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Fitness Costs of Early Life Adversity in Non-Human Primates

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As arguably the most critical period of mammalian development, early life can be defined as the period from conception to reproductive maturity (Tung et al., 2016). The importance of adequate nutrition and proper maternal care for maximizing the survival and development of offspring has been demonstrated through research findings in various species (Lu et al., 2018). However, these ideal growth conditions are difficult to achieve for wild offspring, who often have to overcome various energetically or socially challenging conditions that limit their development in early life. This paper will focuses on the effect that environmental and social adversities have on the fitness of wild and captive non-human primates as measured by lifespan and reproductive success. Current research suggests that early life adversity in non-human primates reduces individual fitness by decreasing lifespan, fertility, and offspring survival. This paper explores and discusses the various factors that contribute to this fitness reduction. These factors include but are not limited to increased risk of physical illness and behavioral disorders, social isolation, maternal death, intergenerational effects, reduced female fertility, maternal stress, delayed sexual maturation, and lower adult body size.

Introduction

Early life adversity can affect important developmental outcomes, ranging from social behavior, gene regulation and expression, and cognition and neuroanatomically functions (French & Carp, 2016). Causes of early life adversity can be broadly classified into two categories: environmental (e.g., resource limitation, predation, disease, and natural disasters) and social (e.g., dominance rank, maternal affiliative social connectedness, maternal death, and sibling competition). The main mechanism through which early life adversity modifies an individual's development is through adaptive plasticity, defined as the ability of

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genetically similar individuals to develop potentially adaptive phenotypic differences in response to different early life experiences (Lu et al., 2018). Given the profound impact early life adversity has on offspring survival and development, it is important to understand the underlying developmental and evolutionary mechanisms behind adaptive plasticity.

There are two major competing views regarding the fitness cost-benefit analysis of early life adversity and adaptive plasticity: the developmental constraints hypothesis and the predictive adaptive response (PAR) hypothesis. The developmental constraints hypothesis states that offspring born in adverse early environments are at a fitness disadvantage relative to their conspecifics, regardless of adult environmental conditions (Lea et al., 2015). Under this hypothesis, short-term adaptive changes to adverse early life conditions come with long-term survival and reproductive costs. The PAR hypothesis, on the contrary, states that adverse early environments prompt adaptive phenotypic adjustments that prepare animals for similar challenges in adulthood (Lea et al. 2015). This suggests that early life adversity may bring fitness advantages to individuals by preparing them for an equally adverse adult environment. Current research in long-lived species, such as primates, appears to support the developmental constraint model where individuals raised in adverse conditions suffer lifelong fitness disadvantages compared to their conspecifics regardless of their adult environment. Offspring born and raised in adverse environments experience higher mortality rates and reduced ability to care for their own offspring (Zipple et al., 2019). The research data and results that support the developmental constraints hypothesis are discussed next.

Reduced Lifespan

An individual's lifespan can serve as a reliable indicator of their fitness. This is especially true in most primate species where there is little to no post-reproductive period. Tung et al. (2016) found there are strong correlations between an individual's age at death and total number of offspring who survived to at least age 1. Individuals with longer lifespans will have more opportunities to conceive and time to raise their offspring. In wild female baboons, those who experience three or more sources of early adversity die on average 10 years earlier than females who experience little to no adverse conditions (Tung et al., 2016). This is consistent regardless of the match between early life and adult environmental conditions. Their significantly shortened lifespan is likely caused by early life malnourishment and an accumulation of environmental aggravations that steadily weaken their physical conditions (Tung et al., 2016).

The detrimental effects accumulated through early life are seldom reversed in adulthood despite adequate resource availability (Lea et al., 2015). Offspring

raised in adverse conditions often have low-ranking mothers whose own physical condition is relatively poor (Zipple et al., 2020). There is little chance for the offspring to move up the social hierarchy, as their weakened condition significantly reduces their resource competition ability. In wild baboons, females who experience the most adversity are also more socially isolated as adults (Tung et al., 2016). Strong social bonds are a known factor associated with increased reproductive success and longevity in baboons (Silk et al., 2010). This suggests that reduced social bond strength experienced by high adversity females can have a negative impact on their physical health and their lifespan.

Higher Prevalence of Physical Illness and Behavioral Disorders

One of the more obvious ways in which early life adversity can reduce fitness is by increasing the offspring's susceptibility to both physical illnesses and behavioral disorders.

In experimental studies conducted by Conti et al. (2012), captive rhesus macaques raised by either humans or surrogate mothers (warm water bottles) have higher rates of developing physical illnesses than conspecifics raised by their biological mothers. Behavioral stereotypies, such as inappropriate vocalizations, are also more prevalent in these individuals (Conti et al., 2012). Nursery-reared macaques also demonstrate greater behavioral inhibition and abnormal social affective behavior compared to their mother-reared counterparts in adulthood (Corcoran et al., 2011). These behavioral deviations can be detrimental to their social relationships with other macaques as adults and lead to isolation. Since macaques are a very social species, this social isolation can lead to poor physical health, much like the effects seen in baboons (Corcoran et al., 2011). Social isolation can also heighten individual susceptibility to predation and reduce ability to obtain resources, both of which can significantly decrease the individual's lifespan and reproductive success (Tung et al., 2016).

Maternal Death

Most mammalian species rely on their mother for food, safety, and learning important survival skills during early life. It is predicted, then, that maternal death during this period would have a significant impact on offspring survival. Indeed, adult female baboons who lost their mothers prior to maturity were three times more likely to die than their conspecifics (Tung et al., 2016). Similar results have been found in multiple wild Old World and New World primate species (Zipple et al., 2020). However, offspring survival is reduced well

before the mother faces imminent death. This can be explained by the maternal conditions hypothesis, which states that mothers who are in poor physical conditions are more likely to die. Thus, imminent maternal death can serve as a proxy for poor maternal condition, which can then result in decreased ability to provide and care for offspring (Zipple et al., 2020). In addition, female offspring who experience early maternal death have reduced ability to produce and successfully rear their own offspring to maturity in adulthood (Zipple et al., 2020). These females likely have weakened physical conditions that make gestation and lactation highly taxing on their physical health as it severely interferes with their resource-gathering abilities. This suggests that early adversity experienced in the form of maternal death may have intergenerational effects.

Intergenerational Effects of Early Life Adversity

The intergenerational and long-term effects of early life adversity have been overlooked by previous literature for some time due to a lack of long-term data. As cumulative data becomes available in recent years, studies have revealed some striking finds regarding the intergenerational effects of early life adversity in wild baboons. Offspring who did not experience early adversity of their own but whose mother experienced early adversity exhibit a 48% higher mortality rate in the first four years of life than their unaffected conspecifics (Zipple et al., 2019). Females who experienced early adversity also demonstrated reduced ability to care for their own offspring near the end of life compared to their conspecifics. The reduction in offspring rearing ability could be the result of these females' own poor physical condition as a consequence of early adversity. It could also be due to a lack of offspring rearing skills, as they may have little opportunity to observe and practice these skills if their mothers died early. This is a classic example of the parental effect, where the environment experienced by an individual can affect their own phenotype and thus their offspring's phenotype (Zipple et al., 2019). This then forms a vicious cycle where one's present predicament as a result of early adversity causes one's offspring to suffer through the same. The exact mechanism for this intergenerational effect is still under investigation. Based on these findings, it is clear that early life adversity can bring long-term reductions on both the direct and the indirect fitness of offspring across generations.

Reduced Fertility in Wild Female Amboseli Baboons

Early life adversity can also have a direct impact on reproductive success by reducing fertility during extreme adverse conditions in adulthood. Long-term

field data from the Amboseli Baboon Research Project in Kenya indicates that females born in low-quality environments showed greater decrease in fertility during drought years than females born in high-quality environments. This reduction in fertility is associated with reduction in these females' fitness since they produce less offspring than conspecifics. This directly opposes the PAR hypothesis, since it is not the case that females whose early life conditions matched with adulthood conditions gain a fitness advantage. Instead, they are at a disadvantage during adverse conditions compared to conspecifics. Interestingly, females who are reared by high-ranking mothers during adverse environmental conditions did not experience this reduction in fertility. In fact, each improvement of one maternal rank position would increase resumption of cycling probability and conception probability during severe drought years by 1.8% and 1.3%, respectively (Lea et al., 2015). This suggests that adequate resource provisioning acquired through high maternal social status and support can buffer offspring against adverse natural conditions.

Reduced fertility may be an adaptive reproductive trade-off where females suspend reproduction in order to invest more attention and resources to their current offspring during adverse conditions. Yet, research data in savannah baboons suggests that this increase in maternal investment by low-ranking females did not increase offspring size or survival (Altmann & Alberts, 2005). Mothers who experienced early life adversity often have very limited resource access and poor physical conditions (Altmann & Alberts, 2005). These significant limitations to their ability for offspring care simply cannot be compensated through effort alone.

Maternal Stress

High-ranking female baboons and those with high affiliative social connectedness also experience lower maternal stress (Lea et al., 2015). This is likely due to the affiliative gestures such as reciprocal grooming and possible protection from predators and infanticide that one's social partners may provide. Glucocorticoids are a class of steroid hormones linked with various inflammatory and immune responses. The reduction in stress and relatively stable glucocorticoid levels has been linked with stronger immune defense and lower inflammatory response in baboons (Campos et al., 2021). Chronic stress and high glucocorticoid levels experienced by early adversity offspring are linked with significant reductions in lifespan by as much as 5.4 years (Campos et al., 2021). Offspring raised by mothers who are under chronic stress may be neglected and experience elevated stress levels as well, further perpetuating the cycle of affective instability. Studies that focus on neuroendocrinology involving glucocorticoids and gut

microbiome are underway to explore the epigenetic and other biological changes that can affect an individual's long-term health outcomes (Lu et al., 2018). They serve as practical measures of physical attributes that can give important insight into an individual's physical condition and well-being. Understanding these physical effects of early life adversity can provide clues to the biological mechanisms by which early life adversity predicts adult fitness.

Delayed Sexual Maturation and Reduced Adult Body Size

Delayed sexual maturation and smaller adult body size observed in savannah baboons raised in resource-limited environments counter the PAR hypothesis. Altmann and Alberts (2004) found that offspring raised in resource-rich environments attained accelerated growth rate and earlier sexual maturation than their resource-limited conspecifics. They also achieved a larger relative and absolute body size than their counterparts (Altmann & Alberts, 2004). According to the PAR hypothesis, the opposite pattern should be observed where, in order to compensate for reduced expected lifespan suggested by environmental cues in early life, offspring that experience early life adversity should have a faster sexual maturation rate so that they can produce offspring earlier than their conspecifics. Yet, the research data directly counters this prediction. Once again, offspring who experience early life adversity are at a fitness disadvantage in terms of growth and reproductive success.

Other Considerations

Maternal Capital Model

Both the developmental constraints and PAR models place their emphasis on offspring survival and fitness. The maternal capital model, however, focuses on the survival of the mother and the decisions and strategies employed to maximize her own fitness (Lu et al., 2018). This model suggests that developmental processes are designed to increase maternal rather than offspring fitness. Offspring receive environmental information indirectly through their mother, who may filter this information to suit her own fitness needs (Lu et al., 2018). Major developmental decisions, such as weaning age and resource allocation, are based on the mother's needs rather than the offspring's. This suggests that offspring development is mainly dependent on their mother's fitness cost-benefit analysis. More attention should be given to test and investigate the extent of maternal control on offspring development trajectories.

Sibling Competition

Sibling competition is a social factor that could be considered as an adversity since it increases resource and maternal capital competition of the offspring. Research found that female baboons with close-in-age younger siblings were twice more likely to die at every age than females without siblings (Tung, 2016). Another study in wild baboons by Zipple et al. mirrored this result in intergenerational competition where offspring whose mother has close-in-age siblings experience 39% higher mortality than their counterparts (Zipple et al., 2019). Sibling competition is well documented in birds but is currently lacking in primate studies. It can have a powerful effect on offspring development, especially considering the slow life histories of primates. Given that gestation and lactation are incredibly energetically costly processes for mothers, having multiple offspring in short birth intervals can severely exhaust the mother's body and reduce her foraging ability. It can be very difficult to keep up with the demands of two young offspring at once, both resource and attention wise. This might lead to severe reduction in offspring fitness since adequate care for one comes at a cost for their siblings.

Sex Differences

It is noteworthy that many of the studies mentioned in this paper focused on only one sex, usually females. This paints an incomplete picture to the understanding of early life adversity's impact on individual survival and fitness, as different sexes often operate under different social conditions and reproductive strategies. There is conflicting evidence as to the significance of differential effects of sex when it comes to early life adversity in primates (French & Carp, 2016). Future studies should consider both sexes when analyzing research data regarding early life adversity. The effects of such early life adversities can be far-reaching and negatively impact the individuals for the rest of their life.

Conclusion

Early life adversity can have profound impacts on the long-term health and reproductive success of the individual. The exact evolutionary and biological mechanisms by which early life adversity operates to manifest these impacts is currently not fully understood. The two leading theories of developmental constraints hypothesis and PAR hypothesis, plus newer hypotheses such as the

maternal capital model, provide guiding research frameworks that are testable both in the lab and out in the field.

Non-human primates are human's closest living relatives. Given their biological relatedness and social similarities to humans, non-human primate models can provide insightful clues regarding human growth and development. Many of the adverse conditions in these studies cannot be replicated or experimented on humans as it would raise serious ethical concerns. Therefore, primate studies are the closest route through which human developmental theories can be tested. Experimental data gathered from these studies can be used to develop and improve existing models regarding not only human development but also evolutionary mechanisms of adaptive plasticity in other species as well.

There is still much left to be explored regarding the role of maternal care, environmental conditions, and social adversity in offspring's physical and social development. Since research in this area relies heavily on long-term data, the exciting potential of advances in the field is just starting to be unveiled. Given that the effects of such early life adversities can be far-reaching and negatively impact the individual for the rest of their life, future research should remain conscious of the long-term implications that experiments may have for the test subjects and implement humane mitigations where possible.

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