Parental care at the molecular level: the metabolic division of labour between parents and offspring

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Keywords

parental care; division of labour; metabolic labour; metabolism

Abstract

Parental care during offspring development has traditionally been viewed as a balance between cooperation and conflict. Offspring are imagined to be too helpless to find resources, or build protection, or generate warmth themselves. According to this view, the only work carried out by the offspring is through diverse acts of supplication for these vital resources. These are the traits, therefore, that have become the focus for analysing conflict with parents. Recent work analysing parental care at the molecular and metabolic level reveals that offspring have more agency than previously supposed and therefore that development should be seen as more of a shared endeavour. It involves a dynamic metabolic division of labour between parents and offspring, from before conception to independence, which can be precisely characterised at the molecular level. We propose a framework that classifies parental care at the molecular level into three broad areas: (1) resource transfer, (2) environmental buffering and protection, and (3) information transfer. This metabolic division of labour framework provides a common currency for understanding when cooperation tips into conflict

(and vice versa) by quantifying the precise costs and benefits of specific molecular transfers. The molecular approach generates insights into the evolution of the genetic pathways that underpin parental care and how parent-offspring conflicts are resolved at the biochemical level. It allows the blending of traditional theoretical approaches for analysing care with state-of-the-art comparative methods, based on -omics technologies. It therefore offers fresh insights into how adaptive parental care functions, why it persists, how it evolves and how it continues to contribute to evolution.

Main text

Parental care during offspring development has traditionally been viewed as a balance between cooperation and conflict. On the one hand, parents are performing acts of altruism, working to promote the growth and fitness of their current offspring but at some marginal cost to their own future fitness (Clutton-Brock, 1991). On the other hand, parents and offspring have divergent evolutionary interests that lead to evolutionary conflict over the supply of parental investment (Trivers, 1974), in which offspring are selected to demand more resources than parents are selected to supply. Offspring are imagined to be too helpless to find nourishment, or build protection, or generate warmth themselves, so must seek these essentials from their parents. According to this characterisation, the only work carried out by the offspring is through diverse acts of supplication for these vital resources. These are the traits, therefore, that have become the focus for analysing conflict with parents (Kilner & Johnstone, 1997; Kilner & Hinde, 2012) because even relatively helpless offspring are capable of demanding more resources than parents are selected to provide (Kilner & Hinde, 2012).

Here we show how parental care can be reframed at the molecular level and in terms of diverse metabolic processes. When recast in this way, parental care extends back to include epigenetic modification of gametes and extends forwards to include offspring physiology and behavioural differences that can be induced by parental condition. Seen in this way, offspring are given more agency and parental care becomes more of a shared endeavour involving a dynamic metabolic division of labour from gamete to independence. Offspring take on more and more labour as they near independence. The scope for cooperation and conflict between parents and offspring

thus extends beyond traits for soliciting parental resources. Furthermore, this reframing permits the use of -omics approaches to analyse and provide fresh insights into how parental care functions, why it persists, how it evolved in the first place and how it continues to contribute to evolution.

The metabolic division of labour between parents and offspring

Offspring growth and development involve costly metabolic processes that consume resources that might be allocated to other activities. Recent research suggests that parents and their offspring share the metabolic labour involved in ensuring the offspring's successful growth and development. The work starts at gamete production, a metabolic task borne solely by parents, and ends when offspring assume full metabolic independence, by which point parents are no longer involved. The extent of parental involvement varies widely across taxa. It can be limited to the well-provisioned eggs of marine broadcast spawners (Marshall et al., 2017), for example, or extend to the highly altricial young of mammals that are supported by parental metabolism throughout lengthy pregnancies and lactation periods (Kilner & Hinde, 2012). We consider three ways, which are not mutually exclusive, in which parents can bear some of the metabolic labour involved in their offspring's successful growth and development.

First, parents can help with the energy that offspring need to grow and develop effectively. This could be through a direct supply of energy, through egg yolk or milk for example, or it could be through more indirect means, by providing machinery to subsidise the offspring's energy needs, for example through the provisioning of ribosomes to eggs (Leesch et al., 2023).

Second, parents compensate for survival-related traits that are under-resourced when offspring allocate metabolic resources to growth and development. For example, parents might protect their young against pathogens by providing offspring with antimicrobial proteins while offspring immune defences are still poorly developed (Cotter & Kilner, 2010; Giacomello et al., 2006; Wellman-Labadie et al., 2008).

Finally, parents are a key source of information about risks and opportunities in the wider world to which offspring can flexibly and adaptively adjust their morphological,

physiological and behavioural development. Parents can supply this critical information at the molecular level, for example through hormones (Hinde et al., 2010) or antibodies against specific pathogens (Pullen et al., 2021), to their young while their offspring's mobility and sensory systems have not yet developed to gather information effectively themselves (Al-Shaer et al., 2016; Atherton & McCormick, 2020).

In short, we can classify the types of metabolic labour that parents share with offspring into three categories (Figure 1): (1) resource transfer, (2) environmental protection and buffering, and (3) information transfer.

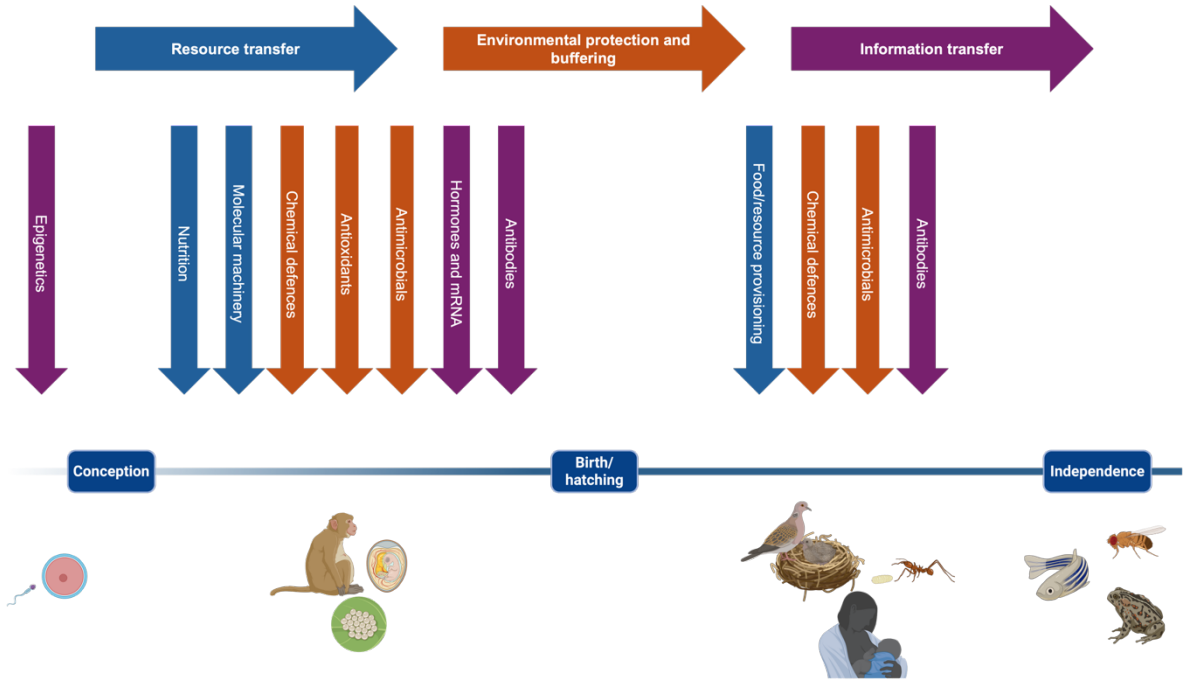

Figure 1: Examples of types of labour that are divided between parents and offspring during development. We classified these into three categories: 1) resource transfer (blue), 2) environmental protection and buffering (orange), and 3) information transfer (purple).

Resource transfer

Offspring require resources to complete growth and development successfully. Mothers provision offspring with specific metabolites, precursors, and sometimes molecular machinery (e.g. hibernating ribosomes) that save the offspring the costs of

production of relevant metabolites or the costs of producing the molecular machinery itself (Bladon, Hakala et al., 2024; Leesch et al., 2023). For example, to build a provisioned protein like a milk casein, the mother also needs to build up ribosomes for translations and acquire or produce the component amino acids, many of which have complex biosynthesis pathways involving several enzymes and cofactors. Cofactors, including several B vitamins, must also be biosynthesized or acquired from diet.

In viviparous and oviparous species, the energy and building blocks required for growth before birth or hatching are entirely provided by the mother in the form of nutrients via the placenta or yolk (Blackburn, 2021; Leesch et al., 2023; Ostrovsky et al., 2016; Safian et al., 2023). At this stage, the cells of the offspring's body begin to assume some of the labour of metabolising nutrients and in building up new molecular machinery and tissues during growth and development. After birth or hatching, parents can continue the labour of provisioning offspring with either unprocessed food or with more metabolically processed resources, such as milk, mucus, regurgitate or trophic eggs (Buckley et al., 2010; Hakala et al., 2023; Negroni & LeBoeuf, 2023; Perry & Roitberg, 2006).

Shifts in the composition and extent of parental provisioning over time reveal a change in division of labour between parent and offspring that are missed if only total provisioning levels are assessed (Galef, 1981; Mainwaring, 2016; Thornton & McAuliffe, 2006). For example, there are complex shifts in the composition of the social fluids that parents transfer to their young as offspring age and mature (Hakala et al., 2023; Morris et al., 2016; Stannard et al., 2020), with component molecules changing in their biosynthetic complexity and in their associated costs of production.

These examples illustrate one of the general advantages to be gained by focusing on care at the molecular level. Theoretical analyses of parental care mostly adopt the phenotypic gambit of quantifying care in terms of fitness gained and fitness lost (Clutton-Brock, 1991; Trivers, 1974). Although this is satisfyingly simple from a theoretical perspective, measures of fitness are notoriously difficult to quantify in reality (e.g. Merilä & Sheldon, 1999; Wolf & Wade, 2001). Measuring care at the molecular level bypasses some of these difficulties. There are at least three approaches that can offer an alternative common currency for assessing offspring and parental perspectives. Most simply, the value of the food passed between parent and offspring

can be quantified using calorimetry rather than the rougher estimate of number of food items or duration of feeding bouts, which have traditionally been reported (Gilby et al., 2011). A second, more granular approach focuses on identifying specific molecular components, including amino acids, proteins, lipids, small molecules and RNAs, and quantifying the number of enzymatic steps required to produce them (Nilsson et al., 2017). Taking such an approach reveals hidden costs borne by parents: they are not only providing nutrients to offspring but they are building custom formulas for offspring that require resource-guzzling molecular machinery to manufacture. A third approach employs bioenergetic techniques to measure the metabolic labour incurred by the different partners, such as through cellular respiration analysis (e.g. de Melo et al., 2025). It thereby tracks the cost to parents of producing particular molecules and measures their beneficial effect on offspring metabolism. Together, these three approaches provide a bridge to previous work on parental care, by generating new ways to the extent of conflict and cooperation within the family, whilst also offering new insights into the function and evolution of parental care.

Environmental protection and buffering

Many behavioural aspects of parental care function to protect the offspring from environmental or immunological threats (Beck et al., 2017; Brewster & Leon, 1980; Clutton-Brock, 1991; Ibáñez-Álamo et al., 2016; Penick & Tschinkel, 2008; Schowalter, 2016). At the molecular level, the strongest evidence is for buffering against pathogen and predation pressure. By exerting energy protecting their offspring, parents not only reduce the likelihood of offspring mortality, they also reduce the energy that offspring themselves must spend on environmental buffering and immunity.

For example, parents assist their offspring with defence from microscopic and chemical threats (Rutkowski et al., 2023), although the precise form of protection changes as offspring develop. Initially, it might involve antioxidants, small molecules and proteins transferred in the egg, which function to protect it against oxidative stress or pathogens. In the freshwater snail *Biomphalaria glabrata*, for example, parents transmit a bactericidal permeability-increasing protein that protects the egg against pathogenic water moulds (Baron et al., 2013). After laying, defence can include

parents spreading antimicrobial or antipredation substances on eggs or nests (Berasategui et al., 2022; Boos et al., 2014; D'Alba & Shawkey, 2015; Duarte et al., 2018; Estes et al., 2013). After hatching, parents of some species transfer antimicrobial substances and beneficial substances directly into the mouths of offspring through trophallaxis or indirectly by depositing substances onto the environment in which the offspring are developing (Diehl et al., 2015; Hakala et al., 2023; Potticary et al., 2024). Parents can also defend offspring from predators using chemical defences. For example, poison frog *Oophaga pumilio* mothers provision their offspring with alkaloids, which protect against spider predation (Stynoski et al., 2014). In many birds, for example great tits *Parus major*, mothers deposit carotenoids into their eggs that buffer embryos against oxidative stress (Watson et al., 2018). The transition from the mother assuming full labour for protecting offspring from pathogenic challenges in utero or in an egg, to assuming some responsibility by improving the microbial environment for offspring in a nest, to relinquishing all responsibility once the offspring disperses, is a clear example of how parental care represents a dynamic division of labour between parents and offspring.

Big data molecular techniques are especially valuable for assessing relative parent and offspring contributions to immune defence. Pairing transcriptomic and proteomic tools can dissociate production from presence of specific molecules such as antimicrobial peptides and lysozymes (Jacobs et al., 2016; Murakami et al., 2005; Reavey et al., 2014; Torati et al., 2017; Xiao et al., 2023). These can be paired with activity assays, for example, turbidity assays, to assess their function by determining the antimicrobial or enzymatic activity of fluids that are produced (Bladon et al., 2024; Cotter & Kilner, 2010; Duarte et al., 2021). Employing these methods at different stages during offspring development means we can elucidate when the division of labour tips from being parentally-biased to offspring-biased as development progresses, by comparing like with like. The common molecular currency facilitates detailed comparisons among families, among populations within species, and among species too. In species where parental care is facultatively supplied, they also make it possible to compare the metabolic load of offspring developing with and without parental care to measure the amount of labour undertaken by parents when they are present (Bladon, Hakala et al., 2024).

Information transfer

At every stage of offspring development, parents are information capacitors. They are a store of information about the wider world, which they may then release to their young in many ways, including at the molecular level. From the perspective of metabolic division of labour, parental information takes two main forms: direct provisioning and conditional cues.

Firstly, parents have valuable information about the world offspring may live in, and sometimes can support offspring by transferring such knowledge. In vertebrates, antibodies of the adaptive immune system prepare offspring for the specific viruses that they may encounter. In placental species, this immune priming begins as early as in utero, when maternal antibodies can transfer to the foetus via the placenta. In species where the placenta does not allow antibody transfer, ingestion of colostrum after birth serves the same function (Alonso-Alvarez & Velando, 2012; Chucri et al., 2010). In non-placental vertebrates, antibodies can be transferred via the egg. In birds, maternal immunoglobulins are transferred directly into the embryo's blood via the egg yolk (Boulinier & Staszewski, 2008). Maternally-derived antibodies help the offspring's body recognise and mount a response against infection by specific pathogens that the mother has encountered. Without these, the offspring might mount a much less precise innate immune response or else get infected by the new virus and develop its own antibodies, risking serious illness (Grindstaff, 2008). In a study in humans, infants breastfed for longer than 2 weeks had fewer enterovirus infections than those not breastfed, and breastfed infants whose mothers had higher enterovirus IgA levels in their breastmilk had fewer enterovirus infections before the age of 1 year than infants of mothers with lower levels (Sadeharju et al., 2007). Maternal antibodies are important for the offspring until it has the ability to mount its own immune response and produce its own antibodies (the timing of which varies greatly depending on body size and metabolism) (Grindstaff et al., 2003). Thus, antibody provisioning represents a metabolic division of labour whereby neonates can rely on their mothers' costly experiences of viral illness, immune memory and antibody production (Boulinier & Staszewski, 2008) until they are developed enough to protect themselves against viruses and build their own immunological catalogue of enemies.

As well as receiving direct help from their parents in defence against attack, offspring can gain information about likely threat through the condition of their parents. Shifting conditions often result in changes in the materials that parents transfer to their offspring which, in turn, have been shown to induce different offspring phenotypes. There are two ways in which parental condition can be a source of information to offspring, which differ in the extent of labour involved by parents. The least labour-intensive from the parent's perspective occurs when parental condition acts as a cue (so-called '**Condition-dependent effects')**. The information transferred to offspring is then simply a by-product of parental condition, perhaps stemming from physiological constraints. For example, if parents are in poor condition they might transfer fewer resources to offspring, which could act as a cue that induces a more 'frugal' phenotype in their young. In *Caenorhabditis elegans* the offspring of starved parents inherit small RNAs that target genes involved in nutrition, for instance (Rechavi et al., 2014). An alternative way of transferring information to offspring involves a greater level of investment by parents through the pro-active inclusion of additional metabolic compounds in the materials transferred to offspring (so-called '**Adaptive or anticipatory effects'**). In this scenario, the compounds are not merely by-products of parental condition but instead have evolved to function as signals that encode environmental information for optimising offspring development.

Current evidence suggests that condition-dependent effects are more common than adaptive anticipatory effects, with meta-analyses finding mixed or weak support for adaptive anticipatory parental effects across taxa (Uller et al., 2013). However, there are instances of adaptive effects operating through epigenetic mechanisms through both sperm and eggs (Chang et al., 2021; Lind et al., 2020; Sun et al., 2018; Weyrich et al., 2016). Whether information can also be transmitted adaptively to offspring after this stage is less clear. In humans, there is some evidence that information about nutrition can be transferred to the offspring *in utero* and during lactation. A review found that maternal diet during these periods influenced infant flavour preferences during infancy. However, whether this was adaptive, and led to beneficial weight outcomes in offspring, remains unclear (Ventura et al., 2021). In many studies to date, it is difficult to assess whether parents take on additional costs to encode information that offspring use. This metabolic division of labour framework may allow future researchers to identify these costs, if they exist.

We have described three functions linked to the metabolic division of labour and, thus far, have treated them as processes that are broadly independent. In reality, they can of course co-occur. For example, viviparity encompasses all three types of labour simultaneously. Through internal gestation, viviparous species integrate resource transfer (via placental or pseudo-placental structures), environmental buffering (through maternal thermoregulation, osmoregulation, and physical protection), and information transfer (through the parent's nervous system interacting with the environment). Viviparity has evolved independently more than 150 times across vertebrate lineages (Whittington et al., 2022), from poeciliid fishes (Furness et al., 2021) to sharks (Blackburn & Hughes, 2024) to mammals (Wildman et al., 2006). In contrast to oviparity, where parents front-load resources and hand over all metabolic labour to their offspring, viviparity's integrated management of all three metabolic division of labour categories may explain its repeated convergent evolution across the vertebrate tree of life. Furthermore, transitions to viviparous development have increased diversification rates in sharks (Mull et al., 2024) and influenced selection patterns in fish (Pollux et al., 2014). Perhaps the capacity to share metabolic labour with offspring, enabled by viviparity, has underpinned further evolutionary innovations.

Future prospects

Much of our current understanding of parental care results from successfully taking the phenotypic gambit to understand adaptive trait evolution. This approach has helped us understand why care persists, who provides care and how its supply is affected by cooperation and conflict. Now new tools for analysing care at the molecular level can provide more precise ways to measure variation in care, and can provide the empirical scope to make like-for-like comparisons among individuals, populations and species. This resolution at the molecular level draws organisms into scope that were previously thought to exhibit no 'caring behaviours' at all (e.g. broadcast spawners) and reveals the extent to which care is a metabolic division of labour between parents and offspring, with parallels to other animal societies that divide tasks among their members (cf Cooper & West, 2018). Offspring are shown to be active participants in this joint enterprise at an earlier stage than previously appreciated, while the effects of parents can linger longer into the offspring's life than previously realised, due to

mechanisms that can potentially reach across the generations. The stage is thus set for a new generation of work that focuses on function, mechanism and evolution, whilst building on the existing adaptive framework for understanding parental care.

Author contributions

All authors made significant contributions to the conceptual development of the manuscript. EKB drafted the initial manuscript. All authors contributed to later versions of the manuscript.

Funding

EKB was supported by post-doctoral funding to RMK from the Department of Zoology, University of Cambridge. ACL received a Human Frontier Science Programme Grant (RGP0023/2022).

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