Oecologia
DOI 10.1007/s00442-015-3266-x

VIEWS AND COMMENTS

Commentary: Parental care and the proximate links between maternal effects and offspring fitness

Matthew B. Dugas

Received: 8 October 2014 / Accepted: 6 February 2015

Abstract Maternal effects influence the phenotype of offspring through non-genetic mechanisms, and thus are important components of individual life-histories and act as drivers of and/or constraints on phenotypic evolution. A maternal effect common in egg-laying vertebrates is provisioning of the yolk with carotenoids, organic pigments that often color sexual ornaments and are hypothesized to play positive and substantial physiological roles. In a recent study, yolks of great tit (*Parus major*) eggs were directly supplemented with carotenoids, and the effects on offspring fitness proxies measured (Marri and Richner in *Oecologia* 176:371–377, 2014a). Nestlings from supplemented broods were heavier early in development and more likely to fledge, but otherwise equivalent to control nestlings. The authors consider in detail the potential physiological mechanisms that might underlie this result, and here I expand on their Discussion by considering a non-exclusive explanation: that parents provided higher quality care to broods that received supplemental carotenoids. I discuss the general non-independence of pre- and post-hatching/parturition maternal effects when parents care for offspring, and then briefly review evidence that carotenoids specifically are tied to the intensity of avian begging displays. Finally, I detail how inclusive fitness opportunities and constraints shape the adaptive landscape in which maternal effects operate, highlighting both theoretical and applied concerns surrounding questions about the adaptiveness of maternal effects.

Communicated by Markku Orell.

M. B. Dugas (✉)
Department of Biology, Case Western Reserve University, DeGrace Hall, 2080 Adelbert Rd., Cleveland, OH 44106, USA
e-mail: matthew.b.dugas@gmail.com

Keywords Begging · Carotenoids · Inclusive fitness · Maternal effects · Offspring–parent communication · Parent–offspring conflict

Introduction

Maternal effects offer mothers non-genetic mechanisms by which to influence the phenotype of their offspring, and thus can be integral to parental life-history strategies (Marshall and Uller 2007; Uller 2008; Wolf and Wade 2009). In a recent issue of *Oecologia*, Marri and Richner (2014a) report the results of an experimental supplementation of one such maternal effect, yolk carotenoids, in great tits (*Parus major*). Carotenoids are organic pigments, synthesized by autotrophs and some bacteria and fungi, that lend yellow, orange, and red coloration to myriad animal and plant tissues, and are nearly ubiquitous in animal ornaments (Svensson and Wong 2011) and in the yolks of vertebrate eggs (Blount et al. 2000). The hypothesized physiological functions of carotenoids (i.e., why they might reveal signaler quality or why they might aid developing embryos) are varied and not uncontroversial, but the preponderance of current evidence suggests that, if a relationship between carotenoids and embryo development or signaler quality exists, it is likely to be a positive one (Blount et al. 2000; Ewen et al. 2008; Svensson and Wong 2011). Great tits are one of the best-studied avian systems with respect to the importance of carotenoids during reproduction, with the role of carotenoids in offspring development followed from maternal intake to offspring survival (Isaksson et al. 2006; Isaksson 2009; Tschirren et al. 2005; Fitze and Tschirren 2006). Previous work on this and several other species has experimentally assessed the effect of pre-laying carotenoid availability to mothers on offspring

Published online: 20 February 2015

fitness (reviewed by Marri and Richner 2014a). However, carotenoid consumption can itself alter parental behavior (Remeš et al. 2007; Thorogood et al. 2011), and so Marri and Richner's (2014a) direct manipulation of yolks fills a void in a larger story about carotenoids, reproduction and avian families.

Marri and Richner (2014a) found that nestlings from carotenoid-supplemented broods were heavier at day 3 (~1/6th of the nestling period) and that, probably at least in part because of this early mass advantage, were more likely to fledge than were controls. Contrary to predictions drawn from an extensive literature (Svensson and Wong 2011), they found no evidence consistent with the hypothesized antioxidant and immune benefits of carotenoids (Marri and Richner 2014a, b), and, somewhat surprisingly, did not find the same effect on nestling plumage coloration revealed by a correlative analysis in the same species (Isaksson et al. 2006). In their Discussion, Marri and Richner (2014a) summarize the current doubt surrounding the antioxidant and immune-enhancing functions of carotenoids in birds (see also Marri and Richner 2014b), and speculate convincingly about how the timing of carotenoid availability during development might explain the patterns they did and did not find. A non-exclusive mechanism that could explain the positive effects of yolk carotenoids is that supplemented offspring benefited from increased parental care relative to controls (see also Discussion in Berthouly et al. 2007), an explanation hinted at when Marri and Richner (2014a) note that, "Possibly the first 3 days after hatching are a crucial period that can influence survival later in the nestling period (Discussion, p. 376)." Here, I expand on this proposition by (1) explicitly considering the non-independence of pre- and post-hatching/parturition maternal effects when parents care for dependent offspring, (2) briefly reviewing evidence that carotenoids influence avian begging displays, including those of great tit nestlings, and (3) highlighting the complex inclusive fitness concerns that underlie both theoretical and applied attempts to assess the adaptive value of maternal effects.

Maternal effects and dependent offspring

Maternal effects exert a causal influence on the phenotype of offspring, which in turn can, but does not necessarily, influence the fitness of offspring (Wolf and Wade 2009). When offspring depend on parental care, any proximate links between offspring phenotype and offspring fitness are necessarily mediated by parents, even if the maternal effect in question is introduced entirely pre-hatching/parturition. For example, nutrient intake requires independent offspring to locate and capture food, while for dependent young, obtaining exogenous nutrients is often a matter of convincing parents to hand them over. Yolk steroid concentration is a well-studied maternal effect in birds, and although hormone titers have diverse physiological and developmental effects, the primary route by which they influence offspring fitness proxies (e.g., mass) appears to be by increasing the frequency and intensity of solicitation displays, and thus the amount of food offspring receive (Schwabl and Lipar 2002; Groothuis et al. 2005). Even a maternal effect that simply increased offspring digestive efficiency (i.e., presumably a "good" effect) would result in increased offspring fitness only with parental cooperation, as parents faced with a brood developing unexpectedly well could plausibly (1) maintain current levels of investment, (2) reduce investment, reserving apparently unneeded reproductive effort for later attempts, or (3) increase investment, taking advantage of higher than expected returns (Mock et al. 2005). When post-hatching/parturition care is present, interpreting the influence of maternal effects on offspring fitness is, then, as much about understanding how and why parents respond to variation in offspring phenotype as it is about understanding the offspring phenotype itself.

Carotenoid-richness and resource extraction by dependent nestling birds

Parents and offspring usually share control of resource allocation, with the relative split varying among species and over the course of development (Mock et al. 2011). Dependent offspring can influence the absolute and relative amount of care they receive with a suite of behavioral, physiological, and morphological traits, often collectively termed "begging" (reviewed by Mock et al. 2011). There is good evidence that carotenoids play an important role in the intensity of avian begging. The most familiar component of this display is probably an outstretched neck and opened gape accompanied by vocalizations. In great tits, nestlings from eggs of carotenoid-supplemented females (i.e., carotenoid-rich eggs) produce nestlings that, at least under some conditions, perform this postural display more intensely (Helfenstein et al. 2008) and perhaps more effectively (Berthouly et al. 2007), and thus seem likely to obtain more food.

Carotenoid availability is also associated with the expression of colorful, carotenoid-based ornamentation in nestling birds, especially mouth coloration (Saino et al. 2000; Thorogood et al. 2008; Dugas and McGraw 2011). The enhanced expression of these carotenoid-dependent colors are typically met with increased parental care, both within (Saino et al. 2000; Dugas 2009) and among (Ewen et al. 2008; Griggio et al. 2009) broods. In house sparrows (*Passer domesticus*), intense carotenoid-based mouth coloration is favored by parents (Dugas 2009), and early within-brood hierarchies in both color and mass are reinforced by parents (Dugas 2012). Carotenoid availability has, in other studies, influenced the expression of carotenoid-based plumage of great tit nestlings (e.g., Tschirren et al. 2003; Isaksson et al. 2006). While carotenoid color intensity per se does not seem to influence parental behavior in this species (Tschirren et al. 2005), ultraviolet (UV) reflectance does (Galvan et al. 2008; Tanner and Richner 2008), and UV reflectance and carotenoid intensity rarely vary independently (reviewed by Dugas and McGraw 2011). Mouth coloration of great tit nestlings is likely also carotenoid-dependent (Hunt et al. 2003), and experimental approaches have not yet resolved whether and how parent great tits respond to variation in this trait (Götmark and Ahlström 1997; Heeb et al. 2003).

Whether nestlings from carotenoid-supplemented eggs displayed more intense solicitation traits and thus received increased investment in Marri and Richner's (2014a) study is impossible to determine using indirect evidence. In a similar study in barn swallows (*Hirundo rustica*) (Saino et al. 2003), a lack of mass differences between treatment groups was interpreted as evidence that parents had not favored offspring from supplemented yolks, although in house sparrows, brood-level food supplementation paired with increased paternal provisioning increases recruitment without increasing mass (Mock et al. 2005). In short, current evidence suggests increased parental care as a result of the maternal effect of carotenoids is as likely an explanation for increased mass and increased fledging success as is a direct physiological benefit of carotenoid pigments. Knowing the extent to which each mechanism contributes to positive effects on offspring is critical to determining how yolk carotenoids influence parent, and offspring, fitness.

Proximate mechanisms and ultimate consequences

When offspring interact with kin following hatching/parturition, estimating the fitness consequences of a maternal effect for both mothers and offspring poses more complex theoretical and practical challenges than when such kin interactions are absent (Moore et al. 1997; Uller 2008). For a dependent offspring, successful foraging events typically carry a direct fitness benefit and an inclusive fitness cost (Mock and Parker 1997; Mock et al. 2011). Therefore, if a maternal effect increases offspring fitness proxies by increasing the offspring's success at extracting costly parental care, concluding that this maternal effect has positive effects on maternal fitness, or even total offspring fitness (direct + indirect), would be premature (Uller 2008). Female rock sparrows (*Petronia petronia*) increase provisioning to broods in which the intensity of an offspring ornament (yellow breast patch) is experimentally increased (Griggio et al. 2009). However, as is typical when brood size is experimentally enlarged (e.g., Nur 1984), mothers that provide enhanced offspring with more food suffer reduced survival (Griggio et al. 2009). Thus, the overall fitness effects of a maternal effect that increased the expression of the yellow breast patch (plausibly, yolk carotenoids) would be unclear.

Maternal effects might influence maternal fitness by providing offspring with accurate information about the environment, or might do so by manipulating offspring (or fathers) to the mother's advantage (Marshall and Uller 2007; Müller et al. 2007; Uller 2008). There is growing evidence that mothers use maternal effects to match offspring demands to the quality of care they intend to provide (Hinde et al. 2009), and the quality of care they intend to provide can vary independently of environmental conditions (e.g., females may intend to invest more in the offspring of an attractive mate; Groothuis et al. 2005). Hormonal maternal effects are perhaps best studied with respect to their influence on post-zygotic care (Schwabl and Lipar 2002; Groothuis et al. 2005), but seem unlikely to be the only maternal effect upon which this selective pressure acts. Carotenoids are, much like androgens, implicated in the efficacy of begging displays, and variation in yolk provisioning could similarly set offspring on particular developmental trajectories (Saino et al. 2002; Dugas 2012). If these pigments are physiologically important and limiting (Blount et al. 2000; Svensson and Wong 2011), when or to what extent they are allocated to displays (vs. maintenance) could offer even more nuanced insights into how parent–offspring conflict is manifested and resolved in the physiological arena.

The identification of maternal effects that explain variation in offspring size, health or viability also has important applied implications. Carotenoid supplementation to reproductive females specifically has proven useful in the management of both wild and captive populations, presumably influencing offspring health via maternal effects (Dugas et al. 2013; Walker et al. 2013). However, the extent to which these direct benefits to offspring impose costs on related individuals will dictate their consequences for the fitness of parents and for the health of populations (Ewen et al. 2008; Thorogood et al. 2011; Walker et al. 2013). Targeted experimental manipulations like that reported by Marri and Richner (2014a) are necessary for understanding both the basic and applied importance of maternal effects. Along with careful behavioral observations, studies like this promise to illustrate the diverse forces that shape how and why generations communicate, cooperate and compete.

Author contribution statement MBD conceived, designed, and executed this study and wrote the manuscript. No other person is entitled to authorship.

Acknowledgments Ryan A. Martin, Michael P. Moore, Douglas W. Mock and an anonymous reviewer provided helpful comments that improved this commentary.

References

Berthouly A, Helfenstein F, Richner H (2007) Cellular immune response, stress resistance and competitiveness in nestling great tits in relation to maternally transmitted carotenoids. Funct Ecol 21:335–343

Blount JD, Houston DC, Møller AP (2000) Why egg yolk is yellow. Trends Ecol Evol 15:47–49

Dugas MB (2009) House sparrow (*Passer domesticus*) parents preferentially feed nestlings with mouth colours that appear carotenoid-rich. Anim Behav 78:767–772

Dugas MB (2012) Cross-fostering reveals that among-brood differences in ornamental mouth coloration mostly reflect rearing conditions in nestling house sparrows. Biol J Linn Soc 106:169–179

Dugas MB, McGraw KJ (2011) Proximate correlates of carotenoid-based mouth coloration in nestling house sparrows. Condor 111:691–700

Dugas MB, Yeager J, Richards-Zawacki CL (2013) Carotenoid supplementation enhances reproductive success in captive strawberry poison frogs (*Oophaga pumilio*). Zoo Biol 32:655–658

Ewen JG, Thorogood R, Karadas F, Cassey P (2008) Condition dependence of nestling mouth colour and the effect of supplementing carotenoids on parental behaviour in the hihi (*Notiomystis cincta*). Oecologia 157:361–368

Fitze PS, Tschirren B (2006) No evidence for survival selection on carotenoid-based nestling coloration in great tits (*Parus major*). J Evol Biol 19:618–624

Galvan I, Amo L, Sanz JJ (2008) Ultraviolet–blue reflectance of some nestling patches mediates parental favouritism in great tits *Parus major*. J Avian Biol 39:277–282

Götmark F, Ahlström M (1997) Parental preference for red mouths of chicks in a songbird. Proc R Soc Lond B 264:959–962

Griggio M, Morosinotto C, Pilastro A (2009) Nestlings' carotenoid feather ornament affects parental allocation strategy and reduces maternal survival. J Evol Biol 22:2077–2085

Groothuis TGG, Müller W, von Engelhardt N, Carere C, Eising C (2005) Maternal hormone as a tool to adjust offspring phenotype in avian species. Neurosci Biobehav Rev 29:329–352

Heeb P, Schwander T, Faoro S (2003) Nestling detectability affects parental feeding preferences in a cavity-nesting bird. Anim Behav 66:637–642

Helfenstein F, Berthouly A, Tanner M, Karadas F, Richner H (2008) Nestling begging intensity and parental effort in relation to prelaying carotenoid availability. Behav Ecol 19:108–115

Hinde CA, Buchanan KL, Kilner RM (2009) Prenatal environment effects match offspring begging to parental provisioning. Proc R Soc Lond B 276:2787–2794

Hunt S, Kilner RM, Langmore NE, Bennett ATD (2003) Conspicuous, ultraviolet-rich mouth colours in begging chicks. Proc R Soc Lond B 270:S25–S28

Isaksson C (2009) The chemical pathway of carotenoids: from plants to birds. Ardea 97:125–128

Isaksson C, Uller T, Andersson S (2006) Parental effects on carotenoid-based plumage coloration in nestling great tits, *Parus major*. Behav Ecol Sociobiol 60:556–562

Marri V, Richner H (2014a) Yolk carotenoids increase fledging success in great tit nestlings. Oecologia 176:371–377

Marri V, Richner H (2014b) Differential effects of vitamins E and C and carotenoids on growth, resistance to oxidative stress, fledging success and plumage coloration in wild great tits. J Exp Biol 217:1476–1484

Marshall DJ, Uller T (2007) When is a maternal effect adaptive? Oikos 116:1957–1963

Mock DW, Parker GA (1997) The evolution of sibling rivalry. Oxford University Press, Oxford

Mock DW, Schwagmeyer PL, Parker GA (2005) Male house sparrows deliver more food to experimentally subsidized offspring. Anim Behav 70:225–236

Mock DW, Dugas MB, Strickler SA (2011) Honest begging: expanding from signal of need. Behav Ecol 22:909–917

Moore AJ, Brodie ED III, Wolf JB (1997) Integrating phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. Evolution 51:1352–1362

Müller W, Lessels CM, Korsten P, von Engelhardt N (2007) Manipulative signals in family conflict? On the function of maternal yolk hormones in birds. Am Nat 169:E84–E96

Nur N (1984) The consequences of brood size for breeding blue tits I. Adult survival, weight change and the cost of reproduction. J Anim Ecol 53:479–496

Remeš V, Krist M, Bertacche V, Stradi R (2007) Maternal carotenoid supplementation does not affect breeding performance in the great tit (*Parus major*). Funct Ecol 21:776–783

Saino N, Ninni P, Calza S, Martinelli R, de Bernardi F, Møller AP (2000) Better red than dead: carotenoid-based mouth colouration reveals infection in barn swallow nestlings. Proc R Soc Lond B 267:57–61

Saino N, Bertacche V, Ferrari RP, Martinelli R, Møller AP, Stradi R (2002) Carotenoid concentration in barn swallow eggs is influenced by laying order, maternal infection and paternal ornamentation. Proc R Soc Lond B 269:1729–1733

Saino N, Ferrari R, Romano M, Martinelli R, Møller AP (2003) Experimental manipulation of egg carotenoids affects immunity of barn swallow nestlings. Proc R Soc Lond B 270:2485–2489

Schwabl H, Lipar J (2002) Hormonal regulation of begging behaviour. In: Wright J, Leonard M (eds) The evolution of begging: competition, cooperation and communication. Kluwer, Dordrecht, pp 221–244

Svensson PA, Wong BBM (2011) Carotenoid-based signals in behavioural ecology: a review. Behaviour 148:131–189

Tanner M, Richner H (2008) Ultraviolet reflectance of plumage for parent-offspring communication in the great tit (*Parus major*). Behav Ecol 19:369–373

Thorogood R, Kilner RM, Karadas F, Ewen JG (2008) Spectral mouth colour of nestlings changes with carotenoid availability. Funct Ecol 22:1044–1051

Thorogood R, Ewen JG, Kilner RM (2011) Sense and sensitivity: responsiveness to offspring signals varies with the parents' potential to breed again. Proc R Soc Lond B 278:2638–2645

Tschirren B, Fitze PS, Richner H (2003) Proximate mechanisms of variation in the carotenoid-based plumage coloration of nestling great tits (*Parus major* L.). J Evol Biol 16:91–100

Tschirren B, Fitze PS, Richner H (2005) Carotenoid-based nestling colouration and parental favoritism in the great tit. Oecologia 243:477–482

Uller T (2008) Developmental plasticity and the evolution of parental effects. Trends Ecol Evol 23:432–438

Walker LK, Armstrong DP, Brekke P, Chauvenet ALM, Kilner RM, Ewen JG (2013) Giving hihi a helping hand: assessment of alternative rearing diets in food supplemented populations of an endangered bird. Anim Conserv 16:538–545

Wolf JB, Wade MJ (2009) What are maternal effects (and what are they not)? Philos Trans R Soc Lond B 364:1107–1115