

### **Literature Review 3: Topic Summary (Revised)**

Female zebra finches passively allocate resources to developing eggs to maximise total fitness returns in response to environmental cues such as mate attractiveness (Gilbert et. al. 2006) and quality of parental care (Navara et. al. 2006). The pattern of maternal effects can be explained by two hypotheses: differential allocation and compensatory investment. The differential allocation hypothesis predicts that maternal resource allocation to developing eggs increases when copulation occurs with an attractive male (Bolund et. al 2009). Gilbert et. al. (2006) suggests that attractive males can provide more protection and food provisioning because they are naturally more dominant and have higher mass. As a result, females will allocate more resources to offspring because future environmental conditions are perceived to be safer. However, Kathryn et. al. (2016) suggests that less attractive males compensate for their phenotypic shortcomings by providing more parental care, including food provision for the female during the nesting period. If the female is in better condition, she can withstand the costs of increased egg provisioning. Therefore, the compensatory investment hypothesis predicts that copulation with a mate of lower attractiveness leads to higher resource investment in offspring (Kathryn et. al. 2016).

Researchers interested in understanding maternal effect patterns can influence perceived male attractiveness and parental quality to observe resulting patterns of sexual selection and variation in maternal effects. Mate attractiveness is manipulated through artificial ornaments (Pariser et. al. 2010) and song rate (Balzer and William 1998). Artificial red ornaments are naturally preferred by females but are also associated with increased song rate through a socially mediated feedback mechanism (Pariser et. al. 2010). Parental care can also be controlled by subjecting females to different levels of parental care activities and nest-defense behaviours by males (Burley 1988). Manipulation of these variables leads to measurable differences in yolk androgen and antioxidant levels, body mass, begging duration, and quality of egg properties (Griffith and Buchanan, 2010). To explore the phenotypic consequence of hormone levels in offspring, researchers have artificially injected androgens into the yolk of offspring and found that allocated hormones influence sex-ratio and levels of immunocompetence (Navara et. al 2006). Together, these studies have found that maternal effect patterns align with both the differential allocation and compensatory investment hypothesis but interact in a complex and context-dependent manner (Griffith and Buchanan, 2010). They suggest that costs of maternal egg provisioning vary among individuals and circumstances (Griffith and Buchanan, 2010).

Hormonal influences on maternal effect patterns are essential to understanding these variations in maternal egg provisioning costs and associated fitness benefits in offspring. Yolk androgens have an overall positive effect on the growth and survival of offspring (Rutkowska et. al., 2007) but can cause impaired T cell immunity and oxidative stress at high concentrations (Pariser et. al., 2012). Yolk antioxidants have been shown to mitigate the negative effects of maternally deposited androgens, as they protect growing tissues from oxidative damage (Pariser et. al., 2012). Griffith and Buchanan (2010) found that females who copulate with an attractive male will tend to increase the ratio of allocated androgens to antioxidants to compensate for low parental expenditure (Griffith and Buchanan, 2010). Increasing androgen content in developing eggs leads to greater begging duration, which may act as a strategy to increase parental contribution (Griffith and Buchanan, 2010). Other hormonal influences include deposition of

carotenoids. It is suggested that females are more likely to use compensatory investment of carotenoids when mated to a male of low attractiveness (Griffith and Buchanan, 2010). Carotenoid deposition can be used to compensate for phenotypic shortcomings because they aid in the development of body colour (Bolund et. al., 2009).

Overall, these studies suggest that allocation strategies are flexible within individuals, and therefor maternal effects will differ depending on environmental conditions and partner quality (Navara et. al., 2006). A clear pattern of manipulation is suggested, but the underlying mechanism and adaptive function of maternal effect patterns have yet to be understood (Griffith and Buchanan, 2010). The question of whether allocation of yolk hormones results in biologically meaningful effects for the offspring needs to be addressed in order to determine the adaptive function of this behavior (Griffith and Buchanan, 2010). I suggest future studies address this question by studying the phenotypic effects of antioxidant to androgen ratios.

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