Supplemental Information

Reproductive Conflict

and the Evolution of Menopause in Killer Whales

Darren P. Croft, Rufus A. Johnstone, Samuel Ellis, Stuart Nattrass, Daniel W. Franks, Lauren J.N. Brent, Sonia Mazzi, Kenneth C. Balcomb, John K.B. Ford, and Michael A. Cant
Figure S1. Survival curves (+ standard error) for the observed data splitting the data by conflict type (A) and birth order (B). Related to figure 3.
Table S1. Model fitting results with imputations for missing covariates. Related to figure 3.

| Model                                      | \( \beta \)                                      | Log-Likelihood | AIC   |
|--------------------------------------------|--------------------------------------------------|----------------|-------|
| \( h(t) = h_0(t) \exp\{\beta_1 G_o + \beta_2 B_o + \beta_3 G_C\} \) | \(0.6172, 0.4000, -0.6935\) | -814.0842      | 1634.168 |
| \( h(t) = h_0(t) \exp\{\beta_1 G_o B_o G_C\} \) | 0.1166                                          | -816.1838      | 1634.368 |
| \( h(t) = h_0(t) \exp\{\beta_1 (G_o + B_o + G_N)\} \) | 0.5110                                          | -814.2988      | 1630.598 |
| \( h(t) = h_0(t) \exp\{\beta_1 (G_o + B_o) + \beta_2 G_N\} \) | 0.5075, 0.6978                                  | -814.1612      | 1632.322 |
| \( h(t) = h_0(t) \exp\{\beta_1 G_Y B_o G_C\} \) | -0.0518                                         | -817.2525      | 1636.505 |
| \( h(t) = h_0(t) \exp\{\beta_1 (G_Y + B_o + G_N)\} \) | 0.1317                                          | -817.1199      | 1636.24  |
| \( h(t) = h_0(t) \exp\{\beta_1 (G_Y + B_o) + \beta_2 G_N\} \) | 0.0963, 0.2804                                  | -816.6687      | 1637.337 |

\( G_o = 1 \) if older generation in conflict  
\( G_Y = 1 \) if younger generation in conflict  
\( G_C = 1 \) if in conflict  
\( G_N = 1 \) if not in conflict  
\( B_o = 1 \) if oldest calf in conflict cohort (i.e. born earliest)  
\( B_{no} = 1 \) if not oldest calf in conflict cohort (i.e. not born earliest)
Supplemental Experimental Procedures

Details of the Theoretical Model: To determine the evolutionarily stable levels of competitive effort for females of different age ranks, we adopt an adaptive dynamic approach, assuming that evolution proceeds by the successive substitution of mutations of small effect, with a clear separation of time scales between demographic and evolutionary processes. For any given vector of age-rank-specific competitive effort levels \( x \) (where element \( x_a \) denotes the competitive effort by females of age rank \( a \)), we determine the coefficients of relatedness between individuals of different sexes and age ranks at demographic equilibrium, as well as the reproductive values of individuals of different sexes and age ranks (as detailed below). We then use these to determine the selection gradient acting on each competitive effort level, i.e. the slope of fitness with respect to competitive effort for a mutant allele (of small effect) that affects the behaviour of females of that particular age rank (again as detailed below). Repeated updating of the vector of competitive effort levels \( x \) by addition of the vector of selection gradients leads ultimately to a convergently stable equilibrium at which all selection gradients are equal to zero, which we take as the solution of the model.

Calculating relatedness at demographic equilibrium

Each group contains \( 2n \) individuals. In the main text we indexed these by sex and age rank, writing for instance \( \mu_{sa} \) for the mortality rate of individuals of sex \( s \) and age rank \( a \). Here, for simplicity, which we assign to each a single unique index, which runs from 1 to \( 2n \), with individuals ordered first by sex and then by age rank, \{\( F_1, \ldots, F_n, M_1, \ldots, M_n \}\}. We then write \( r_{jk} \) for the relatedness between individuals \( j \) and \( k \) (where \( r_{jk} = 1 \) for \( j=k \)). Now, let \( I_{ijk} \) denote the probability, following the death and replacement of individual \( i \), that a gene copy carried by newly-labelled individual \( j \)
is derived from that previously carried by the formerly-labelled individual \( k \). Since the diploid case yields the same results if one assumes additive allelic effects, we focus on the haploid case for simplicity (assuming that gametes are produced clonally and pair to form diploid zygotes, which then undergo meiosis to form a new generation of haploid individuals). To illustrate, when the oldest female in a group of size \( n = 2 \) dies, the formerly younger female \( F_2 \) becomes the new older female \( F_1 \), so that \( I_{111} = 0 \) and \( I_{112} = 1 \) (because a gene copy carried by the new \( F_1 \) was formerly carried by \( F_2 \)). At the same time, the position of younger female is now filled by a newly recruited juvenile who might have inherited a gene copy from any local breeder (either male or female) if locally born and sired, or might be non-locally sired and/or an immigrant from another group (in which case its gene copy may not be derived from any local breeder). Given the assumptions stated in the main text, we thus have \( I_{121} = (1/2)h_f p_1/(p_1+p_2) \), where \( p_1 \) and \( p_2 \) denote the fecundities of females of age ranks 1 and 2 (which depend on the vector of age-rank-specific female competitive effort levels \( x \)), and \( h_f \) the probability that a female breeding vacancy is filled by a locally produced offspring; the factor of \((1/2)\) reflects the probability that the offspring derives its gene copy from its mother rather than its father. Other elements of the full array \( I \) are derived in a similar way.

At demographic equilibrium, we must have

\[
\bar{r}_g = \sum_{i=1,2n} \frac{\mu_i}{2n \bar{\mu}} \sum_{x=1,2n} \sum_{y=1,2n} I_{ix} I_{iy} r_{xy}
\]

where

\[
\bar{\mu} = \frac{1}{2n} \sum_{i=1,2n} \mu_i
\]
denotes the mean mortality rate among all group members. The right hand side of the first equation above gives the expected value of $r_{jk}$ after the next death and replacement in the local patch, averaging over all possible deaths (indexed by $i$), weighted according to their relative probabilities; the expected relatedness in each case is given by summing the probabilities that individuals $j$ and $k$ derive their gene copies from each possible pair of local individuals $x$ and $y$, multiplied by the relatedness between $x$ and $y$. This yields $2n(2n-1)$ simultaneous equations that we can solve for the equilibrium coefficients of relatedness between different group members.

**Calculating reproductive values at demographic equilibrium**

Next, we derive the vector $v$, of which element $v_j$ denotes the reproductive value of individuals of type $j$. To derive equilibrium values for all types, we first define $f_j$ and $m_j$, the rates at which individuals of type $j$ produce and transmit a gene copy to non-local female and male offspring. For females, i.e. for types $j = 1...n$, we have

$$f_j = \frac{1}{2} \sum_{k=1}^{n} \frac{\mu_l(1-h_l)p_j}{\sum_{k=1}^{n} p_k}$$

and

$$m_j = \frac{1}{2} \sum_{k=1}^{n} \frac{\mu_l(1-h_m)p_j}{\sum_{k=1}^{n} p_k},$$

while for males, i.e. for types $j = n+1...2n$ we have

$$f_j = \frac{1}{2} \sum_{k=1}^{n} \frac{\mu_l(1-h_l)p_j}{\sum_{k=1}^{n} p_k}$$

and

$$m_j = \frac{1}{2} \sum_{k=1}^{n} \frac{\mu_l(1-h_m)p_j}{\sum_{k=1}^{n} p_k}.$$
where the element \( p_j \) of vector \( p \) denotes the relative fecundity (for females) or mating output (for males) of individuals of type \( j \), which depends on the vector of age-rank-specific female competitive effort levels \( x \).

For individuals of type \( j \), it then follows that \( v_j \) satisfies

\[
v_j = \left( \sum_{k=1}^{2n} \mu_k \sum_{i=1}^{2n} I_{i,j} v_k + f_j (v_j + \frac{1}{2} v_n) + m_j (v_j + \frac{1}{2} v_{2n}) \right) / \left( \sum_{i=1}^{2n} \mu_i + f_j + m_j \right)
\]

The right hand side is obtained by taking a probability-weighted sum over all possible events that might affect the fitness of the focal individual, including both local deaths and replacements and production of non-local offspring; note also that newly produced offspring are always the youngest in their group, and are thus of value \( v_n \) for females and \( v_n \) for males. This yields \( 2n \) equations, but the system has rank \( 2n-1 \); we can, however, solve for all reproductive values by setting, for example, \( v_1 = 1 \), and solving any \( 2n-1 \) of the equations (the baseline value chosen does not alter the predictions of the model, for which all that matters are the reproductive values of the different classes relative to one another).

**Calculating selection gradients**

To determine how selection acts on the age-specific levels of competitive effort, we next determine the marginal rate of change of fitness with respect to competitive effort for mutant alleles (of small effect) that affect the behaviour of individuals of different types. To do so, we use the direct fitness approach of Taylor & Frank [S1] to capture the effects of local kin interaction. We first write down
the fitness of a mutant allele carried by an individual of type \( j \), as a function of the vector \( \hat{\mathbf{p}} \), of which element \( \hat{p}_k \) denotes the fecundity (for females) or mating success (for males) of the individual of type \( k \) in the focal group. This local fecundity or mating success depends on the local levels of competitive effort given by the vector \( \hat{\mathbf{x}} \), and may thus differ from the population typical value given by the vector \( \mathbf{p} \), due to changes in competitive effort induced by the focal allele and copies of it born by other, related individuals in the group.

We will write \( \hat{I}_{ijk}(\hat{\mathbf{p}}) \) for the probability, following the death and replacement of individual \( i \) in the focal group, that a gene copy carried by newly-labelled individual \( j \) is derived from that previously carried by the formerly-labelled individual \( k \). Similarly, \( \hat{f}_j(\hat{\mathbf{p}}) \) and \( \hat{m}_j(\hat{\mathbf{p}}) \) will denote the rates at which an individual of type \( j \) in the focal group transmits a gene copy to non-local female and male offspring. The fitness, \( w_j \) of a gene copy carried by an individual of type \( j \) in the focal group can then be approximated as

\[
w_j = \left( \sum_{k=1}^{2n} \mu_k \sum_{i=1}^{2n} \hat{I}_{ijk}(\hat{\mathbf{p}}) \nu_k + \hat{f}_j(\hat{\mathbf{p}})(\nu_j + \frac{1}{2} \nu_n) + \hat{m}_j(\hat{\mathbf{p}})(\nu_j + \frac{1}{2} \nu_{2n}) \right) / \left( \sum_{i=1}^{2n} \mu_i + f_j(\hat{\mathbf{p}}) + m_j(\hat{\mathbf{p}}) \right)
\]

The selection gradient on competitive effort level \( x_a \), denoted \( S_a \), which represents the marginal rate of change of fitness with respect to competitive effort for a mutant allele that affects the behaviour of females of age rank \( a \), is then given by
Where

\[
S_a = \frac{1}{2n} \sum_{i=1}^{2n} \sum_{j=1}^{2n} \frac{\partial w_j}{\partial \hat{p}_k} \frac{\partial \hat{p}_k}{\partial \alpha_{ij}} r_{ij}
\]

gives the fecundity (for females) or mating success (for males) of individual \(k\) in the local group as a function of the vector of local competitive effort levels \(\hat{\mathbf{x}}\). To obtain the selection gradient \(S_i\) we average over each class \(j\) of individual in which the focal gene copy might be found, summing in each case the product of the relatedness coefficient \(r_{ij}\) and the marginal impact on the fitness of the focal individual \(j\) of a change in the competitive effort of individual \(i\); the latter value is itself obtained by summing, over all individuals \(k\) in the local group, the marginal impact of a change in \(i\)'s behaviour on \(k\)'s fecundity or mating success, multiplied by the marginal impact of a change in \(k\)'s fecundity or mating success on \(j\)'s fitness.

Above, we have assumed (as stated in the main text) that total female fecundity and male mating success of the group are a decreasing function of the total competitive effort of all females,

\[
f\left(\sum_{a=1}^{n} \hat{x}_a\right)
\]

while a female’s share of that total is a function of her individual competitive effort.
compared to the mean competitive effort of her rivals in the group, \( g\left( x_{\alpha}, \frac{1}{n-1} \sum_{b=\alpha}^{n} x_{b} \right) \). The results shown in the main text are for the illustrative case in which \( n = 2 \) and

\[
\begin{align*}
  f(x_1 + x_2) &= 1 - \frac{1}{2} (x_1 + x_2) \\
  g(x_a, x_b) &= \frac{1}{2} \left( 1 + \tanh(x_a - x_b) \right)
\end{align*}
\]
Supplemental Reference

S1. Taylor, P.D., and Frank, S.A. (1996). How to make a kin selection model. J. Theor. Biol. 180, 27-37.