How competing trade-offs affect parental care

David Cohen
Department of Biology
Lake Forest College
Lake Forest, Illinois 60045

Abstract

Past and current research have revealed that parental care is rare among species. In this review article, I am going to analyze the reasons that parental care might be rare among most species, and then dive into the evolutionary processes that allowed a certain subset of species to develop some mode of parental care. Parental care can come in many forms, whether it is only maternal care or only paternal care, or both, as in biparental care. The purpose of this review is not going to be differentiating between the different modes of parental care, rather, it is going to be looking at how species are able to afford parental care altogether as it is supposedly rare. Initially, I will be providing reasons as to why many species do not provide parental care due to the parents' associated costs, such as reduced future reproduction or the amount of energy that is required, lowering parents' fitness. I will then use many different species to analyze why parental care might have evolved or changed overtime, such as from no care to uniparental care (male or female only) or uniparental care to biparental care. It was revealed that there are many trade-offs that present themselves when it comes to parental care, which was one barrier species had to deal with or overcome for parental care to be worthwhile. This review looks at similar patterns that were seen in different species to try to trace factors that led to the emergence of parental care, even with the costs involved. Overall, it was the fact that the benefits to the offspring, increasing parents' lifetime fitness, must outweigh the costs to the parents for parental care to evolve and be consistent in species.

Introduction

In the study of life-history evolution, parental care is one of the topics that is researched the most (Klug and Bonsall, 2007). Parental care consists of acts or motivation provided by the parent to increase offspring survival or fitness. There are many different forms of parental care that can either directly benefit the offspring or indirectly provide benefits. Even though the main purpose of parental care is to increase offspring survival, the true reason parental care evolved is to increase the parents' life-time fitness (Sheldon et al., 1997). By increasing the chance that their offspring survives to adulthood, parents are ensuring that the energy they expended on their offspring is paying off as their genes will be passed onto future generations. On the flip side, parental care is rare in most species. With most good things in life, there is an associated cost, and the same is true with parental care. By parents providing care to their offspring, they are also hurting themselves by having lower survival rates and less future reproduction (Reguera and Gomendio, 1999). Parental survival rates are low due to an increasing predation rate to parents who care for their young (Reguera and Gomendio, 1999). Additionally, by parents investing more into their current offspring, it reduces their ability to either find additional mates to reproduce again, or continue to mate with their current partner, as most of their energy is being spent on their current young (Reguera and Gomendio, 1999).

Even though parental care might be rare due to the associated costs, many species still find it beneficial. In some species, such as reptiles, when mothers abandon their eggs there is very low hatching success and survival rates of the offspring (Huang, 2006). However, when mothers remain present with their eggs and provide a form of parental care, the rate of survival and hatching success increases dramatically (Huang, 2006). Aside from the benefits that the offspring receive, mother survival rates decrease, as they are more prone to attacking predators in hopes of protecting their young (Huang, 2006). This is just one example which demonstrates that mothers make the decision to protect their young, reducing their current fitness, but promoting offspring survival, increasing life-time fitness (Huang, 2006). The trade-off now presents itself; benefiting offspring, promoting better life-time fitness, must outweigh the associated costs to the parent. This trade-off was demonstrated in the example with the reptiles; however, it is seen in every case in which parental care is exhibited. Williams' Principle (Figure 1) explains the tradeoff: investment into the present comes at a cost to investment to the future (Gross, 2005). The trade-off can also be seen when parental care is not displayed, as parents find that it is not more beneficial to provide care to their offspring based on the costs that would be involved (Jockusch and Mahoney, 1997). In instances where species can continually reproduce and continually lay eggs, they find that the benefits of caring for their offspring do not outweigh the associated costs (Jockusch and Mahoney, 1997). The mothers know that not all their offspring are going to survive, so instead of trying to protect them, the mother's find it more energetically favorable to continue to produce more offspring, with the hope that at least some will survive until reproductive maturity (Jockusch and Mahoney, 1997). By producing more offspring, that is the mechanism that the parents use to increase their life-time fitness, in those species.

There are multiple factors that affect parental care and lead to its presence; ecological and environmental factors consisting of two of them (Zeh and Smith, 1985). Where there are harsh or dangerous environments, or when parents must provide highly prized resources, the appearance of parental care is increased (Zeh and Smith, 1985). The environment has an effect because parents find that it is necessary to protect their young from both biotic hazards and predation (Zeh and Smith, 1985). Regarding highly prized resources, parents are providing their young with these sought-after resources, and not utilizing them themselves, so by providing care to their offspring, they are ensuring that the resources do not go to waste (Zeh and Smith, 1985). Another factor, such as certainty of offspring relatedness, increases parental care because parents know that by providing care to the offspring, it is directly increasing their fitness by passing on genes known to be their own (Sutton and Wilson, 2019). Since parental care is seen in some species and not others, it demonstrates that parental care is not a necessity for species success. This is shown by the fact that different species have different mechanisms for increasing their life-time success and overtime, both species that have parental care and do not have parental care have survived, adapted, and evolved.

Non-Caring species

Many species find that benefits the parents would receive for providing care to their young would not outweigh the associated costs, thus parental care remains absent. Salamanders are one species, in particular, where parental care is absent due to the presence of communal oviposition (Jockusch and Mahoney, 1997). Communal oviposition is when mothers lay eggs together with other conspecific eggs in the same nest; a lot of time this is accompanied with clutch abandonment (Jockusch and Mahoney, 1997). The study by Jockusch and Mahoney (1997) looked at different species among the genus, *Batrachoseps*, and observed the oviposition sites to try to determine if parental care was absent or not. They found that in most cases they did not find adult salamanders present at the clutch sites, and even when they did find adults present, brooding was never seen (Jockusch and Mahoney, 1997). In combination with the lack of parental care, the study pointed to the fact that communal oviposition sites were more common (Jockusch and Mahoney, 1997). This might point to the fact that mothers felt that by laying eggs where others are already present, protection might be accomplished by other individuals (Jockusch and Mahoney, 1997). By not spending energy protecting their eggs, the mothers are now able to find additional mates and lay more eggs to help increase their life-time fitness.

Another example in which parental care is lacking is the Eurasian penduline tit, where offspring desertion is prone (Pogany et al., 2008). Desertion is beneficial to the parent as it improves the chances of future reproduction, while there is a large cost if the parent decides to stay and provide care (Pogany et al., 2008). In most instances, desertion is seen by one parent, while the mate is left to care for the offspring. However, in the Eurasian penduline tit, biparental desertion is often seen (Pogany et al., 2008). It is believed that intense sexual conflict leads to this phenomenon, as both mates want to increase their fitness by having improved future reproductive success (Pogany et al., 2008). Even though the biparental desertion leads to increased future success of both parents, the offspring typically perish without any form of parental care (Pogany et al., 2008). The examples of the salamanders and the Eurasian penduline tit are not exhaustive, however, they provide insight as to why some species prefer to avoid caring for their young. Additionally, in both examples, the main purpose of not providing care is to increase the individual parents' life-time

fitness with improved future reproduction, aiding the fact that parental care is typically rare in most species.

Species that provide parental care

Even though it has been discussed that parental care is rare, there are many instances where parental care is established, and with varying degrees. Parental care stems from the idea of parents investing in their current offspring, creating more fit offspring, which then increases those parents' life-time fitness. One direct form of parental care is protection from predators, which is observed in some reptiles such as the long-tailed skink (Huang, 2006). In a study by Huang (2006) there was evidence which proved that when maternal care is absent, predation on clutches is increased, compared to when maternal care is present. This discovery led to the belief that maternal care evolved to protect their eggs and offspring from predation (Huang, 2006). Additionally, when maternal care is present, offspring survival is increased, but maternal survival is decreased as mothers are more willing to attack predators, especially when clutch sizes are large (Huang, 2006). Larger clutch sizes increase the mother's willingness to attack, due to the idea that if the mother doesn't survive to continue to protect her clutch, there is a better chance some of her offspring will survive to reproductive maturity (Huang, 2006).

Another form of parental care is seen in the pine engraver beetles, where paternal care is witnessed early on in offspring development, but then disappears as males leave their mates (Robertson and Roitberg, 1998). Evidence shows that paternal care might have evolved as male care and male reproductive success are positively correlated (Robertson and Roitberg, 1998). Paternal care in the pine engraver beetles is shown by males assisting their mates in forming nests to lay eggs as well as protecting mates during oviposition (Robertson and Roitberg, 1998). Even though male care is seen early in the pine engraver beetle, male care is abandoned as males find it more beneficial to find additional mates to reproduce with to increase their individual fitness (Robertson and Roitberg, 1998). As mentioned, parental care is rare, but the presence of monogamous species is even more rare, which is a relationship between an adult male and female for reproductive purposes. In a species of birds, the northern flicker, monogamy is present and with that, biparental care is seen (Wiebe and Elchuk, 2003). Since monogamy is present in this species of birds, they find that it is more beneficial to continue to reproduce with the same mate, rather than search for additional partners (Wiebe and Elchuk, 2003). Since the monogamous pair continues to mate with each other, it is determined that providing care to their offspring is the best way they can increase their life-time fitness (Wiebe and Elchuk, 2003). In the northern flicker, different forms of parental care are seen for both the male and female, nonetheless, the energetic contributions are the same (Wiebe and Elchuk, 2003). The forms of care seen in the northern flicker are provisioning, foraging, and time in nest for protection (Wiebe and Elchuk, 2003).

In some unique instances of species providing care, filial cannibalism is present, which is the consumption of one's own offspring (Klug and Bonsall, 2007). There is increasing evidence which shows that filial cannibalism has co-evolved alongside parental care, due to trade-offs of current and future reproductive success (Klug and Bonsall, 2007). The evidence points to the idea that filial cannibalism emerges from energetic requirements which are obtained by parents from consuming their offspring, which is then re-invested into future reproduction (Klug and Bonsall, 2007). Parents can decide to consume only the 'weak' offspring, which can contribute to current reproductive success, as only the 'best' most fit offspring will survive to reproductive maturity (Klug and Bonsall, 2007). Or parents can decide to consume all their offspring and invest all the energy and nutrients that was obtained into future reproduction (Klug and Bonsall, 2007). In terms of parental care, filial cannibalism is rare, however, it demonstrates an avenue caring parents can take to increase their future reproductive success while, in some instances, still providing care to their current offspring. As described, parental care is shown in a multitude of ways either stemming from maternal care, paternal care, or biparental care, all nevertheless, for the sole purpose of increasing parents' individual life-time fitness.

Why parental care might have evolved overtime

There are numerous factors which have led to the investment of parental care in species overtime. One factor in particular that led to the evolution of parental care is certainty of offspring relatedness (Sheldon et al., 1997). In another species of birds, the collared flycatcher, the level of care shown by males is directly related to the level of certainty of relatedness to his offspring (Sheldon et al., 1997). Evidence showed that when females were absent from males during insemination periods, the male was not certain that the offspring were related to him, as the females could have been inseminated by additional males (Sheldon et al., 1997). This led to the presence of paternal care being lower, compared to instances where the males were not absent from the females from the time of insemination to the time of egg laying (Sheldon et al., 1997). When males, in particular, know that the offspring is related to them, they are more willing to provide care because they know that by increasing the fitness of the offspring, it is directly increasing the fitness of themselves (Sheldon et al., 1997).

Another example of offspring relatedness is shown in the male-care dominated bony fish species (Sutton and Wilson, 2019). In these species external fertilization is common, which is when mothers spawn their eggs over an area and then males fertilize the eggs with their sperm (Sutton and Wilson, 2019). As males are visibly able to witness their sperm fertilize the female eggs, they are ensuring their relatedness to the offspring which induces the presence of male care (Sutton and Wilson, 2019). Aside from knowing that the offspring are related to the parents, another factor which leads to increased parental care is the quality of the parents (Klug et al., 2013). When parents are not of great quality or fitness, they find that it is in their best interest to provide care to the offspring they currently have, rather than attempt to find additional mates (Klug et al., 2013). When parents know that they might die soon, either of old age or of a disease/illness, rates of parental care are elevated because it is their last stich effort to increase their overall life-time fitness by promoting the most fit offspring (Klug et al., 2013). Another underlying factor which increases parental care is the initial investment made by the parents (Klug et al., 2013). When parents invest a lot early on in offspring development, parental care is high as the parents don't want their energy or resources to go to waste (Klug et al., 2013). When females make a large contribution regarding egg formation, it reduces their ability to reproduce in the future and thus promotes more maternal care (Klug et al., 2013). Maternal care is also shown to be elevated in some species because of anisogamy, as females must make a greater contribution to the zygote relative to males (Klug et al., 2013). Additionally, when parents notice that their offspring are not able to strive without parental care, it might create a situation for parental care to evolve. Such a case was seen with salamander species, as parental care lacks in most instances, however, researchers found evidence that different species of salamanders exhibited parental care as it led to decreased rate of fungal infection, decreased predation rate, and decreased desiccation of the offspring (Jockusch and Mahoney, 1997). Furthermore, parental care comes with both benefits and costs, so it is up to the individual species to weigh both aspects against each other, to determine what mechanisms will increase their life-time fitness most effectively.

Evolutionary Historical Approach

Lastly, we looked at if parental care has been increasing or decreasing overtime by studying phylogenetics of taxa where parental care has evolved. Ray-finned fishes are a model species for this approach as it exhibits varying degrees of parental care due to under-lying factors such as fertilization method (Mank et al., 2005). A major factor that the study by Mank et al. (2005) revealed is that parental care evolved in different forms repeatedly and independently over time. The study revealed that mode of fertilization, whether it be internal or external, was the main driver of appearance of male-only care or female-only care (Mank et al., 2005). When internal fertilization was selected for, female-only care was observed, while when external fertilization was selected, male-only care was present (Mank et al., 2005). In combination with the mode of fertilization, sexual selection was observed to further drive evolutionary changes (Mank et al., 2005). The phylogenetic data did not answer the question if parental care has increased or decreased overtime, rather it was used to explain that parental care involves independently over time based on fertilization patterns (Mank et al., 2005).

An additional study where phylogenetic data was used to trace the origins of parental care used insects as their model species (Wong et al., 2013). This study determined that there are a few hypotheses that might explain how parental care evolved over time; the major one being iteroparous species evolving from semelparous ancestors (Wong et al., 2013). What this means is that species that reproduce more than once in their lifetime evolved from ancestors that only reproduce once, creating the need for parental care (Wong et al., 2013). Another one of the hypotheses

was that species that only reproduce once in their lifetime was a cost of parental care (Wong et al., 2013). This hypothesis explains that different lineages could have evolved, one in which care was seen in species that reproduce more than once in their life, and another lineage where care is not seen and the species only reproduces once in their lifetime (Wong et al., 2013). This study of insects is useful in trying to use species history to trace what lead to parental care, however, it did not provide conclusive evidence, rather it proposed theories. All in all, the use of phylogenetic data is useful in tracing patterns that lead to the emergence and disappearance of parental care, although more research needs to be accomplished in this field to determine if parental care is increasing or decreasing or is just an independent mechanism.

Conclusion

All in all, based on current research regarding parental care within species, a trade-off is the main mechanism that either induces parental care or explains its lack thereof. As Williams' Principle (Figure 1) describes, there is an inverse relationship between investment to the present and investment to the future (Gross, 2005). In other terms, if a parent decides to invest in their current offspring, their ability to invest in future offspring will be reduced. There are numerous mechanisms that have been discussed which contribute to some species providing care while others do not. Species that provide some level of parental care, regardless if it is maternal, paternal, or biparental, have decided at some point that taking care of their current offspring is more beneficial to their overall lifetime fitness than the associated costs, such as reduced future reproductive success and reduced survival (Reguera and Gomendio, 1999). There are many ways parents can provide care, whether it be territory defense, nest building, incubation of eggs, provisioning, protection from predators, and learning/teaching, and depending on the species, the level of care will vary (Silver et al., 1985). On the other hand, species that do not provide any level of care have determined that the benefits they would receive for caring for their current offspring do not outweigh the associated costs. Typical in these species is the ability to continually reproduce, as they know that most of their offspring will not survive due to the lack of parental care, so by reproducing more and creating more offspring, it is increasing the parents' overall fitness as at least some of their offspring will survive to reproductive maturity (Nager et al., 2000). Additionally, due to the increased energy expenditure of providing care, parental care is rare in most species.

Lastly, reflecting on the current information that is available in respect of parental care, there is not one answer to the question: is parental care a requirement for species success. Different species have different mechanisms when it comes to reproduction, which is a major determinant regarding if parental care is helpful or not. Some species have evolved to provide parental care while some species have evolved the lack of parental care, with both avenues creating increased parental life-time success. Overall, the only question that is unresolved is if parental care has increased or decreased overtime in species, or if care's appearance or disappearance is its own independent event.

References

Gross, M. R. (2005). The evolution of parental care. The Quarterly Review of Biology, 80(1): 37-46.

Huang, W. (2006). Parental care in the long-tailed skink, Mabuya longicaudata, on a tropical Asian island. Animal Behavior, 72(4): 791-795.

Jockusch, E. L., and Mahoney, M. J. (1997). Communal oviposition and lack of parental care in Batra hoseps nigriventris (Caudata: Plethodontidae) with a discussion of the evolution of breeding behavior in Plethodontid Salamanders. Copeia, 1997(4): 697-705.

Klug, H., and Bonsall, M. B. (2007). When to care for, abandon, or eat your offspring: the evolution of parental care and filial cannibalism. The American Naturalist, 170(6): 886-901.

Klug, H. Bonsall, M. B., and 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.

Mank, J. E., Promislow, D. E. L., and Avise, J. C. (2005). Phylogenetic perspective in the evolution of parental care in ray-finned fishes. Evolution, 59(7): 1570-1578.

Nager, R. G., Monaghan, P., and Houston, D. C. (2000). Within-clutch trade-offs between the number and quality of eggs: experimental manipulations in gulls. Ecological Society of America, 81(5): 1339-1350.

Pogany, A., Szentirmai, I., Komdeur, J., and Szekely, T. (2008). Sexual conflict and consistency of offspring desertion in Eurasian penduline tit Remz pendulinus. BMC Evolutionary Biology, 8(242):

Reguera, P., and Gomendio, M. (1999). Predation costs associated with parental care in the golden egg bug Phyllomorpha laciniata (Heteroptera: Coreidae). Behavioral Ecology, 10(5): 541-544.

Robertson, I. C., and Roitberg, B. D. (1998). Duration of paternal care in pine engraver beetles: why do larger males care less? Behavioral Ecology and Sociobiology, 43: 379-386.

Sheldon, B. C., Rasanen, K., and Dias, P. C. (1997). Certainty of paternity and parental effort in the collard flycatcher. Behavioral Ecology, 8(4): 421-428.

Silver, R., Andrews, H., and Ball, G. F. (1985). Parental care in an ecological perspective: a quantitative analysis of Avian subfamilies. American Zoologist, 25(3): 823-840.

Sutton, F. B., and Wilson, A. B. (2019). Where are all the moms? External fertilization predicts the rise of male parental care in bony fishes. Evolution, 73(12): 2451-2460.

Wiebe, K. L., and Elchuk, C. L. (2003). Correlates of parental care in Northern Flickers Colantes auratus: do the sexes contribute equally while provisioning young? Ardea, 91(1): 91-101.

Wong, J. W. Y., Meunier, J., and Kolliker, M. (2013). The evolution of parental care in insects: the role of ecology, life history and the social environment. Ecological Entomology, 38: 123-137.

Zeh, D. W., and Smith, R. L. (1985). Parental investment by terrestrial arthropods. American Zoologists, 25(3): 785-805.

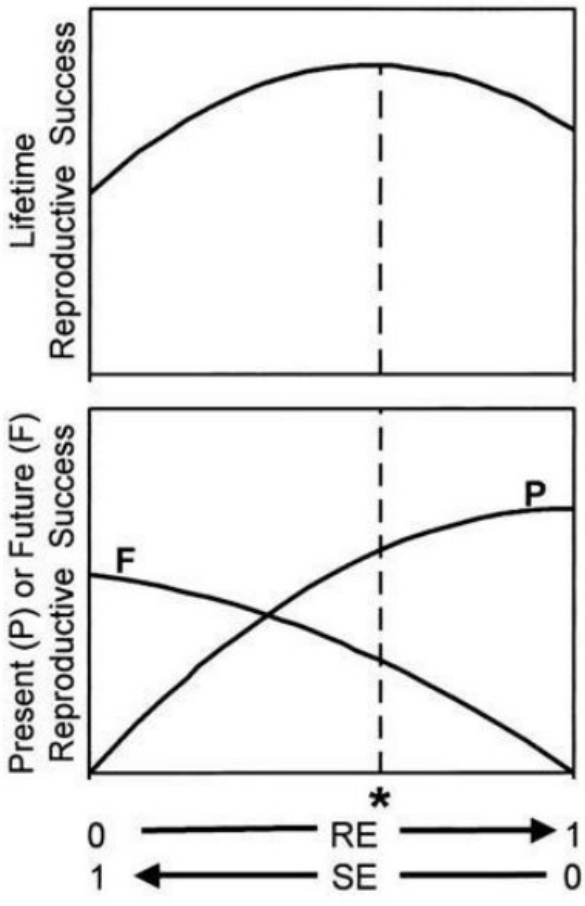

Figure 1: Williams' Principle. (Reproduced from Gross, 2005). This figure demonstrates how the investment to current offspring, increasing present reproductive success, has an inverse relationship with future reproductive success.