Annotated bibliography

The articles in this bibliography are organized based on the discovery of ultimate to proximal maternal effects in zebra finches in response to mate quality. I chose to finish with a review article as it summarizes the strengths and weakness of the primary literature on this topic.

Primary literature citation:

Burley, N. (1988). The differential-allocation hypothesis: An experimental test. *The American Naturalist*, *132*(5), 611– 628. https://doi.org/10.1086/284877

Article summary:

Traditional studies on sexual selection have focused on polygynous species, where male reproductive success varies tremendously. This leads to the evolution of male ornamental traits, in attempts to maximize reproductive success. This study advances previous knowledge on sexual selection by researching the evolution of aesthetic traits in both male and female zebra finches, and their effect on allocation of resources to developing offspring. Burley (1988) hypothesized that attractive individuals can enhance their fitness by acquiring mates with higher reproductive success. Individuals can also enhance their fitness by allocating parental investment, such that unattractive mates can enhance their mating opportunities by incurring a greater amount of parental investment; a concept known as the differential-allocation hypothesis. This study tests the differential-allocation hypothesis by determining whether band colour influences paternal expenditure and reproductive success. Parental care activities and nest-defense behaviours were measured over 30 months in four experiments on domesticated zebra finches: female banded, male-banded, neither-sex banded, and bands exchanged after formation of pair bonds. Attractive ornaments were coloured black in females and red in males. Whereas unattractive ornaments were coloured blue in females and green in males. The results of the study found that the correlation between individual attractiveness and parental expenditure was negative for males and positive for females, as hypothesized by the differential-allocation hypothesis. It was also found that half of the attractive males became bigamists, which further decreased parental expenditure. This finding showed that polygynous males could lower parental investment in offspring to reach a behavioural-polygyny threshold. Overall, the findings were significant in that they revealed a correlation between unattractive males, high parental expenditure, low reproductive success, and shorter life span. This work also reveals a series of potential follow up questions on the proximal mechanism in which allows zebra finches to associate colour bands with mate quality.

Article contribution:

This study provides a mechanism of sexual selection in a monogamous species with biparental care, which contradicts most sexual selection studies that focus primarily on promiscuous species. It therefor advances previous knowledge on sexual selection by researching the evolution of aesthetic traits and reproductive success in both male and female specimens. This article was included in my literature review because it provides fundamental information on the effect of mate attractiveness on parental investment. It is also cited by multiple sources of literature and is there for an excellent resource for finding additional information.

Primary literature citation:

Kathryn, E.A., Lucy, G., Helen, E.G., Kate, J.G., Aileen, A., & Ruedi, G.N. (2016). Paternal attractiveness and the effects of differential allocation of parental investment. *Animal Behaviour*, *113*, 69–78. https://doi.org/10.1016/j.anbehav.2015.12.013

Article summary:

The classical differential allocation hypothesis predicts that female zebra finches will invest more resources into offspring of attractive males. However, differential allocation is difficult to predict in socially monogamous species with biparental care. If attractive mates contribute less parental care, then females may invest more resources into offspring from unattractive mates who compensate by providing more parental care. This pattern is not frequently seen in previous studies, but few studies have investigated the investment by both males and females. This study aims to investigate positive and negative differential allocation in egg formation in response to mate attractiveness, by looking at the investment of both sexes. 20 male zebra finches were banded with red (attractive) or green (unattractive) leg rings. 21 females were banded with orange (neutral) leg rings. Once clutches were complete, eggs were cross fostered between nests. Egg characteristics, parental feeding behaviour, nestling behaviour, and offspring performance as adults were measured. Positive differential allocation was observed at the egg stage: eggs reared or incubated from red-ringed fathers had higher yolk to albumen ratios and higher hatchling mass. Negative differential allocation was also observed at the rearing stage: parents from green-ringed pairs fed their nestlings more frequently. These findings are significant because they reveal an inconsistency in the reproductive investment patterns in response to mate attractiveness. This inconsistency suggests that the costs and benefits of differential allocation vary among individuals and circumstances. This study opens further research on how positive and negative investment balance in zebra finch reproduction and the implications this may have on offspring phenotype. It also provides a series of follow up questions on the role of environmental cues in the investment patterns of monogamous birds, a field that has yet to be quantified or understood by researchers.

Article contribution:

This article advances previous studies by investigating the complex interaction of both positive and negative differential allocation. The results align with previous findings on positive differential allocation, such that egg provisioning increases with higher mate quality. However, negative differential allocation has been observed less frequently in previous studies as most fail to investigate both maternal and paternal effects. This article was included in my literature review because it investigates a variety of scenarios and environmental cues that can shift the balance of differential allocation. It therefore analyses maternal effects using a method that better reflects what is seen in nature.

Primary literature citation:

Balzer, A.L., & Williams, T.D. (1998). Do female zebra finches vary primary reproductive effort in relation to mate attractiveness? *Behaviour*, *135*(3), 297–309.
https://doi.org/10.1163/156853998793066230

Article summary:

Previous studies suggest that reproductive effort of female zebra finches is positively correlated with male attractiveness, both prior to copulation and during parental care. However, it is not clear whether this correlation is due to resources associated with mate quality that allow for increased reproductive effort, male-male competition resulting in higher quality mates pairing with females, or simply to the facultative adjustment of reproductive effort by females. Balzer and Williams (1998) explored the notion that females facultatively adjust reproductive effort in egg production. They investigated primary reproductive effort, including clutch size, timing of laying, and mean egg mass, when females were paired sequentially to a preferred and non-preferred mate. 33 females were paired randomly to a single male in a separate cage until a preferred and non-preferred mate was identified for each female. The proportion of time each female bird spent interacting with the male was used as an indication of mate quality. Females were then permitted to breed sequentially with both their preferred and non-preferred mate, and female reproductive effort was recorded after two weeks. The study found that females preferred mates with high song duration and frequency, which confirms the notion that females prefer attractive and high-quality mates. Male attractiveness also had a weak positive correlation to clutch size, but no significant results were found on egg mass, timing of laying, and egg quality. These findings are significant because they suggest that the components of primary reproductive effort (egg size, clutch size, and laying date) are determined by relatively non-plastic traits. However, previous studies on the maternal effects of different species have found that secondary reproductive effort traits are much more variable. Thus, this study opens further research on the effects of male quality on the secondary reproductive effort of female's zebra finches during parental care.

Article contribution:

Balzer and Williams (1998) studied the effects of mate quality on primary reproductive efforts, whereas previous studies have focused on secondary reproductive efforts. They advance knowledge in the field by suggesting that traits involved in primary reproductive effort are relatively non-plastic. This supports the significance of previous findings on secondary reproductive efforts. I included this study in my literature review because it provides basic, yet valuable, information on the underlying criterion for mate choice. The article reveals that song rate is the most important criterion for sexual selection in finches, which contradicts most previous studies that focus on beak colour.

Primary literature citation:

Bolund, E., Schielzeth, H., & Forstmeier, W. (2009). Compensatory investment in zebra finches: Females lay larger eggs when paired to sexually unattractive males. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1657), 707–715. https://doi.org/10.1098/rspb.2008.1251

Article summary:

The compensatory investment hypothesis predicts that female zebra finches will invest more resources into offspring when their mate is lower quality. Low genetic quality offspring require more maternal resources including egg volume and yolk carotenoid content. Previous studies show conflicted findings that support both the compensatory investment and positive differential allocation hypothesis. Bolund et. al. (2009) predicts that these conflictions are due to an entangled analysis of both indirect (quality genes) and direct (parental abilities) benefits. This study adopted a different approach that separated these benefits by measuring the effects of male attractiveness and male parental quality independently. The study investigated female primary reproductive investment in relation to selected mates with either extreme values of sexual attractiveness or parental quality. In the first treatment, 16 females were each sequentially paired with two males with maximal difference in attractiveness but similar parental quality. In the second treatment, 16 fecund females were each sequentially paired with two males with maximal difference in parental quality but similar attractiveness. Pairs were given 42 days to copulate. Egg volume, yolk mass, number of eggs, and yolk testosterone were measured. It was found that females invested more nutrients and laid larger eggs when mated to males of lower sexual attractiveness. The results for mates of lower parental care showed the same pattern but had a weaker correlation. These results are significant because they confirm that male behaviour and quality influences female investment. Males of lower attractiveness are predicted to focus their reproductive investment on their mate rather than seek more copulations. This could stimulate within-pair investment and cause the female increase egg provision. This study reveals a new approach of disentangling the direct and indirect benefits of male attractiveness that can be adopted by future studies to further study unknown proximal mechanisms of maternal allocation.

Article contribution:

Previous studies on maternal effects in response to mate quality show conflicting results due to simultaneous analysis of parental care and mate attractiveness. This article advances knowledge in the field by adopting a new approach that measures the effects of male attractiveness and male parental quality independently. The maternal effect patterns in this study align with previous findings. However, it differs because the direct and indirect benefits of mate quality are analysed separately to determine a more specific mechanism of sexual selection; a significant distinction from other studies that led me to include this study in my literature review.

Primary literature citation:

Gilbert, L., Williamson, K.A., Hazon, N., & Graves, J.A. (2006). Maternal effects due to male attractiveness affect offspring development in the zebra finch. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1595), 1765–1771. https://doi.org/10.1098/rspb.2006.3520

Article summary:

Mate attractiveness is a potential environmental factor that could influence offspring phenotype through maternal effects, even in cases where the mate does not contribute any parental care. Previous studies on finches show that mate quality is positively correlated to larger eggs, and deposition of more androgens and immunoglobulins. However, these studies have yet to control for overriding effects of genetic quality and parental care. This study aims to investigate mate attractiveness-dependent maternal effects on the development of offspring in zebra finches. Factors of parental care and genetic quality are controlled so that only sexual selection of leg rings can be investigated. Thus, it can be assumed that any variance in egg resource provision is likely a response to mate attractiveness. 36 captive male zebra finches were randomly assigned red (attractive) or green (unattractive) leg bands and paired to a female until chicks were reared. Effect of nestling care was controlled for by cross fostering clutches. Yolk androgen content, egg mass, maturation rate, begging duration, and body size were measured following copulation. It was found that egg mass, begging duration, and body size significantly increased when females copulated with attractive mates. This suggests that attractive males can provide more protection and food provisioning because of their phenotypic advantages. As a result, females will allocate more resources to offspring to maximize survival of late-hatched chicks because future environmental conditions are perceived to be safer. This study is significant because it confirms a direct correlation between mate attractiveness and maternal resource allocation. However, factors of parental care and genetic quality can affect this correlation in nature. This opens future research on the isolated effects of parental care and genetic quality on maternal allocation. These factors can then be combined to investigate a maternal resource allocation mechanism that is more commonly seen in nature.

Article contribution:

This article provides insight on egg provisioning in response to mate attractiveness by overriding the effects of parental genetic quality and parental care. It advances knowledge by using a cross fostering technique to study the isolated effects of ornamental traits, which have been found to positively correlate with increased egg provision. This finding supports previous research on maternal effect patterns but provides a more proximal mechanism of differential allocation that's based merely on mate attractiveness. This article was included in my literature review because it adopts a different approach on studying maternal effects by investigating individual factors of mate quality.

Primary literature citation:

Pariser, E.C., Mariette, M.M., & Griffith, S.C. (2010). Artificial ornaments manipulate intrinsic male quality in wild-caught zebra finches (*Taeniopygia guttata*). *Behavioral Ecology*, *21*(2), 264–269. https://doi.org/10.1093/beheco/arp185

Article summary:

Coloured leg bands have been used in previous studies to manipulate the attractiveness of zebra finches. Red colouration is a signalling quality of male attractiveness that is naturally preferred by females. Most studies using this method of sexual selection assume that ornaments do not influence intrinsic male quality and that female preference does not last after the band is removed. Pariser et. al. (2010) investigated the long-term effects of color bands on male socialization and attractiveness. The study predicted that banded birds housed in a social environment will vary in condition and quality of sexually selected traits, even after the bands are removed. 67 wild-caught zebra finch males were given either a red, green, or control band, and housed in a single-sex aviary for 5 months. Changes in mass and condition were recorded. The males were then introduced to females and courtship display (song rate) was observed. It was found that males wearing red bands were in better condition and had higher body-mass and song rate than green-banded males. Male song rate also increased when female response was positive, revealing a socially mediated feedback mechanism between interacting birds. In this feedback mechanism, red-bands or dominant nature directly affect other aspects of male attractiveness including song rate. Therefore, socialization of zebra finches with artificial ornaments does affect intrinsic male quality. This result is significant because it reveals an effect of artificial ornaments on physiological and behavioral parameters, rather than just the appearance of the individual. These effects should be accounted for in future studies to prevent inaccurate data analysis. This study opens further research on the mechanism that relates band colour to changes in intrinsic male qualities. It also raises the question of whether females pay less attention to physical band colour compared to the courtship display associated with that colour.

Article contribution:

Previous studies attribute maternal effect patterns to female preference of external male ornaments. This study provides new insight on maternal effects by investigating the effects of ornamental traits on physiological and behavioral traits of male zebra finches. It advances knowledge by investigating the direct effects of socialization on intrinsic quality of males with diverse ornamental traits. This article was included in my literature review because it provides a proximal mechanism that relates ornamental traits to sexual selection by females. This mechanism can be used to analyse the results of previous studies on maternal effects in response to perceived mate attractiveness.

Primary literature citation:

Rutkowska, J., Wilk, T., & Cichoń, M. (2007). Androgen-dependent maternal effects on offspring fitness in zebra finches. *Behavioral Ecology and Sociobiology*, *61*(8), 1211–1217. https://doi.org/10.1007/s00265-007-0351-0

Article summary:

Maternal hormones play a role in offspring sex-adjustment and offspring viability. It has been found that increased yolk androgen levels result in a male-biased sex ratio. It also negatively affects the survival of sons but has positive effects on survival of daughters. However, little is known about the costs of androgen-mediated mechanisms. Rutkowska et. al. (2007) investigated the phenotypic effects of androgens by observing changes in offspring growth and cell-mediated immune response. Eggs were analyzed from two experimental groups: female zebra finches injected with testosterone during egg laying and control females with no treatment. Eggs were also cross fostered to account for any differences in incubation and laying sequence. Nestlings were weighed and injected with a non-pathogenic antigen to assess immunocompetence. It was found that male offspring of testosterone-treated mothers had slower growth rate and impaired immune response compared to the control group. On the contrary, female offspring benefitted from increased androgen levels and had enhanced immune response. Males produce naturally high levels of testosterone so androgen injections can lead to high rates of aromatization. This leads to a decrease in competitive ability. On the other hand, female offspring show enhanced competitive ability when subject to androgen injections. These results are significant because they reveal a complex trade-off between biased sex-ratio and offspring survival. Although androgens can be used as a mechanism of sex determination, the quality of offspring may be negatively impacted by high androgen levels. This study opens further research on the context-dependent effects of androgens, such as mate attractiveness or quality of parental care. It also questions the mechanism that causes opposite responses to androgens in male and female offspring.

Article contribution:

This article advances knowledge of maternal effects in zebra finches by investigating the phenotypic effects of yolk androgens. Previous studies have yet to understand the costs associated with androgen-mediated mechanisms. This study provides a new insight on the complex trade-off between biased sex-ratio and offspring survival mediated by androgen deposition. A major cost of androgen deposition is slow growth rate and impaired immunocompetence in male offspring. These effects are important to understanding mechanisms of maternal effects in response to mate quality; a reason why I decided to include it in my literature review.

Primary literature citation:

Navara, K.J., Hill, G.E., & Mendonça, M.T. (2006). Yolk androgen deposition as a compensatory strategy. *Behavioral Ecology and Sociobiology*, *60*(3), 392–398. https://doi.org/10.1007/s00265-006- 0177-1

Article summary:

Androgens are mediators that have an overall positive effect on the growth and survival of offspring when deposited into eggs. Previous studies on avian maternal effects have investigated incubation, provisioning, and protection of offspring, but few have researched the effects of androgen deposition. Research on this topic has found that strategies of androgen deposition vary based on environmental and social context, such as mate quality. This study investigated the deposition of yolk androgens according to the differential allocation hypothesis: preferential allocation of resources to offspring reared from more attractive and high-quality mates. Thus, it is predicted that females with more attractive mates will deposit more yolk androgens into their eggs. Male ornamental quality, female condition, and yolk androgen concentration were measured from 15 nest boxes within a population of wild house finches. Yolk androgens, including testosterone, androstenedione, and dihydrotestosterone, in the first laid egg were separated and analyzed using chromatography and a radioimmunoassay. It was found that females deposited more androgens into eggs sired by less attractive males. This finding is significant because it reveals a connection to the compensatory investment hypothesis: preferential allocation of resources to offspring reared from less attractive mates. It is suggested that lower-quality males compensate for their ornaments by providing more parental care, including food provision for the female during the nesting period. If the female is in a better condition, she can withstand more of the costs associated with high androgen deposition. However, the compensatory distribution hypothesis is flexible and therefore can be explained by multiple different environmental, social, and physiological circumstances. This opens further research on the complex costs and benefits of androgen deposition that can then be used to understand the significance of this maternal effect in finches.

Article contribution:

This article provides insight on the mechanism of yolk androgen deposition in response to mate attractiveness in finches. It advances knowledge on the compensatory distribution of yolk androgens, which were previously thought to be distributed based on positive differential allocation. It also proposes explanations for the complex variation in androgen deposition when exposed to different environmental, social, and physiological circumstances. Many studies on maternal effects patterns have yet to observe a significant pattern of yolk androgen deposition in response to mate quality. I decided to include this article in my literature review because it contributes to this gap in knowledge.

Primary literature citation:

Pariser, E.C., Gilbert, L., Hazon, N. Arnold, K.E., & Graves, J.A. (2012). Mind the gap: The ratio of yolk androgens and antioxidants varies between sons and daughter's dependent on paternal attractiveness. *Behavioral Ecology and Sociobiology*, *66*(4), 519–527. https://doi.org/10.1007/s00265-011-1300-5

Article summary:

Female zebra finches can manipulate androgen and antioxidant levels among offspring in an environment-dependant way to maximize fitness returns. Increased yolk androgens have a positive effect on growth but can cause impaired T-cell immunity at high concentrations. Antioxidants have been shown to mitigate the costs of androgens and are critical for embryonic development. However, previous studies have yet to investigate the collective effects of both androgens and antioxidants on the growth and survival of offspring. This study aims to investigate the effect of male attractiveness on the ratio of androgens to antioxidants in zebra finch offspring, and whether females allocate resources in a sex-specific way. 12 males were labelled with either red (attractive) or green (unattractive) leg rings, and randomly paired to a female until eggs were collected. The yolk androgens and antioxidants were measured in each egg, as well as the egg sex and clutch sex ratio. It was found that females paired with attractive males deposited more antioxidants than androgens in males. This trend was also seen in female offspring when the mother was paired with an unattractive male. Antioxidants are more expensive to deposit than androgens. An increase in antioxidant deposition is usually only observed when female condition improves, or copulation occurs with an attractive mate. While maternal manipulation of androgens and antioxidants is evident, the trends were not consistent with any theories of differential or compensatory allocation. However, the findings are significant because they suggest that maternal allocation of androgens and antioxidants depend on both environmental cues and female condition. Patterns of maternal allocation can be better interpreted if the fitness consequences of egg constituent ratios are known. This opens further research on the manipulation of antioxidant and androgen rations in order to determine resulting phenotypes of developing offspring.

Article contribution:

Pariser et. al (2012) provide a new insight on the effects of mate attractiveness on the maternal allocation of androgens and antioxidants in developing zebra finch eggs. The study synthesizes new knowledge on maternal effects by investigating the role of ornamental traits, an environmental cue, on the complex interaction of androgens and antioxidants. Previous studies have yet to investigate this interaction; rather they have focused on the independent properties of either androgens or antioxidants. This article investigates a proximal mechanism of maternal allocation that supports and helps to explain the findings of other articles in my literature review.

Secondary literature citation:

Griffith, S.C., & Buchanan, K.L. (2010). Maternal effects in the zebra finch: A model mother reviewed. *Emu - Austral Ornithology*, *110*(3), 251–267. https://doi.org/10.1071/MU10006

Article summary:

The Zebra Finch provides an excellent model for studying maternal effects in response to mate quality because is it a socially monogamous species, meaning the fitness of the female is closely linked to that of the male. This article performed a meta-analysis on resource allocation to developing eggs in response to mate quality. The studies have examined maternal effects through provisioning behaviour, sex allocation, hormone levels, and incubation behaviour. This article provides logical explanations for the variation in maternal investment patterns generated from a comparison of these studies.

Female Zebra Finches can optimize their reproductive success by altering the phenotype of offspring to better adapt to the environment they are likely to encounter. They are also able to allocate passive transfer of hormones between reproductive events in relation to mate quality. Females prefer males with red bands compared to green because they stimulate a sensory preference for red ornaments seen in nature. Color bands can also affect intrinsic male quality, as males wearing red bands tend to become more dominant and have increased body-mass. Overall, females were found to invest more resources in developing eggs when mated to a male of lower attractiveness and parental quality. Many of the studies on maternal allocation of hormones failed to consider the level of parental care as a factor of mate attractiveness; a factor that partly attributes to the inconsistency between studies. However, the most studied conclusion states that the variation between hormone levels of developing eggs is a result of the circulating levels of hormones within a female during the period of egg-production. It is hypothesized that female hormone levels vary based on mate quality, the ability of females to assess quality, the likelihood of a female to switch mates, and the extent to which differential investment affects future reproductive potential.

Article contribution:

This article explores maternal resource allocation in response to mate quality. However, the synthesis of patterns on sex allocation, egg size, hormones, and provisioning levels show contrasting results and complex interactions between traits. This article highlights these flaws and helps to provide explanations for the variation in conflicting patterns. It also focuses on the specific mechanisms that still need to be studied to better understand the maternal effects of Zebra Finches. This review also mentions multiple sources of primary literature that have studied the maternal effects of Zebra Finches and is therefore an excellent resource for finding additional information.