the wait duration plot.

Results

Territory Reuse

In the natural variation experiment, the probability of territory reuse declined with arrival day (χ^2 = 8.156, df = 1, P = .0043) and did not differ between years (NS; statistics for overall model: Wald's χ^2 = 8.161, df = 2, P = .0169). In the 2 yr combined, 25 of the 78 females who settled (32%) had their territories reused at least once. In the 1999 density experiment, territory reuse did not differ among the high- (12 of 28 territories reused) and low-density pens (seven of 27 territories reused; χ^2 =

1.743, df = 1, P = .19). Nineteen of the 55 females who defended territories (35%) had their territories reused at least once. The maximum density of spawning females was similar to that observed in the open channel (Y. E. Morbey, unpublished data).

Seasonal Variation in Longevity and Wait Duration

In the natural variation experiment, longevity varied seasonally and differed between years (fig. 3*A*; R^2 = 0.598, F = 63.16, df = 2, 85, P < .0001). Early-arriving females lived longer than did late-arriving females (t = −7.26, df = 85, P < .0001), with longevity declining 0.629 ± 0.087 d for each successive arrival day. Females lived about 7.5 d longer in 1999 than in 1998 (F = 70.23, df = 1, 85, P < .0001). The wait duration among territorial females declined seasonally but did not differ between years (fig. 3*B*; R^2 = 0.261, F = 13.22, df = 2, 75, P < .0001; year effect: F = 1.34, df = 1, 75, P = .25). Wait duration declined 0.614 ± 0.125 d for each successive arrival day (t = −4.93, df = 75, P < .0001).

The Effect of Density

Initial female density was not an important factor affecting longevity and waiting. In the 1998 density experiment, density did not affect longevity (F = 0.611, df = 2, 26, NS) or wait duration (F = 2.059, df = 2, 19, P = .16). In the 1999 density experiment, longevity did not differ among pens and was unaffected by density (R^2 = 0.044, F = 0.72, df = 3, 54, NS). There was a trend toward longer waiting in the low-density pens (15.44 d) than in the high-density pens (12.36 d; F = 2.97, df = 1, 51, P = .09), with no difference among pens (nested within density; NS). However, the full model was not significant (R^2 = 0.060, F = 1.08, df = 3, 51, P = .37).

Proximate Factors Affecting Longevity

In the natural variation experiment, water temperature affected longevity differently in the 2 yr (F = 6.09, df = 1, 80, P = .0157), so the 2 yr were analyzed separately. In 1998, longevity was greater among territorial females (11.97 ± 4.44 d, n = 32) than among females who never defended territories (8.92 ± 3.90 d, n = 13; F = 6.75, df = 1, 39, P = .0132). There was a nonsignificant tendency for females to live longer when water temperature on arrival was warmer (t = 1.74, df = 39, P = .08). Longevity was unaffected by maturation status and fork length (P's > .3). When controlling for all proximate factors, longevity still declined with arrival day (t = −4.23, df = 39, P = .0001; statistics for full model: R^2 = 0.526, F = 8.66, df = 3, 39, P < .0001).

In 1999, maturation status was the only significant proximate factor affecting longevity ($F = 5.16$, df $= 1, 37$, $P = .0290$; statistics for full model: $R^2 = 0.490$, $F = 7.10$, df $= 5, 37$, $P < .0001$). Immature females lived for more days (20.07 ± 4.71 d, $n = 28$) than did mature females (14.27 ± 3.59 d, $n = 15$). Detecting any effect of nesting success was difficult in 1999 because only two of 43 females did not defend territories compared with 13 of 45 in 1998. Likewise, detecting an effect of maturity was difficult in 1998 because only eight of 45 females arrived mature compared with 15 of 43 females in 1999. Although fork length was unimportant within years, the greater fork length of females in 1999 (21.71 ± 0.74 cm, $n = 48$) than in 1998 (20.31 ± 0.57 cm, $n = 47$; $R^2 = 0.535$, $F = 107.14$, df $= 1, 93$, $P < .0001$) may have contributed to their increased longevity.

Female state of maturity affected longevity in the 1999 maturity experiment (fig. 4A; $R^2 = 0.411$, $F = 7.92$, df $= 3, 34$, $P = .0004$). Very immature females lived about 8 d longer (31.47 ± 3.58 d, $n = 15$) than did females in the control pens (23.83 ± 5.32 d, $n = 23$; $F = 23.06$, df $= 1, 34$, $P < .0001$). Pens (nested within treatment) did not differ significantly in longevity. Sampling of newly arriving females in 1999 indicated a marked increase in the proportion of mature females from zero at the beginning of the season to 90% at the end of the season.

Proximate Factors Affecting Wait Duration

In the natural variation experiment, water temperature affected wait duration differently in the 2 yr ($F = 5.43$, df $= 1, 70$, $P = .0227$), and arrival day affected wait duration differently depending on female maturation status ($F = 3.13$, df $= 1, 70$, $P = .08$), so years and maturity levels were analyzed separately. Mature females settled within about 4 d in 1998 (wait duration $= 3.63 \pm 2.50$ d, $n = 8$) and 1999 (wait duration $= 3.60 \pm 2.87$ d, $n = 15$). Arrival day, fork length, and water temperature on arrival did not affect the wait duration of mature females in 1998 ($R^2 = 0.339$, $F = 0.68$, df $= 3, 4$, NS) or 1999 ($R^2 = 0.015$, $F = 0.06$, df $= 3, 11$, NS).

In contrast to mature females, immature females took much longer to settle in 1998 (8.42 ± 4.41 d, $n = 24$) and 1999 (11.45 ± 6.06 d, $n = 31$). In 1998, females waited longer before defending territories when they arrived earlier ($t = -3.11$, df $= 20$, $P = .0056$) and when the water was warmer ($t = 2.47$, df $= 20$, $P = .0228$; statistics for full model: $R^2 = 0.525$, $F = 7.37$, df $= 3, 20$, $P = .0016$). Fork length did not affect wait duration significantly. In 1999, there was a nonsignificant tendency for immature females to wait less time before settling when larger ($t = -1.91$, df $= 27$, $P = .07$; statistics for full model: $R^2 = 0.168$, $F = 1.82$, df $= 3, 27$, $P = .17$). Neither ar-
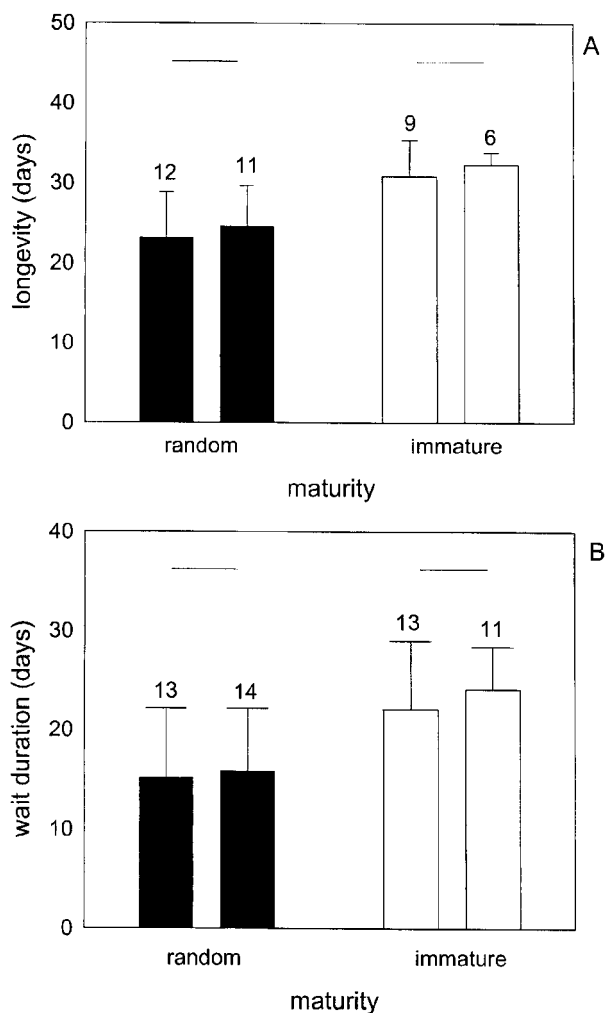
Figure 4: Very immature female kokanee lived longer (*A, open bars*) and waited longer before establishing territories (*B, open bars*) than did randomly selected females (*filled bars*) in the 1999 maturity experiment. Averages (with SDs and sample sizes) for each of the two pens in each treatment are shown. Lines above the bars join pens with statistically similar longevities or wait durations on the basis of the ANOVA results. Females who had to be killed are excluded from the longevity plot, and females who did not defend territories are excluded from the wait duration plot.

rival day nor water temperature affected the wait duration of immature females in 1999 (P's $> .25$).

Female state of maturity affected wait duration in the 1999 maturity experiment (fig. 4B; $R^2 = 0.285$, $F = 6.25$, df $= 3, 47$, $P = .0012$). Very immature females waited about 8 d longer (23.00 ± 5.83 d, $n = 24$) than did control females (15.44 ± 6.60 d, $n = 27$; $F = 18.45$, df $= 1, 47$, $P < .0001$). Pens (nested within treatment) did not differ significantly in wait duration.

The Benefit of Waiting

In the natural variation experiment, the effect of arrival day on reproductive life span differed among immature and mature females ($F = 3.64$, df $= 1, 71$, $P = .06$). Among immature females, reproductive life span depended on wait duration, year, and arrival day but not fork length ($R^2 = 0.645$, $F = 22.72$, df $= 4, 50$, $P < .0001$), and among mature females, reproductive life span depended on year and arrival day but not wait duration or fork length (fig. 5; $R^2 = 0.785$, $F = 16.40$, df $= 4, 18$, $P < .0001$). Immature females who waited an additional day spent 0.351 ± 0.077 d fewer in egg deposition and territory defense (fig. 5A; $t = -4.57$, df $= 50$, $P < .0001$). Thus, waiting for 1 d increased the longevity of immature females by about 0.65 d. The lack of a significant effect of fork length suggests that high-quality females did not spend more time waiting or more time in spawning activities. Reproductive life span was greater in 1999 than in 1998 among both immature ($t = 28.63$, df $= 50$, $P < .0001$) and mature ($t = 28.15$, df $= 18$, $P < .0001$) females (fig. 5).

Discussion

Game-theoretic reasoning shows that in Pacific salmon, both longevity and waiting can be adjusted as tactics to reduce nest dig-up. In line with the hypotheses of McPhee and Quinn (1998) and Hendry et al. (1999), and as recorded in several populations (Neilson and Banford 1983; Perrin and Irvine 1990; McPhee and Quinn 1998; Hendry et al. 1999; but see van den Berghe and Gross 1986; Fukushima and Smoker 1997), our models predict a seasonal decline in female longevity. In Meadow Creek kokanee, the longevity of females declined about 0.6 d for each successive arrival day.

The models also demonstrate that early-arriving females can prolong longevity and further reduce dig-up by conserving energy during a prespawning waiting phase. Kokanee in Meadow Creek appear to use this strategy (cf. Foote 1990) because wait duration declined seasonally and accounted for most of the variation in longevity within years. Quinn et al. (2000) also observed a seasonal decline in the period between arrival to spawning areas and gonadal maturation in chinook salmon. Given the widespread occurrence of prespawning waiting in salmon populations (e.g., pink salmon: Mattson and Rowland 1963; sockeye salmon: Hoopes 1972; Brett 1995), a seasonal decline in wait duration may be a common dig-up avoidance tactic. Waiting could have consequences on female productivity. As waiting becomes less energetically expensive, females should allocate more of their somatic energy to fecundity. As waiting becomes more expensive, females
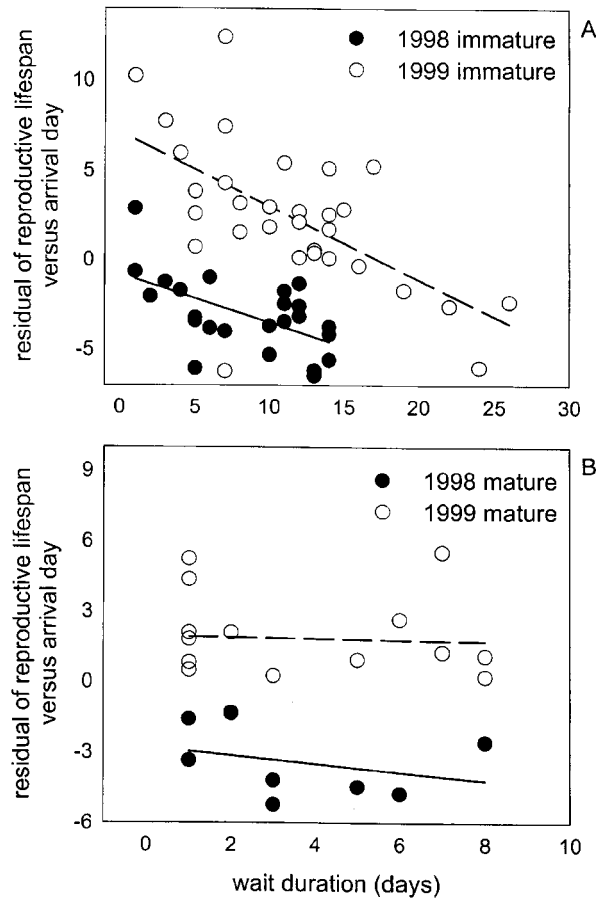
Figure 5: Effect of wait duration on the reproductive life span of female kokanee who arrived immature (*A*) and mature (*B*) in 1998 (*filled circles, solid lines*) and 1999 (*open circles, dashed lines*). Arrival day also affected reproductive life span, so the residual of reproductive life span versus arrival day is presented on the *Y*-axis in both plots. The lines represent the best-fitting linear regressions for each year. Among immature females, reproductive life span declined 0.35 d for each additional day of waiting. Among mature females, there was less variation in wait duration than there was among immature females (compare the ranges of wait duration in the two plots), and reproductive life span was not affected by wait duration. Reproductive life span was greater in 1999 than in 1998, regardless of maturity.

should invest less in fecundity than in the nonwaiting situation.

Our game-theoretic models reveal the conditions favoring seasonal declines in longevity and waiting, and the life history of kokanee and the specific characteristics of the Meadow Creek population are consistent with these conditions. First, dig-up is probably a significant source of offspring mortality. The digging activity of females creates obvious depressions in the gravel of the Meadow Creek spawning channel and probably subjects developing

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, μ_e, and C_e. However, by using realistic guesses for the set of parameters ($N_f = 10,000$, $N_s = 10,000$, $\mu_f = 0.01$, $\mu_e = 0.50$, $C_e = 10$ eggs, $B_w = 0.65$ d), the model predicts prolonged waiting and longevity comparable to when $B_w = 0.75$ in figure 2A.

Our game-theoretic models suggest some predictions, and depending on whether females respond at evolutionary or ecological time scales, these should be testable among or within populations. For example, wait duration may be responsive to ecological factors experienced on the spawning grounds, whereas allocation to longevity is likely fixed before arrival at spawning areas. The current study provided an opportunity to test the prediction of increased wait duration with increased female density. However, the role of density was unclear. In the 1998 density experiment, females seemed to settle on territories sooner in the lowest-density pen, but insufficient power made it impossible to detect statistical significance. In contrast, females tended to settle sooner in the high-density pens in 1999 when the sample sizes were larger. Many explanations are possible for this annual difference, including different experimental setups among years or differences in territory quality among pens. Alternatively, the absence of a significant density effect could reflect the similarity in territory reuse among high- and low-density pens. A pressing question is whether females can vary their wait duration in response to ecological cues of the probability of dig-up.

Parasitism of Nest Defense

The longevity model predicts that the earliest-arriving females should adopt an alternative phenological tactic and invest little in longevity (and therefore wait duration) when the probability of dig-up is low or when dig-up avoidance tactics are costly. Under these conditions, females can take advantage of the inadvertent defense of later-arriving, longer-lived females who reoccupy their territories. This apparent parasitism of nest defense is reminiscent of egg dumping in birds (Petrie and Møller 1991) and insects (Brockmann 1993), although in contrast to egg dumping, it may not be costly for females to defend an additional clutch. Such a pattern may not have been observed in kokanee because of inappropriate conditions, and the presence of this tactic in other populations is unknown. Further modeling is necessary to determine whether the two dig-up avoidance tactics (egg protection through parental defense and egg protection through inadvertent defense by others) could coexist among females with similar arrival timing.

Proximate Explanations of Longevity and Waiting

Female state of maturity was an important factor producing the seasonal decline in longevity and wait duration of females. In general, immature females took longer to settle on territories and longer to die than did mature females. An effect of maturation status on longevity was not detected in the 1998 natural variation experiment possibly because of the relatively low number of females who arrived mature. The seasonal decline in the maturity of newly arriving females is consistent with the seasonal decline in wait duration and longevity, and female state of maturity accounted for most of the seasonal variation in longevity in 1999. Another important proximate factor affecting longevity, which was not measured in this study, is energy allocation to somatic tissue. In anadromous sockeye salmon, early-arriving females allocate less energy to gonads and retain more energy for metabolism and thus live longer compared with late-arriving females (Hendry et al. 1999).

Ectoparasite load and water temperature may have contributed to the greater longevity of females in 1999 than in 1998. In 1998, most females hosted multiple leeches throughout their residence on the spawning grounds and hosted extensive fungal growth as they senesced. In contrast, leeches were uncommon and fungal infections were minimal in 1999. The greater parasite load in 1998, coupled with slightly warmer water and the smaller size of females, may have accelerated senescence in 1998 (cf. Brett 1995). The metabolic rate of salmonids increases with water temperature because they are poikilotherms (Fry 1971).

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; Parenskiy 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 seasonal declines in wait duration are unknown.

Fourth, living longer may allow females to spawn over more days as a hedge against uncertainty in the timing of optimal environmental conditions or territory reuse (see Philippi and Seger 1989). However, females typically spawn over a short period of time (3–5 d) relative to the duration of waiting (current study) or relative to the duration of territory defense (McPhee and Quinn 1998). Fifth, females in poorer condition (and with fewer energy reserves) may arrive later because they must first acquire sufficient energy reserves for breeding or may delay breeding as an adaptive tactic (e.g., Schultz et al. 1991). The lack of any seasonal variation in fork length in kokanee females is inconsistent with this hypothesis.

Why Wait Instead of Arrive Late?

The model demonstrates that phenological strategies incorporating waiting can be evolutionarily stable. But this begs the question of why females would arrive early and wait rather than arrive late and not wait. The latter would reduce dig-up as effectively, would minimize the time spent exposed to predators on the spawning grounds before spawning, and may allow females to invest more in fecundity. A common idea is that waiting is necessary for the completion of reproductive maturation (Groot and Margolis 1991). This explanation is better viewed as a mechanism of waiting than as an alternative adaptive hypothesis or a physiological constraint. If females benefit from waiting because of reduced dig-up (or if waiting serves a different adaptive function), it is possible that arriving immature is a mechanism for prolonging waiting. Furthermore, a necessary waiting phase is inconsistent with the arrival of mature females later in the season. If state of maturity was a physiological constraint and waiting was not adaptive, newly arriving, mature females should have greater reproductive success than do newly arriving, immature females.

Several adaptive hypotheses may help explain why some female salmon arrive early and wait. All of these expla-

nations imply differential benefits of early arrival for different individuals; otherwise, all females would arrive early and wait. Salmon may benefit by migrating while immature even if this necessitates prespawning waiting. Given that very immature females are cryptic in coloration (Y. E. Morbey, personal observation), a potential benefit of migrating while immature is safety from predators. Migrating while immature also may improve energy efficiency. In the latest stages of gonadal maturation, female sockeye salmon mobilize muscle protein (Hendry 1998) and, as a result, may compromise their swimming performance (Davison and Goldspink 1977). Concluding the feeding stage and migrating early may also allow females to avoid predators in the premigratory habitat (e.g., Kootenay Lake for Meadow Creek kokanee).

Early arrival followed by waiting near suitable spawning areas may also be advantageous if it allows nest-searching females to minimize aggression with territorial females. Later-arriving females must migrate past aggressive, territorial females and risk injury from attacks. Another possible advantage of arriving immature early in the season is flexibility in spawning timing, which could be important when social or physical conditions are unpredictable or when females are prevented from spawning. Although both arrival to spawning areas and maturation timing have a strong genetic basis (e.g., chinook salmon: Quinn et al. 2000), less is known about the ability of female salmon to vary their wait duration in response to internal or external stimuli. Flexibility in breeding timing has been observed in brook trout under a varying social environment (Blanchfield 1998). The best evidence for flexible spawning timing in kokanee is that in 1998, immature females delayed territory settlement when the water was warmer. Furthermore, when controlling for arrival day, immature female kokanee waited for a variable length of time and spent fewer days in territory defense when waiting for a longer period.

Guarding Behavior and the Benefits of Being Last

Our model of tactical reproductive timing highlights an important benefit of being late relative to others. Although our model considered the specific case of nest guarding by female Pacific salmon, the predictions are more general and can apply to other species that guard their nests against conspecific takeovers (e.g., burying beetles *Nicrophorus orbicollis*: Scott 1990) or guard their eggs against cannibalism (see Clutton-Brock 1991 for a review of parental care). In such species, our model would predict a longer period of parental care and perhaps delayed breeding among the earliest breeders. Nest defense against conspecifics is not the only phenomenon providing benefits to being last. For example, postcopulatory mate guarding by males reduces

the risk of extrapair copulations and results in greater paternity assurance (Birkhead and Parker 1997). Similar to cascading selection to be early (Kokko 1999), cascading selection to minimize extrapair copulations could play an important role in prolonging the optimal duration of postcopulatory mate guarding.

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