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Abstract

Two models are proposed to simulate population growth of species with mature stage and immature stage in which there are parental cares for immatures. It is assumed that the protection of matures to their immatures reduces mortality of immatures at the cost of reduction of reproduction. Dynamical adaptation of parental cares is incorporated into the models, one of which is described with the proportional transition rate from immatures to matures (ODE model) and the other one is described with a transition rate from immatures to matures according to a fixed age (DDE model). For the ODE model, it is shown that the adaptation of parental care enlarges the possibility of species survival in the sense that population is permanent under the influences of the adaptation, but becomes extinct in the absence of adaptation. It is proved that the outcome of the adaptation makes the population in an optimal state. It is also observed that there are parental care switches, from non-care strategy to care strategy, as the natural death rate of immature individuals increases. The analysis of the DDE model indicates that the adaptation also enlarges the opportunity of population persistence, but the stage delay has the tendency to hinder the movement of population evolution to the optimal state. It is found that the loss rate of immatures in the absence of parental cares can induce different patterns to disturb the adaptation of population to optimal state. However, it is shown that the adaptation of parental care approaches to the optimal state when parental care is required for the survival of the population, for example, when the loss rate of immatures or competition among matures increases or the fecundity decreases.

Key Words: Parental care; Adaptation; Stage; Stability; Optimal.

1 Introduction

Parental care is a fundamental biological activity because matures of many organisms provide their immature offsprings with food and protection. Biological studies of this topics are related to parental care patterns (uniparental care by either sex, sex-biased parental care, or biparental care) and parental care investments (Lessells, 1998; Seno and Endo, 2007; Yaniv, 2005). It is recognized that parental care increases offspring survival, but reduces parental fecundity and mating opportunities (Reynolds et al., 2002). Indeed, if a mature spends more time in searching food to have more benefits for reproductions, its immatures face more risks to be lost due to poor living conditions, or attack from enemies. These have been observed and studied from biological point of view including experiments. Bruno et al. (2007) conducted experimental manipulations to identify and quantify the costs and benefits of parental cares of the harvestman. They found that in a removal experiment of parental cares that lasted 14 days, larvae without parental cares survived 75.6% less than those with parental cares. By monitoring females' reproductive success for 2 years, they found that parents experimentally prevented from guarding their larvae produced new offspring more frequently and had mean lifetime fecundity 18% higher than that of control guarding parents.

There have been a few of mathematical considerations to find strategies of parental investments, among which are game analyses done in Forbes and Mock (1998) and Houston et al. (2005). It seems that game analysis is better applicable when population is in a steady state and individuals know all information to choose the best strategy. To consider dynamical influences of parental care, Wang, Nakaoka, and Takeuchi (2008) and Wang, Takeuchi, Saito, and Nakaoka (2006) proposed mathematical models that incorporate trade-offs between the protection of immatures and the reproduction of matures. However, all the parameters are constants over time in the models of Wang et al. (2008) and Wang et al. (2006), which means that the adaptation of parental care is ignored. Notice that parental care time is a behavioral strategy that can be adjusted by matures to contribute better fitness. Motivated by recent works of DeAngelis et al. (2006); Abrams (2007); Abrams et al. (2007); Krivan (2007), we propose two models with the adaptation of parental care where the parental care time is continuously adjusted to represent the natural selection of matures to achieve better fitness through learning favorable strategy. Our models have two stages (immature and mature), between which there is a transition from immature to mature.

64 The organization of this paper is as follows. In the next section, we present
65 the model formulation of a population with parental care described with a pro-
66 portional transition rate from immature individuals to mature individuals. Our
67 analysis shows that the adaptation of parental care enlarges the possibility of pop-
68 ulation survival in the sense that population is permanent under the influences of
69 the adaptation, but becomes extinct if there is no adaptation. We also prove that
70 the adaptation makes the population in an optimal state. In section 3, we introduce
71 another mathematical model with the adaptation of parental care with the transi-
72 tion from immature individuals to mature individuals according to a fixed age. It
73 is shown that the adaptation also enlarges the opportunity of population persis-
74 tence, but the stage delay has the tendency to hinder the movement of population
75 evolution to the optimal state.

76 **2 Model with proportional transition**

77 **2.1 Model**

78 To consider dynamical behavior of parental care, we use a stage-structured model
79 that splits a population into two categories: immature class and mature class. Con-
80 tinuous stage structured models were proposed or studied by Nisbet and Gurney
81 (1983), Aiello and Freedman (1990); Aiello et al. (1992), Thieme (2003), de Roos
82 et al. (2003), Gourley and Kuang (2004, 2005), Kostova et al. (1999), Wang and
83 Chen (1997); Wang et al. (2001); Wang and Zhao (2005, 2006). Basically, modeling
84 approaches are divided into two types according to the rate of transition: ODE ap-
85 proach and DDE approach. We start from the ODE method. Let y_1 be the density
86 of immature individuals, y_2 be the density of mature individuals, c be the fraction
87 of parental care time in one unit time and s be the fraction of searching time in
88 one unit time. Then $c + s = 1$. Care time c is a behavioral strategy for matures.
89 As a trait, it can adapt and evolve because of learning of individuals. We hope to
90 find influences of adaptation of care time c on population dynamics.

91 To derive the recruitment rate of population, we assume that the resource input
92 is constant r , which is a reasonable approximation in the first step and simplifies
93 the dynamics. Moreover this assumption can be reasonable if the resource recovers
94 very fast to become steady state. Then one mature admits the resource r/y_2 . If
95 a_0 is the searching efficiency of the resource for one mature, since the fraction of
96 searching time becomes $1 - c$ because of parental care, the searching efficiency is

now reduced to $a_0(1 - c)$. As a result, the uptake rate of resource for one mature is $x = a_0(1 - c)r/y_2$. To incorporate the saturation effect converting the nutrient x into offsprings, we select the simplest candidate of Beverton-Holt recruitment function $\frac{kx}{1+hx}$ to obtain per capita birth rate of one mature:

$$k \frac{a_0(1 - c) \frac{r}{y_2}}{1 + a_0(1 - c)h \frac{r}{y_2}} = \frac{a(1 - c)}{b(1 - c) + y_2}$$

with $a = ka_0r$ and $b = a_0hr$. Now, without evolution of c , we can assume that population dynamics is described by

$$\begin{cases} \frac{dy_1}{dt} = \frac{a(1 - c)y_2}{b(1 - c) + y_2} - d_1y_1 - \alpha(1 - c)y_1 - \nu y_1, \\ \frac{dy_2}{dt} = \nu y_1 - d_2y_2, \end{cases} \quad (2.1)$$

where α gives the loss rate of immatures in the absence of parental cares per unit time, d_1 and d_2 are the natural per capita death rates of immature individuals and mature individuals and ν is the transition rate from immature stage to mature stage. That is, we assume that the average maturation time is $1/\nu$. This is a simple way to model stage structures when ages of immature individuals are not easily measured or maturation is size-dependent (Thieme, 2003). Another advantage of this methodology is that the transition rate from immature stage to mature stage can be easily obtained by statistical method such as linear regression.

To include adaptation of parental care in (2.1), we must define the fitness of the population. Without a stage structure, it is just the per capita net growth rate of the species (Metz et al., 1992; Geritz et al., 2004). Now, because one mature is a representative of one ‘family’ (one mature together with its immature members) and an adult should consider the future of whole family, its care time and reproduction are connected to a family. Thus, it is reasonable to consider that costs and benefits should be calculated according to a family. Hence, we define the fitness by

$$F = \frac{a(1 - c)}{b(1 - c) + y_2} - (d_1 + \alpha(1 - c)) \frac{y_1}{y_2} - d_2.$$

Here note that

$$F = (\frac{dy_1}{dt} + \frac{dy_2}{dt})/y_2.$$

Following the spirit of adaptation (Dieckmann and Law, 1996; Hofbauer and Sigmund, 1998; Abrams, 2000), we assume that adaptation equation takes the form:

$$\frac{dc}{dt} = \beta(c) \frac{\partial F}{\partial c} = \beta(c) \left(-\frac{ay_2}{(b(1-c) + y_2)^2} + \alpha \frac{y_1}{y_2} \right),$$

where $\beta(c)$ satisfies: $\beta(0) = \beta(1) = 0$, $\beta(c) > 0$ for $0 < c < 1$ to ensure c lies between 0 and 1. Thus, the full model is

$$\begin{cases} \frac{dy_1}{dt} = \frac{a(1-c)y_2}{b(1-c) + y_2} - d_1y_1 - \alpha(1-c)y_1 - \nu y_1, \\ \frac{dy_2}{dt} = \nu y_1 - d_2y_2, \\ \frac{dc}{dt} = \beta(c) \left(-\frac{ay_2}{(b(1-c) + y_2)^2} + \alpha \frac{y_1}{y_2} \right). \end{cases} \quad (2.2)$$

To be specific, we choose $\beta(c) = wc(1-c)$ with a positive constant w . Indeed, mathematical analysis and computer simulations below show that the change of adaptation coefficient $\beta(c)$ does not influence qualitative behavior of (2.2), though the adaptation speed is altered. w is always fixed at 1 for numerical computations.

We transform (2.2) by $u = y_1/y_2$ to obtain

$$\begin{cases} \frac{du}{dt} = \frac{a(1-c)}{b(1-c) + y_2} - (d_1 + \alpha(1-c) + \nu - d_2)u - \nu u^2, \\ \frac{dy_2}{dt} = y_2(\nu u - d_2), \\ \frac{dc}{dt} = wc(1-c) \left(-\frac{ay_2}{(b(1-c) + y_2)^2} + \alpha u \right). \end{cases} \quad (2.3)$$

Note that (2.3) or (2.2) is defined only for $y_2 > 0$ because we consider the fitness according to a family of predators.

2.2 Optimal versus Dynamical Adaptation

Appendix A shows that (2.1) has a globally stable positive equilibrium point $E_{00} = (\bar{y}_1, \bar{y}_2)$ when (A-3) is satisfied. On the other hand, adaptation system (2.2) has an asymptotically stable positive steady state $E^* = (y_1^*, y_2^*, c^*)$ when (A-6) is satisfied (see Theorem A in Appendix B and Table 1). Let us consider the relationship between E_{00} and E^* . Let $f(s) = \bar{y}_1 + \bar{y}_2$ be the total number of the population described by (2.1) at globally stable steady state $E_{00} = (\bar{y}_1, \bar{y}_2)$. With $s = 1 - c$ we have

$$f(s) = \left(1 + \frac{\nu}{d_2}\right) \frac{a\nu - (d_1 + \alpha s + \nu)bd_2}{\nu(d_1 + \alpha s + \nu)} s.$$

144 Function $f(s)$ attains a maximal value for $s \in (0, \frac{a\nu - bd_2(d_1 + \nu)}{bd_2\alpha})$ at

$$145 \quad s_m := \frac{1}{\alpha} \left\{ \sqrt{\frac{a\nu(d_1 + \nu)}{bd_2}} - (d_1 + \nu) \right\} = s^*,$$

146 where $s^* = 1 - c^*$ (see (A-12)). Thus, we have from (A-13)

$$\begin{aligned} f(s_m) &= \left(1 + \frac{\nu}{d_2}\right) \frac{a\nu - bd_2 \sqrt{\frac{a\nu(d_1 + \nu)}{bd_2}}}{\nu \sqrt{\frac{a\nu(d_1 + \nu)}{bd_2}}} s^* \\ 147 \quad &= \left(1 + \frac{d_2}{\nu}\right) \left(\frac{a\nu}{d_2} \sqrt{\frac{bd_2}{a\nu(d_1 + \nu)}} - b \right) s^* \\ &= \left(1 + \frac{d_2}{\nu}\right) y_2^* = y_1^* + y_2^*. \end{aligned}$$

148 Therefore, the equilibrium $E^* = (y_1^*, y_2^*, c^*)$ of (2.2) presents the optimal care time
149 c^* such that population size attains maximal value $y_1^* + y_2^*$. This means that the
150 outcome of adaptation makes the population in optimal state.

151 Now, we can present that the adaptation of population enhances its persistence.
152 Indeed, the case that $c = 1$ is uninteresting because there is no reproduction. For
153 $0 \leq c < 1$, if we set

$$\begin{aligned} A_0 &= \frac{bd_2(d_1 + \nu)}{\nu}, & A_c &= \frac{bd_2(d_1 + \alpha(1 - c) + \nu)}{\nu}, \\ 154 \quad A_1 &= \frac{bd_2(d_1 + \alpha + \nu)}{\nu}, & A_2 &= \frac{bd_2(d_1 + \alpha + \nu)^2}{\nu(d_1 + \nu)}, \end{aligned}$$

155 it is easy to see

$$156 \quad A_0 < A_c \leq A_1 < A_2.$$

157 Then Table 1 follows easily from comparison of existence and stability of positive
158 equilibrium E_{00} of (2.1) and equilibria E_1 and E^* of (2.3) (see Appendix A and B).
159 In fact, from Table 1 we obtain Figure 1. In region B ($A_c < a < A_2$) and region C
160 ($A_0 < a < A_c$), positive equilibrium E^* of (2.3) that incorporates the adaptation of
161 parental care is asymptotically stable. Moreover, numerical simulations show that
162 positive equilibrium E^* is globally stable (see Figure 2). Hence, the population
163 survives in this case. However, since positive equilibrium E_{00} of (2.1) does not
164 exist in region C , the population without adaptation of parental care becomes
165 extinct (see Appendix A). Therefore, the adaptation of the parental care enlarges
166 the possibility of species survival.

a	$a < A_0$	$A_0 < a < A_c$	$A_c < a < A_1$	$A_1 < a < A_2$	$A_2 < a$
E_{00}	no existence	no existence	existence(+)	existence(+)	existence(+)
E_1	no existence	no existence	no existence	existence(-)	existence(+)
E^*	no existence	existence(+)	existence(+)	existence(+)	no existence

Table 1: Comparison of existence and stability of equilibria of model (2.1) and model (2.3) where the sign $-$ means the equilibrium is unstable and the sign $+$ indicates the equilibrium is asymptotically stable (see Appendix A and B).

Figure 1: Distribution of equilibrium E_{00} of (2.1) and equilibria E_1 and E^* of (2.3) in the plane of a (fecundity) and c (parental care), where region A gives “no relevance to adaptation”, B indicates “advantageous parental care” and C presents “adaptation mediated survival”.

Figure 2: Graphs that show global stability of positive equilibrium E^* of (2.3).

167 We now reveal the mechanisms of parental care. In region A ($a > A_2$), E_{00}
168 and E_1 are stable. From the definition $a = ka_0r$, region A implies that resource
169 is rich (r is large), or searching efficiency of the species is high (a_0 is large) or
170 the conversion coefficient k is large. In this case, having more reproductions is
171 more important than reducing the loss of immatures, and hence parental care time
172 $c(t) \rightarrow 0$ as $t \rightarrow \infty$, indicated in Figure 3 by arrows. On the other hand, in region
173 B , the population adapts its strategy to the curve $1 - c = s_m$ of optimal care time
174 in order to achieve maximal population size. In region C where the population
175 becomes extinct without adaptation, the strategies of adaptation of care time are
176 to move to the ‘good’ region B first, and then approach to the curve of optimal
177 care time, indicated by arrows in Figure 3.

Figure 3: Strategies of parental care where arrows indicate the directions of reducing or increasing parental care times.

178 2.3 Resource Competition and Parental Care

179 We now point out that model (2.3) admits an interesting phenomenon of stability
180 switches of equilibrium E_1 as the natural mortality rate d_1 of immatures varies.
181 Indeed, let

$$182 \quad S = a - \frac{bd_2(d_1 + \alpha + \nu)^2}{\nu(\nu + d_1)}.$$

183 It follows from (A-14) that E_1 is stable if $S > 0$, whereas E_1 is unstable if $S < 0$.
184 If we fix $b = 2$, $d_2 = 0.1$, $a = 18$, $\nu = 0.1$ and $\alpha = 2$, then we see that E_1 is unstable
185 when $d_1 < 0.9$ or $d_1 > 3.9$, and is stable when $0.9 < d_1 < 3.9$ by Table 1 (see the
186 left panel of Figure 4).

187 Notice that the change of stability of E_1 means the occurrence (at $d_1 = 3.9$)
 188 or disappearance (at $d_1 = 0.9$) of parental care. The stability switches imply that
 189 there are parental care switches as the natural death rate of immature individuals
 190 increases. The parental care is effective if the death rate of immatures is large
 191 (see the right panel of Figure 4 for $d_1 > 3.9$). Thus it is reasonable to see that
 192 E_1 is unstable on the region for larger d_1 . It remains to know why the population
 193 needs to spend its time for parental care even though the death rate of immatures is
 194 small (see the right panel of Figure 4 for $d_1 < 0.9$). One possible explanation which
 195 could answer the question is the limitation of resource available to the population.
 196 If the death rate of immatures is small, a large number of them could be matured.
 197 It subsequently leads to the strong resource competition among matures, because
 198 of the Beverton-Holt functional response. Hence, the resource competition would
 199 decrease the effectiveness of searching food. We have a trade-off between the time
 200 for searching food and that for protecting immatures. The population is now
 201 advantageous to behave as spending more time to parental care.

Figure 4: Left panel shows stability switches of E_1 and right panel indicates transitions of care times as d_1 increases.

3 Model with transition by age

3.1 Model

204 Another common way to model a stage structure is to use delayed differential
 205 equations (DDE) when the duration of immature stage can be easily measured.
 206 Following the modeling approach in the last section, without evolution of c , we

207 assume that the population dynamics is described by

$$\begin{cases} \frac{dy_1}{dt} = \frac{a(1-c)y_2(t)}{b(1-c) + y_2(t)} - (d_1 + \alpha(1-c))y_1(t) - T, \\ \frac{dy_2}{dt} = T - d_2y_2(t), \end{cases} \quad (3.1)$$

208 where T is the transition rate from immatures to matures, defined by

$$209 \quad T = \frac{a(1-c)y_2(t-\tau)}{b(1-c) + y_2(t-\tau)} \exp\{-(d_1 + \alpha(1-c))\tau\},$$

210
211 in which τ gives the time for immatures to mature. Here T represents the imma-
212 tures born at time $t-\tau$ (with the mature birth $a(1-c)y_2(t-\tau)/\{b(1-c)+y_2(t-\tau)\}$)
213 that survive to time t (with the immature death rate $d_1 + \alpha(1-c)$). This gives the
214 immatures transition from the immature population entering the mature popula-
215 tion at time t . The similar formulation can be found in many papers, for example,
216 Aiello and Freedman (1990).

By similar arguments in the previous section, we introduce the adaptation equa-
tion

$$\frac{dc}{dt} = wc(t)(1-c(t)) \left(-\frac{ay_2(t)}{(b(1-c(t)) + y_2(t))^2} + \alpha \frac{y_1(t)}{y_2(t)} \right),$$

217 and obtain the full model:

$$\begin{cases} \frac{dy_1}{dt} = \frac{a(1-c(t))y_2(t)}{b(1-c(t)) + y_2(t)} - (d_1 + \alpha(1-c(t)))y_1(t) \\ \quad - \frac{a(1-c(t-\tau))y_2(t-\tau)}{b(1-c(t-\tau)) + y_2(t-\tau)} \exp\left\{-\int_{t-\tau}^t (d_1 + \alpha(1-c(\theta)))d\theta\right\}, \\ \frac{dy_2}{dt} = \frac{a(1-c(t-\tau))y_2(t-\tau)}{b(1-c(t-\tau)) + y_2(t-\tau)} \exp\left\{-\int_{t-\tau}^t (d_1 + \alpha(1-c(\theta)))d\theta\right\} - d_2y_2(t), \\ \frac{dc}{dt} = wc(t)(1-c(t)) \left(-\frac{ay_2(t)}{(b(1-c(t)) + y_2(t))^2} + \alpha \frac{y_1(t)}{y_2(t)} \right). \end{cases} \quad (3.2)$$

218 Note that c is now time dependent and we need the transition term expressed with
219 integral form in the above.

220 3.2 Optimal versus Dynamical Adaptation

221 Table 2 presents the distribution of the equilibria of (3.2). Here $E_0 = (0, 0, 0)$ is an
222 extinct steady state, $E_1 = (y_{10}, y_{20}, 0)$ is an equilibrium state without parental care
223 and $E^*(y_1^*, y_2^*, c^*)$ is one with parental care for (3.2), respectively (see Appendix C
224 and Theorem B). See further the definition of $\tau^*, \tau^{**}, \tau_0$ in Appendix C.

τ	$\tau < \tau^*$	$\tau^* < \tau < \tau_0$	$\tau_0 < \tau < \tau^{**}$	$\tau^{**} < \tau$
E_0	no existence	no existence	no existence	existence
E_1	existence(+)	existence(-)	no existence	no existence
E^*	no existence	existence	existence	no existence

Table 2: Equilibria of model (3.2) as the stage delay varies, where the sign $-$ means the equilibrium is unstable and the sign $+$ indicates the equilibrium is asymptotically stable (see Appendix C).

225 Numerical calculations show that E_0 is globally stable when $\tau^{**} < \tau$, E^* is
226 globally stable whenever it exists, and E_1 is globally stable for $\tau < \tau^*$ (see Figures
5 and 6). Thus, there is no need for parental care when the stage delay is small

Figure 5: Graphs that show global stability of E_0 and E^* of (3.2). The parameters for the graphs are fixed by $a = 5, d_1 = 1, d_2 = 0.5, \alpha = 0.5, b = 1$ ($\tau_0 = 1.54$, $\tau^* = 1.31$ and $\tau^{**} = 2.30$). The delay for the left panel is taken as $\tau = 3.0 > \tau^{**}$ and the delay for the right panel is given by $\tau = 2.0$ ($\tau_0 < \tau < \tau^{**}$).

227
228 (ref. the right panel of Fig. 6), and parental care is necessary when the stage delay
229 is in a medium size (ref. the right panel of Fig. 5 and the left panel of Fig. 6).

230 To see whether the adaptation can enlarge the possibility of population survival,
231 we consider the stability of model (3.1) where there is no population adaptation.
232 Let

$$\tau < \frac{1}{d_1 + \alpha(1-c)} \ln \frac{a}{bd_2} := \tau_c. \quad (3.3)$$

233 (3.1) admits a globally stable positive equilibrium $E_{01} = (y_{01}, y_{02})$ where

$$\begin{aligned} y_{02} &= \frac{a(1-c)e^{-(d_1+\alpha(1-c))\tau}}{d_2} - b(1-c), \\ y_{01} &= \frac{a(1-c)y_{02}}{(b(1-c) + y_{02})(d_1 + \alpha(1-c))} (1 - e^{-(d_1+\alpha(1-c))\tau}). \end{aligned} \quad (3.4)$$

Figure 6: Graphs that show global stability of E^* and E_1 of (3.2). The parameters are fixed as the same as Figure 5 ($\tau_0 = 1.54$, $\tau^* = 1.31$ and $\tau^{**} = 2.30$). The delay for the left panel is taken as $\tau = 1.4$ ($\tau^* < \tau < \tau_0$) and the delay for the right panel is given by $\tau = 1$ ($\tau < \tau^*$).

Furthermore, if $\tau > \tau_c$, positive solutions of (3.1) approach $(0, 0)$ as $t \rightarrow \infty$. Note that $\tau_c < \tau^{**}$ when $0 \leq c < 1$, and that the population in (3.2) can survive when $\tau_c \leq \tau < \tau^{**}$ (see Table 2). It follows that the adaptation increases the possibility of population persistence.

Motivated by the observations on ODE model (2.3), we hope to know whether the adaptation of population makes the population in an optimal state in the sense that $y_1^* + y_2^*$ gives the maximal value of $y_{01}(c) + y_{02}(c)$ when $c = c^*$. We assume that $y_{01}(c) + y_{02}(c)$ achieves a maximum value at $c = \bar{c}$. Note that y_1^* and y_2^* satisfy (A-23) and (A-24). If we fix $c = c^* = 1 - s^*$ in (3.4) with s^* satisfying $f(s^*) = g(s^*)$ in the proof of Theorem B, we obtain $y_1^* = y_{01}(c^*)$ and $y_2^* = y_{02}(c^*)$. Hence, we have

$$y_1^* + y_2^* \leq y_{01}(\bar{c}) + y_{02}(\bar{c}), \quad (3.5)$$

and the inequality holds unless $c^* = \bar{c}$. The following example shows that the population size at the positive equilibrium is less than the optimal population size.

Example 1 We take $\tau = 1, \alpha = 1, b = 0.5, d_1 = 0.2, d_2 = 0.5, a = 0.8$. By (3.4) we obtain

$$y_{01} = \frac{0.5(1.6 \exp(-0.2 - s)s - 0.5s)(1 - \exp(-0.2 - s))}{\exp(-0.2 - s)(0.2 + s)},$$

$$y_{02} = 1.6 \exp(-0.2 - s)s - 0.5s$$

with $s = 1 - c$. Then $y_{01} + y_{02}$ achieves a maximal value 0.2572 at $s = 0.4453$.

251 However, we have $y_1^* = 0.1065, y_2^* = 0.1463, s^* = 0.5093$. Since $y_1^* + y_2^* = 0.2528 <$
 252 0.2572 , the evolution of the population does not arrive at the ideal state.

253 3.3 Effects of Stage Delay on Parental Care

254 Example 1 shows that the stage delay has the tendency to reduce the opportunity
 255 for the population to move to the optimal state. To see influences of stage delay
 256 on the outcomes of adaptation, we first consider the effect of the stage delay τ on
 257 y_{01} and y_{02} . By direct calculations, we obtain

$$\begin{aligned} y'_{02}(\tau) &= -\frac{as}{d_2}(d_1 + \alpha s)e^{-(d_1 + \alpha s)\tau} < 0, \\ y'_{01}(\tau) &= (ae^{-2(d_1 + \alpha s)\tau} - bd_2)e^{(d_1 + \alpha s)\tau}s, \end{aligned}$$

259 and

$$y'_{01}(\tau) + y'_{02}(\tau) = \left\{ a\left(1 - \frac{d_1 + \alpha s}{d_2}\right)e^{-(d_1 + \alpha s)\tau} - bd_2e^{(d_1 + \alpha s)\tau} \right\}s.$$

261 Hence, the density of matures at the equilibrium is a decreasing function of τ , and
 262 the density of immature individuals at the equilibrium increases for $0 < \tau < \tau_c/2$,
 263 decreases for $\tau_c/2 < \tau < \tau_c$. Further, the density of whole population at the
 264 equilibrium increases for

$$0 < \tau < \frac{1}{2(d_1 + \alpha s)} \ln \left\{ \frac{a}{bd_2} \left(1 - \frac{d_1 + \alpha s}{d_2} \right) \right\},$$

266 and decreases for

$$\frac{1}{2(d_1 + \alpha s)} \ln \left\{ \frac{a}{bd_2} \left(1 - \frac{d_1 + \alpha s}{d_2} \right) \right\} < \tau < \tau_c$$

268 (see Figure 7). From Figure 7, we see that parental care time $\bar{c}$, which gives the
 269 maximal total population size, increases as the stage delay increases.

270 Next, we consider the influences of stage delay on the difference between the
 271 optimal population size and the population size at the positive equilibrium with
 272 the adaptation. If we fix $a = 3.0, b = 0.5, d_1 = 0.1, d_2 = 0.6$ and vary α , we obtain
 273 three different types of figures that show interesting phenomena about influences
 274 of stage delay on the adaptation (see Figure 8). As the loss rate α of immatures
 275 in the absence of parental cares becomes larger, the conflicts between reproduction
 276 and parental care become more severe. As a result, the curve for the difference,
 277 i.e., $y_{01}(\bar{c}) + y_{02}(\bar{c}) - (y_1^* + y_2^*)$, undergoes the transitions from a decreasing manner
 278 to the shape with one hump (increasing first, and then decreasing), and then to
 279 the shape with two humps. We examine how the difference can be influenced as

Figure 7: The graph of $y_{01}(\bar{c})$, $y_{02}(\bar{c})$, $y_{01}(\bar{c}) + y_{02}(\bar{c})$ and $\bar{c}$ versus τ where $\alpha = 0.2$, $b = 0.5$, $d_1 = 0.1$, $d_2 = 0.6$, $a = 3.0$.

Figure 8: Graphs that show the adapted parental care time c^* and differences of $y_{01}(\bar{c}) + y_{02}(\bar{c}) - (y_1^* + y_2^*)$ where $\alpha = 0.1$ for the top left panel, $\alpha = 0.2$ for the top right panel, $\alpha = 0.4$ for the bottom left panel, and $\alpha = 2.0$ for the bottom right panel. The other parameters are always fixed as $a = 3.0$, $b = 0.5$, $d_1 = 0.1$ and $d_2 = 0.6$.

Figure 9: Graphs that show the adapted parental care time c^* and differences of $y_{01}(\bar{c}) + y_{02}(\bar{c}) - (y_1^* + y_2^*)$ where $a = 1.5$ and $b = 0.5$ for the left panel whereas $a = 3.0$ and $b = 1.5$ for the right panel. The other parameters are fixed as same as one of the panel in Figure 8; $\alpha = 0.2$, $d_1 = 0.1$ and $d_2 = 0.6$.

the loss rate α of immatures varies. Among four panels in Figure 8, we observe that τ^* becomes smaller as α increases (c.f., (A-28)). The adapted parental care time c^* rapidly saturates to 1 as α increases. Thus matures are forced to spend more time to care for immatures even though stage delay is small. Moreover, the difference $y_{01}(\bar{c}) + y_{02}(\bar{c}) - (y_1^* + y_2^*)$ becomes smaller as α increases, in the sense that the difference rapidly decreases to become small for almost stage delay.

Now we consider the influences of fecundity a and competition among matures b on the adaptation of parental care time. Compare the top right panel of Figure 8 and the left panel of Figure 9, where the latter panel has a smaller value of fecundity a . We observe that τ^* and the difference $y_{01}(\bar{c}) + y_{02}(\bar{c}) - (y_1^* + y_2^*)$ become smaller and c^* rapidly saturates to 1 when fecundity is smaller. The same tendencies are also observed for larger competition among matures (compare the top right panel of Figure 8 and the right panel of Figure 9).

Note that adaptation is rapid if the right hand side of the adaptation equation in (3.2) is large. Above observations together with the adaptation equation in (3.2) suggest that the population undergoes adaptation toward increasing parental care, provided that either α is large, a is small or b is large. In other words, the more parental care is required, the smaller the difference becomes. Hence the population state approaches to the optimal state as parental care is required for the survival of the population.

4 Discussions

In this paper, by dividing a population into immature stage and mature stage, we have proposed two models with stage structures to simulate the adaptation of dynamical parental care of matures to their offsprings. We have defined the population fitness according to families. Then we have given the rule of adaptation that matures adjust their care times according to the direction of gradient of fitness. For the proportional transition case (ODE model), we have shown that this is a perfect way of adaptation because the adaptation makes the population in an optimal state, and the adaptation of parental care enlarges the possibility of species survival in the sense that population is permanent under the influences of the adaptation, but becomes extinct in the absence of adaptation. We have also found the counterintuitive phenomenon that lower death rate of immature individuals induce parental care. For the model with transition by age (DDE model), we have verified that the adaptation also enlarges the opportunity of population persistence, but the stage delay has the tendency to hinder the movement of population evolution to the optimal state. Biological mechanism behind this is that the model with the stage structure induces trade-off between matures and immature members. The model with the proportional transition rate admits the nice property that mature individuals achieve optimal state together with their children. However, the model with the transition from immature individuals to mature individuals according to a fixed age has the nonlinear transition rate, which produces certain gap between the optimal occurrence of matures and the optimal occurrence of immatures. The numerical simulation suggests that the gap decreases as the loss of the immatures without parental care increases or the fecundity decreases or competition among matures increases. Under these circumstances, the adaptation approaches to the optimal state.

APPENDIX

APPENDIX A

Stability of Equilibria of (2.1)

We define $\frac{a(1-c)y_2}{b(1-c)+y_2} = 0$ at $(0, 0)$ since the reproduction rate is 0 when $y_2 = 0$ and $c = 1$. Then (2.1) is well defined for $y_1 \geq 0, y_2 \geq 0$ and $0 \leq c \leq 1$. Note that

331 (2.1) is a cooperative system when $0 \leq c < 1$. Linearizing (2.1) at $(0, 0)$, we obtain

$$\begin{cases} \frac{dy_1}{dt} = -(d_1 + \alpha(1 - c) + \nu)y_1 + \frac{a}{b}y_2, \\ \frac{dy_2}{dt} = \nu y_1 - d_2 y_2. \end{cases} \quad (\text{A-1})$$

332 The coefficient matrix of the right-hand side of (A-1) has a negative dominant
333 eigenvalue if

$$d_2 d_1 b + d_2 \alpha b(1 - c) + d_2 \nu b > a \nu, \quad (\text{A-2})$$

334 and has a positive dominant eigenvalue if

$$d_2 d_1 b + d_2 \alpha b(1 - c) + d_2 \nu b < a \nu. \quad (\text{A-3})$$

335 It follows from similar arguments (Takeuchi et al., 2006) that system (2.1) exhibits
336 extinct of the population if (A-2) holds, and the population is persistent if (A-3)
337 holds. Indeed, the theory of monotonic flows (Smith, 1995; Zhao, 2003) implies that
338 system (2.1) has a positive equilibrium, denoted by E_{00} , that is globally stable.

339 APPENDIX B

340 Stability of Equilibria of (2.3)

341 First, we consider the case where $c = 0$. Let u_0 be the unique positive solution
342 of the following equation:

$$343 \quad \frac{a}{b} - (d_1 + \alpha + \nu - d_2)u - \nu u^2 = 0.$$

344 Then $E_0 = (u_0, 0, 0)$ is an equilibrium point of (2.3). When

$$345 \quad a \nu > d_2 b(d_1 + \alpha + \nu),$$

346 another equilibrium $E_1 = (\frac{d_2}{\nu}, y_{20}, 0)$ occurs where

$$347 \quad y_{20} = \frac{a \nu - d_2 b(d_1 + \alpha + \nu)}{d_2(d_1 + \alpha + \nu)}.$$

348 It is easy to see that E_0 is a saddle point. The stability of E_1 is not trivial. The
349 Jacobian matrix at E_1 is

$$\begin{bmatrix} -d_1 - \alpha - \nu - d_2 & -\frac{a}{(b + y_{20})^2} & -\frac{a}{b + y_{20}} + \frac{a b}{(b + y_{20})^2} + \frac{\alpha d_2}{\nu} \\ \nu y_{20} & 0 & 0 \\ 0 & 0 & w \left(-\frac{a y_{20}}{(b + y_{20})^2} + \frac{\alpha d_2}{\nu} \right) \end{bmatrix}.$$

350 The characteristic equation is

$$351 \quad (\lambda - w(-\frac{a y_{20}}{(b + y_{20})^2} + \frac{\alpha d_2}{\nu}))((d_1 + \alpha + \nu + d_2 + \lambda) \lambda + \frac{a \nu y_{20}}{(b + y_{20})^2}) = 0.$$

352 Hence, E_1 is asymptotically stable if

$$\frac{a y_{20}}{(b + y_{20})^2} > \frac{\alpha d_2}{\nu}, \quad (\text{A-4})$$

353 while E_1 is unstable if

$$\frac{a y_{20}}{(b + y_{20})^2} < \frac{\alpha d_2}{\nu}. \quad (\text{A-5})$$

354

355 **Theorem A:** (2.3) has a unique asymptotically stable positive equilibrium $E^* =$
 356 (u^*, y_2^*, c^*) if we have

$$b d_2 (d_1 + \nu) < a \nu < \frac{b d_2 (d_1 + \nu + \alpha)^2}{d_1 + \nu}. \quad (\text{A-6})$$

357 **Proof:**

358 If $E^* = (u^*, y_2^*, c^*)$ is a positive equilibrium of (2.3), by the second equation of
 359 (2.3) we obtain $u^* = \frac{d_2}{\nu}$. Set $s^* = 1 - c^*$. By the third equation of (2.3), we have

$$\frac{a y_2^*}{(b s^* + y_2^*)^2} = \alpha u^*. \quad (\text{A-7})$$

360 Further, the first equation of (2.3) gives

$$\begin{aligned} \frac{a s^*}{b s^* + y_2^*} &= (d_1 + \alpha s^* + \nu - d_2 + \nu u^*) u^* \\ &= (d_1 + \alpha s^* + \nu) u^*. \end{aligned} \quad (\text{A-8})$$

361 Then (A-7) and (A-8) imply

$$\frac{a}{\alpha u^*} \left(\frac{a s^*}{(d_1 + \alpha s^* + \nu) u^*} - b s^* \right) = \frac{a^2 (s^*)^2}{(d_1 + \alpha s^* + \nu)^2 (u^*)^2}, \quad (\text{A-9})$$

362 which leads to

$$a(d_1 + \alpha s^* + \nu) - b(d_1 + \alpha s^* + \nu)^2 u^* = a \alpha s^*. \quad (\text{A-10})$$

363 A simplification of (A-10) yields

$$b(d_1 + \alpha s^* + \nu)^2 u^* = a(d_1 + \nu). \quad (\text{A-11})$$

364 As a consequence, we obtain

$$s^* = \frac{1}{\alpha} \left\{ \sqrt{\frac{a(d_1 + \nu)}{bu^*}} - (d_1 + \nu) \right\}, \quad (\text{A-12})$$

365 and

$$y_2^* = \left(\sqrt{\frac{ab}{u^*(d_1 + \nu)}} - b \right) s^*. \quad (\text{A-13})$$

366 Note that (A-6) implies that $y_2^* > 0$ and $0 < s^* < 1$. Therefore, the existence and
367 uniqueness of the positive equilibrium is verified.

368 The Jacobian matrix at E^* is

$$369 \quad J := \begin{bmatrix} -(d_1 + \alpha(1 - c^*) + \nu - d_2) - 2\nu u^* & -\frac{a(1 - c^*)}{(b(1 - c^*) + y_2^*)^2} & 0 \\ \nu y_2^* & 0 & 0 \\ \alpha w c^*(1 - c^*) & -a w c^*(1 - c^*) \frac{b(1 - c^*) - y_2^*}{(b(1 - c^*) + y_2^*)^3} & \chi \end{bmatrix}$$

370 where

$$371 \quad \chi = -w c^*(1 - c^*) \frac{2ab y_2^*}{(b(1 - c^*) + y_2^*)^3} < 0.$$

372 Note that

$$373 \quad -(d_1 + \alpha(1 - c^*) + \nu - d_2) - 2\nu u^* = -(d_1 + \alpha(1 - c^*) + \nu) - \nu u^* < 0.$$

374 It is easy to see that all characteristic roots of J have negative real parts. The
375 proof is complete. $\square$

376 We now give interesting comparisons between the dynamics of model (2.3) and
377 the dynamics of model (2.1). Let $E_{00} = (\bar{y}_1, \bar{y}_2)$ be the globally stable equilibrium
378 of (2.1). Note that $\bar{y}_2 = \frac{\nu}{d_2} \bar{y}_1$ and

$$379 \quad \bar{y}_1 = (1 - c) \frac{a\nu - (d_1 + \alpha(1 - c) + \nu)bd_2}{\nu(d_1 + \alpha(1 - c) + \nu)}.$$

380 This equilibrium exists if and only if (A-3) holds.

381 Now we consider relations among stability conditions of various equilibria of
382 (2.3). Note that the second inequality in (A-6)

$$a\nu < \frac{bd_2(d_1 + \nu + \alpha)^2}{d_1 + \nu} \quad (\text{A-14})$$

383 is equivalent to (A-5). In fact, from the definition of y_{20} , we have

$$384 \quad y_{20} + b = \frac{a\nu}{d_2(d_1 + \alpha + \nu)},$$

385 which, together (A-14), implies

$$386 \quad \frac{ay_{20}}{(b + y_{20})^2} = \frac{d_2(d_1 + \alpha + \nu)(a\nu - bd_2(d_1 + \alpha + \nu))}{a\nu^2} < \frac{\alpha d_2}{\nu}.$$

387 Thus, (A-14) leads to (A-5). The fact that (A-5) implies (A-14) can be easily ob-
 388 tained from above inequality. Hence, E^* is asymptotically stable under conditions
 389 (A-5) and $bd_2(d_1 + \nu) < a\nu$. Furthermore, E_1 is asymptotically stable under

$$a\nu > \frac{bd_2(d_1 + \nu + \alpha)^2}{d_1 + \nu}. \quad (\text{A-15})$$

390

391 APPENDIX C

392 Stability of Equilibria of (3.2)

393 We now consider stability of (3.2). First, we find equilibria when $c = 0$. When
 394 $c = 0$, (3.2) is reduced to

$$\begin{cases} \frac{dy_1}{dt} = \frac{ay_2(t)}{b + y_2(t)} - (d_1 + \alpha)y_1(t) - \frac{ay_2(t - \tau)}{b + y_2(t - \tau)}e^{-(d_1 + \alpha)\tau}, \\ \frac{dy_2}{dt} = \frac{ay_2(t - \tau)}{b + y_2(t - \tau)}e^{-(d_1 + \alpha)\tau} - d_2y_2(t). \end{cases} \quad (\text{A-16})$$

395 It is easy to verify that (A-16) has a positive equilibrium $E_{10} = (y_{10}, y_{20})$ with

$$396 \quad y_{20} = \frac{ae^{-(d_1 + \alpha)\tau}}{d_2} - b, \quad y_{10} = \frac{ay_{20}}{(b + y_{20})(d_1 + \alpha)} (1 - e^{-(d_1 + \alpha)\tau})$$

397 if

$$\frac{ae^{-(d_1 + \alpha)\tau}}{d_2} > b. \quad (\text{A-17})$$

398 Note that the second equation can be separated from the first equation in (A-
 399 16) and that the flow of the second equation of (A-16) is monotonic. It follows
 400 from Smith (1995) and Zhao (2003) that E_{10} is globally stable whenever it exists.
 401 Furthermore, if the inequality in (A-17) is reversed, $(0, 0)$ is globally stable for
 402 (A-16).

403 For the reason of mathematical techniques, we consider the stability of $E_1 =$
 404 $(y_{10}, y_{20}, 0)$ for (3.2), and leave the stability of $E_0 = (0, 0, 0)$ to computer simula-
 405 tions. We linearize (3.2) at E_1 to obtain

$$\begin{aligned}
 \frac{dy_1}{dt} &= -(d_1 + \alpha)y_1(t) + \frac{ab}{(b + y_{20})^2}y_2(t) - \frac{abe^{-(d_1+\alpha)\tau}}{(b + y_{20})^2}y_2(t - \tau) \\
 &\quad + \left(\alpha y_{10} - \frac{ay_{20}^2}{(b + y_{20})^2} \right) c(t) - \frac{\alpha ay_{20}e^{-(d_1+\alpha)\tau}}{b + y_{20}} \int_{t-\tau}^t c(\theta) d\theta \\
 &\quad + \frac{ay_{20}^2 e^{-(d_1+\alpha)\tau}}{(b + y_{20})^2} c(t - \tau), \\
 \frac{dy_2}{dt} &= \frac{abe^{-(d_1+\alpha)\tau}}{(b + y_{20})^2} y_2(t - \tau) + \frac{\alpha ay_{20}e^{-(d_1+\alpha)\tau}}{b + y_{20}} \int_{t-\tau}^t c(\theta) d\theta - d_2 y_2(t) \\
 &\quad - \frac{ay_{20}^2 e^{-(d_1+\alpha)\tau}}{(b + y_{20})^2} c(t - \tau), \\
 \frac{dc}{dt} &= wc(t) \left(-\frac{ay_{20}}{(b + y_{20})^2} + \alpha \frac{y_{10}}{y_{20}} \right).
 \end{aligned} \tag{A-18}$$

406 If

$$\frac{ay_{20}}{(b + y_{20})^2} > \alpha \frac{y_{10}}{y_{20}}, \tag{A-19}$$

407 it follows from the third equation of (A-18) that $c(t) \rightarrow 0$ as $t \rightarrow \infty$. By the theory
 408 of asymptotically autonomous differential equations, we see that E_1 is asymptot-
 409 ically stable for (3.2). Furthermore, it is easy to see that E_1 is unstable if we
 410 have

$$\frac{ay_{20}}{(b + y_{20})^2} < \alpha \frac{y_{10}}{y_{20}}. \tag{A-20}$$

411 For the existence of positive equilibrium of (3.2), we have

412 **Theorem B:** (3.2) admits a unique positive equilibrium $E^* = (y_1^*, y_2^*, c^*)$ if and
 413 only if

$$\begin{cases} \frac{a}{bd_2} > e^{d_1\tau}, \\ \frac{\alpha + d_1}{\alpha e^{-(\alpha+d_1)\tau} + d_1} > \frac{ae^{-(\alpha+d_1)\tau}}{bd_2}. \end{cases} \tag{A-21}$$

414 **Proof:**

415 Set $E = e^{-(d_1+\alpha s)\tau}$ with $s = 1 - c$. Then we have

$$\alpha \frac{y_1}{y_2} = a \frac{y_2}{(bs + y_2)^2}, \tag{A-22}$$

$$a \frac{sy_2}{bs + y_2} (1 - E) = (d_1 + \alpha s)y_1, \tag{A-23}$$

$$a \frac{sy_2}{bs + y_2} E = d_2 y_2. \tag{A-24}$$

416 To get equations for s , we solve y_2 from (A-24) to obtain

$$y_2 = \frac{aE - bd_2}{d_2}s. \quad (\text{A-25})$$

417 It follows from (A-22) that

$$y_1 = \frac{ay_2^2}{\alpha(bs + y_2^2)^2} = \frac{(aE - bd_2)^2}{a\alpha E^2}. \quad (\text{A-26})$$

418 Substituting (A-25) and (A-26) into (A-23), we obtain

$$419 \quad as(1 - E) = (d_1 + \alpha s) \frac{aE - bd_2}{\alpha E}.$$

420 It follows that

$$\frac{aE}{bd_2} = \frac{\alpha s + d_1}{\alpha s E + d_1}. \quad (\text{A-27})$$

421 To derive conditions such that (A-27) admits a unique solution in $(0, 1)$, we define

$$422 \quad f(s) := \frac{aE}{bd_2}, \quad g(s) := \frac{\alpha s + d_1}{\alpha s E + d_1}.$$

423 Note that $f(s)$ is a decreasing function of s and has a maximum $f(0) = \frac{a}{bd_2}e^{-d_1\tau}$.

424 Since $E' = -\alpha\tau E$, we have

$$\begin{aligned} g'(s) &= \frac{1}{(\alpha s E + d_1)^2} \{ \alpha(\alpha s E + d_1) - (\alpha s + d_1)(\alpha E - \alpha s \cdot \alpha\tau E) \} \\ 425 \quad &= \frac{1}{(\alpha s E + d_1)^2} \{ \alpha d_1(1 - E) + (\alpha s + d_1)\alpha s \cdot \alpha\tau E \} > 0. \end{aligned}$$

426 Hence, (A-27) admits a unique solution s^* in $(0, 1)$ if and only if $f(0) > g(0)$ and
427 $f(1) < g(1)$. The former corresponds to the first inequality of (A-21), while the
428 latter corresponds to the second inequality of (A-21). From (A-27), we see that

$$429 \quad aE(s^*) = \frac{\alpha s^* + d_1}{\alpha s^* E(s^*) + d_1} bd_2 > bd_2.$$

430 It follows from (A-25) and (A-26) that when $c = c^* = 1 - s^*$, we have

$$431 \quad y_2^* = \frac{aE(s^*) - bd_2}{d_2}s^* > 0, \quad y_1^* = \frac{(aE(s^*) - bd_2)^2}{a\alpha E^2(s^*)} > 0.$$

432 This completes the proof. $\square$

433 Note that the first inequality of (A-21) is satisfied if (A-17) holds. Further, it
434 is easy to see that the second condition in (A-21) is equivalent to (A-20). Further,
435 (A-21) can be rewritten as

$$\tau^* := \frac{1}{d_1 + \alpha} \ln \frac{ad_1 + \sqrt{(ad_1)^2 + 4a\alpha bd_2(\alpha + d_1)}}{2bd_2(\alpha + d_1)} < \tau < \frac{1}{d_1} \ln \frac{a}{bd_2} := \tau^{**}. \quad (\text{A-28})$$

436 The left inequality of (A-28) ensures that $E_1 = (y_{10}, y_{20}, 0)$ is unstable. If we define

437
$$\tau_0 = \frac{1}{d_1 + \alpha} \ln \frac{a}{bd_2},$$

438 by summarizing above discussions, we obtain Table 2 that presents the distribution
439 of equilibria of (3.2).

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