



PATERNITY PROTECTION CAN PROVIDE A KICK-START FOR THE EVOLUTION OF MALE-ONLY PARENTAL CARE

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Sperm competition and uncertainty of paternity hamper the evolution of male parental care. Thus, maternal care predominates in most taxa. What if males can, however, limit cuckoldry by guarding the eggs postmating? Here, we show that this provides a reason to reconsider an old and nowadays rather discredited hypothesis: that external fertilization is associated with male care because the parent who releases its gametes first can depart leaving the other in a “cruel bind,” having to care for the offspring. In our model, protection of paternity provides an additional incentive for the male to stay associated with its young. When we then assume that offspring survive better if guarded, paternity protection proves enough to kick-start the evolution of male-only parental care from a scenario with no care. This fits with data from fishes, where male-only care is associated with external fertilization, whereas female-only care almost always evolves after an initial transition to internal fertilization. Our model unifies disparate hypotheses regarding parental care roles and provides support for the idea that care roles can be influenced by sex differences in selection to be physically close to the offspring, including selection that is initially not based on offspring survival.

KEY WORDS: Fish, mate guarding, mode of fertilization, parental care, paternity.

In many taxa, the survival of offspring is dependent on parental care, which is defined as any trait that enhances the fitness of offspring and originated / is maintained for this function (Smiseth et al. 2012). Among species with parental care, exclusive or predominate maternal care is more common than male care (terrestrial arthropods: Zeh and Smith 1985; birds: Lack 1968; Møller and Cuervo 2000; mammals: Clutton-Brock 1991; reptiles: Shine 1988; review: Kokko and Jennions 2012). This female bias is predicted by anisogamy—the initial sex inequality in investment into gametes (review: Kokko and Jennions 2008). Anisogamy promotes female-biased parental care via two indirect pathways. First, it can lead to multiple mating by females and sperm competition, thus reducing males’ certainty of paternity such that mothers are, on average, more closely related to their offspring than their social mates are. This means that females stand to lose more than males by deserting their offspring (Queller 1997). Second,

anisogamy promotes competition among males and nonrandom mating by females. This results in only an elite subset of males actually ever getting to mate (Queller 1997). For these males, then, the potential benefits of additional matings outweigh the costs of desertion (Kokko and Jennions 2008).

The teleost fishes (Superclass Osteichthyes) are unique in that they show a strong bias toward male-only parental care (approx. 61% care-giving families: Gross and Shine 1981; Gross and Sargent 1985; Reynolds et al. 2002; around twice the number of evolutionary transitions [22–27] than female-only care [12–17]: Mank et al. 2005; Fig. 1). The extent and mode of male parental care varies greatly across species, from nest building to mouth brooding and even male pregnancy (reviews: Ridley 1978; Blumer 1979). In the majority of species, however, male-only care simply means protecting fertilized eggs from predators (approx. 95% care-giving species: Gross and Sargent 1985). It should be

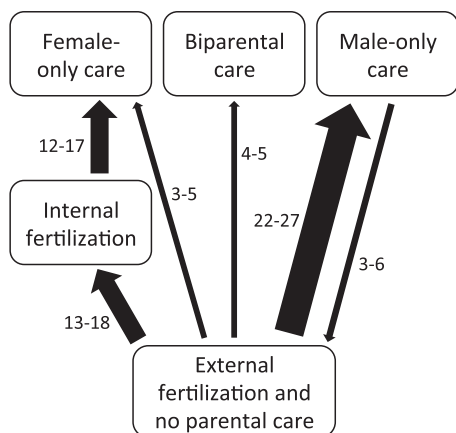


Figure 1. Evolutionary transitions of parental care and mode of fertilization in teleost fishes (redrawn from Mank et al. 2005). Arrow widths are proportional to mean number of transitions and adjacent numbers are the range estimates. Only transitions with lower bound estimates greater than zero are shown.

noted, however, that in many of these cases it has not been empirically demonstrated that this guarding is true parental care (i.e., that offspring fitness is improved).

Several authors have suggested that male-only care is favored in fish because male fish have a reduced cost of parental care compared to other taxa (reviews: Smith and Wootton 1995; Gross 2005). For example, in species where males may care for multiple broods at a time (e.g., sticklebacks; Wootton 1984), males need not sacrifice future mating opportunities to care for their current brood (Gross and Shine 1981; Gross and Sargent 1985). This can promote male-only parental care when males have many mating opportunities (e.g., females spend little time recuperating resources after reproduction; Manica and Johnstone 2004). This is likely to be especially true when females actually prefer already-caring males (e.g., Ridley and Rechten 1981; Forsgren et al. 1996; Reynolds and Jones 1999). In addition, in territorial species where males already spend a large amount of time defending a small area, caring for offspring might not represent much of an alteration to their normal daily activities (Trivers 1972; Williams 1975). Although male-only parental care is associated with territoriality, phylogenetic evidence suggests that territoriality alone is not sufficient for male care to evolve (Ah-King et al. 2005).

That benefits of care can be easily shared among many young is clearly important for promoting male care in fishes (Alonzo and Klug 2012), but within this taxon care roles also show strong associations with the mode of fertilization. In the majority of fish species fertilization occurs externally. The only other vertebrate taxon with external fertilization is the amphibians, which interestingly display the second highest prevalence of male-only care among vertebrate groups (males and females care equally often;

Gross and Shine 1981). This potential link between fertilization mode and patterns of parental care was examined in detail in a phylogenetic study by Mank et al. (2005), who showed that almost all the evolutionary transitions to maternal care in fishes were preceded by a transition from external to internal fertilization (Fig. 1; but this pattern is not as clear in anurans: Beck 1998).

Why should male parental care be associated with external fertilization? Williams (1975) pointed out a simple fact: parental care is not typically feasible unless there is an association (i.e., physical proximity) between parent and offspring (review: Gross 2005). In external fertilizers, parents are not necessarily close to the zygote when fertilization happens (e.g., broadcast spawners), but in spawning vertebrates, gametes and zygotes do not travel far from either the male or the female. A focus on this situation led to the order of gamete release hypothesis, which suggests that the first parent to release gametes can desert, leaving the other in a game-theoretic “cruel bind” (Dawkins and Carlisle 1976): if offspring die without care, it is better for a parent to stay, even if it would have been better to be able to leave first and make the other sex care. However, empirical data do not support this simple model. In fish species where gamete release is simultaneous, male-only parental care still predominates (Ridley 1978; Gross and Shine 1981), even when males actually release their gametes before females (e.g., Forsgren et al. 1996).

Recently, Kvarnemo (2006) pointed out that uncertainty of paternity is a far more complex issue for the evolution of male care than it being a simple negative selective pressure (Kokko 1999; Sheldon 2002; see also Alonzo and Heckman 2010 and Kvarnemo 2010 for the insight that we must consider the total number of offspring, not only the ratio of own to total young). Although there is evidence that the degree of male care is negatively related to paternity uncertainty at the species (e.g., Møller and Birkhead 1993) and individual levels (e.g., Sheldon et al. 1997; Neff 2003), the causality is not unidirectional. Males might reduce the level of sperm competition they face, and thus uncertainty of paternity, by having traits that make them stay near the young during fertilization. In this way, the implied causality of the correlation between paternity uncertainty and male care is reversed.

Here, we produce a model to extend on the ideas put forward by Kvarnemo (2006) and ask: can male strategies evolved to reduce cuckoldry (e.g., guarding unfertilized eggs from rival males) also promote the evolution of postfertilization male parental care (e.g., guarding the developing offspring from predators)? We focus particularly on fish and other external fertilizers, but many of the concepts raised will be broadly applicable to the evolution of male-only care across all taxa. Throughout, we will use the term “guarding” to refer to any time either parent spends with the eggs post gamete release, irrespective of the type of benefits obtained. The benefits can include paternity protection, improved offspring

survival, or both. We will only use the term “care” when there is an offspring survival benefit.

The Idea

Consider a species of fish with no parental care. During mating, a female deposits her eggs (e.g., on a substrate), and a male releases his sperm. At this point, both parents desert their offspring-to-be. After gamete release, there is, however, a short period of time before the eggs are actually fertilized. This time provides a window of opportunity for other males who can release their own sperm on the eggs and potentially steal some paternity from the original male.

Imagine now that, instead of deserting, a male remains with the eggs for a short time after mating. Will he be able to limit the amount of cuckoldry he would otherwise suffer? It seems plausible that such male behavior would be highly advantageous, and that this risk of partial cuckoldry would select for all males to spend a short time after gamete release with the eggs “protecting paternity.”

Here, we consider the subsequent evolutionary trajectories if males that guard eggs not only protect paternity, but also provide their offspring with a survival benefit. This requires us to link two different time scales: paternity protection is completed relatively quickly (cuckoldry can no longer occur once all eggs are fertilized), whereas a significant reduction of predation risk requires a much longer commitment. We show that a relatively short duration of paternity protection can actually kick-start evolution toward male rather than female care in externally fertilizing taxa.

The Model

The model requires linking selection for males to stay, caused by a potentially brief fertilization window, with the clearly longer duration of egg development, during which eggs benefit through increased survival from being guarded (which can subsequently also lead to other forms of care). Females, too, may be selected to stay with young, based on benefits to egg survival. Without loss of generality, we set egg development time (fertilization to independence) to 1. The time from gamete release to independence is consequently $t + 1$, where t is the time it takes for an egg to be fertilized, which is distributed with probability density function $f(t)$. Here, t has a negative exponential distribution with mean k . The larger the value of k , the more time it takes for local sperm to find and fertilize the egg. For example, if $k = 0.01$ and gametes are released at time 0, the average egg will achieve independence at time $k + 1 = 1.01$.

We assume that both the male and female are present at the point of gamete release (i.e., we are not dealing with broadcast

spawners). After egg release, the male can stay and guard the egg for a duration T_M , and the female for duration T_F ; these are the evolving traits in our model. We assume that neither T_M nor T_F will exceed the actual development time until independence ($t + 1$). We thus assume that parents do not stay guarding an empty nest but are free to join the mating pool after the offspring leave. To avoid unnecessary computational complications, we consider one egg at a time; in a multi-egg brood, real guarding times may become marginally longer if parents must stay until the last egg (rather than an average egg) reaches independence. Approximating such systems with a one-egg model is unlikely to bias our argument with respect to *which* sex, if any, should guard until eggs are independent.

Our task, then, is to derive the probabilities that an offspring reaches independence when its parents use guard durations T_M (male) and T_F (female). Offspring can fail to do this because of predation, which we assume occurs only when an egg is left unguarded by either parent. Predation risk under those circumstances equals μ per time unit, which means that survival of an egg over one unit of unguarded development time is $e^{-\mu}$. Here, we assume that the presence of only one parent is necessary to avoid egg predation. Although guarding against egg predators is more efficient when performed by both parents in some species (e.g., biparental-caring cichlids: Lehtonen et al. 2011), the predominance of single-parent care across all fish groups (Gross and Sargent 1985; Mank et al. 2005; Fig 1) suggests this is a reasonable assumption to make.

There is a male–female asymmetry in the fitness benefits gained when an offspring survives and becomes independent. This is because the male present at release (the social father) is not necessarily the sire. We assume that the probability that the social father is the sire is P_G if the egg is fertilized while he guards (i.e., if $t \leq T_M$), and P_U if it is fertilized after he has deserted ($t > T_M$). Note that P_U is not necessarily zero, because a male’s sperm can remain in the vicinity of unfertilized eggs after the male has departed. We also assume that the paternity *not* gained by the social father (i.e., $1 - P_G$ if the social father guards, $1 - P_U$ if he does not) is instead shared equally among all the males currently available to mate. However, males dynamically gain parasitic fertilizations while still trying to find a mate (e.g., Vliieger and Candolin 2009; Järvi-Laturi et al. 2011; Rezucha et al. 2012).

DERIVING FEMALE FITNESS

Our first goal is to derive R_F , the reproductive success that a female can expect from one breeding event, and how this changes if her guarding duration T_F changes. Selection on female guarding depends on whether she currently stays with the young for longer than the male, or shorter. We first consider the mathematically simpler case where males currently guard for longer than females.

Assuming $T_F < T_M \leq 1$, eggs are left vulnerable for a duration that lasts from T_M to $t + 1$, whereas if $T_M > 1$, there are some eggs that are totally safe (those fertilized between 0 and $T_M - 1$). Female fitness gain from this bout is therefore

$$R_F = \begin{cases} \int_0^\infty f(t)e^{-\mu(t+1-T_M)} dt & \text{if } T_M \leq 1, \\ \int_0^{T_M-1} f(t)dt + \int_{T_M-1}^\infty f(t)e^{-\mu(t+1-T_M)} dt & \text{if } T_M > 1. \end{cases} \quad (1)$$

This can be solved in closed form given the exponentially distributed fertilization time with parameter k ,

$$R_F = \begin{cases} e^{-\mu(1-T_M)}/(1+k\mu) & \text{if } T_M \leq 1, \\ 1 - \frac{k\mu}{1+k\mu} e^{-(T_M-1)/k} & \text{if } T_M > 1. \end{cases} \quad (2)$$

From this we can notice that neither expression depends on T_F . Thus, little-guarding females would benefit by an increase in male guarding duration, but not by increasing their own duration. There is no selection on females to improve the survival of eggs, as the male already takes care of this.

Next, we consider the case where females currently guard for longer than males ($T_F > T_M$). Female expected reproductive success from this breeding event is derived as above, giving us

$$R_F = \begin{cases} e^{-\mu(1-T_F)}/(1+k\mu) & \text{if } T_F \leq 1, \\ 1 - \frac{k\mu}{1+k\mu} e^{-(T_F-1)/k} & \text{if } T_F > 1. \end{cases} \quad (3)$$

The derivative of interest here is

$$\frac{\partial R_F}{\partial T_F} = \begin{cases} \mu e^{-\mu(1-T_F)}/(1+k\mu) & \text{if } T_F \leq 1, \\ \mu e^{-\frac{(T_F-1)}{k}}/(1+k\mu) & \text{if } T_F > 1. \end{cases} \quad (4)$$

Note that both R_F and its derivative have the same limit at $T_F = 1$ irrespective of the direction of approach. High predation risk selects for longer guarding duration, as does a sluggish rate of fertilization (because it then takes longer for eggs to be independent).

Ultimately, we are interested in the gains and losses that a female makes if she guards for an infinitesimally longer time than the population mean T_F . The gains such a female makes are given by $\partial R_F/\partial T_F$, but she also pays an opportunity cost in the form of a delay in starting a new breeding attempt. Given that a female who is not guarding mates and starts new breeding events at a rate a , and each of these will give her R_F offspring, female fitness changes with T_F according to

$$\frac{\partial W_F}{\partial T_F} = \frac{\partial R_F}{\partial T_F} - aR_F. \quad (5)$$

DERIVING MALE FITNESS

Calculating male reproductive success from one reproductive event, R_M is more complicated than it is for females because paternity levels interfere with reproductive gains. As above, we first consider the case where males guard for longer than females. And, again as above, the case $T_M \leq 1$ has to be dealt with separately from $T_M > 1$, but we also now have to consider that an egg may become fertilized before or after T_M , because this impacts paternity.

We first consider the case where $T_M \leq 1$ and males currently guard for longer than females ($T_M > T_F$). The male reproductive gain is

$$R_M = \int_0^{T_M} P_G f(t)e^{-\mu(t+1-T_M)} dt + \int_{T_M}^\infty P_U f(t)e^{-\mu(t+1-T_M)} dt \\ = \frac{P_G e^{-\mu(1-T_M)} - (P_G - P_U) e^{-(\mu+T_M/k)}}{1+k\mu}. \quad (6)$$

Its derivative is

$$\frac{\partial R_M}{\partial T_M} = \frac{P_G k \mu e^{-\mu(1-T_M)} + (P_G - P_U) e^{-(\mu+T_M/k)}}{k(1+k\mu)}. \quad (7)$$

However, when $T_M > 1$ and $T_M > T_F$, the derivation changes to

$$R_M = \int_0^{T_M-1} P_G f(t)dt + \int_{T_M-1}^{T_M} P_G f(t)e^{-\mu(t+1-T_M)} dt \\ + \int_{T_M}^\infty P_U f(t)e^{-\mu(t+1-T_M)} dt \\ = \frac{P_G(1+k\mu(1-e^{(1-T_M)/k})) - (P_G - P_U) e^{-(\mu+T_M/k)}}{1+k\mu} \quad (8)$$

and

$$\frac{\partial R_M}{\partial T_M} = \frac{P_G k \mu e^{-\frac{1-T_M}{k}} + (P_G - P_U) e^{-\mu(1-T_M)}}{k(1+k\mu)}. \quad (9)$$

Next, we consider the case where females guard for longer than males ($T_M < T_F$). When $T_F \leq 1$ (and $T_M < T_F$), all eggs are vulnerable to predation from T_F to $t+1$, whereas male fertilization probability depends on t relative to T_M . Thus,

$$R_M = \int_0^{T_M} P_G f(t)e^{-\mu(t+1-T_F)} dt + \int_{T_M}^\infty P_U f(t)e^{-\mu(t+1-T_F)} dt \\ = \frac{P_G e^{-\mu(1-T_F)} - (P_G - P_U) e^{-\mu(1-T_F+T_M)-T_M/k}}{1+k\mu}. \quad (10)$$

The derivative in this case is

$$\frac{\partial R_M}{\partial T_M} = \frac{(P_G - P_U) e^{-\mu(1-T_F+T_M)-T_M/k}}{k}. \quad (11)$$

This makes intuitive sense; the expression is directly proportional to the paternity difference between guarding and nonguarding. Furthermore, mean time to fertilization, k , is alone

in the denominator and thus plays a more important role than the mortality risk of unguarded eggs, μ (the latter is taken care of by females in this case where $T_F > T_M$).

Finally, when females guard longer than males and $T_F > 1$, we additionally have to distinguish between subcases where the difference between T_M and T_F is smaller or greater than unity, because this determines whether there are eggs with guaranteed survival that are fertilized after the male has deserted (unguarded fertilization). We first deal with the case $T_F - T_M \leq 1$, which obviously requires that T_M is large enough so that $T_F - 1 \leq T_M$:

$$R_M = \int_0^{T_F-1} P_G f(t) dt + \int_{T_F-1}^{T_M} P_G f(t) e^{-\mu(t+1-T_F)} dt + \int_{T_M}^{\infty} P_U f(t) e^{-\mu(t+1-T_F)} dt = \frac{P_G(1 + k\mu(1 - e^{-\frac{1-T_F}{k}})) - (P_G - P_U)e^{-\mu(1-T_F+T_M)-T_M/k}}{1 + k\mu} \tag{12}$$

The derivative in this case is the same as described above (eq. (11)). Our final calculations are for the case where females guard longer such that $T_F - T_M > 1$, which requires a small male care duration ($T_M < T_F - 1$):

$$R_M = \int_0^{T_M} P_G f(t) dt + \int_{T_M}^{T_F-1} P_U f(t) dt + \int_{T_F-1}^{\infty} P_U f(t) e^{-\mu(t+1-T_F)} dt = P_G(1 - e^{-\frac{T_M}{k}}) + \frac{P_U(e^{-\frac{T_M}{k}}(1 + k\mu) - e^{-\frac{1-T_F}{k}})}{1 + k\mu} \tag{13}$$

The derivative in this subcase is

$$\frac{\partial R_M}{\partial T_M} = \frac{e^{-\frac{T_M}{k}}(P_G - P_U e^{-\mu(1-T_F+T_M)})}{k} \tag{14}$$

Because of the Fisher condition (i.e., males cannot sire more offspring than females produce eggs; Houston and McNamara 2002) male lifetime fitness, W_M , for any values of T_M and T_F must equal $W_M = W_F/r$, where r is the operational sex ratio (OSR; the ratio of males to females among those individuals who are ready to mate) and W_F is female fitness. However, the Fisher condition does not prevent individual males from benefiting by deviating their guarding duration from the population average. We are therefore interested in the gains and losses that a male makes if he guards for an infinitesimally longer time than the population mean T_M . The gains such a male makes are given by $\partial R_M/\partial T_M$, whereas his losses are any mating opportunities he forgoes by guarding (note that we do not assume that he can add new broods while guarding, because we are interested whether the causal route from paternity protection to male care can work on its own, that is, in the absence of other arguments produced for paternal care in fishes). Mating opportunities arise at a rate equal

to aR_F/r , where a is the rate at which females breed, and R_F is the breeding success per female breeding event. By multiplying this with the inverse of the OSR, $1/r$, this modifies the above rates to a rate that applies for males who are currently competing for matings (not guarding an egg). Therefore, male fitness changes with T_M according to

$$\frac{\partial W_M}{\partial T_M} = \frac{\partial R_M}{\partial T_M} - \frac{aR_F}{r} \tag{15}$$

The OSR, here denoted r , is calculated according to equation (A9) in Kokko and Jennions (2008), where we assume that the adult mortality rate is identical for males and females whether they guard or seek new matings (we denote this by μ_A). The rate at which females meet suitable mates (which is always assumed to lead to a mating), a , is consequently $Mr^{1/2}$ where M is a species-specific mate encounter rate (see Kokko and Jennions 2008).

In the following, we assume that evolutionary change is proportional to the values $\partial W_M/\partial T_M$ and $\partial W_F/\partial T_F$, which is appropriate given the lack of any a priori reason that one sex should, more often than the other, lack the necessary genetic variation to respond to a prevailing selection pressure.

Results

We are particularly interested in the evolution of guarding from initial conditions where neither sex has yet evolved any guarding behaviors. In many of the scenarios discussed later (Fig. 2), there is little or no selection on the sex that currently has the smaller guarding duration to stay for longer. If, for example, males already guard eggs for longer than females do, it is beneficial for females to shorten their stay and depart immediately, as this has no negative impact on offspring survival. This means that there is positive feedback (Lehtonen and Kokko 2012): the sex that is already guarding less can diminish its effort further.

IF MALES CANNOT LIMIT CUCKOLDRY, NEITHER SEX IS MORE LIKELY TO CARE

Unsurprisingly, when there is no benefit of parental guarding to either parent in terms of offspring survival and no benefit to paternity certainty, both parents are selected to desert their offspring as soon as possible (i.e., no parental guarding). When offspring survival improves with parental guarding (but there is no paternity benefit to guarding males, $P_U = P_G$; Werren et al. 1980), the abovementioned positive feedback is perfectly symmetrical. Male and female care are expected to evolve equally often, because whichever sex starts with a longer guarding duration will be selected to become the sole carer (Fig. 2A). If we measure guarding duration from the time the first parent releases its gametes and assume some temporal asynchrony in gamete release, then this case confirms the simple logic of Dawkins and Carlisle's (1976)

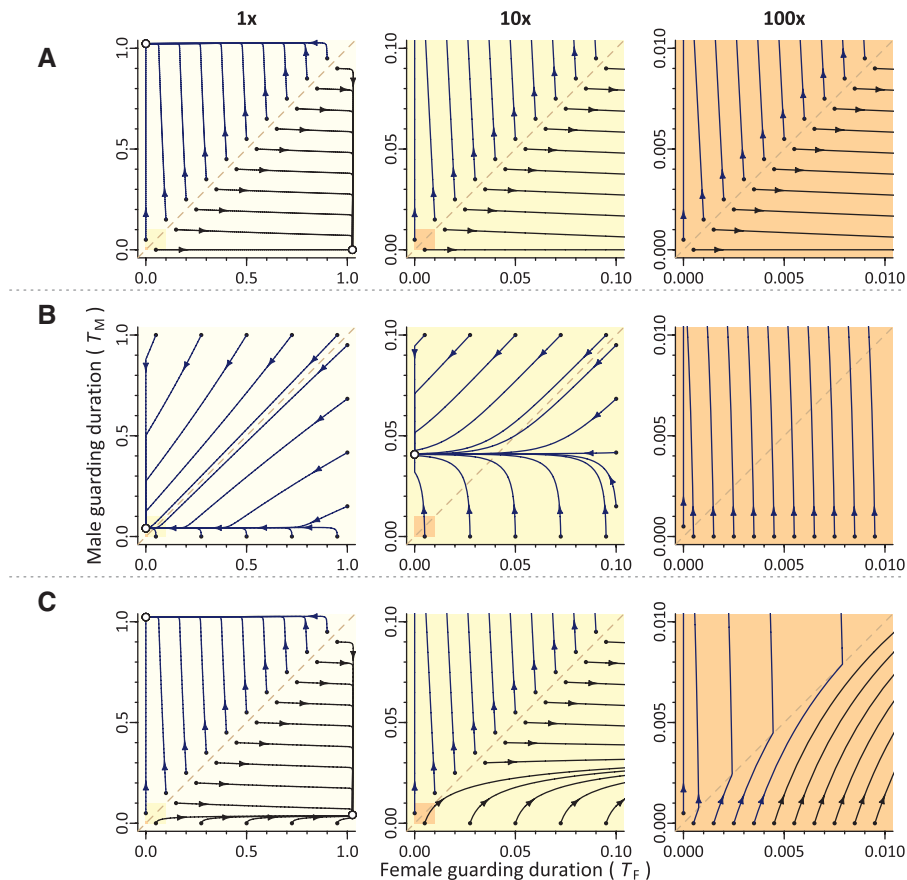


Figure 2. Evolutionary trajectories of male versus female guarding duration when: (A) there is an offspring survival ($\mu = 25$), but not a paternity benefit of guarding ($P_G = P_U = 0.8$); (B) there is a paternity ($P_G = 0.8$, $P_U = 0.2$), but not offspring survival ($\mu = 0$) benefit of guarding; and (C) when there is both an offspring survival and a paternity benefit of guarding ($\mu = 25$, $P_G = 0.8$, $P_U = 0.2$). Other parameters: $k = 0.01$, $\mu_A = 0.01$, $M = 1$. For each scenario, we present three different “magnifications” to view evolutionary trajectories near the origin: 100x, 10x, and 1x “zoom” from left to right. Evolution starts from the black points (starting values chosen for illustrative purposes) and progresses to the white points. Trajectories that lead to males guarding for longer than females are shown in blue. When males have the additional benefit of paternity protection as well as increasing offspring survival, a bias toward male-only parental care is predicted when starting at low guarding durations (i.e., near the origin in 100x magnification of scenario C).

order of gamete release hypothesis. Interestingly, these findings are true even when males are not guaranteed full paternity of the brood they are guarding (Fig. 2A). The evolutionary endpoint has one parent guarding for a duration where most offspring have reached independence.

WHEN MALES CAN LIMIT CUCKOLDRY, PATERNITY PROTECTION EVOLVES

When fathers are able to reduce the risk of cuckoldry by guarding after gamete release ($P_G > P_U$; Kvarnemo 2006), they are selected to do so only until the majority of eggs are fertilized (Fig. 2B). If we assume guarding has no impact on egg survival, the male will not stay for the entire egg development duration, and females depart even sooner (immediately after egg release; Fig. 2B).

If we consider Figures 2A and 2B together, we can imagine a species that first experiences selection for brief guarding by the male for paternity protection with females deserting after gamete

release (Fig. 2B). If offspring survival then becomes dependent on parental guarding, longer male-only care will evolve because initial guarding duration will be greater for males than females (Fig. 2A).

PATERNITY PROTECTION PROMOTES THE EVOLUTION OF MALE-ONLY PARENTAL CARE

This result is confirmed by considering the case (Fig. 2C) where both paternity and egg survival are improved by guarding (obviously only the latter is relevant for female fitness). The overall pattern features positive feedback as described above (compare Fig. 2A and 2C). To predict the prevalence of male versus female care, however, it is essential to consider ancestral conditions. Crucially, low initial guarding durations now reveal an asymmetry, favoring evolution toward male care.

If selection on guarding near the origin (i.e., from a no-care scenario) was perfectly symmetrical (as in Fig. 2A, where

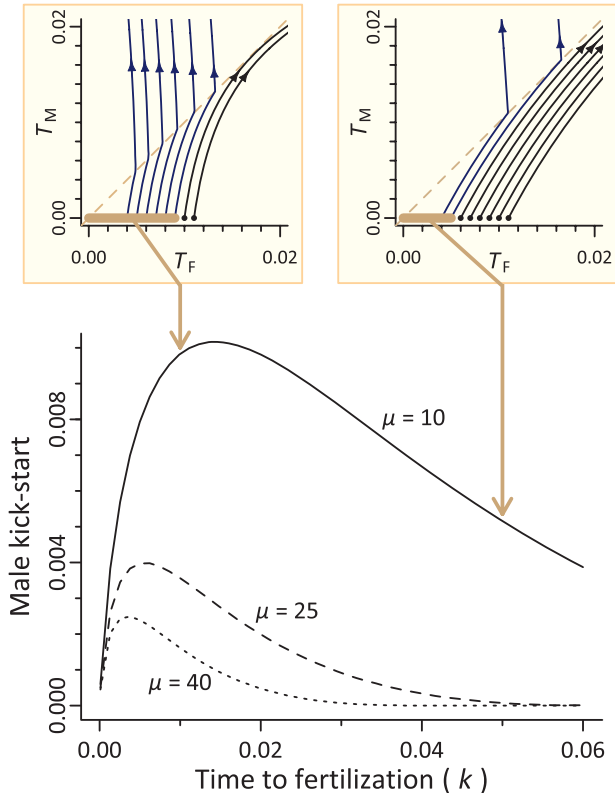


Figure 3. The effect of time to fertilization (k) and offspring mortality when unguarded (μ) on the male kick-start—the likelihood of male-only care evolving from a no-care situation. The two inset figures illustrate how this male kick-start (switch from male-only to female-only parental care indicated by the brown bar) looks in terms of evolutionary trajectories (as in Fig. 2) for different points of the top curve in the main figure: (left) $k = 0.01$, (right) $k = 0.05$. Other parameters: $P_G = 0.8$, $P_U = 0.2$, $\mu_A = 0.01$.

there is no paternity protection benefit), then we predict no bias in the prevalence of males or females as the caring sex; any minute sex difference in the initial guarding duration becomes self-reinforcing. However, if paternity protection provides a “male kick-start,” it can be measured by asking the following question: how female-biased can the initial guarding asymmetry be, such that the evolutionary endpoint is still male-biased care? The answer to this question is the magnitude of the kick-start (e.g., Fig. 3).

Consider the evolutionary trajectories that start with no male guarding and short female guarding duration ($T_M = 0 < T_F < 0.01$; Fig. 2C 100 \times zoom). Male guarding initially does not improve offspring survival (because the short duration that eggs are protected is already provided by females, $T_F > T_M$) but it improves his paternity. Because paternity can matter greatly (the male reason to guard) while limited guarding by the female is unlikely to impact offspring survival much, selection to increase guarding duration is stronger for males than for females. However, as the

male guarding duration increases, it becomes more difficult for the male to keep increasing paternity by guarding longer (eggs are likely to have been fertilized already). The trajectories consequently are of a curvilinear shape, with male guarding duration initially, but not necessarily later, increasing faster than female guarding duration ($\partial W_M / \partial T_M > \partial W_F / \partial T_F$).

The evolutionary endpoint depends on whether paternity protection initially selects for males to begin guarding for longer than females. If, from an initial state of $T_M < T_F$, male guarding evolves to exceed T_F , female guarding no longer matters for offspring survival. Because this removes the reason behind female guarding, selection now favors a reduction of female guarding and a strong increase in male guarding duration, as male guarding now matters not only for paternity but also for egg survival.

If the trajectories do not reach equality ($T_M = T_F$) when they are initiated from female-biased guarding durations, the evolutionary endpoint is female-only parental care. In these cases, although, males are still selected to remain with the eggs for a short period of time to maximize their paternity, even though there is no additive offspring survival benefit of having both parents present.

Consequently, our model clearly demonstrates that guarding by males—initially favored by a reduction in paternity uncertainty—can indeed kick-start the evolution of male-only parental care: male care evolves from male biased as well as somewhat female-biased initial guarding durations. It is necessary to provide a quantitative assessment of the phrase “somewhat female-biased”: if the majority of all possible ancestral events lead to male care, we expect it to be more ubiquitous than if the situation remains nearly symmetrical (all but the mildest female biases lead to female care and all initial male biases lead to male care). In other words, which sex ends up caring is still highly sensitive to the initial guarding durations (i.e., evolutionary history), but if the male kick-start is strong, we expect a higher prevalence of male care in nature.

The male kick-start is the maximum initial guarding duration of females that still leads to male-only parental care when males do not initially guard ($T_M = 0$). Graphically, it can be identified as the last point along the x-axis before the evolutionary trajectories switch from leading to male-only to female-only care (e.g., approximately 0.004 in Fig. 2C, 100 \times zoom). The greater the male kick-start, the more likely male-only care is to evolve from no parental care because stochastic events are less likely to impact the direction of selection.

FERTILIZATION TIME MATTERS . . .

Compared to the total time from gamete release to offspring independence, fertilization presumably occurs rapidly. One might intuitively predict that the above kick-start only works if fertilization is relatively slow. However, our model reveals the opposite: male-only parental care is most likely to evolve when fertilization

occurs relatively quickly (in the window of approximately 0.5–2% of the time from gamete release to offspring independence; e.g., $k = 0.005$ – 0.015 in Fig. 3). This somewhat surprising result can be explained by changes in the relative cost of paternity protection with different fertilization times. When fertilization is instantaneous, no male kick-start exists because males gain no paternity benefit by guarding. Conversely, very-long fertilization times make initial increases in guarding duration an inefficient means to protect against cuckoldry, thus reducing the net benefit of paternity protection and hence the overall male kick-start. This is why the kick-start effect works best at intermediate fertilization windows.

AND SO DOES OFFSPRING MORTALITY RISK ...

Offspring mortality risk when unguarded has a strong effect on the male kick-start: the smaller the mortality risk, the stronger the male kick-start (Fig. 3). Again this pattern can be explained by considering the costs and benefits of paternity protection versus increasing offspring survival. For females, only the latter is of importance; for males, both are. If offspring rarely survive without guarding, the need to protect them tends to override all other fitness considerations, thus making the positive feedback symmetrical (little male kick-start based on paternity). It is, of course, difficult to assess how well offspring tended to survive in an ancestral no-care scenario, as their needs may coevolve with the care provided. However, because parental care in fish frequently evolves from a no-care scenario (Mank et al. 2005), the survival chances of unguarded offspring must have been adequate enough to maintain a persisting population. This means that the conditions for a strong male kick-start are generally satisfied in ancestral no-care situations.

AS WELL AS THE PATERNITY BENEFIT OF GUARDING ...

Finally, our model predicts that, as the absolute paternity benefit ($P_G - P_U$) of male guarding increases, so does the magnitude of the male kick-start (Fig. 4). In other words, male-only parental care is more likely to evolve when guarding males receive a large paternity bonus compared to deserters. This effect is independent of the baseline level of paternity social fathers gain when they desert (e.g., the male kick-start is equally significant when guarding improves paternity from $P_U = 0.5$ to $P_G = 1$ as it is when it improves it from $P_U = 0.25$ to $P_G = 0.75$). One could interpret this result as follows: high levels of sneaking (low P_U) can make male-only care more likely to evolve, but only if guarding the eggs is an efficient means to limit the impact of sneaking.

Discussion

Sperm competition and multiple paternity are generally thought of as negative selection pressures on male parental care (Kokko

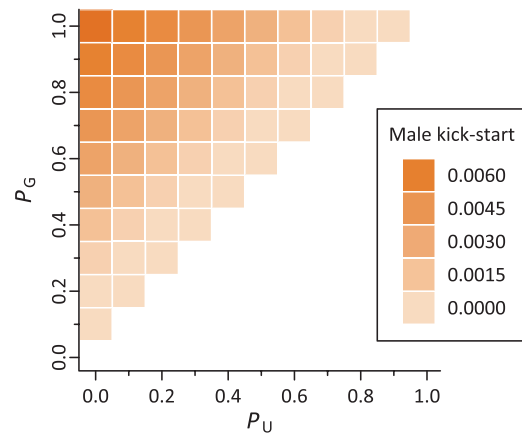


Figure 4. The magnitude of the male kick-start depending on the social father's paternity when the eggs are guarded (P_G) or unguarded (P_U). Here, $k = 0.01$, $\mu = 25$ and $\mu_A = 0.01$.

1999; Sheldon 2002) yet the causality is reversed if, by caring, males are able to limit the risk of cuckoldry (Kvarnemo 2006). Here, we have demonstrated that, in externally fertilizing species, a paternity benefit of guarding offspring postmating can promote the evolution of male-only care. When males can limit the risk of cuckoldry by staying near eggs until they are fertilized, males are selected to protect paternity. This paternity protection is analogous to post-copulatory mate guarding in taxa with internal fertilization (e.g., Hammers et al. 2009; Schubert et al. 2009; Ancona et al. 2010), except here, the mother has the opportunity to desert her offspring after gamete release. We considered what happens if the initial reason to guard sets the stage for further elongation of this guarding duration, now for the sake of offspring survival. Our model shows that this process can work: as male guarding durations increase, the reason for prolonging it shifts from paternity to offspring survival, but selection can remain positive throughout, until the guarding duration matches the time it takes for offspring to reach independence. This combination of factors has great potential to explain the prevalence of male care in externally fertilizing taxa.

By incorporating both paternity protection and offspring survival benefits, our model predicts that male-only care will evolve from a no-care scenario whereas female-only care is more difficult to achieve. Phylogenetic evidence suggests that transitions from no care to male-only parental care are indeed the most common evolutionary transition of parental care in fish (Mank et al. 2005; Fig. 1). Furthermore, our model demonstrates that there is strong positive feedback in which sex cares, making evolutionary transitions from male-only to female-only care (or vice versa) unlikely. Instead, such a transition could only occur via a return to a no-care scenario, again fitting well with what we know about the evolution of parental care in fish (Mank et al. 2005).

The link between mode of fertilization and which sex cares in fishes has long been known (Gross and Shine 1981). The argument that parental care behaviors evolve according to simple principles of spatial or temporal association between parent and offspring go back to Williams (1975), with Dawkins and Carlisle (1976) providing a potential explanation for a sex asymmetry by focusing on the order of gamete release. Although this has largely been repudiated (Ridley 1978; Gross and Shine 1981), we here show that the time a parent is selected to associate with its young can matter, when we take into account that the reason changes over time as the length of the association evolves. Sperm competition, together with the ability of males to reduce it by guarding, can provide the necessary kick-start for a male association with its young, confirming Kvarnemo's (2006) verbal model. Essentially, we are shifting the focus away from the timing of gamete release (*sensu* Dawkins and Carlisle 1976) to the timing of fertilization, which helps explain why there can be a sex difference in initial departure decisions. Sperm competition does not make a female's relatedness to her young depend on the timing of her departure, but it creates a potentially strong link between a male's departure decision and his paternity.

It is instructive to contrast our findings with other models of parental care evolution, where paternity uncertainty reduces male care (e.g., Werren et al. 1980; Kokko and Jennions 2008; Alonzo 2012). Our model identifies positive feedback: the longer guarding sex is typically selected to extend its guarding, whereas Kokko and Jennions (2008) found negative feedback where the sex that spends less time caring will remate at a slower rate (due to biased OSR), and is therefore selected to care for longer. This made biparental solutions common in Kokko and Jennions (2008), whereas our model predicts uniparental care despite taking the OSR feedback into account. The predictions are different because in Kokko and Jennions (2008) being cared for by two parents was assumed to be better for offspring survival than being cared for by just one parent, whereas in our model, we assume that one parent's guarding makes the other's guarding superfluous. Although the truth may lie somewhere in between, the high frequency of uniparental care in fishes (Gross and Sargent 1985) is suggestive of a relatively high capacity of a single parent to raise young.

Another difference is that our model is, to our knowledge, the only one that explicitly incorporates a paternity benefit of guarding. Thus, although our model agrees with Alonzo (2012) who shows that male care can be an evolutionary endpoint despite relatively low paternity, the underlying reasons are different. In Alonzo (2012, see also Alonzo and Heckman 2010), male care can evolve despite low paternity if males who stay with young attract additional females; in our model (and in Kvarnemo's 2006 verbal model), paternity uncertainty selects for male care because it is a prerequisite for paternity differences between males who

guard for different durations after gamete release. Obviously, in nature both factors can interact, which should further promote male care.

Female mate preferences could also be important in the sense that females might prefer males who are able to protect their own paternity, assuming that female interests might be best served if many of her eggs are fertilized by her chosen mate rather than other males stealing paternity. It may be difficult, however, for a female to judge a male's ability (future guarding duration and efficiency) in this respect. Furthermore, there is mounting evidence that sneaker males are not always less desirable to females—indeed females may be able to get the best of both worlds (good genes and parental care) by mating in the presence of sneakers (review: Reichard et al. 2007). Therefore, our modeling approach where female departure decisions do not depend on paternity patterns in the brood appears justified.

DO FISH ACTUALLY CUCKOLD AND CAN FATHERS DO ANYTHING ABOUT IT?

Multiple paternity is well documented in a large number of fish species with male-only parental care, and occurs at a similar rate to other vertebrate groups (reviews: Taborsky 1998; Coleman and Jones 2011). In many cases, sneaker males represent an alternative reproductive tactic (e.g., Mackiewicz et al. 2005; Neff and Clare 2008), whereas in others males both sneak and mate with social partners throughout their lives (e.g., Vliieger and Candolin 2009; Järvi-Laturi et al. 2011; Rezuca et al. 2012); or do both simultaneously (e.g., Lee and Bass 2004). Given that the most common form of male-only care in fish is simple guarding against con- and hetero-specifics (Gross and Sargent 1985), it seems likely that, by caring for offspring, fathers can also reduce levels of cuckoldry (Kvarnemo 2006). Potential evidence comes from males of the cichlid *Pterophyllum scalare*, who triple their aggression levels toward other males immediately after females release their eggs compared to before egg release or after hatching (Yamamoto et al. 1999). Such mate-guarding aggression is also known in the wrasse *Symphodus ocellatus* (Alonzo and Warner 2000). Empirical tests of the paternity benefit of these aggressive behaviors could be done relatively easily in species with sneaker / satellite males by removing social fathers immediately after they release sperm and comparing levels of cuckoldry between these broods and un-manipulated ones.

WHAT ABOUT INTERNAL FERTILIZATION AND FEMALES?

Female-only parental care is almost exclusively associated with internal fertilization in fishes (Mank et al. 2005; Fig. 1). How does internal fertilization fit with our model? In internal fertilizers, the female (or sometimes the male: Kvarnemo and Simmons 2004) must, by definition, hold the eggs until fertilization. Therefore, the

smallest possible guarding duration of females is constrained to be greater than males, given that paternity protection alone selects for males to guard less than 100% of the fertilization time. In our model, if T_F is constrained such that it exceeds the male kick-start, evolution proceeds to female-only care (e.g., Fig. 3). Thus, if there is a significant lower boundary for T_F , we predict female-only care to be the predominant pattern. Therefore, given the current phylogenetic evidence, our model is fully compatible with the association between internal fertilization and female-only care.

HISTORY IS IMPORTANT

Our model also demonstrates that the evolution of which sex provides care is highly sensitive to initial guarding durations (i.e., we predict phylogenetic inertia: Lehtonen and Kokko 2012). This means that chance events are likely to affect the outcome of evolution, particularly under conditions that predict a small magnitude of the male kick-start. Thus, although our model predicts a preponderance of male-only parental care, it does not strictly exclude the evolution of female-only care from no care. More precisely, we can predict that the incidences of female-only parental care in external fertilizers should be more common in species where fertilization time (relative to total parental care duration) is long or instantaneous.

When testing any predictions from this model one must, however, be cautious about using the life history of extant species to predict past evolution. For example, consider a species that displays a very clear paternity benefit of guarding, but mothers care for the offspring until independence. One could argue that such a species counters our predictions here. However, the importance of protecting paternity may have changed over time (e.g., because the species lives at a different density than before) and if it is currently greater than when care first evolved, female-only care is predicted to be just as likely as male-only care. Indeed, if female care evolves, it may simultaneously intensify sperm competition (make P_U lower) because female-only care makes the operational sex ratio more male biased. However, if P_U becomes low only once females are already firmly the caring sex, the evolutionary outcome is unchanged due to phylogenetic inertia.

Similarly, and crucially, our model does not require any paternity benefit of guarding to be maintained once male-only parental care has evolved. Consider the three scenarios discussed above (Fig. 2). If both a paternity and an offspring survival benefit arise simultaneously, the evolution of male-only care from no care is predicted (Fig. 2C). If this paternity benefit now disappears, male-only care is predicted to be maintained (Fig. 2A). The only way for female-only care to evolve in this scenario is by a transition to no care first. Again, this appears to be true in the evolutionary history of fishes (Mank et al. 2005; Fig. 1), thus our model appears, as a whole, consistent with the general phylogenetic pattern.

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