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Maternal allocation in cooperative breeders: should mothers match or compensate for expected helper contributions?

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Among species with variable numbers of individuals contributing to offspring care, an individual's investment strategy should depend upon both the size of the breeding group and the relative contributions of each carer. Existing theoretical work on carer investment rules has, however, largely focused on biparental care, and on modelling offspring provisioning in isolation from other stages of investment. Consequently, there has been little exploration of how maternal investment prior to birth might be expected to influence carer provisioning decisions after birth, and how these should be modified by the number of carers present. In particular, it is unclear whether mothers should increase or decrease their investment in each offspring under favourable rearing conditions, and whether this differs under alternative assumptions about the consequences of being ‘high quality’ at birth. We develop a game-theoretical model of cooperative care that incorporates female control of prebirth investment, and allow increased maternal investment to either substitute for later investment (giving offspring a ‘head start’) or raise the value of later investment (a ‘silver spoon’). We show that mothers reduce prebirth investment under better rearing conditions (more helpers) when investment is substitutable, leading to concealed helper effects. In contrast, when maternal prebirth investment primes offspring to benefit more from postbirth care, mothers should take advantage of good care environments by investing more in offspring both before and after birth. These results provide novel mechanisms to explain contrasting patterns of maternal investment across cooperative breeders.

Classic life history theory dictates that mothers should vary their investment in reproduction according to both current ecological conditions and the potential for future reproduction (Stearns, 1992; Williams, 1966), and that this investment can be used to produce either large numbers of small offspring or small numbers of large offspring, generating an offspring size–number trade-off (Lack, 1947; Roff, 2002; Williams, 2001). More recently, evidence has accumulated that mothers can also tactically vary their level of investment in each offspring prior to birth, independently of the number of offspring produced, to better match the potential benefits of current conditions (Cunningham & Russell, 2000; Fox, Thakar, & Mousseau, 1997; Verboven et al., 2003). When the fitness of offspring is determined by the total investment they receive across all stages of their development, mothers can tactically increase prebirth investment and compensate for poorer rearing conditions (e.g. Bolund, Schielzeth, & Forstmeier, 2009), or reduce it and transfer costs to other carers (e.g. Russell, Langmore, Cockburn, Astheimer, & Kilner, 2007). However, the assumption that investment can be easily substituted across stages may not always hold, for example if offspring that are larger at birth are more likely to survive the rearing period (Williams, 1994), or more likely to become dominant as adults (Royle, Lindström, & Metcalfe, 2005), as this will increase the value of caring for them after birth. Similarly, if larger offspring require more food during development, higher prebirth investment may require higher postbirth investment for the potential benefits of larger size to be realized. The potential for this ‘dynamic complementarity’ (sensu Heckman, 2007) between the value of investment across developmental stages has thus far been largely overlooked in the literature on parental care.

Cooperative systems provide an excellent test of adaptive plasticity in maternal allocation strategies because helper number represents a highly variable aspect of current ecology that has predictable effects on maternal fitness (Russell & Lummaa, 2009).

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Larger groups are capable of delivering more food to the breeding female and/or offspring than smaller groups, and so mothers can gain higher breeding success with more helpers. However, group sizes are rarely static, and the number of helpers available will vary both spatially and temporally. Interestingly, across species mothers appear to invest differently in their offspring prebirth in response to variation in helper number. For example, in studies of cooperative meerkats, *Suricata suricatta* (Russell, Brotherton, McIlrath, Sharpe, & Clutton-Brock, 2003), increasing helper number indirectly increases pup mass at burrow emergence, as helpers boost maternal weight at conception, and heavier mothers produce heavier pups. By contrast, in fish species (Taborsky, Skubic, & Bruintjes, 2007) and a range of birds (Canestrari, Marcos, & Baglione, 2011; Paquet, Covas, Chastel, Parenteau, & Doutrelant, 2013; Russell, Langmore, et al., 2007; Santos & Macedo, 2011), studies have generally reported a reduction in prebirth investment with increasing group size (for an exception see Koenig, Walters, & Haydock, 2009), without a corresponding change in the number of offspring produced.

Here, we present a formal model of how females breeding in cooperative groups should alter their prebirth investment in offspring as group size changes. We hypothesize that the key influence on maternal strategy is the relationship between prebirth investment and later outcomes for offspring, with this determining whether mothers enjoying good conditions (i.e. more helpers) should invest more to exploit current conditions, or save resources to increase their future survival probability. To this end, we explore two possible effects of increased maternal investment on outcomes for offspring: a ‘head start’ relationship under which greater prebirth investment leads to lower postbirth investment from the entire care group (Paquet et al., 2013; Russell, Langmore, et al., 2007), and a ‘silver spoon’ relationship under which prebirth investment has long-term effects on offspring phenotype (Eising, Müller, & Groothuis, 2006; Strasser & Schwabl, 2004), but may lead to greater demands during rearing, for example if larger offspring require more food (Clutton-Brock, Albon, & Guinness, 1985; Klaassen & Bech, 1992). This approach contrasts with previous theoretical work on parental care, which has focused on either postbirth investment in isolation (Houston & Davies, 1985; McNamara, Gasson, & Houston, 1999) or maternal control of offspring number rather than offspring ‘quality’ (Savage, Russell, & Johnstone, 2013a, 2013b).

The ‘head start’ and ‘silver spoon’ paradigms lead to different predictions about how mothers should alter prebirth investment in offspring in response to favourable breeding conditions. When maternal investment gives offspring a ‘head start’, total investment in offspring should remain similar across a range of group sizes (Russell, Langmore, Gardner, & Kilner, 2008), as only the sum of investment across the pre- and postbirth stages is important. Previous work by Hatchwell (1999) has shown that in cooperative bird species parents compensate for the presence of helpers (when nestling starvation is rare) by reducing their provisioning rate, and a similar argument can be applied to prebirth investment when it has no indelible effects on offspring fitness (Russell, Langmore, et al., 2007). Conversely, we predict mothers should increase prebirth investment with group size when higher early investment leads to lasting advantages for offspring by providing a ‘silver spoon’ that complements future investment. This strategy probably occurs in meerkats, in which greater numbers of helpers indirectly lead to both higher offspring weights at emergence (Russell et al., 2003) and an increased probability of offspring breeding once mature (Russell, Young, Spong, Jordan, & Clutton-Brock, 2007). Unlike a ‘head start’ relationship, offspring that receive greater maternal investment may suffer during poor rearing conditions (Oksanen, Jokinen, Koskela, Mappes, & Vilpas, 2003) under a ‘silver spoon’ relationship, as prebirth investment interacts with postbirth investment, rather than simply adding to it.

Our primary aim in this article is to provide a theoretical explanation for the range of maternal tactics found in the empirical literature, by exploring how breeding conditions (specifically group size), the costs of producing and rearing offspring, and the ultimate benefits to offspring interact to generate different optimal maternal tactics. The scope for these maternal tactics will be constrained by the relative importance of pre- and postbirth investment in the species in question, and so we also explore how altriciality and precociality influence our model predictions under different breeding conditions. Further complications arise through species differences in dispersal, leading to paternal and/or maternal-related helpers, as the latter benefit more from removing costs from the breeding female (Savage et al., 2013a). Although our model is framed in terms of cooperative breeding systems, with group size as the environmental variable, our results generalize to other environmental factors, in biparental or cooperative systems (e.g. mate quality, weather, food availability), that are predictable within the timescale of a single breeding attempt (Burgess & Marshall, 2014).

THE MODEL

We model a cooperative breeding attempt as a two-step process involving a breeding pair and a variable number of helpers. The female first chooses the amount of investment delivered to the offspring prebirth, and then the whole group plays a standard ‘sealed bid’ investment game (sensu Houston & Davies, 1985) to determine their individual investment levels during the offspring rearing period. Our model follows a similar two-step structure to Savage et al. (2013b), but explores maternal control of offspring ‘quality’ rather than the number of offspring produced. Previous theoretical work has not investigated how parental care should differ when prebirth investment varies in its downstream effects on offspring, or how variation in the importance of pre- and postbirth investment should influence carer decisions. Consequently, our model focuses on two possible relationships between prebirth and later investment, termed ‘head start’ and ‘silver spoon’, and on the degree of altriciality, while leaving offspring number fixed. Empirical studies support this approach by generally reporting no adjustment of offspring number when offspring ‘quality’ is found to vary (e.g. Russell, Langmore, et al., 2007; Taborsky et al., 2007; Santos & Macedo, 2011; Canestrari et al., 2011). In our model we use the generic term ‘quality’ to represent any characteristic of offspring that is both observable by all carers and potentially related to the need for care (e.g. offspring size or activity level at birth). All calculations and plots were made using Wolfram Mathematica (v7.01, Wolfram Research, Long Hanborough, U.K.), and all solutions are analytical.

The cooperative group consists of H helpers and a breeding pair (female and male). All group members choose their level of investment in offspring care during the second, postbirth step with full knowledge of the investment made by the female during the first, prebirth step. In empirical terms this represents nonmaternal carers being able to accurately assess the relevant aspect(s) of offspring ‘quality’ shortly after they are first able to contribute to care: this may be immediately after birth (as in many cooperative birds), or after some postbirth development if mothers initially care for offspring alone (e.g. cooperative mammals without allolactation). The breeding female and male are related to helpers by the relatedness parameters r_{fh} and r_{mh}, respectively, are unrelated to each other, and are each related to the offspring by $r_{\mathrm{fo}} = r_{\mathrm{mo}} = 0.5$. Helpers are assumed to be identical to each other in their cost parameters and relatedness to other group members, and are related to each other by r_{hh} and to the offspring by r_{ho}.