Protaendry models and their application to salmon

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Mating systems characterized by restricted breeding seasons, male polygamy, and female monogamy are common among animals. In such systems (e.g., butterflies), the earlier emergence of males than females to breeding areas (protaendry) is a typical phenological pattern. Protandry likely results from a timing strategy that maximizes mating opportunities by males. In Pacific salmon (Onchorhynchus spp.), males typically arrive at the spawning grounds in advance of females. Using arrival-timing models, I found that under the mate-opportunity hypothesis, the mating system of salmon favors protandry. Protandry is predicted under a range of competitive scenarios, and the degree of protandry is especially sensitive to the duration of male spawning activity. Greater protandry is expected with increasing population sex ratio (i.e., more males) when there is mate guarding, but lower protandry is expected with increasing population sex ratio when interference competition among males reduces male longevity. The timing of unequal competitors is expected to be similar, but among years, protandry may be less variable in the better competitor. Key words: arrival timing, Onchorhynchus, protandry, salmon. [Behav Ecol 13:337–343 (2002)]

In mating systems characterized by a greater frequency of mating by males than females, males tend to arrive at breeding areas earlier on average than females (e.g., arthropods: Thornhill and Alcock, 1983; ground squirrels: Mchener, 1984; Pacific salmon: Morbey, 2000). This form of sex-biased timing, called protandry, theoretically allows males to maximize their mating opportunities with females (e.g., Boteverweg, 1982; Iwasa et al., 1983; Wiklund and Fagerstrom, 1977). Protandry (and the less frequent, opposite pattern called protogyny) may occur for different reasons in different taxa. For example, in many migrant bird species, competition for territories may select for the earlier arrival of the territorial sex (usually males) (Ketterson and Nolan, 1976; Myers, 1981). Most theoretical work on protandry has focussed on the mate-opportunity hypothesis and how it relates to protandry in arthropods. I assessed how well the mate-opportunity hypothesis explains protandry in a different taxon, Pacific salmon (Onchorhynchus spp.). The biology of salmon seems consistent with the mate-opportunity hypothesis because reproduction is highly seasonal and because male salmon mate with several females and have a longer period of mating or spawning activity than females (e.g., chum salmon O. keta; Schroder, 1982; sockeye salmon O. nerka: McPhee and Quinn, 1998). Alternative hypotheses for protandry also are generally inconsistent with salmonid biology (Morbey, 2000).

I first determined whether the maximization of mating opportunities selects for protandry in salmon by using biologically realistic parameters in a modified version of an existing arrival-timing model. Competitive inequalities are a feature of the salmonid breeding system, and so my second objective was to incorporate competitive inequalities in arrival-timing models to quantify their effect on protandry. For example, large male salmon often have an advantage when competing against small males for access to females (coho salmon O. kisutch: Fleming and Gross, 1994; sockeye salmon: Quinn and Foote, 1994). Males in mate-guarding positions also may acquire familiarity with local habitat features, which helps them during male–male competition (sockeye salmon: Chebanov, 1997; Foote, 1990). Previous models of protandry in insects consider how the benefits of large male size, attained through prolonged development, affect optimal protandry (Zonneveld 1996a,b). I did not consider such a trade-off between early arrival and large size. My third objective was to examine how well arrival-timing models predict protandry in salmon by comparing the predictions to observed protandry from my earlier study (Morbey, 2000).

The model
I followed the modeling approach of Iwasa et al. (1983) and Parker and Courtney (1983) and assumed that selection acts on male arrival timing. The model is a game with n players, and the strategy set contains a continuous set of timing options (i.e., arrival days at breeding areas) (Maynard Smith, 1982). This type of model is often referred to as an ideal free distribution in time because males are assumed to have complete knowledge of the female arrival distribution and are free to arrive (i.e., are not prevented from arriving) on any day of the season (Fretwell and Lucas, 1970). The evolutionarily stable strategy is a probability distribution of arrival days, with the fitness of males among arrival days equal.

I began with an equal competitors model with the same general assumptions of Iwasa et al.’s (1983) and Parker and Courtne y’s (1983) models. Males were assumed to engage in scramble competition for unmated females on each day while alive and were subject to both prearrival mortality and postarrival mortality. My model differs in the form of postarrival mortality and in the frequency of mating by females. I assumed that postarrival mortality occurs mainly due to senescence (e.g., Groot et al., 1995) and that male longevity (period between arrival and death) declines with arrival day (English et al., 1992; Hendry, 1998; McPhee and Quinn, 1998; Neilson and Banford, 1983; Neilson and Geen, 1981; Perrin and Irvine, 1990; but see Fukushima and Smoker, 1997; van den Berghe and Gross, 1986). Daily predation risk while spawning was not considered because it is likely low in most

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populations. Salmon can use deep areas as refuges, and important predators such as bears tend to be more successful at capturing older, postspawning salmon (e.g., chum salmon: Reimchen, 2000). However, predation on spawning adults may be substantial in some years and in some populations (e.g., sockeye salmon: Ruggeroni et al., 2000) and, if present, would affect protandry in the same way as reduced longevity. I assumed that females spawn once per day for 3 days, which is close to the observed duration of spawning by female sockeye salmon (McPhee and Quinn, 1998).

Following Iwasa et al. (1983), the fitness of a cohort of males arriving on day \( t \), \( \phi(t) \), is the expected number of spawning events they participated in from day \( t \) until death:

\[
\phi(t) = e^{-\mu_\text{ps} t} \sum_{s=0}^{10.2} \frac{F(s)}{M(s)} e^{-\mu ps(s-t)} ds.
\]

\( F(s) \) and \( M(s) \) are the number of spawning females and males present on day \( s \), respectively, and are determined from the female arrival distribution, the duration of egg deposition, the male arrival distribution not accounting for mortality, \( \mu_\text{ps} \), and the longevity function. A male’s spawning success on day \( s \), \( F(s)/M(s) \), is inversely proportional to the number of male competitors. Initial population size was set to 200 females and 200 males; neither population size nor population sex ratio affects protandry (Iwasa et al., 1983; cf. the two-patch continuous input model of habitat selection: Sutherland and Parker, 1992). An estimate of prearrival mortality (0.0012 per day) was based on Parker’s (1962) estimate of mortality during the coastal phase of the return migration of pink salmon \( O. gorbatscha \). The daily mortality rate after arrival, \( \mu_\text{ps} \), equals 0 and the daily mortality rate before arrival, \( \mu_\text{ps} \), equals 0.0012. Quantitative information on the relationship between longevity and arrival day is available for male sockeye salmon (Hendry, 1998). I used a range of longevity functions, \( L(t) \), that approximated the seasonal decline reported in Hendry’s (1998) study [shallow: \( L(t) = 10.2 - 0.2t \); intermediate: \( L(t) = 15.3 - 0.3t \); steep: \( L(t) = 20.4 - 0.4t \)].

Female arrival was modeled as a normal distribution with a mean of 13.5 and SDs of 3, 5, or 7, which correspond to 10, 18, or 22 day periods, respectively, during which 95% of females arrive. Although arrival can be highly irregular, generally it is neither synchronous nor uniform (e.g., analysis of data used in Morbey, 2000); a normal distribution was used. Season length, \( T \), was set to 32 days to cover a 30-day female arrival period plus 2 days when the last-arriving females were still actively spawning.

At the evolutionary stable strategy (ESS), \( \phi(t) \) must be equal for all \( t \). The ESS was found using replicator dynamics programmed in Quick Basic (see Parker and Courtney, 1983). The simulation began by randomly assigning arrival probabilities for each timing option or cohort. During each iteration of the simulation, \( \phi(t) \) was calculated for each cohort \( t = 0, \ldots, T \), and then each cohort was replicated in direct proportion to its relative fitness. If the longevity of a cohort had a noninteger value, the survival of that cohort in its last day of life was set to the truncated fraction. For example, if male longevity was 5.2 days, survival at age 6 days was 0.2. The iterations were continued for 500 generations so that \( \phi(t) \) approximated a constant. Discretization produced irregularities in the shape of the optimal male arrival distribution, but these do not affect the interpretation of the results.

After the simulation was complete, the resultant protandry was calculated as the area (in units of days) between the cumulative-percent-differences of the arrival days of males and females:

\[
\text{protandry} = \frac{1}{100\%} \sum_{t=1}^{T} [M(t) - F(t)] s .
\]

where \( s = 1 \) day intervals (Morbey, 2000). In calculating protandry, the expected arrival distribution after mortality is important, so \( M(t) \) was adjusted by subtracting prearrival mortality from the ESS. Protandry represents the number of days between the arrival of an equal proportion of males and females, with positive values representing the earlier arrival of males. This measure was used in my earlier descriptive study (Morbey, 2000).

The model just described effectively assumes all males are equal competitors (Model A). I also investigated how protandry was affected by interference competition among males, by mate guarding, and by phenotypic differences in competitive ability among males.

**Model B: interference competition**

Interference among male competitors may reduce longevity because males compete more aggressively when sex ratios are male biased (Fleming and Gross, 1994; Schroder, 1982) and consume energy reserves at a higher rate (Hendry A, personal communication). Breeding density also can shorten male longevity (Hendry, 1998; van den Berghe and Gross, 1986). To model this scenario, I reduced male longevity by an amount relative to the degree of interference \( r \) on each day \( s \), where:

\[
r(s) = \begin{cases} 1 - \exp \left( - \frac{c (M(s) - F(s))}{F(s)} \right) & \text{if } M(s) \geq F(s) \\ 0 & \text{if } M(s) < F(s) \end{cases}
\]

This function was chosen because \( r(s) = 0 \) days with no excess males and \( r(s) \) asymptotes at 1 day. The constant \( c \) \((0.05, 0.1, \text{or } 0.2) \) determines how quickly interference reduces male longevity. These values of \( c \) correspond to half-day reductions in longevity when the number of excess males per female equals 13.9, 6.9, or 3.5, respectively, and were assumed to reflect a realistic range of natural conditions.

**Model C: mate-guarding**

Male salmon may guard a female for several days during her egg deposition phase due to an acquired competitive advantage (Chebanov, 1997; Foote, 1990). This contrasts with the ideal despotic distribution of Fretwell and Lucas (1970), in which mate-guarding males are intrinsically superior. I assumed that males pair with females and continue mate guarding for an additional day (during a female’s 3 days of egg deposition) with probability \( p_g \). Without mate guarding, \( p_g = 0 \) and the model is equivalent to model A. Males paired with females participated in spawning on the current day, and males who mate guarded the female for an additional day participated in spawning on the next day. Sneaking also was allowed as an alternative mating tactic (e.g., sockeye salmon: Foote et al., 1997). The proportion of a clutch fertilized by a sneaking male was set to 0.5 (see Chebanov et al., 1983; Foote et al., 1997; Maekawa and Onozato, 1986; Mjølnersød et al., 1998; Schroder, 1982). On all days while alive, unpaired males either paired randomly with unguarded females or sneaked. One unpaired male per spawning event used the sneaking tactic to fertilize eggs. A male’s lifetime fertilization success was his accumulated daily fertilization success. The model was run with the intermediate longevity function, two levels of \( p_g \) (0.5 or 1) and population sex ratio (0.75:1 or 1.25:1), and with or without sneaking.
sensitive to some parameters than others. For example, vari-
dicted protandry ranges from 2.67 to 7.74 days and is more
All the models predict protandry in salmon (Tables 1–3). Pre-
Results

Interference

Competitive effect | Sex ratio | Predicted protandry | Sensitivity
---|---|---|---
Low ($c = 0.05$) | 0.75:1 | 4.251 | $-0.143$
1.00:1 | 4.012 | $-0.191$
1.25:1 | 3.811 | $-0.231$
Medium ($c = 0.1$) | 0.75:1 | 3.825 | $-0.228$
1.00:1 | 3.509 | $-0.292$
1.25:1 | 3.261 | $-0.342$
High ($c = 0.2$) | 0.75:1 | 3.302 | $-0.334$
1.00:1 | 2.935 | $-0.408$
1.25:1 | 2.667 | $-0.462$

Probability of mate guarding

<table>
<thead>
<tr>
<th>Competitive effect</th>
<th>Sex ratio</th>
<th>Predicted protandry</th>
<th>Sensitivity</th>
</tr>
</thead>
</table>
| High ($p_L = 1$) | 0.75:1 | 5.241 | 0.057
1.25:1 | 5.364 | 0.082
| Low ($p_L = 0.5$) | 0.75:1 | 5.102 | 0.029
1.25:1 | 5.139 | 0.037

Sensitivity analyses

Sensitivity analyses were conducted to assess the importance and robustness of each parameter. Most parameters were var-
ated independently. Testing every parameter combination
would have required an enormous amount of time, and I did not detect any interactions among the parameters during pre-
liminary testing. Sensitivity was calculated as (protandry for the alternative model—protandry for the basic model)/ (pro-
tandry for the basic model). The version of model A with the
intermediate longevity function and 1:1 sex-ratio was used as the basic model.

Results

All the models predict protandry in salmon (Tables 1–3). Pre-
dicted protandry ranges from 2.67 to 7.74 days and is more
sensitive to some parameters than others. For example, vari-
ation in male longevity affects protandry much more than the
details of male–male competition or the pattern of female arrival (Tables 1 and 2). However, novel predictions about
protandry emerge when such details are considered.

In the equal competitors model, greater protandry is fa-
vored when males live longer (Table 1). Compared to an in-
termediate male longevity at the beginning of the season, lon-
ger and shorter male longevity changes protandry by about
50%. This can be understood by considering a scenario in
which males can spawn for only 3 days (the same period that
females spend depositing eggs). Under this condition, male
arrival should match the female arrival distribution, and no
male could improve his spawning success by arriving earlier.
But this would not be stable if males lived for 4 days because
the peak of male presence would be shifted later, leading to
greater competition among late males than among early
males. The longer males live, the earlier they should arrive
relative to females.

In contrast, the pattern of female arrival affects protandry
only slightly (Table 1). Greater protandry is favored when fe-
male arrival is more protracted, possibly because of the in-
creased availability of females earlier in the year. By arriving
slightly earlier, males have opportunities to spawn with these
early arriving females. The greater longevity of early-arriving
males also allows them to closely match the longer period of
concentrated female spawning activity.

Greater interference competition among males, caused by
an increased cost of interference or an increased population
sex ratio, reduces male longevity and so favors less protandry
(Table 2). Compared to the equal competitors model, inter-
ference favors males who arrive and mate slightly later in the
year, when there are fewer males per female (Figure 1). At
the most extreme conditions for interference, protandry is
46% less than the basic equal competitors model.

Mate guarding favors greater protandry than does the equal
competitors model because earlier arrival allows males to pair
with newly arriving females (Table 2). Newly arriving females
are more valuable than previously arrived females because
they offer more spawning opportunities for mate-guarding
males and also are more likely to be unguarded. There was only a 1% reduction in protandry when sneaking was allowed (results not presented). Successful sneaking favors slightly less protandry because the availability of all females becomes important. An increase in male–male competition caused by an increase in the population sex ratio or an increase in the probability of continued mate guarding favors greater protandry because of increased selection to pair earlier and monopolize females. The temporary advantage held by mate-guarding males does not strongly affect protandry, however. When male–male competition is at its most extreme, protandry is only about 8% higher than the basic equal competitors model.

When large males fertilize more eggs than small males, an infinite number of arrival distributions are possible for each competitor type (represented by each line in Figure 2). At each equilibrium, large males have higher spawning success than small males (when the former are competitively superior), but spawning success is the same among the same-sized males. One possible equilibrium is for large and small males to have similar arrival timing and match the protandry predicted from the basic equal competitors model. Large males may arrive earlier than small males or vice versa. Average protandry is similar to that predicted by the basic equal competitors model, but small males show slightly less protandry than large males (Table 3).

One interesting property of the unequal competitors model is the greater range of protandry equilibria for small males than for large males (Figure 2). This occurs because small males can be excluded from the mid-season period, when female availability is at its greatest, by the presence of large, competitively superior males. Small males cannot monopolize females during this period and therefore cannot exclude large males. The slope relating protandry among the two size classes represents the degree to which large males exclude small males from this period and is the ratio between the competitive weight of small males to that of large males.

**DISCUSSION**

Although the different protandry models used salmon-specific parameters, the predictions of the models are general and can be tested on a wide range of species with similar mating systems. The most important requirement is that males attempt to mate more often than females. Thus, these predictions apply less well to more monogamous species (e.g., birds) because the timing of males relative to females has less direct fitness consequences. The assumptions of each model also must be met for its predictions to be applicable. Support for the predictions would not only uphold the mate-opportunity hypothesis, but also would provide insight into how different

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**Table 3**

<table>
<thead>
<tr>
<th>CW</th>
<th>Male size</th>
<th>Predicted protandry</th>
<th>Sensitivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>20</td>
<td>Large</td>
<td>5.246 ± 1.111</td>
<td>0.058</td>
</tr>
<tr>
<td></td>
<td>Small</td>
<td>4.943 ± 0.056</td>
<td>-0.003</td>
</tr>
<tr>
<td>2</td>
<td>Large</td>
<td>5.088 ± 0.412</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td>Small</td>
<td>4.891 ± 0.206</td>
<td>-0.013</td>
</tr>
<tr>
<td>1</td>
<td>Large</td>
<td>4.939 ± 0.391</td>
<td>-0.004</td>
</tr>
<tr>
<td></td>
<td>Small</td>
<td>4.974 ± 0.391</td>
<td>0.003</td>
</tr>
</tbody>
</table>

Protandry is shown as the mean and SD of 30 simulations; sensitivity is calculated as (predicted protandry −4.957)/4.957. All models used the intermediate longevity function and the 1:1 population sex ratio.
selective factors affect male arrival timing. The models also suggest that some factors (e.g., male longevity) will affect mating opportunities, and therefore protandry, more strongly than other factors (e.g., mate guarding by males).

The effect of longevity

The key feature favoring protandry in salmon is the longer period of spawning activity among males than females. Unlike previous models of protandry in arthropods, I explicitly included senescence by constraining longevity. Despite the difference in how longevity was modeled, my results are consistent with Parker and Courtney’s (1983) prediction of increased protandry with increased male longevity. If male salmon survive and spawn throughout the entire spawning period, they all should arrive on the first day. All else being equal, less protandry and greater tracking of female availability by males is predicted when males expect to live and spawn for fewer days. Analogously, in polygynous species returning to breed in subsequent seasons (e.g., reptiles and amphibians), greater protandry is predicted when males allocate more time to mating activity.

The modeling shows how protandry leads to equality of spawning success despite seasonal differences in longevity. Intuitively, it would seem that increased longevity would translate into greater spawning success, but this is not necessary if shorter-lived males face fewer competitors but access to more spawning females. However, one might question whether the seasonal pattern of longevity assumed in the models is evolutionarily stable, because selection could operate on male longevity as well as on arrival timing. Early in the year, it makes sense for males to live longer because they could participate in more spawning events (Hendry et al., 1999). Presumably, the allocation of somatic energy stores to longevity would be balanced by the costs of such allocation (e.g., smaller gonads or secondary sexual characteristics). I propose that a combination of protandry and a seasonal decline in longevity is evolutionarily stable, perhaps even in arthropods, but this hypothesis awaits testing.

Contrasting effects of interference competition and mate guarding

Protandry is less sensitive to the details of male–male competition than to the longevity of males. At the equilibrium solution of the basic equal competitors model, male–male competition is at its highest earlier in the year (Figure 1). A seasonal decline in male–male competition (at least during the male arrival period) also occurs in species that experience greater prearrival mortality for delaying arrival (e.g., butterflies: Iwasa et al., 1983). If interference competition among males reduces male longevity, males should minimize male–male competition by arriving later and exhibiting less protandry. Conditions that increase male–male competition should lead to decreased protandry. This prediction may apply to other species with interference competition among males. For example, in dense breeding aggregations of amphipods, male–male competition for females may increase the energy expenditure by males and, in turn, may reduce how long males spend breeding. However, information about how male survival and the duration of reproductive activity vary seasonally is needed to predict how increased interference competition affects protandry.

The mate-guarding model represents a scenario where males benefit from early arrival relative to both sexes. The model predicts greater protandry with increasing population sex ratio (more males per female) because of increasing selection to be early relative to other males (cf. Kokko, 1999). Mate-guarding prevents later-arriving males from participating in spawning events. By arriving earlier, males have more opportunities to pair with and monopolize newly settling females than by arriving later. The mate-guarding model can be tested in other species with precopulatory mate guarding (Ridley, 1983). It also can apply to territorial species (including birds) if earlier arriving males acquire higher quality territories that attract more mates, because the early arrival of males relative to other males also would have direct fitness consequences.

The observed relationship between population sex ratio and protandry could provide insight into the relative importance of interference competition and mate guarding on male-arrival timing. Depending on the strength of interference and the probability of mate guarding, the relationship between population sex ratio and protandry could be positive, negative, or flat. However, a flat relationship would result if neither factor affected protandry. In Morbey’s (2000) study of protandry in Pacific salmon, the observed flat relationship in six of seven populations suggests that both factors affect protandry equally or that neither factor affects protandry (the observed positive correlation between population sex ratio and protandry in Auke Creek pink salmon warrants further study). Such counteracting effects make it difficult to assess whether males can respond to factors affecting mating opportunities.

The effect of size-based competitive asymmetries

The inclusion of size-based inequalities in competitive ability has little effect on the timing of different-sized males and on protandry. A range of protandry equilibria is possible for each size class, and average predicted protandry is slightly less for small males than large males. Among years or populations, a greater range in protandry is predicted in small males than in large males because the latter monopolize the mid-season period with the greatest availability of females. The greater the relative competitive ability of large males, the greater the exclusion. Although not stated explicitly, the two-patch unequal competitor model of habitat selection also predicts a negative correlation between the proportion of good and poor competitors in the good patch that equals $-CW_{good}/CW_{poor}$, where CW refers to the competitive weight of good or poor competitors (Milsinski and Parker, 1991; Parker and Sutherland, 1986).

The effect of phenotypic differences in competitive ability on the timing of different-sized males has been considered previously. Thornhill and Alcock (1983) suggested that male wasps with a short life span but superior ability to monopolize and mate with females should arrive at the peak of female availability. Males with increased longevity and lower competitive abilities should arrive when competition is lower. Hastings (1989) also suggested that small male wasps should avoid competition with large males, and presumably delay emergence. In light of my modeling, males expecting to live for a short period should arrive at peak female availability regardless of their competitive ability. The effect of competitive ability depends on how competitors differ. If the relative payoff among competitor types is constant regardless of arrival day, they should exhibit similar protandry. Extrapolating from Milsinski and Parker’s (1991) model, in which relative payoff among competitor types varies among patches, differential arrival of different-sized males would be possible when large males achieve higher spawning success than small males on days with high densities of females.

In support of the unequal competitors model, younger age classes did not arrive consistently earlier or later than older age classes within several salmon populations (Morbey, 2000). The observation of similar arrival timing regardless of com-
petitive ability (or size) is unusual. In several species, time constraints imposed by seasonality are expected to produce a seasonal decline in body size. For example, in arthropods with overwintering larvae and rapid development (months as opposed to years in Pacific salmon), greater time pressure to reach sexual maturity or reduced food availability later in the season may cause a seasonal decline in development time and therefore body size (e.g., grasshoppers Spharrium purpurascens: Cueva del Castillo and Núñez-Fárfán, 1999). In iteroparous fish, a seasonal decline in body size may result because time constraints cause smaller males to delay reproduction and preferentially allocate energy to growth early in the season (e.g., smallmouth bass Micropterus dolomieui: Ridgway et al., 1991). In birds, males in better condition may be able to take advantage of early arrival while suffering fewer costs than males in poor condition (Kokko, 1999). In Pacific salmon, time constraints may be less important because they do not have to allocate energy for future reproduction, because seasonality in feeding conditions is probably less severe than for bass breeding in northern lakes, and because males are not territorial.

**Observed versus predicted protandry**

Depending on the assumptions made about male longevity and the nature of male–male competition, predicted protandry (2.49–7.74 days) spans the observed population average of 2.84 days (n = 7 populations of 4 species) but is slightly greater than the observed range of 0.90–5.18 days (n = 105 years; analysis of data from Morbey, 2000). Observed protandry (2.84 days) differs statistically from the protandry predicted by the basic model with the intermediate longevity function (4.96 days, one sample t test: t = −3.65, p = .0108) and, notably, 4.96 days far exceeds the average protandry observed in the two sockeye salmon populations (about 1 day).

The different models offer potential explanations for why protandry was overestimated. First, perhaps males spawn for fewer days than indicated by the intermediate longevity function. This could happen if males senesce more quickly than assumed, become weaker and less effective at spawning as they age, or suffer predation risk on the spawning grounds. Significant prespawning mortality also can occur when abiotic conditions are suboptimal (e.g., Groot and Margolis, 1991). Second, interference competition may affect longevity more strongly than assumed. Thus, the mismatch between observed and predicted protandry indicates a need to identify the factors limiting the duration of male reproductive activity in salmon.

Another explanation for the lower-than-predicted protandry is related to postarrival waiting (Morbey, 2000). If in the model, I assumed that males and females commence spawning activities immediately after arrival. However, salmon may wait for days or weeks before initiating spawning activities (e.g., pink salmon: Mattson and Rowland, 1963; sockeye salmon on Brett, 1995; Hoopes, 1972; Morbey, personal observation). Males do not begin mate searching until females have settled on nest sites. Once the first female settles, all previously arrived males suddenly can begin mate searching. Therefore, in populations with postarrival waiting, protandry in arrival would underestimate protandry in the commencement of spawning activities. This may explain why the model overestimated protandry, particularly in sockeye salmon.

**Conclusions**

The biology of Pacific salmon is more consistent with the mate-opportunity hypothesis than with alternative hypotheses (Morbey, 2000), and the modeling confirms that selection should favor protandry under a range of competitive scenarios. However, observed and predicted protandry do not match well, there is little support for the predictions of the different models, and population differences in protandry are not yet understood. Further research is needed to determine whether early arrival relative to females has direct fitness consequences for males. A realistic goal is to first test for a positive correlation between male longevity and protandry among years within a population. This would require accurate data on annual and seasonal variation in predation risk, the duration of male and female reproductive activity, and prespawning waiting. It also would be essential to calculate protandry using accurate measurements of male and female arrival timing.

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