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Adaptive variation in senescence: reproductive lifespan in a wild salmon population

Andrew P. Hendry[1*], **Yolanda E. Morbey**[2], **Ole K. Berg**[3] **and John K. Wenburg**[4]

[1]*Redpath Museum and Department of Biology, McGill University, 859 Sherbrooke Street West, Montréal, Québec H3A 2K6, Canada*
[2]*Department of Zoology, University of Toronto, 25 Harbord Street, Toronto, Ontario M5S 3G5, Canada*
[3]*Department of Biology, Norwegian University of Science and Technology NTNU, N-7491 Trondheim, Norway*
[4]*Conservation Genetics Laboratory, Alaska Region, US Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, AK 99503, USA*

The antagonistic pleiotropy theory of senescence postulates genes or traits that have opposite effects on early-life and late-life performances. Because selection is generally weaker late in life, genes or traits that improve early-life performance but impair late-life performance should come to predominate. Variation in the strength of age-specific selection should then generate adaptive variation in senescence. We demonstrate this mechanism by comparing early and late breeders within a population of semelparous capital-breeding sockeye salmon (*Oncorhynchus nerka*). We show that early breeders (but not late breeders) are under strong selection for a long reproductive lifespan (RLS), which facilitates defence of their nests against disturbance by later females. Accordingly, early females invest less energy in egg production while reserving more for nest defence. Variation along this reproductive trade-off causes delayed or slower senescence in early females (average RLS of 26 days) than in late females (reproductive lifespan of 12 days). We use microsatellites to confirm that gene flow is sufficiently limited between early and late breeders to allow adaptive divergence in response to selection. Because reproductive trade-offs should be almost universal and selection acting on them should typically vary in time and space, the mechanism described herein may explain much of the natural variation in senescence.

Keywords: ageing; aging; reproductive trade-offs; energy allocation; adaptation-by-time; sockeye salmon

1. INTRODUCTION

Evolutionary theory posits that the strength of selection declines with advancing age, leading to two major mechanisms by which senescence can evolve (Medawar 1952; Williams 1957; Hamilton 1966; Rose 1991; Partridge & Gems 2002). In one (antagonistic pleiotropy; AP), genes or traits that enhance early-life performance (i.e. survival or reproduction) have detrimental effects on late-life performance. In the other (mutation accumulation; MA), deleterious mutations that are expressed late in life accumulate to a greater degree than those expressed early in life. AP and MA have been examined in a number of laboratory experiments, which have variously yielded inconclusive results, supported AP or supported MA (Kirkwood & Austad 2000; Hughes *et al.* 2002; Partridge & Gems 2002). However, determining which mechanism is most important in nature requires studies of wild populations, and yet such studies are surprisingly rare.

Any theory seeking to explain senescence must account for the dramatic variation observed in nature (Promislow 1991; Rose 1991; Ricklefs 1998; Reznick *et al.* 2002). Most studies examining such variation have compared different populations or species, attributing the observed variation to differences in extrinsic mortality. In general, higher rates of extrinsic mortality should lead to fewer individuals reaching a given age, and therefore to weaker selection on genes expressed at that age. Accordingly, higher rates of extrinsic mortality are typically associated with senescence that starts sooner or progresses more rapidly (Austad 1993; Tatar *et al.* 1997; Ricklefs 1998; Dudycha & Tessier 1999), although exceptions are possible (Promislow 1991; Abrams 1993; Williams & Day 2003). An additional effect is that the strength of selection acting on age-specific mutations will be influenced by how fecundity changes with age (Williams 1957; Reznick *et al.* 2002).

Studies of natural populations have thus demonstrated that variation in senescence can be consistent with evolutionary expectations, but most of these studies cannot discern the underlying mechanism (AP versus MA). In general, AP can be inferred if increased early-life performance is accompanied by earlier or faster senescence, i.e. a trade-off between early-life and late-life performances (Partridge & Gems 2002). Unfortunately, studies that examine natural variation in senescence rarely test for such trade-offs (for an exception see Dudycha & Tessier (1999)). Here, we take the novel approach of investigating variation in senescence *within* a natural population, showing that it is adaptive and the result of AP.

AP can be caused by several processes, one of which is a trade-off between energy invested in current reproduction and energy reserved for subsequent tasks (e.g. reproductive effort versus future survival; Roff 1992). All else being equal, individuals investing more energy in current reproduction should exhibit earlier or faster senescence. The optimal allocation between current reproduction and subsequent tasks should then vary with the strength of selection acting on each component. The

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[*] Author for correspondence (andrew.hendry@mcgill.ca).

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study of such trade-offs is greatly simplified in organisms that breed only once in their life (semelparous), use stored energy to fuel reproduction (capital breeding) and defend their nest but do not otherwise care for their young. Here, the primary trade-off for females is between energy invested in egg production and energy retained as somatic stores for use during subsequent nest defence. Increased investment in egg production should lead to decreased somatic energy, which should cause earlier or faster senescence and a shorter period of nest defence. Moreover, groups experiencing stronger selection for nest defence should decrease investment in egg production and increase investment in somatic stores, allowing delayed or slower senescence. We demonstrate how this mechanism generates adaptive variation in senescence in sockeye salmon (*Oncorhynchus nerka*).

Sockeye salmon are semelparous capital breeders, and females defend their nests after oviposition but do not otherwise care for their young (Burgner 1991; Brett 1995). Maturing adults return from the ocean to their natal lake, where they complete maturation adjacent to their natal stream (Burgner 1991). Mature females then enter the stream, select a nest site, dig a nest in the gravel, oviposit in the nest (with simultaneous external fertilization by males), cover the eggs with gravel and finally defend the nest until death (Burgner 1991). Nest digging and egg deposition by a given female typically lasts a few days, with subsequent nest defence lasting days to weeks (McPhee & Quinn 1998; Hendry *et al.* 1999, 2001*a*). Barring predation, death results from rapid physical deterioration (senescence) associated with the depletion of energy stores (Dickhoff 1989): breeding females deplete *ca.* 74% of their energy stores (Brett 1995; Hendry & Berg 1999). The length of time between the start of breeding by an individual and its death (reproductive lifespan; RLS) thus provides an indication of how early or rapidly females senesce.

Principal factors determining the reproductive success of female sockeye salmon include egg number, egg size, nest quality and nest defence (Foote 1990; McPhee & Quinn 1998; Essington *et al.* 2000; Quinn *et al.* 2001; Fleming & Reynolds 2004; Morbey & Ydenberg 2003). Nest defence is important because it influences whether or not a female's nest is superimposed (dug up) by another female. Superimposition is common in dense breeding populations, where it causes very high egg mortality (McNeil 1964; Fukushima *et al.* 1998; Essington *et al.* 2000). Nest defence is an effective countermeasure because a resident female is rarely displaced by an intruding female (Foote 1990; McPhee & Quinn 1998; Morbey & Ydenberg 2003). Selection should therefore favour nest defence to a degree that depends on a female's relative breeding date. Early females should be subject to strong selection for a long RLS to defend their nests against the many females that will arrive later. Conversely, late females need not live very long because few females will arrive even later to potentially disturb their nests. We experimentally demonstrate this difference in selection and show how it causes adaptive variation in energy allocation and RLS between early and late breeders. Our results provide evidence of adaptive variation in senescence driven by AP.

2. MATERIAL AND METHODS

First, we determined the relationship between breeding date and RLS. In 1995 and 1996, we used a seine net to collect maturing females from Lake Nerka at the mouth of Pick Creek, Alaska (59°33′00″ N, 159°04′18″ W). Each female was anaesthetized with MS222, tagged with an individually coded 2 cm Peterson disc tag and released back into the lake. These capture and tagging procedures are standard for salmon and do not influence breeding behaviour or RLS (Quinn & Foote 1994; McPhee & Quinn 1998; Hendry *et al.* 1999, 2001*a*; Quinn *et al.* 2001). After a tagged female completed maturation in the lake, she entered the creek and immediately engaged in her first breeding activity. Thus, the date a female entered the creek was taken as the date she completed the transition to the breeding state.

We performed daily surveys of the entire 2 km length of the creek to determine each female's breeding date (the date she was first observed in the creek) and RLS (one plus the last day a female was observed alive minus the breeding date). This metric standardized RLS (and therefore senescence) to the date that each individual underwent the critical life-history transition, as opposed to a particular calendar date. Breeding date and RLS estimates were very accurate because Pick Creek has very clear and shallow water that allows for the easy identification and observation of all tagged individuals. For more details on these procedures, see Hendry *et al.* (1999, 2001*a*). We also examined the carcasses of all dead tagged fishes to determine the cause of death: senescent (no obvious wounds) or killed by a predator (very obvious wounds; see Quinn *et al.* 2001).

Using these data, we first considered the relationship between breeding date and RLS for all tagged fishes recovered at death. However, because females killed by predators cannot be used to establish patterns of senescent mortality, we focused all subsequent analyses on females known to have died of senescence (1995, $n = 69$; 1996, $n = 113$). (In this population, the length of time a female has been breeding in the creek does not influence the probability that she will be killed by a bear, even after taking breeding date into consideration (Gende *et al.* 2004).)

Second, we quantified energy allocation in relation to breeding date. In 1996, 10 females that had just started breeding (judged by their physical appearance; see Quinn & Foote 1994) were captured in the creek and killed on 21 July (early), 1 August (middle) and 12 August (late). Each carcass was divided into eggs and soma, which were separately weighed, homogenized in a blender and frozen at −20 °C. These samples were then analysed using standard biochemical assays that measure water, fat, protein and ash content (Hendry & Berg 1999; Hendry *et al.* 1999). The amounts of energy each female had allocated to her eggs and her soma were estimated by multiplying the amounts of fat and protein in each tissue by the appropriate energy equivalents: 36.4 kJ g^{-1} for fat and 20.1 kJ g^{-1} for protein (Brett 1995). Only a subset of the somatic energy in a fish is available for subsequent metabolism, simply because some energy remains even at death. Similar biochemical analyses of 23 tagged females collected at their senescent death showed that the amount of somatic energy at death averaged 4277 kJ (s.e. = 211 kJ) and was not correlated with breeding date ($r^2 = 0.01$, $p = 0.627$). We therefore estimated the amount of somatic energy 'available' for metabolism as a female's total somatic energy at the start of breeding minus 4277 kJ (Hendry *et al.* 1999).

Third, we estimated gene flow between early and late breeders in Pick Creek. In 1997, 25 males and 25 females that had just started breeding (judged by their physical appearance) were captured in Pick Creek on 22 July (early) and 20 August (late). A small piece of adipose fin tissue was removed from each fish and used to screen for genetic variation at nine microsatellite loci: *Ots107*, *Ots3*, *One102*, *One103*, *One105*, *One108*, *One109*, *One111* and *One114*. Our goal in this part of the study was to determine whether gene flow was sufficiently limited between early and late breeders to allow adaptive divergence in response to selection. Adaptive divergence is constrained by the *rate* of gene flow (i.e. the *proportion* of genes exchanged, m; Hendry *et al.* 2001*b*) rather than the effective number of migrants ($N_e m$). We therefore used the maximum-likelihood coalescent program MIGRATE (Beerli & Felsenstein 1999) to estimate m between early and late breeders. Further details of the microsatellite analyses are provided in electronic Appendix A (available on The Royal Society's Publications Web site).

Fourth, we estimated the cost to a female of her nest being superimposed. In 2000, we injected non-toxic dye (Brilliant Black BN, Sigma-Aldrich product number 211842, dissolved in Ringers solution) into the body cavities of females that we tagged for superimposition experiments (described below). This procedure dyed a female's eggs before oviposition without influencing her breeding behaviour. We then monitored each female to see whether her nest was superimposed: i.e. the central nest area substantially disturbed by another nest-building female. At the end of the breeding season, we fully excavated the nests of two females whose eggs we had dyed. Each nest site was well defined and located in shallow water, but one was clearly superimposed by a female with undyed eggs, whereas the other was clearly not superimposed. Excavations involved carefully removing by hand all of the gravel from the entire nest area (*ca.* 2 m^2) to a depth of at least 25 cm (which exceeds the depth at which females bury their eggs). All dyed and undyed eggs thus exposed were collected in a net. We then partially excavated the nests of two other females with dyed eggs: one superimposed by an undyed female and the other not superimposed. For these partial excavations, we used a shovel to dig through the gravel and a net to collect any dyed and undyed eggs that were exposed.

Statistical analyses were based on the numbers of dyed and undyed eggs recovered from each excavated nest site. For the full excavations, we first determined the expected number of eggs deposited by each female based on her body length (superimposed = 414 mm; not superimposed = 514 mm) and the known relationship between length and egg number in Pick Creek ($\log_e(\text{egg number}) = -5.57 + 2.26 \times \log_e(\text{length})$; $n = 28$, $r^2 = 0.59$, $p < 0.001$). We then used a one-tailed Fisher's exact test of the prediction that the ratio of observed dyed eggs to expected dyed eggs was lower for the nest that was superimposed than for the nest that was not superimposed. For the full and partial excavations considered together, we used a one-tailed t-test of the prediction that the proportion (arcsine square-root transformed) of excavated eggs that were dyed was lower for nests that had been superimposed ($n = 2$) than for nests that had not been superimposed ($n = 2$). The number of nests we excavated was few because excavations were very time consuming and the results were unambiguous.

Fifth, we determined how superimposition imposes selection on RLS. In 2000, we established grids above two stream sections, each 35 m in length. Newly mature females arriving in each section were captured in salmon landing nets, individually tagged (as above) and released to allow natural breeding. Each female was then observed daily to determine the location of her nest, how long she defended her nest and whether or not her nest was superimposed. To increase variation in RLS and generate phenotypes not typically present in the population (early breeders with a short RLS), two or three tagged females defending their nests were captured and killed every 2–3 days. The experiment recorded the fates (superimposed or not) of the nests of 136 females, out of which 70 started breeding 'early' (21–30 July, average date of 25 July) and 66 started breeding 'late' (3–20 August, average date of 9 August). We then used standard regression methods to determine the effect of each trait (breeding date and RLS) on relative fitness (see electronic Appendix A for details). When interpreting these results, it is important to remember that they reflect selection resulting only from superimposition.

Sixth, we modelled and interpreted age-specific survival using the LIFETEST and LIFEREG procedures in SAS v. 8.02 (Allison 1995). These analyses were restricted to tagged females that died of senescence and had known breeding and death dates. LIFETEST estimates age-specific survival probabilities and confidence limits using the Kaplan–Meier method, as well as age-specific hazard functions using the life-table method. Plots of these and related functions provide information for assessing the best-fit parametric survival model. LIFEREG then uses maximum likelihood to estimate the parameters of a specified survival model. We used LIFETEST to compare the age-specific survivals of early and late females in 2000, and LIFEREG to estimate parameters and choose among nested exponential, Weibull and generalized gamma models for females in 1995, 1996 and 2000. Log-likelihood ratio tests were used to compare nested models and breeding date was included as a covariate (β_1).

Finally, we applied a game-theory model of reproductive timing (Morbey & Ydenberg 2003) to the Pick Creek population. This model provided a more refined test of adaptive expectations because it simultaneously considered multiple factors that influence female reproductive success. The model derives the evolutionarily stable strategy (ESS) RLS for female salmon that start breeding on different dates. For this analysis, we assumed that female fitness was influenced by the number of eggs deposited, the probability of superimposition and the number of eggs lost in the event of superimposition. We parameterized these effects for the Pick Creek population (see electronic Appendix A) and ran the model for 1000 generations to determine whether the seasonal decline in RLS was an ESS.

3. RESULTS

For fishes that died of all causes (senescence and predation), RLS was negatively correlated with breeding date (years pooled: $r^2 = 0.328$, $p < 0.001$; see also Hendry *et al.* 2001*a*). For fishes that died of senescence, the relationship was even stronger (years pooled: $r^2 = 0.525$, $p < 0.001$; see also Hendry *et al.* 1999), was evident in both years (figure 1) and was particularly dramatic. For example, females that started breeding on the first day of the breeding season in 1996 lived a predicted 22 subsequent days, whereas those that started breeding on the twenty-third day of the breeding season lived a predicted 11 subsequent days.

The longer RLS of early females was achieved through the allocation of less energy to eggs and more energy to somatic stores (figure 2). Early females contained an average of 5344 kJ of energy when they started breeding

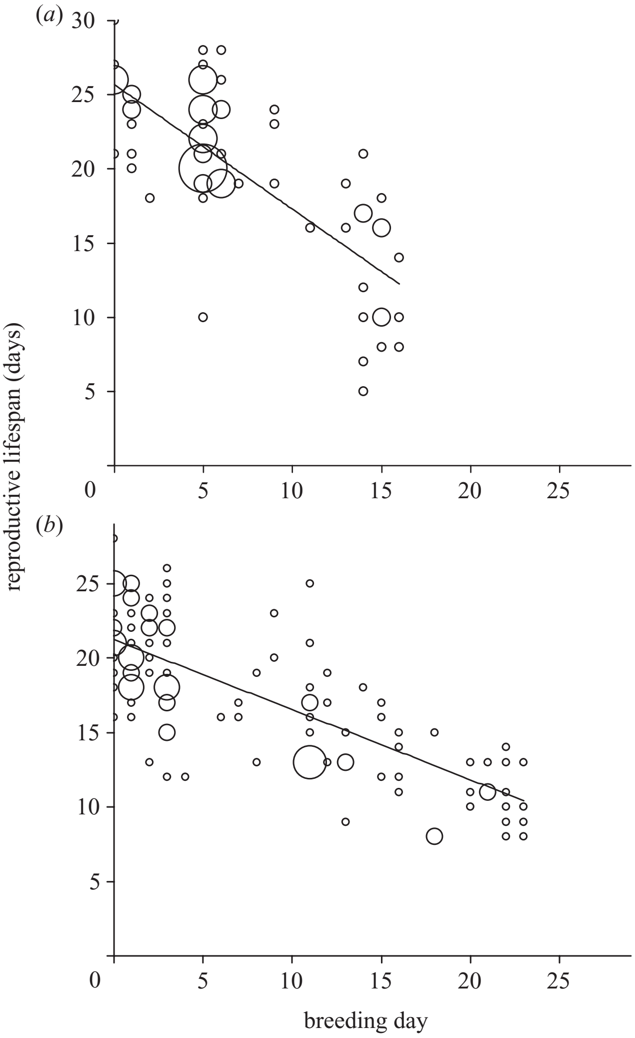

Figure 1. The relationship between breeding day (date of first breeding) and reproductive lifespan (1+ date of death – date of first breeding) for female sockeye salmon in Pick Creek. (*a*) 1995 females ($r^2 = 0.56$, $p < 0.001$); (*b*) 1996 females ($r^2 = 0.53$, $p < 0.001$). Circle diameter is proportional to the number of data points for a given combination.

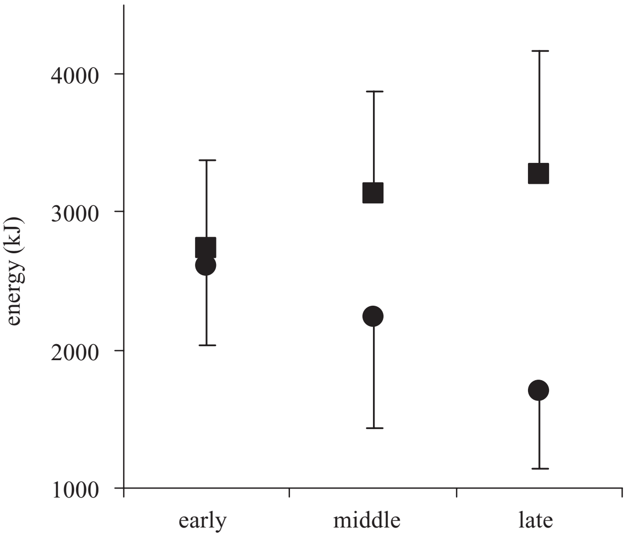

Figure 2. The effect of breeding day on the trade-off between energy allocated to gonads (squares) and somatic stores available for subsequent metabolism (circles). Early and late breeders show different allocation patterns: $p = 0.035$ for the interaction term in a two-way ANOVA analysing breeding date (early, middle, late) and energy allocation (gonad, available soma). Error bars represent 95% CIs.

(excluding the energy that would remain at death), divided almost equally between eggs (2731 kJ) and soma (2613 kJ). Late females had 4984 kJ of energy when they started breeding, and allocated a greater proportion to eggs (3280 kJ) than to soma (1704 kJ). Gonadosomatic index (percentage of total body mass comprising eggs) was 17.8% for early breeders, 20.0% for middle breeders and 21.8% for late breeders (one-way ANOVA: $p = 0.001$; Tukey tests: early versus middle, $p = 0.083$; middle versus late, $p = 0.135$; early versus late, $p = 0.001$). In short, early and late females occupy opposite extremes along the trade-off between energy invested in eggs and energy reserved for active metabolism, with the result that late females have a shorter RLS than early females.

Neutral genetic divergence (microsatellites) between early and late breeders was low (see electronic Appendix A), as expected for samples taken only 29 days apart in a small stream. From the program MIGRATE (N_e, effective population size; μ, mutation rate; m, migration rate), maximum-likelihood parameter estimates were $4N_e\mu = 2.7457$ for late breeders, $4N_e\mu = 1.7311$ for early breeders, $4N_em = 5.7219$ from early to late breeders and $4N_em = 4.6249$ from late to early breeders. Assuming $\mu = 10^{-4}$ (a reasonable mutation rate for microsatellites), these estimates would yield a total N_e of 11 192 and a total N_em of 2.5867, generating a gene-flow estimate of $m = 0.000\,23$. If instead, $\mu = 10^{-3}$ then $m = 0.0023$, or if $\mu = 10^{-5}$ then $m = 0.000\,023$. All of these rates of gene flow are low enough that substantial adaptive divergence is possible in the presence of divergent selection (see figures in Hendry *et al.* 2001*b*).

Superimposition imposed a substantial fitness cost. For our full excavations, the nest that was superimposed had 532 dyed eggs and the nest that was not superimposed had 2664 dyed eggs. The expected numbers of eggs in these nests were 3128 (95% confidence interval (CI) of 2905–3370) and 5102 (95% CI of 4448–5852), respectively. Thus, we recovered a substantially smaller proportion of the expected eggs from the nest that was superimposed (17.0%) than from the nest that was not superimposed (52.2%) ($p < 0.001$). For our full and partial excavations combined, a smaller proportion of the excavated eggs were dyed in the two nests that were superimposed (19.3% and 37.6%) than in the two nests that were not superimposed (73.8% and 89.0%) ($t = 4.03$, $p = 0.028$). These results unambiguously support previous work in showing that females whose nests are superimposed lose a substantial fraction of their eggs.

Directional selection resulting from superimposition favoured late breeding and a long RLS (table 1) because both reduced the probability of superimposition. However, it is important to remember that other selective factors will favour early breeding (e.g. better access to preferred nesting sites and earlier emergence of offspring) and short RLS (e.g. increased energy for egg production). Significant negative correlational selection (quadratic

Table 1. Estimates of how superimposition imposes selection on breeding date and RLS for female sockeye salmon in Pick Creek. (Shown are partial logistic regression coefficients, their *p*-values and the equivalent linear coefficients (see electronic Appendix A for details).)

type of selection	trait	logistic coefficient (± s.e.)	*p*-value	linear coefficient
total directional	breeding date	2.109 ± 0.404	< 0.001	0.289
	RLS	0.118 ± 0.186	0.525	0.026
direct directional	breeding date	3.591 ± 0.617	< 0.001	0.312
	RLS	1.990 ± 0.461	< 0.001	0.173
quadratic (univariate)	breeding date	−1.269 ± 0.723	0.079	−0.201
	RLS	−1.322 ± 1.107	0.232	−0.193
quadratic (bivariate)	breeding date + RLS	−3.580 ± 1.310	0.006	−0.545

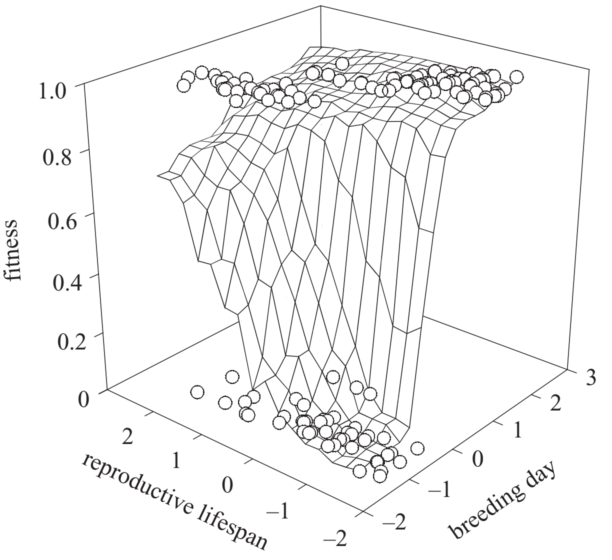

Figure 3. Cubic spline estimation (Schluter & Nychka 1994) of the fitness surface relating the probability of superimposition (0 = superimposed, 1 = not superimposed) to breeding day and reproductive lifespan (RLS), each standardized by subtracting the mean and dividing by the standard deviation for female sockeye salmon in Pick Creek. For breeding day, smaller values indicate earlier breeding. For RLS, smaller values indicate a shorter life.

bivariate coefficient in table 1) indicated that superimposition favoured early breeding and long RLS, late breeding and short RLS or both. We discriminated among these possibilities by examining selection on RLS separately for early and late females. This partitioning revealed strong selection for a long RLS in early females (logistic coefficient (± s.e.) = 2.173 ± 0.516, $p < 0.001$, linear coefficient = 0.147) but not in late females (logistic coefficient = −2.020 ± 0.963, $p = 0.036$, linear coefficient = −0.037) (figure 3). The longer RLS of early females is clearly adaptive with respect to superimposition.

Analyses of age-specific survival rates revealed a strong signature of senescence that differed between early and late breeders. In 2000, the period of rapid senescence preceding death corresponded to marked age-specific decreases in survival and increases in hazard (figure 4). Moreover, late females began rapid senescence sooner after they began breeding (figure 4). The Weibull model was qualitatively the most appropriate because of near-linear relationships between ln(−ln(survival distribution function)) and ln(time since arrival). Using Lifereg with breeding date as a covariate, a constant-hazard model (exponential model) was rejected in favour of a Weibull model in 1995, 1996 and 2000 ($p < 0.001$; see electronic Appendix A). The increase in hazard for each additional day after a female started breeding was 23.0% in 1995, 17.7% in 1996 and 17.8% in 2000. In each year, late-breeding females had shorter expected times until death.

The ESS model predicted a strong seasonal decline in RLS for Pick Creek females. The earliest females were predicted to live for 73% of the arrival period (26 days in a 35 day season), which was similar to the figure observed for early females in Pick Creek (figure 1). The latest females were predicted to live for the minimum period that we set for successful egg deposition (5 days). The observed RLS of late females in Pick Creek was longer than this prediction (figure 1), but we did not tag the very latest females. Moreover, females may hedge against uncertainty in the length of the breeding season and in their relative breeding date. The model also predicted that early females should suffer a high probability of superimposition (*ca.* 40%), a level slightly lower than but qualitatively similar to that observed in Pick Creek (54% based on the females who began breeding within the first 5 days of the 2000 experiment and whose lives we did not artificially shorten). Thus, the seasonal decline in RLS in Pick Creek is remarkably consistent with ESS predictions.

4. DISCUSSION

We propose a two-part mechanism for the evolution of adaptive variation in senescence. The first part is a trade-off between energy invested in current reproduction and energy reserved for subsequent tasks; in our system, this trade-off was between energy invested in egg production and energy reserved as somatic stores for post-oviposition nest defence (figure 2). The second part is spatial or temporal variation in the strength of selection acting on the elements of the trade-off. In our system, early females were under strong selection for a long RLS so that they could defend their nests against disturbance by later females (figure 3). Late females were not subject to the same selection because few females would arrive even later to potentially disturb their nests. This difference in selection led to dramatic adaptive variation in senescence (figure 4), manifested as an RLS that was twice as long for early females as for late females (figure 1). The mechanism outlined above has its basis in antagonistic pleiotropy (AP): increased early-life performance (here egg production) negatively affects late-life performance (here

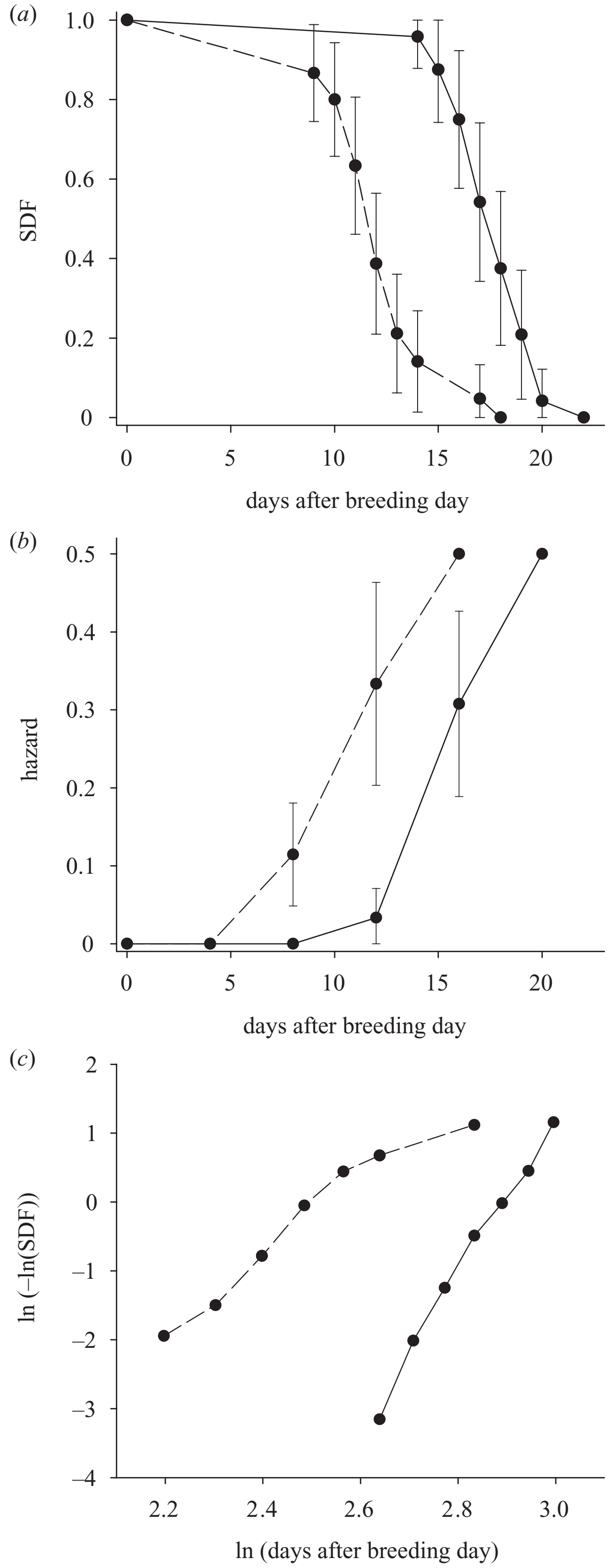

Figure 4. Age-specific (*a*) survival distributions (SDF) and (*b*) hazards for early (solid lines) and late (dashed lines) Pick Creek females in 2000. Age is shown as days after an individual starts breeding. Estimates and 95% CIs were obtained using the LIFETEST procedure in SAS. The near-linear relationships in (*c*) indicate a close fit to Weibull survival models.

nest defence). An important difference from previous work is that variation in selection for late-life performance was not the result of extrinsic adult mortality but rather of the need to protect an existing reproductive investment.

Similarly dramatic seasonal declines in RLS are common in other sockeye salmon populations and Pacific salmon species (e.g. McPhee & Quinn 1998; Hendry *et al.* 1999; Dickerson *et al.* 2002; Morbey & Ydenberg 2003). The mechanism we have here proposed probably provides a general explanation for this recurring pattern, simply because capital breeding, semelparity and nest superimposition are typical in Pacific salmon (Fleming & Reynolds 2004). RLS also varies dramatically *across* salmon populations (e.g. compare McPhee & Quinn 1998 with Hendry *et al.* 1999). Much of this among-population variation may reflect adaptation to extrinsic mortality (e.g. predation by bears; Quinn *et al.* 2001) but some may also reflect adaptation to superimposition. For example, superimposition should be more likely in populations with protracted breeding seasons and higher densities. Such populations should experience stronger selection for a long RLS, leading to later or slower senescence, but lower egg production. These predictions have yet to be tested.

Previous studies examining natural variation in senescence have compared different species or populations. We took the novel approach of examining variation within a single population, wherein early and late breeders differed dramatically in selection, allocation, RLS and senescence. This seasonal variation might arise through at least three different mechanisms. First, individual status or condition might jointly determine breeding date and energy allocation, with the latter then influencing RLS. Such 'condition dependence' occurs in birds (e.g. Price *et al.* 1988) and some other organisms, but its effect on the evolution of senescence is unknown. Second, the population might be genetically monomorphic, with all individuals randomly playing different tactics (breed early and invest less in gonads or breed late and invest more in gonads) at ESS probabilities (a mixed ESS; Parker 1984). Third, individuals may be genetically predisposed to breed at particular times and to allocate energy appropriately for those times. All of these mechanisms could contribute to the observed variation but we have several reasons for favouring the third.

Breeding date can play an important role in structuring genetic variation within populations (e.g. Borash *et al.* 1998). Pacific salmon are exceptional in this regard because breeding dates vary considerably within populations and offspring breed on essentially the same date as their parents ($h^2 = 0.4$–1.0; e.g. Smoker *et al.* 1998; Quinn *et al.* 2000). As a result, breeding date is one of the primary causes of neutral genetic differentiation in salmon (Tallman & Healey 1994; McGregor *et al.* 1998; Woody *et al.* 2000). This temporal constraint on gene flow, which we have called 'isolation-by-time' (Hendry *et al.* 1999), results in partial reproductive isolation between early and late breeders within populations. When selective regimes vary through the breeding season, as we have here shown for superimposition, early and late breeders should be able to adapt, at least in part, to the conditions they experience ('adaptation-by-time'; Hendry *et al.* 1999). Indeed, our microsatellite data indicate that the proportion of genes exchanged between early and late breeders in Pick Creek ($m \approx 0.000\,23$) is low enough to allow substantial adaptive divergence in response to divergent selection (see figs in Hendry *et al.* 2001*b*).

The mechanism we have described herein may make a substantial contribution to adaptive variation in senescence in many animal taxa, simply because its two major parts should be almost universal. First, reproductive trade-offs resulting from energy limitation are common (Roff 1992). Such trade-offs may sometimes be difficult to detect at the population level, owing to variation in energy acquisition across individuals, but they should nevertheless be present at the individual level. That is, when an individual invests more energy in eggs, it will have less available for other tasks. Second, the relative strength of selection acting on the components of this trade-off should often vary spatially and temporally. One component of this variation is probably rates of extrinsic mortality but selection should be similarly variable for other tasks. Future studies examining the evolution of senescence might profit from examining the role of varying selection acting on reproductive trade-offs.

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