

LIFE HISTORY, MATING DYNAMICS, AND THE ORIGIN OF PARENTAL CARE

Tamjeed Azad^{1,2}, Suzanne H. Alonzo^{3,4}, Michael B. Bonsall^{5,6}, and Hope Klug^{1,7*}

¹ Department of Biology, Geology, and Environmental Science, University of Tennessee at Chattanooga

² Department of Computer Science, Columbia University

³ Ecology and Evolutionary Biology Department, University of California Santa Cruz

⁴ Institute of Marine Sciences, University of California Santa Cruz

⁵ Mathematical Ecology Research Group, Department of Zoology, University of Oxford

⁶ St. Peter's College, University of Oxford

⁷ SimCenter, University of Tennessee at Chattanooga

*corresponding author

Additional Author Information:

Tamjeed Azad, tamjazad@gmail.com, <https://orcid.org/0000-0001-6959-5928>

Suzanne H. Alonzo, <https://orcid.org/0000-0001-7757-0528>, shalonzo@ucsc.edu

Michael B. Bonsall, <https://orcid.org/0000-0003-0250-0423>, michael.bonsall@zoo.ox.ac.uk

Hope Klug, <https://orcid.org/0000-0003-3169-2452>, hope-klug@utc.edu

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Abstract

Parental care, mating dynamics, and life history co-evolve. Understanding the diversity of reproductive patterns found in nature is a major focus of evolutionary ecology research. Previous research suggests that the origin of parental care of eggs will be favored when egg and adult death rates and juvenile survival are relatively high. However, the previous research that explored the link between care and life history did not account for among-species variation in mating dynamics. As mating dynamics are generally expected to influence care, we explore, theoretically, the life-history conditions (stage-specific rates of maturation and survival) that favor parental care across three mating scenarios: reproductive rate 1) is unaffected by males (assuming that some males are present), 2) increases as male abundance increases, or 3) decreases as male abundance increases. Across scenarios, all forms of care were most strongly favored when egg and adult death rates, juvenile survival, and female egg maturation rates were relatively high. When reproductive rate was unaffected by male abundance or increased as male abundance increased, as we might expect in systems in which females are mate limited, all forms of care were most strongly favored when male egg maturation rate (i.e., the rate at which male eggs develop, mature, and hatch) was moderate or high. When greater male abundance inhibited reproduction, which might occur in systems with intense male-male competition, all forms of care were most strongly favored when male egg maturation rate was low to moderate. These results suggest that life history affects the evolution of parental care, and sex-specific life history can interact with mating dynamics to influence the origin of care.

Key words: parental care, life history, mating, mate competition, paternal care, bi-parental care, maternal care

Introduction

Parental care is a behavior that is found in many animal groups (reviewed in (1, 2)). In nature we see extensive diversity in whether post-fertilization parental care is provided and if so, whether males, females, or both sexes provide care. In many animal groups, such as fishes, anurans, many invertebrates, and squamate reptiles, it is typical for no post-fertilization parental care to be provided (1-3). In contrast, bi-parental care is common in birds, and maternal care is prevalent in mammals (1-4). Within groups, though, there are exceptions to these patterns. For instance, in fishes, bi-parental care is common in cichlids (3). While most non-cichlid fishes and amphibians lack parental care, when parental care does occur in non-cichlid fishes and amphibians, it tends to be paternal (1, 3). Likewise, in leeches, insects, and polychaete worms, male and/or female parents of some species attend to and guard offspring, feed their young, and/or carry offspring (4-6). A large body of research has focused on understanding why such variation in sex-specific patterns of parental care exist (1, 2, 7-23). In particular, both mating dynamics and basic life history (i.e., stage-specific rates of mortality and maturation) have independently been found to influence the evolution of parental care by males and females (7, 9, 19, 21, 24, 25).

With regard to mate availability, mate limitation of one sex can influence the costs and benefits of investing in mating versus caring for current young, which can in turn influence the evolution of sex-specific patterns of parental care (7, 19, 21, 26). For example, if males are highly mate-limited, we would in some cases expect selection to favor male investment in parental care, as caring for young can increase fitness more than competing for highly limited female mates (19). In other cases, though, there is no negative trade-off between parental care and mating rate (10,

27). In addition, empirical studies have found a range of effects of male and female abundance on reproduction. For instance, in some species such as fruit flies (*Drosophila melanogaster*), the reproductive success of males is thought to be largely limited by the availability of female mates (28). In contrast, in sex-role reversed species such as the broadnosed pipefish (*Syngnathus typhle*), female reproduction is limited by the availability of male mates (29). In still other cases, male-male competition can reduce reproduction when male abundance is relatively high. In the European bitterling (*Rhodeus sericeus*), for example, courtship and reproduction can in some cases be negatively impacted due to male-male aggression and greater male abundance (30).

With regard to basic life history, previous theoretical research found that the origin of maternal, paternal care, and bi-parental egg care will be most strongly favored when egg death rates in the absence of care, adult death rates, and juvenile survival rates are relatively high (24). Some empirical work supports these findings. For example, care is more likely to occur in insects when offspring predation is high (31), and previous research has found that fish species with shorter lifespans are more likely to provide parental care (32). Further, sex differences in embryo maturation rate have been documented in birds and mammals (33-35), and previous research suggests that such sex differences can influence the evolution of maternal, paternal, and bi-parental care (24, 25). Specifically, previous theoretical research found that paternal care or bi-parental care were more likely to originate if males had relatively low egg maturation rates (i.e., if male eggs matured and hatched relatively slowly) and females had relatively high egg maturation rates (i.e., if female eggs matured and hatched relatively quickly) (24). In contrast, maternal care was most likely to originate if both males and females had relatively high egg maturation rates (i.e., if eggs of both sexes matured and hatched relatively quickly) (24). Given

these earlier studies (7, 9, 19, 24, 36), we know that both mating dynamics and basic life history can independently influence the evolution of maternal, paternal, and bi-parental care. However, to the best of our knowledge, no previous work has explored how basic whole-organism life history (i.e., stage specific maturation and mortality rates) influences the evolution of care across different mating scenarios. Given this, no previous work has explored the evolution of care in relation to stage-specific life history and mating dynamics within a single theoretical framework. In the current study, we aim to bridge this gap.

To enhance our understanding of how mating dynamics influence the evolution of care, we explore the effect of stage-specific mortality and maturation rates on the evolution of maternal, paternal, and bi-parental care across mating scenarios. Specifically, we use a mathematical model to explore the effect of basic life-history parameters on the origin of parental care of eggs in the following different scenarios: 1) reproductive rate (i.e., the rate of egg fertilization in the population) is unaffected by males (assuming that at least some males are present), which may follow when females, but not males, limit reproduction; 2) reproductive rate increases when more adult males are present, which may follow if reproduction is in general limited by both male and female abundance; and 3) reproductive rate decreases when more adult males are present, which may follow if the presence of additional males inhibits reproduction. Such a scenario might be expected if there is, for instance, interference competition among males and male mating success is reduced when more males are present (37). We focus on these three general scenarios, as they represent a broad array of mating scenarios that could apply to a range of systems, and because there is empirical evidence of such relationships in animals (discussed above). Based on previous research (7, 9, 18, 24, 25, 36), we hypothesized that both basic life-

history parameters and the mating-dynamic scenario considered would influence the origin of maternal, paternal, and bi-parental care.

Materials & Methods

Model Overview:

We developed a mathematical model in which individuals pass through egg and juvenile stages and reproduce as adults. In the model, a rare mutant that displays maternal, paternal, or bi-parental care attempts to invade a resident population in which individuals exhibit a no-parental-care strategy. The mutant strategy of maternal, paternal, or bi-parental care is assumed to be rare relative to the resident strategy of no-care. Each form of parental care is incorporated into the model through trade-offs reflecting each form of care (discussed below). Other than the trade-offs associated with parental care (described below), the resident and mutant individuals were assumed to have the same baseline parameters (i.e., the same parameters before any costs and benefits of care were accounted for). We then used evolutionary invasion analyses (see, e.g., (24, 38)) to explore the basic life-history conditions (stage specific survival and maturation rates) under which each form of parental care was able to invade the resident strategy when 1) reproductive rate (i.e., the rate of egg fertilization in the population) is unaffected by males, 2) reproductive rate increases when more adult males are present, and 3) reproductive rate decreases when more adult males are present. In doing so, we identify the life-history conditions under which each form of care is most likely to be selected for across three general mating scenarios.

Model Dynamics:

A generalized description of the model, which follows directly from the model outlined in (24), is described below. The model assumes a stage-structured system in which individuals have the potential to pass through egg and juvenile stages and reproduce as adults. For the resident strategy, the number of eggs (E) in the population increases as adults reproduce and decreases as eggs either die or mature and leave the egg stage, such that

$$\frac{dE}{dt} = rA(t)a_f\left(1 - \frac{A(t)}{K}\right) - E(t)(d_{Em}e_m + d_{Ef}e_f + m_{Em}e_{sm} + m_{Ef}e_{sf}). \quad (1)$$

In the above equation, r is the rate of egg fertilization in the population (i.e., the reproductive rate at any point in time, t). Overall, reproduction depends on the rate of females entering the adult stage, a_f , and the number of adults present $A(t)$. Reproduction is also assumed to be density dependent with a population-level carrying capacity of K . The number of male and female eggs that die depends on the number of eggs in the population at a given time, $E(t)$, the rates at which male and females are produced, e_m and e_f , respectively ($e_m = e_f = 0.5$ in all cases considered), and the male and female egg death rates, d_{Em} and d_{Ef} , respectively. Likewise, the number of male and female eggs that mature depends on the number of eggs in the population at a given time, the rate of male and female eggs surviving the egg stage, e_{sm} and e_{sf} , and male and female egg maturation rates, m_{Em} and m_{Ef} . The rate of males entering the adult stage is a_m .

The number of male and female adults decrease in the population as adults die and increase as individuals survive, mature, and pass through the egg and juvenile stages and enter the adult stage, such that:

$$\frac{dA}{dt} = \sigma_{Jm}E(t - \tau_m)e_{mm} + \sigma_{Jf}E(t - \tau_f)e_{mf} - A(t)(d_{Af}a_f + d_{Am}a_m), \quad (2)$$

where σ_{Jm} and σ_{Jf} are the male and female juvenile survival rates, τ_m and τ_f are the male and female juvenile stage durations, e_{mm} and e_{mf} are the rates of males and females surviving the egg stage and maturing into juveniles at the time t , and d_{Af} and d_{Am} are the rates of death for adult females and males. Adults that are male and female at time t is a function of the rate of individuals surviving the egg stage, maturing, and surviving and passing through the juvenile stage. The rate at which males and females enter the adult stage at time t , a_m and a_f , equals $e_m(1 - d_{Em})m_{Em}\sigma_{Jm}$ and $e_f(1 - d_{Ef})m_{Ef}\sigma_{Jf}$. Additional details of these rates and modeling dynamics can be found in (24).

The resident strategy is assumed to be at equilibrium in the population. The density of the adults exhibiting the resident strategy at equilibrium (i.e., when $\frac{dE}{dt}$ and $\frac{dA}{dt}$ equal zero) is:

$$A^* = K \left[1 - \frac{(\omega[a_md_{Am} + a_fd_{Af}])}{a_fr(e_{mf}\sigma_{Jf} + e_{mm}\sigma_{Jm})} \right], \quad (3)$$

where $\omega = e_{sf}m_{Ef} + e_{sm}m_{Em} + e_fd_{Ef} + e_md_{Em}$.

The mutant strategy, which is denoted by the superscript \bullet , is modeled using the following equations (see also (24)) and by incorporating the trade-offs that reflect parental care (discussed below and in Table 1). As with the resident strategy, mutant eggs increase in the population as adults reproduce, and eggs decrease in the population as eggs die and as eggs mature and leave the egg stage, such that:

$$\frac{dE^\bullet}{dt} = r^\bullet A^\bullet(t) a_f^\bullet \left(1 - \frac{A^\bullet}{K^\bullet}\right) - E^\bullet(t) (d_{Em}^\bullet e_m^\bullet + d_{Ef}^\bullet e_f^\bullet + m_{Em}^\bullet e_{sm}^\bullet + m_{Ef}^\bullet e_{sf}^\bullet), \quad (4)$$

where the parameters are as described previously for the resident dynamics. In the equation above, A^\bullet , which is the resident's equilibrial density (eqn. 3), replaces $A(t)$ because the mutant is rare in the population. As the mutant is rare in the population, the mutant's reproduction is thus limited by competition with the resident (see also discussion of this standard assumption in invasion analyses in (38)). Adults exhibiting the mutant strategy increase in the population as eggs survive, mature, and pass through the juvenile stage and decrease as adults die, such that:

$$\frac{dA^\bullet}{dt} = \sigma_{jm}^\bullet E^\bullet(t - \tau_m^\bullet) e_{mm}^\bullet + \sigma_{jf}^\bullet E^\bullet(t - \tau_f^\bullet) e_{mf}^\bullet - A^\bullet(t) (d_{Af}^\bullet a_f^\bullet + d_{Am}^\bullet a_m^\bullet), \quad (5)$$

where the parameters are as described previously for the resident dynamics.

Costs and Benefits of Parental Care:

Mutant adults are assumed to provide some form of parental care to their eggs. Our model therefore assumes that parents who provide care are physically associated with their eggs and remain alive to provide care to their young. As mentioned above, we consider the cases in which the mutant either provides paternal, maternal, or bi-parental care. The mutant strategies considered (paternal, maternal, or bi-parental care) are assumed to arise from a genetic mutation that allows individuals to provide care to their offspring. In the case of paternal and maternal care, this assumes that the expression of mutation underlying parental care is sex-specific.

In previous modeling using this framework (24) and in the current model, we distinguish between initial egg investment (i.e., resource investment into eggs) and post-fertilization parental care (herein referred to as parental care). We assume that females initially invest resources into their eggs. Baseline egg death rate (i.e., egg death rate in the absence of care) is our measure of initial egg investment, and egg survival, by definition, therefore increases as initial egg investment from mothers increases. Initial egg investment is costly to females, and as initial egg investment increases, female survival decreases relative to baseline survival (baseline survival = the survival rate before the costs of investment are accounted for) (Table 1). To isolate the effects of adult males on reproductive rate and the fitness of each form of care (see also mating scenarios, which are described below), in the current model, we do not assume that initial egg investment directly decreases female egg production rate. However, as initial egg investment decreases adult female survival, females who invest a relatively large amount of resources into their eggs will have reduced survival and overall reduced future reproductive opportunities. This lack of a trade-off between female initial egg investment and female egg production is one way in which the current model differs from that of Klug et al. 2013 (24). This difference, as

mentioned above, allows us to isolate the effect of our mating scenarios (described below) on fitness because in the current model, mating scenario is the only trade-off associated with reproductive rate. That is, across forms of parental care, reproductive rate is only directly affected by mating scenario. As reproductive rate is the measure of egg fertilization in the population, there is no way to impose sex-specific costs of care in relation to r , and therefore costs of care and initial egg investment are associated with reduced adult survival (discussed further below).

Post-fertilization parental care is provided by mutant parent(s) to their mutant eggs and increases egg survival relative to baseline egg survival. The total level of care that eggs receive is the sum of the care provided by their male and female parents ($c_m + c_f$) (Table 1). Providing care is costly to the parent that provides care, and specifically, as the level of care increases, adult survival decreases relative to baseline adult survival (i.e., survival before the costs of care are accounted for) (Table 1). For all trade-offs (i.e., costs and benefits of care) mentioned above, we assume non-linear trade-off functions ((Table 1); see also (24)).

The costs and benefits associated with parental care provide an initial look at how parental care can influence fitness. However, to identify whether a given form of parental care will be able to invade a resident strategy of no care given the stage-structured life-history conditions and ecology of our model, we must utilize invasion analyses (as described above and below), which allow us to ask whether paternal, maternal, and/or bi-parental care can invade an ancestral state of no care given a set of specified male and female life-history parameters. This, in turn, allows us to explore the male and female life-history mortality and maturation rates that are most likely

to select for the origin of paternal, maternal, and/or bi-parental care across the mating scenarios considered (described below).

Mating Scenarios:

As mentioned previously, the current model differs from that of Klug et al. 2013 (24) as we consider three mating scenarios in the current model. Specifically, we explore the origin of paternal, maternal, and bi-parental care when: 1) reproductive rate r is unaffected by the rate at which males enter the adult stage, which is the scenario assumed in Klug et al. 2013 (24), such that $r = r_0$ and $r^* = r_0$, where r_0 and r_0 are the baseline reproductive rate of the resident and mutant individuals, respectively; 2) reproductive rate increases linearly with the rate at which males enter the adult stage, which would be expected if female reproduction is in general limited by male abundance, such that $r = r_0 + zr_0a_m$ and $r^* = r_0 + zr_0a_m$; and 3) reproductive rate decreases linearly as the rate of males entering the adult stage increases, which would be expected if having additional males present inhibits reproduction, such that $r = r_0 - zr_0a_m$ and $r^* = r_0 - zr_0a_m$. In the above equations, z is a parameter that reflects the magnitude of the effect that males have on reproductive rate. In all results presented z was assumed to be a constant and equal to 1. We also explored cases in which the rate at which males enter the adults stage had a greater effect on reproductive rate. Specifically, in these additional analyses, we assumed that $z = 8$, as this parameterization allowed us to consider cases in which males had a relatively large impact on reproductive rate, yet reproductive rate was still biologically realistic (i.e., reproductive rate was a positive value). That is, we considered cases in which the absolute slope of the relationship between the rate of males entering the adult stage and reproductive rate was one versus eight. Performing these additional analyses allowed us to ensure that we

considered a relatively broad range of effects of males on reproductive rate (i.e., cases in which males had relatively small versus large effects on reproduction, $z = 1$ versus 8). In all cases, the qualitative patterns of these additional analyses were identical to the results from the scenarios outlined in the previous paragraph. As these results were qualitatively identical to the case in which $z = 1$, we present only the results from the initial scenarios above in which $z = 1$.

In considering these three broad mating scenarios, we are able to explore whether three general patterns of mating dynamics will influence the life-history conditions under which paternal, maternal, and bi-parental care can be selected for and originate. The mating dynamic scenario considered (i.e., scenario 1-3 above) were assumed to be the same for mutant and resident individuals for each analysis. Importantly, this assumes that the origin of a given mating system precedes the origin of care. Given that mating dynamics and care can co-evolve (7), it is possible that the resident and mutant could have different mating dynamics, which is a worthy focus of future research but beyond the scope of the current study.

Fitness and Invasion Dynamics:

The fitness of the mutant is the mutant's per-capita population-level growth rate and can be thought of as the fitness of a given form of parental care (maternal, paternal, bi-parental) relative to the fitness of the no-care resident strategy (24, 38). The fitness of the mutant strategy is found by taking from the determinant of the following invasion matrix:

$$\begin{pmatrix} B & C \\ D & F \end{pmatrix}, \quad (6)$$

$$\text{where } B = \lambda + d_{Em}^{\bullet} e_m^{\bullet} + d_{Ef}^{\bullet} e_f^{\bullet} + m_{Em}^{\bullet} e_{sm}^{\bullet} + m_{Ef}^{\bullet} e_{sf}^{\bullet}, \quad (7)$$

270
$$C = -r^{\bullet}a_f^{\bullet}\left(1 - \frac{A^*}{K^{\bullet}}\right), \quad (8)$$

271
$$D = -\sigma_{jm}^{\bullet}\exp(-\lambda\tau_m^{\bullet})e_{mm}^{\bullet} - \sigma_{jf}^{\bullet}\exp(-\lambda\tau_f^{\bullet})e_{mf}^{\bullet}, \text{ and } (9)$$

272
$$F = \lambda + d_{Af}^{\bullet}a_f^{\bullet} + d_{Am}^{\bullet}a_m^{\bullet} \quad (10)$$

273

274 and solving the resulting characteristic equation for λ , which is then the fitness associated with
275 the form of parental care considered (24, 38). When λ is positive, the mutant strategy of paternal,
276 maternal, or bi-parental care is expected to invade the resident population; when λ is negative,
277 the resident strategy of no care will persist in the population.

278

279 We hypothesized that 1) stage-specific maturation and survival rates and 2) the mating scenario
280 considered would interact to determine whether maternal, paternal, and bi-parental care evolve.
281 To test this hypothesis, we used the invasion dynamics outlined above (eqns. 6-10) to analyze the
282 relationship between each basic life-history parameter (male and female egg maturation rates,
283 male and female egg death rates, male and female juvenile survival rates, and male and female
284 adult death rates) and the fitness of care. Analyzing the relationship between the fitness of each
285 form of care in relation to life-history trait values across the three mating scenarios allowed us to
286 explore the impact of life history and scenarios reflective of mate limitation and interference
287 competition on the fitness of various forms of parental care. Importantly, in these analyses, we
288 focus on parameter combinations that potentially allow care to invade; this allows us to focus on
289 the qualitative relationship between the fitness of care and each life-history trait across scenarios.
290 If the parameter values were changed (parameter values provided in figures) for a given scenario,
291 the numerical value of fitness would be expected to potentially change; however, the qualitative

relationship between fitness and care would not be expected to change. When examining the results (Fig. 1-4), it is thus important to focus on the qualitative relationship between each life-history trait and the fitness of care to determine which life-history conditions are most likely to select for a given form of care under each mating scenario.

Results

The life-history parameters (stage-specific mortality and maturation rates) influenced the fitness associated with maternal, paternal, and bi-parental care relative to a no-care strategy (Fig. 1-4). The observed effects of life history on the fitness associated with care were qualitatively similar across parental care forms and across mating scenarios in most cases (Fig. 1-4). That is, in most cases, the fitness associated with maternal, paternal, and bi-parental care were identical or very similar for most scenarios considered (see overlapping lines in Figs. 1-4). Specifically, relatively high female and male egg (Fig. 1 A-F) and adult (Fig. 2 A-F) death rates and relatively high rates of female and male juvenile survival (Fig. 3 A-F) favor the evolution of maternal, paternal, and bi-parental care across mating scenarios (i.e., scenarios in which the rate of males entering the adult stage does not influence fertilization rate, decreases the rate of egg fertilization, or increases the rate of egg fertilization). The finding that all forms of care had similar fitness values across most life-history parameters and across the three mating scenarios suggests that in some cases life history (e.g., high offspring need, high adult mortality that reduces future reproductive potential, high juvenile survival) can lead to similar selection for either maternal, paternal, or bi-parental care.

Maternal, paternal, and bi-parental care were also more likely to result in relatively high fitness when female egg maturation rate is high (Fig. 4 A, C, E) across mating scenarios (i.e., scenarios in which the rate of males entering the adult stage does not influence fertilization rate, decreases the rate of egg fertilization, or increases the rate of egg fertilization). In general, at relatively high female egg maturation rates, paternal care tends to result in slightly greater fitness than bi-parental care, and maternal care tends to result in lower fitness than either paternal or bi-parental care (Fig. 4 A, C, E). Moderate to high male egg maturation rates result in relatively high fitness of maternal, paternal, and bi-parental care when reproductive rate is unaffected by the rate at which males enter the adult stage (Fig. 4 B). In addition, high male egg maturation rates can increase the fitness of all forms of parental care when the rate of males entering the adult stage is positively associated with egg fertilization rate, which we might expect if females are mate limited, a pattern that is common in sex-role reversed systems (Fig. 4 F). However, very high male egg maturation rates reduce the fitness of all forms of parental care when the rate of males entering the adult stage decreases fertilization rate (Fig. 4 D). As a result, when the rate of males entering the adult stage is negatively associated with fertilization rate, which we might expect if interference competition among males inhibits reproduction, all forms of parental care will be most strongly selected for at relatively low to moderate male egg maturation rates (Fig. 4 D). Across mating scenarios, when male egg maturation rates are relatively high, maternal care is associated with greater fitness than bi-parental care, and paternal care is associated with lower fitness than either bi-parental or maternal care (Fig. 4 B, D, F).

337 In summary, in most cases, life-history trait values have a greater impact on the fitness
338 associated with care relative to a no-care strategy than the form of parental care provided
339 (maternal, paternal, or bi-parental) or the mating scenario considered (see, e.g., overlapping
340 fitness functions in Fig. 1-4). These results suggest that various forms of parental care can be
341 favored across mating scenarios and across a range of life-history trait values (Fig. 1-4). This
342 pattern likely occurs as, in some cases and under the assumptions of our model, all forms of care
343 can have substantial positive effects on overall fitness. For example, when offspring survival in
344 the absence of care is low, high offspring need creates a situation in which any form of care will
345 be favored regardless of mating dynamics. Importantly, though, in some cases, the mating
346 scenario considered can interact with life history to influence the likelihood that care will be
347 selected for. In particular, the effect of male egg maturation rate on fitness depends on the
348 relationship between adult male abundance and reproduction. When only females limit
349 reproductive rate (assuming that at least some males are present) or when males positively affect
350 reproductive rate, all forms of parental care will be most strongly favored when female egg
351 maturation rate is high and when male egg maturation rate is moderate or high. This pattern
352 occurs because males either do not impact or positively affect reproductive rate, and as a result,
353 moderate to high male egg maturation rates create population dynamics that allow the overall
354 reproductive success of the mutant strategy to be relatively high. As a result, care can invade a
355 no-care strategy under these conditions. In contrast, when male abundance is negatively
356 associated with reproductive rate, parental care is most likely to be favored when female egg
357 maturation rate is high and male egg maturation rate is relatively low or moderate, as these
358 conditions lead to population dynamics that allow the mutant strategy to increase in the
359 population and invade the no-care strategy. Thus, while life history has strong impacts on the

evolution of some form of parental care, mating dynamics interact with life history to determine when parental care will be most likely to evolve.

Discussion

Maternal, paternal, and bi-parental care of eggs has the potential to originate across a wide range of life-history parameters and under various mating scenarios. In general, all forms of care will be most strongly selected for when 1) eggs survive relatively poorly in the absence of care (i.e., baseline male and female egg death rates are relatively high), 2) adults have reduced potential for survival and future reproduction (i.e., when baseline male and female adult death rates are relatively high), 3) male and female juvenile survival is relatively high, and 4) female egg maturation rate is relatively high. These effects of whole-organism life history on parental care were robust across mating scenarios; that is, they were consistent regardless of any positive or negative effects of male abundance on reproductive rates..

The finding that some form of care will be favored when offspring need care the most (i.e., when egg death rate in the absence of care is relatively high) is consistent with previous theoretical work (24, 36, 39) and the findings of some empirical research. For example, relatively harsh environments, and in particular intense egg predation, are associated with parental care in many insect species (reviewed in (31)). Across bird species, parents are likely to invest relatively more in parental care under harsher environmental conditions (e.g., at higher elevations) (40). The finding that higher egg death rates will favor some form of care is also intuitive as offspring gain

the most from parental care when they survive relatively poorly in the absence of care; that is, parents have the greatest potential to increase offspring survival when offspring survival is low in the absence of care (Table 1). Likewise, the finding that care is most likely to evolve when juvenile survival is relatively high is also intuitive, as parental fitness is likely greatest when parents invest in young that survive to maturity (i.e., it likely would not make sense to invest heavily in egg care if those young were simply going to die at high rates as juveniles). To the best of our knowledge, no empirical studies have examined the relationship between the evolution of parental care and juvenile survival across species. However, our finding that egg-only parental care is selected for when offspring are likely to survive the subsequent life-history stage is consistent with research suggesting that parents invest more heavily in high-quality young. For example, in the cichlid *Pelvicachromis taeniatus*, parents reduced their care of lower quality broods (i.e., broods with small average individual offspring body size) (41). The finding that all forms of parental care were most strongly selected for at relatively high adult death rates, regardless of the mating scenario considered, is also consistent with previous work (24, 36) and classic life-history theory that suggests that parents should invest more in current reproduction and offspring when their likelihood of future reproduction is reduced (e.g., when their mortality is relatively high). In addition, consistent with these predictions, previous empirical work has found a relationship between short lifespan and parental care in fish species (42).

The finding that maternal, paternal, and bi-parental parental care were most strongly favored when egg death rates, juvenile survival rates, and adult death rates were relatively high regardless of the mating scenario considered suggests that whole-organism basic life history can play a relatively important role in the evolution of parental care. While the finding that whole-

organisms life history strongly influences the evolution of parental care might seem intuitive after the fact, there was no *a priori* reason to expect that the life-history parameters favoring the evolution of care would be so similar across forms of care and across the mating scenarios considered, particularly since co-evolutionary feedbacks have previously been found to influence the evolution of care and mating dynamics (7, 9, 19). Specifically, some previous studies have found that sex-specific patterns of parental care will be primarily influenced by the availability of males and females in the mating pool and the costs and benefits of mating (e.g., (7, 19, 43)). Our results, on the other hand, reveal that stage-specific rates of maturation and mortality across an organism's lifespan can also be a primary driver of the evolution of care. Our study differed from previous work in that we explicitly focused on demographic rates of mortality and maturation across life-history stages, whereas other studies have primarily focused on dynamics of the adult stage (e.g., (19)). This difference in focus is likely what allowed us to detect effects of whole-organism life history on the origin of care. Indeed, it is interesting that the life-history parameters favoring the evolution of care can, in some cases, be so uniform across various forms of care.

The male egg maturation rate that is most likely to favor care depends on the mating scenario considered, and moderate to high male egg maturation rates most strongly favor the origin of care when females are not mate limited (assuming that at least some males are present). High male egg maturation rates are expected to favor the evolution of care most strongly when females are mate limited, and low to moderate male egg maturation rates will most strongly favor the evolution of care when an abundance of males inhibit reproduction (e.g., due to interference competition). These qualitative patterns are intuitive, as a given parental care strategy will be more likely to spread in the population when the overall reproductive rate

429 associated with that strategy is greatest. Given that we would expect a strategy to spread in the
430 population when overall reproductive rate is relatively high, it is unsurprising that when females
431 are mate limited, life-history parameters that lead to more adult males, including greater male
432 maturation rates, will increase fitness. Similarly, when males inhibit reproduction due to
433 interference competition, for example, it is intuitive that life-history parameters that prevent large
434 numbers of adult males, including lower male maturation rates, will increase fitness. However,
435 the rate at which males enter the adult stage is ultimately influenced by the production of male
436 eggs, egg survival, egg maturation rate, and juvenile survival. Given this, it is interesting that the
437 qualitative relationship between male egg maturation rate and the fitness associated with each
438 form of care depended on the mating dynamics considered, whereas the qualitative relationship
439 between male egg survival and juvenile survival and the fitness associated with each form of
440 care did not depend on the mating dynamics considered. In our model, the effect of male egg
441 maturation rate on fitness is likely so pronounced because male egg maturation rate ultimately
442 has multiple effects on adult male abundance. When male eggs mature relatively quickly, we
443 would expect more males to mature and ultimately become adults due to the direct effect of a
444 faster maturation rate on adult abundance. In addition, at relatively slower egg maturation rates,
445 individuals will spend more time as eggs; as an individual egg has the potential to die at any
446 point in time, individuals who spend more time in the egg stage are more likely to die as eggs.
447 Thus, faster egg maturation rates make it less likely that an individual will die during the egg
448 stage, which will in turn lead to more individuals surviving and entering the adult stage.
449 Importantly, in some species we might expect a trade-off between egg maturation rate and
450 offspring size, such that slower developing young are larger and have greater overall survival.
451 We did not assume a trade-off between egg maturation rate and offspring size in the current

model. If such a trade-off were assumed, it is possible that the effect of egg maturation rate would be less pronounced in our model, particularly if relatively slow egg maturation rates are associated with higher juvenile survival. Regardless, previous empirical studies have found differences in the rate at which males and females develop during the egg stage in birds and mammals (33, 34). In future work, it would be interesting to explore whether there is an empirical relationship between the form of parental care provided and male and female egg maturation rates across species.

In general, the findings of the present model reveal that pre-adult life history can interact with mating dynamics and parental care to influence the strength of selection on care, and in some cases, there can be a critical life-history parameter that is linked to the success of a given strategy such as care. Indeed, our model suggests that we might expect some form of parental care to be most likely to evolve when: 1) male egg maturation rates are relatively high if females are mate limited, which would be expected, in particular, in species that have reversed sex roles; and 2) male egg maturation rate is relatively low if females are not mate limited and a higher abundance of males inhibits reproduction, which would be expected in species that have strong male-male competition. Ultimately, we would expect these predictions to be applicable to animals that have similar dynamics as those of our model, including egg, juvenile, and adult life-history stages and logistic population growth. If a system had different dynamics (e.g., non-logistic population growth, a different life history), it is possible that other life-history parameters might be relatively more important in determining the evolutionary origin of parental care.

Importantly, our results suggest that maternal, paternal, and bi-parental care have the potential to evolve across a range of mating scenarios. While the mating scenario considered can influence the life-history conditions that most strongly select for some form of parental care, mating dynamics can in some cases have relatively little impact on which form of care originates. Indeed, across mating scenarios, all forms of care will be most strongly selected for when egg and adult mortality and juvenile mortality are high for both females and males. Likewise, across mating scenarios all forms of care will be most strongly favored when female egg maturation rate is relatively high. While the mating scenario considered affects the male egg maturation rates that will most strongly favor some form of care, as discussed above, all forms of care have the potential to invade across a broad range of male egg maturation rates. Thus, whole-organism life history has strong effects on the origin of care, regardless of the mating scenario or the form of parental care provided.

In the present model, we did not assume a trade-off between parental care and reproductive or mating rate, and this is a limitation of our model. The relationship between mating rate and parental care can be complex (27). In some cases, we would expect parental care to lead to mate limitation and decrease mating rate (19, 27), whereas in other cases mating rate and parental effort might not trade-off or there might be a positive relationship between parental effort and mating rate (10, 27). A positive or negative relationship between parental care and mating rate might change the likelihood that paternal, maternal, or bi-parental care will evolve, and this is not considered within the present study. We also did not account for any factors that would predispose a particular sex to provide care (e.g., evolutionary history, fertilization mode), and we did not explicitly consider mate choice or uncertainty of paternity. Likewise, parental conflict

and parental negotiation over care can have strong influences on the amount of parental care provided by each sex, but these factors were not incorporated in the current model. Previous research has demonstrated that such factors can be important in driving sex-specific patterns of care (7, 9, 10, 12, 16, 20, 21, 26). Given this previous research, life history, as well as these previously studied factors, are expected to influence the evolution of care.

In conclusion, the results of the current model and our previous research (24, 36) suggest that the basic life-history characteristics that favor the evolution of care are remarkably consistent across different forms of care and various mating scenarios. In general, across mating scenarios we would expect maternal, paternal, and bi-parental care to be most likely to evolve in systems that have high offspring need (i.e., high egg mortality in the absence of care), high adult mortality such that parents have limited future opportunities for reproduction, high juvenile survival, and high female egg maturation rates. In systems in which females are mate limited, such as sex-role reversed systems, we would expect relatively high male egg maturation rates to favor some form of care. In contrast, in systems with interference competition or intense male-male competition that hinders reproduction, we would expect relatively low male egg maturation rates to favor some form of care.

514 **Figures & Tables.**

515 **Table 1. Trade-offs associated with initial investment in eggs by females and parental care by males and females (c_m and c_f).** The total level
 516 of parental care provided to eggs, c_{total} , is the sum of maternal and paternal care provided (i.e. $c_m + c_f$). Male and female egg death rate decreases as
 517 initial investment in eggs increases and as the total level of parental care increases. Initial egg investment is costly to mothers, such that female
 518 adult death rate increases as initial egg investment increases. Care is costly to parents that provide it, such that as care increases, adult death rate
 519 increases. The term a determines the specific shape of the trade-off function and is equal to 6 in all cases considered. The trade-off functions
 520 described in this table are modelled after those outlined in Table 1 of Klug et al. 2013 (24).

	Strategy:	
	No care	Parental care of eggs
Egg death rate (d_{Em} & d_{Ef})	$\text{♂s: } d_{Em} = d_{Em_0}$ $\text{♀s: } d_{Ef} = d_{Ef_0}$	Egg death rate ↓ as care ↑ $\text{♂s: } d_{Em}^* = d_{Em_0}^* \cdot \exp(-a \cdot c_{total})$ $\text{♀s: } d_{Ef}^* = d_{Ef_0}^* \cdot \exp(-a \cdot c_{total})$
Adult death rate (d_{Am} & d_{Af})	Female adult death rate ↑ as initial egg investment ↑ $\text{♂s: } d_{Am} = d_{Am_0}$ $\text{♀s: } d_{Af} = 1 - [(1 - d_{Af_0}) \cdot \exp(-((1 - d_{Em_0}) \cdot e_m + (1 - d_{Ef_0}) \cdot e_f))]$	Male adult death rate ↑ and as male care ↑ and Female adult death rate ↑ as initial egg investment ↑ and as female care ↑ $\text{♂s: } d_{Am}^* = 1 - [(1 - d_{Am_0}^*) \cdot \exp(-c_m)]$ $\text{♀s: } d_{Af}^* = 1 - [(1 - d_{Af_0}^*) \cdot \exp(-((1 - d_{Em_0}^*) \cdot e_m^* + (1 - d_{Ef_0}^*) \cdot e_f^* + c_f)))]$

Figure 1: Higher baseline egg death rates favor the evolution of maternal, paternal, and bi-parental care across mating scenarios. The fitness gains associated with parental care relative to that of a no-care strategy are illustrated in relation to female (A, C, E) and male (B, D, F) baseline egg death rate for maternal care ($c_m = 0$, $c_f = 0.7$, dotted line), biparental care ($c_m = 0.35$, $c_f = 0.35$, dashed line), and paternal care ($c_m = 0.7$, $c_f = 0$, solid line). We additionally considered the following mating dynamics: (A-B) reproductive rate (i.e., the rate of egg fertilization) is unaffected by the rate of males entering the adult stage, (C-D) reproductive rate decreases as the rate of males entering the adult stage increases, and (E-F) reproductive rate increases as the rate of males entering the adult stage increases. Unless otherwise noted, $d_{Em0} = d_{Ef0} = 0.5$, $m_{Em0} = m_{Ef0} = 0.1$, $d_{Am0} = d_{Af0} = 0.5$, $\sigma_{Jm0} = \sigma_{Jf0} = 0.5$, $\tau_m = \tau_f = 0.1$, $e_m = e_f = 0.5$, $K = 50$, $r_0 = 6$ for both mutants and residents. Note: where a single line is shown, the fitness associated with maternal, paternal, and bi-parental care overlap.

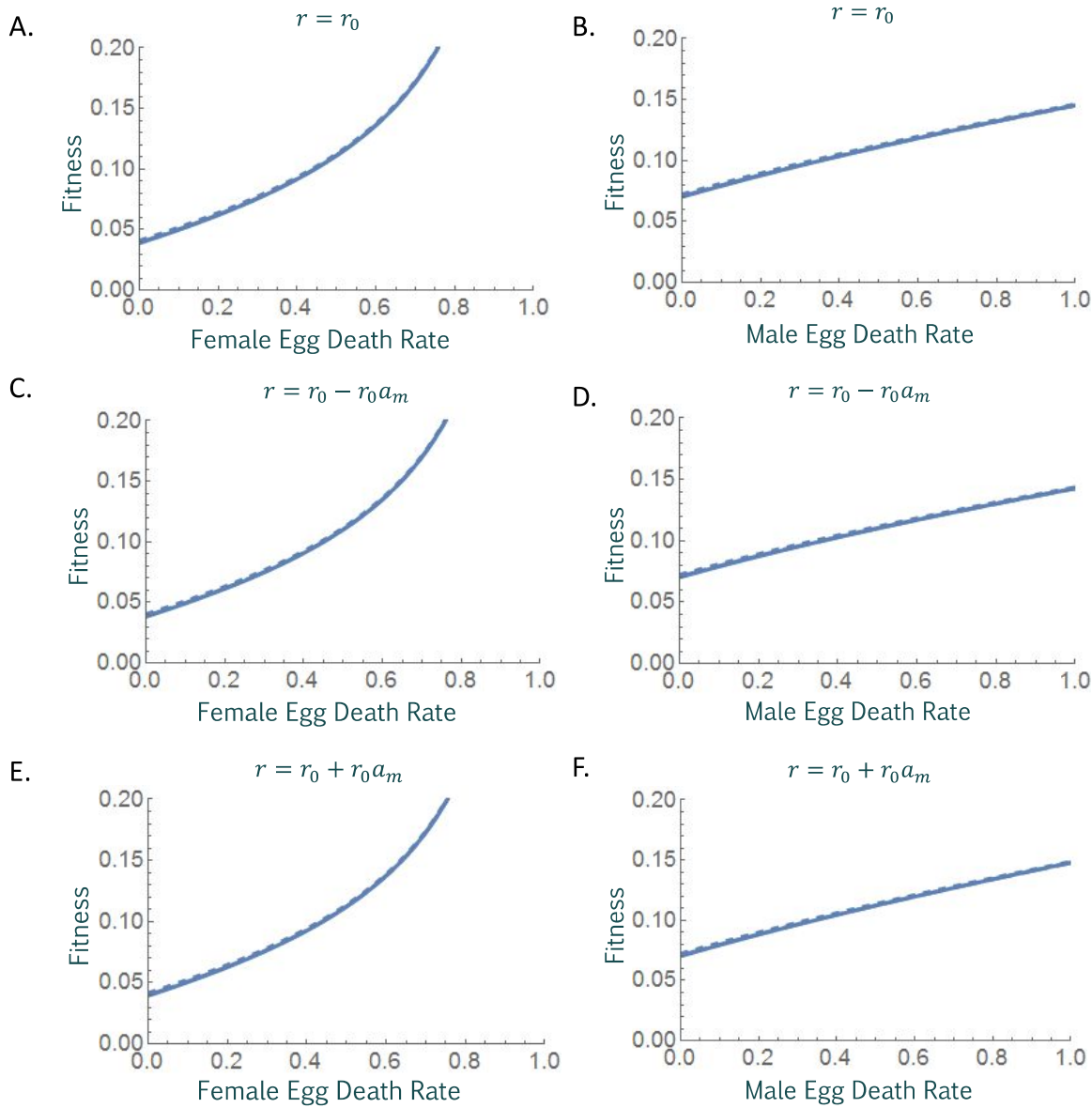


Figure 2. Higher adult death rates favor the evolution of maternal, paternal, and bi-parental care across mating scenarios. The fitness gains associated with parental care relative to that of a no-care strategy are illustrated in relation to female (A, C, E) and male (B, D, F) baseline adult death rate for maternal care ($c_m = 0$, $c_f = 0.7$, dotted line), biparental care ($c_m = 0.35$, $c_f = 0.35$, dashed line), and paternal care ($c_m = 0.7$, $c_f = 0$, solid line). We additionally considered the following mating dynamics: (A-B) reproductive rate (i.e., the rate of egg fertilization) is unaffected by the rate of males entering the adult stage, (C-D) reproductive rate decreases as the rate of males entering the adult stage increases, and (E-F) reproductive rate increases as the rate of males entering the adult stage increases. Unless otherwise noted, $d_{Em0} = d_{Ef0} = 0.5$, $m_{Em0} = m_{Ef0} = 0.1$, $d_{Am0} = d_{Af0} = 0.5$, $\sigma_{Jm0} = \sigma_{Jf0} = 0.5$, $\tau_m = \tau_f = 0.1$, $e_m = e_f = 0.5$, $K = 50$, $r_0 = 6$ for both mutants and residents. Note: where a single line is shown, the fitness associated with maternal, paternal, and bi-parental care overlap.

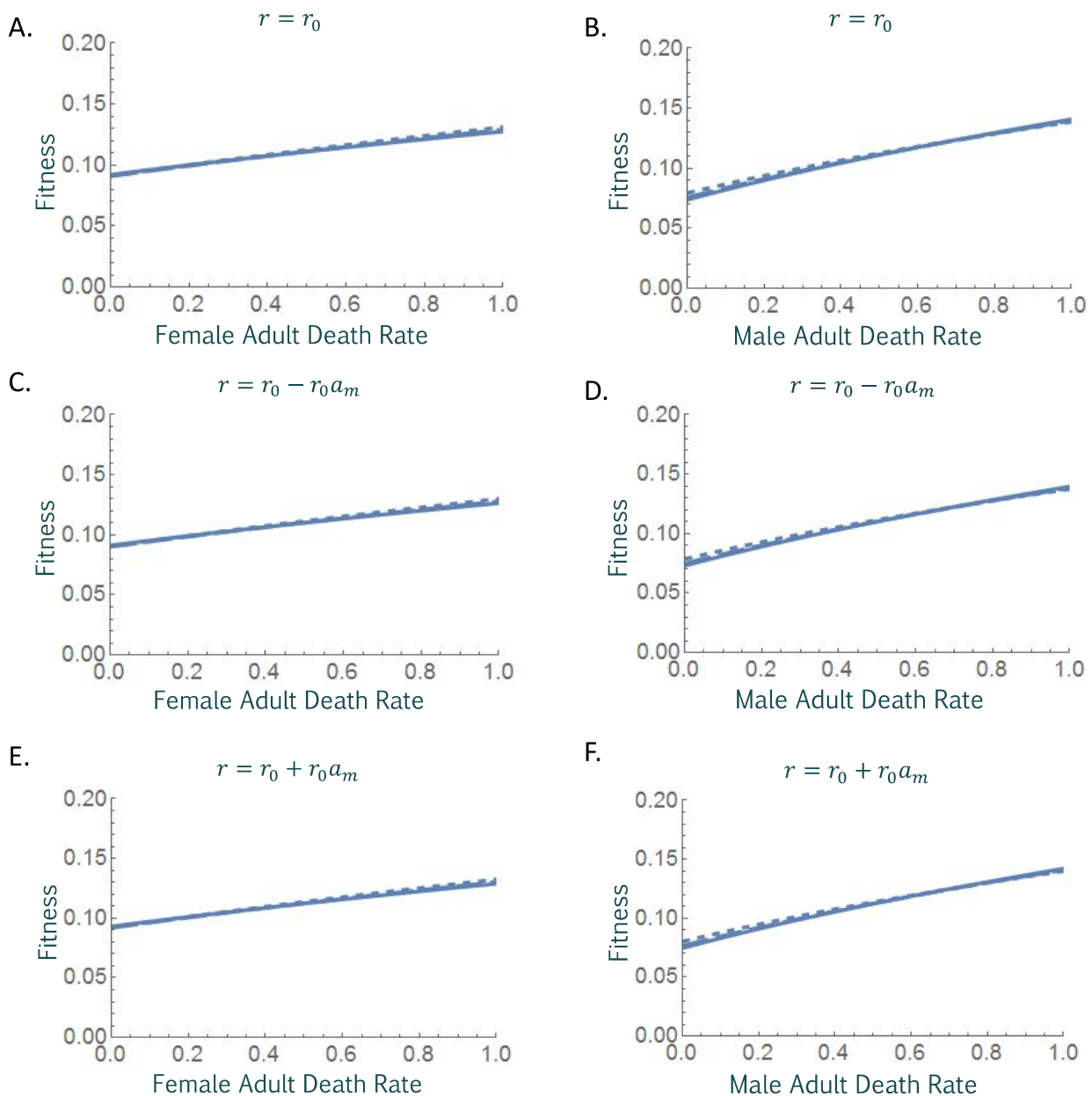


Figure 3. Higher female and male juvenile survival rates favor the evolution of maternal, paternal, and bi-parental care across mating scenarios. The fitness gains associated with parental care relative to that of a no-care strategy are illustrated in relation to female (A, C, E) and male (B, D, F) baseline juvenile survival rate for maternal care ($c_m = 0$, $c_f = 0.7$, dotted line), biparental care ($c_m = 0.35$, $c_f = 0.35$, dashed line), and paternal care ($c_m = 0.7$, $c_f = 0$, solid line). We additionally considered the following mating dynamics: (A-B) reproductive rate (i.e., the rate of egg fertilization) is unaffected by the rate of males entering the adult stage, (C-D) reproductive rate decreases as the rate of males entering the adult stage increases, and (E-F) reproductive rate increases as the rate of males entering the adult stage increases. Unless otherwise noted, $d_{Em0} = d_{Ef0} = 0.5$, $m_{Em0} = m_{Ef0} = 0.1$, $d_{Am0} = d_{Af0} = 0.5$, $\sigma_{Jm0} = \sigma_{Jf0} = 0.5$, $\tau_m = \tau_f = 0.1$, $e_m = e_f = 0.5$, $K = 50$, $r_0 = 6$ for both mutants and residents. Note: where a single line is shown, the fitness associated with maternal, paternal, and bi-parental care overlap.

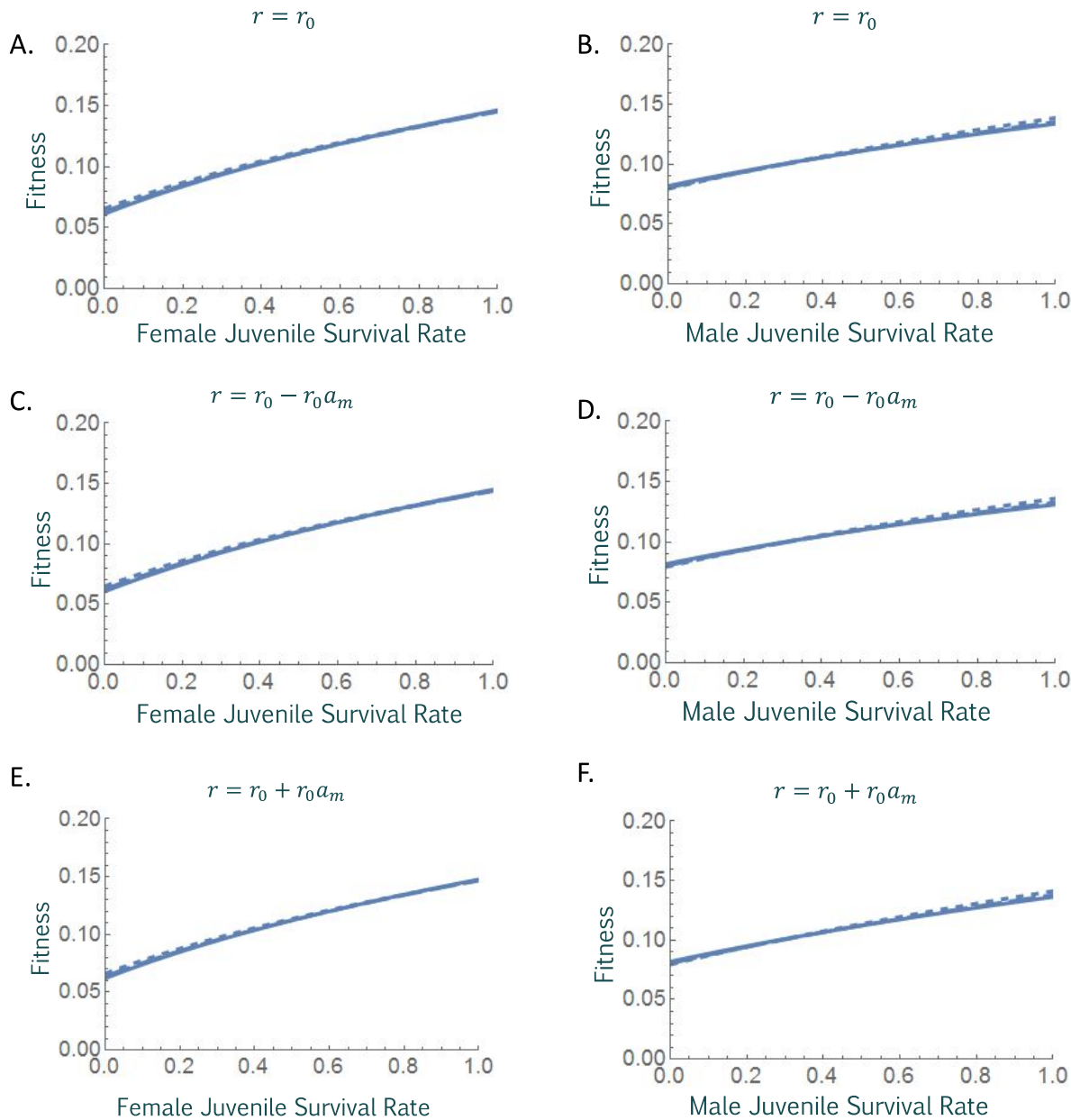
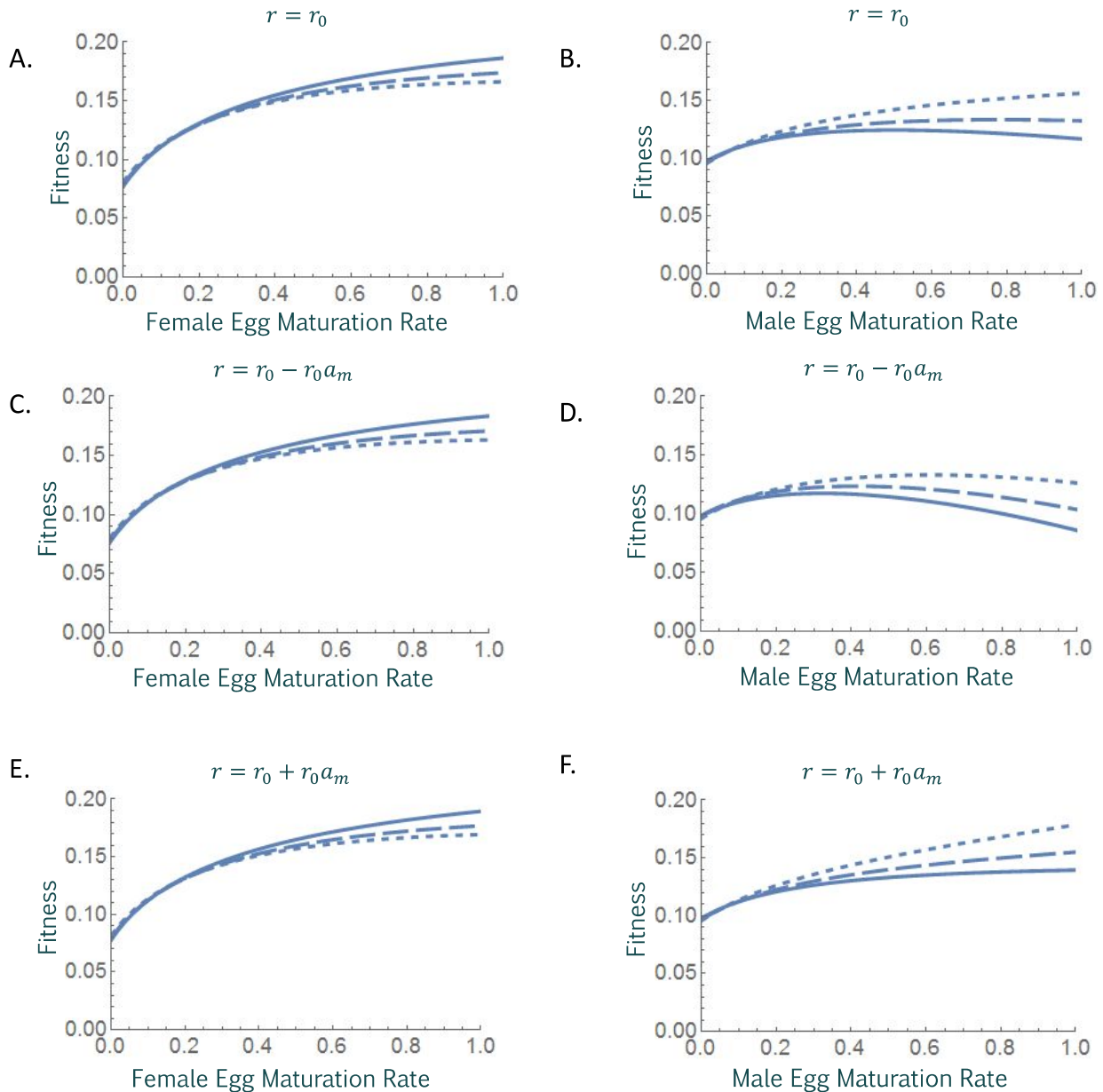


Figure 4. Moderate to high female and male egg maturation rates favor the evolution of maternal, paternal, and bi-parental care across mating scenarios. The fitness gains associated with parental care relative to that of a no-care strategy are illustrated in relation to female (A, C, E) and male (B, D, F) egg maturation rate for maternal care ($c_m = 0$, $c_f = 0.7$, dotted line), biparental care ($c_m = 0.35$, $c_f = 0.35$, dashed line), and paternal care ($c_m = 0.7$, $c_f = 0$, solid line). We additionally considered the following mating dynamics: (A-B) reproductive rate (i.e., the rate of egg fertilization) is unaffected by the rate of males entering the adult stage, (C-D) reproductive rate decreases as the rate of males entering the adult stage increases, and (E-F) reproductive rate increases as the rate of males entering the adult stage increases. Unless otherwise noted, $d_{Em0} = d_{Ef0} = 0.5$, $m_{Em0} = m_{Ef0} = 0.1$, $d_{Am0} = d_{Af0} = 0.5$, $\sigma_{Jm0} = \sigma_{Jf0} = 0.5$, $\tau_m = \tau_f = 0.1$, $e_m = e_f = 0.5$, $K = 50$, $r_0 = 6$ for both mutants and residents. Note: where a single line is shown, the fitness associated with maternal, paternal, and bi-parental care overlap.



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