

Transient polymorphisms in parental care strategies drive divergence of sex roles

Xiaoyan Long^{a, b} and Franz J. Weissing^{a, 1}

^aGroningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen 9747AG, The Netherlands

^bInstitute of Biology I, University of Freiburg, Freiburg im Breisgau 79104, Germany

¹ To whom correspondence should be addressed. Email: f.j.weissing@rug.nl

Mathematical analysis. We applied the evolutionary invasion analysis in the baseline scenario where individuals mate randomly and only switch between the mating state and the caring state by following Fromhage & Jennions (2016). To correspond to the simulation, all mortality rates are set to μ ($\mu = 0.001$). In this case, female care duration T_f and male care duration T_m are allowed to evolve. The sex-specific care duration could affect the operational sex ratio (OSR) r , which results in sex-specific mating rate (a_f for the female and a_m for the male) in the end. Here, the female mating rate is $a_f = \sqrt{r}$ and the male mating rate is $a_m = 1/\sqrt{r}$, where $r = 1 + \frac{A}{2\mu^2} (A + \sqrt{A^2 + 4\mu^2})$, $A = e^{-\mu T_m} - e^{-\mu T_f}$ (p 10 in ref. 1). The sex-biased OSR would in turn, affects the care strategies.

According to Fromhage and Jennions (2016), we determine the fitness of an individual as follows. The fitness w_f of a female with care duration T_f in a population is given by $w_f = \frac{P_f}{1-s_f P_f} \cdot S_{off}$, where $\frac{P_f}{1-s_f P_f}$ is the expected number of matings of the female (p 9 in ref. 1) and S_{off} is the offspring survival probability determined by the care duration of the female and its partner. Here, P_f indicates the mating probability of a female entering the mating state and it is given by $P_f = \frac{a_f}{a_f + \mu}$, where μ is the mortality rate in the mating state for females. And a female has probability $s_f = e^{-\mu T_f}$ of surviving after providing maternal care, where μ is the female mortality rate in the caring state. Moreover, since the parents may die during the period of providing care, the expected care duration (τ_f or τ_m) is used to calculate the offspring survival function:

$S_{off} = \frac{(\tau_f + \tau_m)^2}{(\tau_f + \tau_m)^2 + D^2}$, where $\tau_f = (1 - e^{-\mu T_f})/\mu$, $\tau_m = (1 - e^{-\mu T_m})/\mu$, μ is the mortality rate in the caring phase.

Analogously, the fitness w_m of a male is given by $w_m = \frac{P_m}{1-s_m P_m} \cdot S_{off}$. Then the selection gradient for female care duration can be obtained as $\frac{dw_f}{dT_f w_f} = \frac{s'_f P_f}{1-s_f P_f} + \frac{S'_{off}}{S_{off}}$, where the derivatives $s'_f = -\mu \cdot e^{-\mu T_f}$ and $S'_{off} = \frac{dS_{off}}{d\tau_f} \frac{d\tau_f}{dT_f}$ ($\frac{dS_{off}}{d\tau_f} = \frac{2D^2(\tau_f + \tau_m)}{((\tau_f + \tau_m)^2 + D^2)^2}$, $\frac{d\tau_f}{dT_f} = e^{-\mu T_f}$). Analogously, the selection gradient for male care duration is $\frac{dw_m}{dT_m w_m} = \frac{s'_m P_m}{1-s_m P_m} + \frac{S'_{off}}{S_{off}}$. The vector-field plots in Figure 1a is based on these selection gradients.

Then we consider if any mutant can invade the monomorphic population where all individuals provide the same amount of care. In this situation, we determine the fitness $w_{(T,\hat{T})}$ of a rare mutant with care duration T in a resident population with care duration \hat{T} . The fitness is given by $w_{(T,\hat{T})} = \frac{PS_{(T,\hat{T})}}{1-PS_{(T,\hat{T})}}$, where $P = \frac{a}{a+\mu}$ ($a = 1.0$, since there are always same number of females and males in the mating phase), $S_{(T)} = e^{-\mu T}$ and $S_{(T,\hat{T})} = \frac{(T + \hat{T})^2}{(T + \hat{T})^2 + D^2}$. The pairwise invisibility plots in Supplementary Figure S2 is based this invasion fitness function. We analyse the fitness function by the standard means of adaptive dynamics analysis. The fitness gradient is given by $\frac{\partial w_{(T,\hat{T})}}{\partial T} \Big|_{T=\hat{T}} = \frac{PS'_{(T,\hat{T})} + S_{(T,\hat{T})}PS'_{(T)}}{(1-PS_{(T)})^2} \Big|_{T=\hat{T}}$, where $S'_{(T,\hat{T})} = \frac{2D^2(T + \hat{T})}{((T + \hat{T})^2 + D^2)^2}$ and $s'_{(T)} = -\mu \cdot e^{-\mu T}$. Equalizing this with zero yields the evolutionary singular strategy T^* . The calculation shows that T^* is not evolutionarily stable but convergence stable, hence, an evolutionary attractor. In particular, it is an evolutionary branching point, and dimorphism arise via the repeated invasion of mutations with infinitesimally small effect in both sexes.

We also apply the offspring survival function of Fromhage and Jennions (2016) in the analytical analysis, where $S_{(T,\hat{T})} = e^{-\alpha/(T + \hat{T})}$ (or $S_{off} = e^{-\alpha/(\tau_f + \tau_m)}$ when male care and female care coevolve). Supplementary Figure S5 and S7 are based this offspring survival function (see details in p 9 in ref. 1).

References

Fromhage, L. & Jennions, M. Coevolution of parental investment and sexually selected traits drives sex-role divergence. *Nat. Commun.* **7**, 1–11 (2016).