Abstract

Most species lack parental care and leave their offspring to fend for themselves after copulation. 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

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

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 benefting 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,

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