The evolution and fitness benefits of paternal care

Maeve Barbera
Department of Biology
Lake Forest College
Lake Forest, Illinois 60045

Abstract

Most species lack parental care and leave their offspring to fend for themselves after copulation and birth. Nonetheless, in some species, parental care is essential to the survival of the offspring. It is important to the overall fitness of the parent because with offspring survival, parental genes are passed on in the population. Parental care can come about in many different forms, depending on the species and which parent provides it. Care can be short lived and just aim to help offspring survive past larval stages, or it could also consist of near lifelong bonds that aid in learning for future reproduction. In the species that do exhibit parental care, maternal care is what is expected to arise from the ancestral state of no parental care, since females are the sex that are believed to invest the most in the reproductive process. However, paternal care has been highly selected for over maternal or in addition to maternal care in a variety of species, with males either being the sole providers of resources or both parents aiding in the care for offspring. I aim to identify why and how paternal care has evolved over other forms of parental care in different species and how this has benefitted the overall parental fitness of the given species. In order to do this, I will look at a multitude of different taxa who exhibit solely paternal care and paternal care in addition to maternal care to see how it differs in different taxa, conveying that paternal care has evolved in different areas for different reasons. In addition, investigating specific parental behaviors males display to determine whether these behaviors are more costly or beneficial to their fitness, which helps determine the evolution of male parental care.

Introduction:

Parental care can be defined as any parental behavior that contributes to the increase in fitness of an offspring and these behaviors can occur either before and/or after laying and/or birth (Smiseth, 2021). These behaviors, as we know, can be performed by both sexes, but are dependent on the species and the needs of the other parents and of the offspring. For parental care to be present in a species, the benefits of the care must outweigh the costs. In other words, there will be a tradeoff between benefitting the parents' current offspring versus reduced future reproduction of more offspring (Zeh and Smith, 2015). These costs and benefits do not always come directly from the fitness of the parents but can also come from abiotic and biotic factors from the environment. At times, the environment can be stronger than an individual organism, making the effort put into parental care not worth fighting against the stronger, detrimental effects that come from the outside world (Zeh and Smith, 2015). When looking at the benefits of parental care, they can be summarized into four main categories: (1) increase offspring survival, (2) improve offspring quality, (3) increase offspring reproductive success, and (4) control offspring developmental rate (Klug and Bonsall, 2014). These benefits can be exhibited by both parents to their offspring, or by only one of the parents.

Classical theory suggests that females are much more likely to provide care than males, and this is because they are believed to invest more in gametes and zygotes (Klug et al., 2013). Here, females are investing more prior to mating, and it costs more to replenish those resources in comparison to males. It is expected to see maternal care if they are mated with a more attractive male, when biparental care is not needed to rear offspring, in older animals, or in mammals (Kempenaers and Sheldon, 1997). Mammals need maternal care because lactation is necessary for survival and can only be provided by mothers. Maternal care can be seen by itself, with just the female providing care by herself, or maternal care with the addition of paternal care. Paternal care is assumed to be much rarer and research on this form of care is much newer in comparison to maternal care. Care provided by the male sex is often found in species that have extra-pair paternity, which is a result of copulation between the female and a male, other than her social partner (Kempenaers and Sheldon, 1997). In addition, paternal care is highly affected by female choice, where the fitness benefits of male care can select for female preferences to favor parental males, influencing the male sex to display higher parental qualities (Alonzo, 2012). The variation of the condition that the male is in will affect the care that is provided by the given individual, resources must be provided to increase an individual's own condition for it to be able to first, spread their genes and second, take care of their offspring (Kempenaers and Sheldon, 1997).

Although we see maternal care being more common across many taxa due to costs of reproductive efforts, in some cases sole paternal care or paternal care in addition to maternal care is greatly beneficial to the fitness of the offspring. Within birds an increase in paternal care has been seen in comparison to other species, mostly due to social monogamy (Moller and Cuervo, 2000). There has been an evolution in both paternity and paternal care across the taxa, as paternity has been hypothesized to be related to the evolution of paternal care because there should be selection for males not to invest in broods with uncertain parentage and male extra pair activity is against paternal care (Moller and Cuervo, 2000). Male bird participation in three forms of paternal care behaviors increased with high paternity within their own nests. These behaviors included: nest building, incubation, and provisioning of offspring (Moller and Cuervo, 2000). By spending more time in the nest, before and after copulation, female birds have less of a reason to explore extra-pair copulations, ensuring that most of the offspring are related in the nest and resulting in the male bird investing more resources and energy into a brood he knows is all his genes. Under these circumstances, male birds are increasing the fitness of their offspring so that they can survive after the care of their parents is terminated. Of the three forms of behaviors observed, they fall under the categories of benefits parental care provides (Moller and Cuervo, 2000). Many forms of paternal care have arisen in the wake of sexual selection efforts, where females prefer males who will provide some form of parental care. Being able to provide parental care shows what kind of condition an individual is in, and females prefer to mate with males in higher bodily condition, as mentioned earlier (Alonzo, 2012). The majority of cases of paternal care have been seen in species of bird, as they have arisen to counteract extra-pair copulations (Moller and Cuervo, 2000). Paternal care has also been documented in arthropods as it conveys to the female the quality of the male (Tallamy, 2000), in mammals as it helps stabilize mating systems and promote the evolution of complex behaviors (Stockley and Hobson, 2016), and in frogs male care positively impacts offspring survival (Pettitt et al., 2020). In many of these cases, sole male parental care or male parental care in addition to female parental care is selected for because it increases the female's reproductive success either directly or indirectly. This increase in reproductive success can look very different depending on the taxa exhibiting the behavior, some forms include pre-mating behaviors, while in other taxa it may include post-mating behaviors, or both. In taxa that have a nest some male partners exhibit nest guarding behaviors (Tallamy, 2000), defense of offspring (Tallamy, 2000; Requena and Machado, 2014) or the ability to provision resources for offspring (Requena and Machado, 2014).

We see in most cases of paternal care that it is being selected for by females and that finding mates and successfully mating encourages males to give care to their offspring. By exhibiting certain behaviors males can show females that they are in high condition, which conveys to the female that they will be able to care for offspring (Alonzo, 2012). Females display their preference for males with better condition and for those that will care for offspring when they choose a mate, and therefore, males that display parental like behaviors will be preferred by females and have a higher chance of mating and increasing their fitness (Alonzo, 2012). In addition to female choice on male behavior, males sometimes evolve certain features that can either increase or decrease their likelihood of investing in parental care. The phenotype of individuals can vary, inducing changes in the male that correlate with paternal care, which a female can then select for (Alonzo, 2012). Inversely, the phenotype of a male can also select against paternal care, showing that a male is not fit to give care and will, therefore, not provide for their offspring (Duckworth et. al., 2003). In general parental care is rare across taxa, mainly because it is costly to parents, there is a low life expectancy for many of offspring, and offspring have a chance of maturing early, so there is no reason for parental care in the first place (Doody et al., 2009). When parental care is present, as we know, maternal care is much more prevalent than paternal care, or even paternal care in addition to maternal care. But, as more studies are done into parental care and the male sex as parents, more evidence of paternal care is being found. Since females invest more in their reproductive efforts and males were previously expected to be present to just reproduce and move on to reproduce more, there was no reason for them to provide care. Now, we know females have a preference of males who do provide care, so we see an increase in males exhibiting behaviors that show they are in a good condition to provide the care the female wants to copulate with her. Looking at several different taxa that exhibit paternal care allows for more understanding as to why paternal care has been selected for over maternal care or in addition to maternal care and how it benefits the overall fitness of a given species.

Mammals:

In mammals, we always see parental care in the form of care coming from the mother since lactation is necessary for survival for the early stages of life. An offspring of a mammal tends to stay with their mother until they have received enough resources to be strong enough to be on their own. In many mammalian cases of paternal care, it is assumed that care coming from the male sex evolved because it was critical for offspring survival (Gubernick and Teferi, 2000). Furthermore, biparental care in mammalian species is particularly common among species that demonstrate socially monogamous mating systems (Stockley and Hobson, 2016). In cases looking at California mice and a broad overview of mammal species, the relationships between paternal care, litter size, and offspring survival were investigated. In the monogamous mammal, the biparental California mouse, evidence indicates that paternal behaviors enhance offspring survival; when males are removed it results in lower offspring survival in the father-absent groups compared to father-present groups (Gubernick and Teferi, 2000). Within this species males are seen to provide extensive care to their offspring, both in the field and in the laboratory, and when in the field males spend between 65 to 85% of time in the nest with their young (Gubernick and Teferi, 2000). Except for lactation, males exhibit all the same behaviors the mothers display and to the same extent. When males were taken away from their female partners, new males took up residence with widowed females, but this was usually after lactation was finished. This suggests that the importance of the father being present and providing care is not primarily for the protection against predators, but instead for direct care for their young (Gubernick and Teferi, 2000).

The evolution of paternal care in mammals has also been seen to influence the increase in litter size, as with additional parental care, more offspring are able to be supported. By looking at 427 mammalian species, 119 of those were classified to exhibit paternal care (Stockley and Hobson, 2016). When looking at the data from these species' information based on average litter size, offspring number per teat, neonate mass, weaning mass, inter-litter interval, and number of litters per year were all used to investigate the relationship between paternal care and offspring production (Stockley and Hobson, 2016). There was no evidence found that paternal care has evolved in response to the benefits of supporting females to rear more costly, larger litters or larger offspring. However, evidence suggests the increase in offspring production is likely to follow the evolution of paternal care, especially where males provide direct benefits to offspring (Stockley and Hobson, 2016). Here, the production of larger litters seems to be an evolutionary response to paternal care, rather than a stimulus for paternal care. Overall, it is expected that paternal care plays an important role in stabilizing monogamous mating systems, ultimately promoting complex social and parental behaviors (Stockley and Hobson, 2016).

Birds:

The avian taxon provides some of the best evidence for paternal care, as most species provide biparental care for early stages of their offspring's life. Certainty of paternity plays a major factor into whether a male bird will invest in parental care, playing a role in different offspring life stages (Moller and Birkhead, 1993). Males should provide care to their own offspring, while also attempting to increase their reproductive success by engaging in additional copulations with other females, besides their social partners. Therefore, males should invest in guarding their paternity to increase their certainty of paternity in their own nests and that they are only feeding their offspring, not other males' (Moller and Birkhead, 1993). To determine if there was a relationship between parental care and certainty of paternity, 52 bird species and data on their paternal care and extra-pair paternity were looked at. Here, paternal care is related to the level of male contribution to nest building, courtship feeding, incubation, and feeding of the offspring (Moller and Birkhead, 1993). Males did not provide less parental care during the stages of nest building, courtship feeding, or incubation when the frequency of extra-pair paternity was high. Nevertheless, male engagement in feeding of offspring was significantly negatively related to the frequency of extra-pair paternity (Moller and Birkhead, 1993). The differences in these contributions at different reproductive stages might be explained by the fact that feeding of offspring is energetically the most expensive mode of parental care, so paternal care during provisioning behaviors is likely to be costly to the fitness (Moller and Birkhead, 1993). These variations in behaviors by male birds during different stages suggest the extent of paternal care has been affected by certainty of paternity, while also sex roles during the costliest part of reproduction, offspring provisioning, have been shaped by sperm competition (Moller and Birkhead, 1993).

Variation is common when it comes to paternal care and in other species of bird variation in their plumage determines if they will or will not provide parental care to offspring. We also know that selection should favor variation in reproductive tactics when the combination of different sexual traits and reproductive behaviors that reach the highest fitness differs within males in a population (Duckworth et al., 2003). In a Montana population of house finches, males display a continuous variation in parental tactics: males that exhibited more elaborate (defined as redder) plumage color provided little to no parental care compared to less elaborate (defined as duller) plumage color males. Elevation of prolactin, a pituitary hormone, was closely associated with parental care (Duckworth et al., 2003). Additionally, males who presented a redder plumage color had low prolactin levels, whereas duller plumaged males had high levels of prolactin. These differences in prolactin levels and plumage colors are just a correlation and prolactin levels are not labeled as the cause of variation. The males who exhibited duller plumage also tended to provision for offspring two more times than those who had redder plumage (Duckworth et al., 2003). Here the relationship between variation in plumage and provisioning levels suggests a tactic to avoid the costs associated with parental care. Additionally, duller males previously had higher success in pairing compared to redder males, suggesting that the relationship between plumage color and parental care could reflect the individual optimized parental tactics, not just population (Duckworth et al., 2003). Ultimately, due to most birds providing some form of paternal care, there are high variations in the form of male care that is given, allowing for further expansion and research into what lead to the evolution and later fitness benefits of these systems of care.

Herps:

Similar to what is seen in birds, frogs can also use their genetic composition to display how fit they are to provide care for offspring. Male secondary sexual traits can potentially be used as indicators of direct or indirect fitness benefit to their female counterparts. Direct benefits, for example different paternal care behaviors, are especially important to species that exhibit biparental care (Pettitt, et. al., 2020). Within the golden rocket frog, a species that exhibits biparental care, predictions were tested to explain the evolutionary relationship between male secondary sexual traits and paternal care quality. To determine how these secondary sexual traits affected paternal care, offspring survival influenced by paternal care, relationships between male call and different forms of care, and female preference based on different aspects of male call were measured (Pettitt et al., 2020). It was revealed that when males were removed from their brood's, offspring survival was negatively impacted, indicating that paternal care positively impacts offspring survival. Males that produce longer calls provide higher quality paternal care, in the form of more egg attendance and territory defense, with females preferring these males (Pettitt et al., 2020). Females can gain direct benefits from selecting a mate with good parental qualities based on traits that honestly reveal paternal care quality, rather than males who send false signals (Pettitt et al., 2020). This suggests that males who have better advertisement calls will provide better paternal care behaviors, allowing females to select them based on their display of the given behavior knowing this behavior will directly benefit both of their reproductive fitness.

Costs and benefits are an important factor of deciding if parental care is worth it for an individual. Giant bullfrogs are a good example of a species where the benefits barely outweigh the costs but make it worth it for the male sex to provide care to offspring. Male giant bullfrogs exhibit parental care behaviors through the construction of channels that guide tadpoles to larger bodies of water (Cook et al., 2001). These channels, some exceeding up to 15m in length, allow cooler water to become available to broods living in rapidly drying puddles that can frequently reach critically high temperatures. Eggs of the giant bullfrog that experience temperatures above

38°C died, while the tadpoles present in these high temperatures, and temperatures even higher, were able to survive. Additionally, male bullfrogs actively defend their offspring from predators, which at times, results in the individual being killed while performing this defensive behavior (Cook et al., 2001). However, the survival of eggs and larvae in territorial broods was almost twice as high as non-territorial broods, showing that the large cost of paternal care is offset by even stronger fitness gains. In this biparental species, it is suggested that channel construction and predator defense, both important for tadpole survival, are most efficiently accomplished by larger bodies, which explains why males, rather than their smaller female counterparts perform parental care (Cook et al., 2001). In general, we see paternal care is more likely in frogs, compared to other invertebrates, since paternal care costs are usually low, even if costs are present, as in the giant bullfrog, the benefits highly outweigh the costs, an important factor when determining if parental care will be present.

Invertebrates:

Within arthropods, exclusive postzygotic paternal care is uncommon and both internal fertilization and anisogamy are believed to delay the evolution of this form of parental care by reducing certainty of paternity and increasing male promiscuity (Tallamy, 2000). Evidence has found that these two factors elevate the costs of paternal care over the benefits from offspring survival (Tallamy, 2000). In addition, internal fertilization, the main mechanism arthropods reproduce, discourages paternal care because it typically reduces certainty of paternity and creates a physical disconnect between the male and the eggs he fathered when they are laid. However, exclusive paternal care has evolved in at least eight independent arthropod lineages (Tallamy, 2000). It is believed that exclusive paternal care in arthropods has arisen more as a sexually selected trait for attracting mates compared to a naturally selected mechanism for offspring survival. Further, it was found that male behaviors that enhance female reproductive success either directly by allowing females to not incur parental costs or indirectly by females selecting mates with better genes are traits that sexual selection has acted on, supporting previous hypotheses (Tallamy, 2000). With this, males that are willing to guard young become preferred mates for females who need their eggs to be fertilized. Females also use nest construction or egg guarding behaviors as honest signals for paternal intent and quality when selecting a mate (Tallamy, 2000). The traits that male arthropods exhibit have been acted on by sexual selection as a way of attracting mates, where increased offspring survival comes with the behaviors performed by males.

In another species of arthropod, a Neotropical harvestman, the benefits of nest-related behaviors far outweigh the costs, influencing the male sex to engage in parental behaviors more willingly. Nest-related behaviors have the potential to benefit males by increasing offspring survival and increase their attractiveness to females, but have the costs of limiting males' foraging activity, increase metabolic expenses, and expose them to increased mortality during nest attendance (Requena and Machado, 2014). The females lay eggs solely in nests that have been built, repaired, cleaned, and defended by males, and they may remain there for up to five months. Body conditions of nesting and non-nesting males were taken to determine their survival rates and despite long nest attendance periods, nesting males had good body conditions and had higher survival rates than non-nesting males and females (Requena and Machado, 2014). There is a high supply of food in tropical rainforests that can provide males with frequent access to food within the vicinity to their nests, which can reduce or even eliminate the costs associated with limited foraging opportunities. In addition, predation rates seemed to be directed mostly at roaming individuals, meaning the more they move, the more likely they are to be targeted by predators, which is also reduced by having a stagnant nest (Requena and Machado, 2014). Altogether, nest and offspring defense mechanisms provide many benefits, seeming to impose no costs to males, which influences them to partake in parental care behaviors (Requena and Machado, 2014). Although nest-related behaviors and general reasons behind paternal care are poorly explored in arthropods, further research has started to explain the evolutionary steps that have been taken in forming biparental care and exclusive paternal care across various arthropod species.

Conclusions:

These different models of both exclusive paternal care and paternal care in a biparental care system across distinct taxa exhibit the main causes and pathways of the evolution and the fitness benefits of male parental care. Parental care will be selected for in circumstances where the benefits outweigh the costs, at times males can be larger than females, so even if costs are present, the benefits still outweigh the costs. Larger bodies tend to be more beneficial when it comes to predator defense, seen in the giant bullfrog. Territorial males who actively defend their offspring from predators have higher survival rates for larvae and tadpoles compared to male who do not defend, however, these males' risk being killed in combat (Cook et al., 2001). Despite this risk, the benefit of increasing the survival rate of offspring and in turn increasing their own fitness outweighs the risk of death. Males are more likely to provide care when there is certainty of paternity, a cost is present when males expend energy caring for offspring that are not their own. When a male is certain that the offspring in their nest are their own, they are more likely to provide care. In birds, males give care during reproductive stages prior to birth despite the chance of their social partner engaging in extra-pair paternity. Feeding of offspring is the most energetically costly form of parental care, so males will not invest energy into feeding offspring that are not their own since it will decrease their fitness (Moller and Birkhead, 1993). Female choice is a main contributor in the mechanisms of the evolutionary pathway of paternal care, females tend to choose mates that exhibit traits or behaviors that show they will be good parents or provide care to offspring (Alonzo, 2012). Males will display secondary sexual traits which can further explain other related parental traits of a male to a female. In some birds, their variations in plumage can help determine what levels of parental care the individual will provide. These traits are displayed to females, which can help a female determine which males they want to mate with (Duckworth et al., 2003). Additionally, male frogs who have longer calls are preferred by females over males with shorter calls. These males are in higher fitness and are therefore able to provide higher levels of parental care (Requena and Machado, 2014). When males send honest signals it benefits both themselves and the females, allowing the male to provide adequate parental care, directly benefiting the female, increasing the reproductive fitness of both the male and the female. All these pathways that lead to the evolution of paternal care across different taxa increase the reproductive fitness of both the female and the male, a main factor in selecting for paternal care. When costs are taken away from females and put onto a male, who can incur more costs, a female is able to put more effort into her offspring or reproduce more efficiently. When a male defends his offspring from predators and increases the survival of those offspring, his genes have a higher chance of being passed through the population, increasing his fitness. Overall, we see in all these cases pathways leading to increased fitness of both males and females, which results in paternal care being selected for.

We see a multitude of different pathways that paternal care has evolved in different species, but we see a trend in the result across taxa, care only comes about when benefits outweigh the costs and when fitness is increased by performing the parental behaviors. It was previously believed that females were the only sex that invested in parental care, but we see that males also tend to invest in these behaviors for the aspect of attaining a mate. We also know that sexual selection acts largely on traits for parental care from males. The question of if natural selection plays a factor in selecting for parental care behaviors in males remains unanswered and needs more research done to determine its role. Questions remain unanswered on species who exhibit paternal care, such as the origin and mechanisms of why this form of care has arisen and what its benefits are, more research is needed for questions to be answered.

References

Alonzo, S. H. (2012). Sexual selection favours male parental care, when females can choose. The Royal Publishing Society, 279:1784-1790.

Cook, C. L., J. W. Ferguson, and S. R. Telford. (2001). Adaptive male parental care in the giant bullfrog, Pyxicephalus Adspersus. Journal of Herpetology, 35:310–315.

Doody, J. S., Freedberg, S., Keogh, J. S. (2009). Communal egg-laying in reptiles and amphibians: evolutionary patterns and hypotheses. The Quarterly Review of Biology, 84(3): 229-252.

Duckworth, R. A., A. V. Badyaev, and A. F. Parlow. (2003). Elaborately ornamented males avoid costly parental care in the house finch (carpodacus mexicanus): A proximate perspective. Behavioral Ecology and Sociobiology, 55:176–183.

Gubernick, D. J., and T. Teferi. (2000). Adaptive significance of male parental care in a monogamous mammal. Proceedings of the Royal Society of London. Series B: Biological Sciences, 267:147–150.

Kempenaers, B., Sheldon, B. C. (1997). Studying paternity and paternal care: pitfalls and problems. Animal Behavior, 53: 423-427
Klug, H., and M. B. Bonsall. (2014). What are the benefits of parental care? the importance of parental effects on developmental rate. Ecology and Evolution 4:2330–2351.
Klug, H. Bonsall, M. B., Alonzo, S. H. (2013). Sex differences in life history drive evolutionary transitions among maternal, paternal, and bi-parental care. Ecology and Evolution, 3(4): 792-806
Møller, A. P., and T. R. Birkhead. (1993). Certainty of paternity covaries with paternal care in birds. Behavioral Ecology and Sociobiology, 33:261–268.
Moller, A. P., and J. J. Cuervo. (2000). The evolution of paternity and paternal care in birds. Behavioral Ecology, 11:472–485.
Pettitt, B. A., G. R. Bourne, and M. A. Bee. (2019). Females prefer the calls of better fathers in a Neotropical frog with biparental care. Behavioral Ecology, 31:152–163.
Requena, G. S., and G. Machado. (2014). Lack of costs associated with nest-related behaviors in an arachnid with exclusive paternal care. Oikos, 124:372–380.
Smiseth, P. T. 2021, December 13. Evolution of parental care. https://www.oxfordbibliographies.com/display/document/obo-9780199941728/obo-9780199941728-0014.xml.
Stockley, P., and L. Hobson. (2016). Paternal care and litter size coevolution in mammals. Proceedings of the Royal Society B: Biological Sciences, 283:20160140.
Tallamy, D. W. (2000). Sexual selection and the evolution of exclusive paternal care in arthropods. Animal Behaviour, 60:559–567.
Zeh, D. W., Smith, R. L. (1985). Parental investment by terrestrial arthropods. American Zoologists, 25(3): 785-805.