Animal Behaviour 102 (2015) 189–197

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

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ARTICLE INFO

Article history:
Received 30 July 2014
Initial acceptance 16 September 2014
Final acceptance 8 December 2014
Available online 18 February 2015
MS. number: 14-00618R

Keywords:
cooperative breeding
game theory
maternal effects
parental care
reproductive investment

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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http://dx.doi.org/10.1016/j.anbehav.2015.01.015
0003-3472/

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}.

To find stable investment levels for all individuals during the rearing period, we first calculate the response of all individuals to any quality of offspring the female could produce. All individuals simultaneously choose an investment level x during the postbirth rearing stage, termed $x_{\mathrm{f}}, x_{\mathrm{m}}$ and x_{h}^{i} for the female, male and ith helper, respectively. Cost parameters $(k_{\mathrm{q}}, k_{\mathrm{f}}, k_{\mathrm{m}}, k_{\mathrm{h}})$ specify the relative costs of the female quality investment, and of the female, male and helper rearing investments, respectively. The total costs incurred by the breeding female, denoted c_{f}, are assumed to be a function of her prebirth investment in offspring quality, denoted q, and her postbirth investment during offspring rearing, denoted x_{f}. Males and helpers only contribute during offspring rearing, so their costs, denoted c_{m} and c_{h}, are simply a function of their postbirth investments. For all carers, costs accelerate with increasing investment:

$$c_{\mathrm{f}} = \left(k_{\mathrm{q}} \cdot q^2 + k_{\mathrm{f}} \cdot x_{\mathrm{f}}^2\right)$$

$$c_{\mathrm{m}} = \left(k_{\mathrm{m}} \cdot x_{\mathrm{m}}^2\right)$$

$$c_{\mathrm{h}}^{i} = \left(k_{\mathrm{m}} \cdot x_{\mathrm{h}}^{i2}\right)$$

Offspring are assumed to share the investment of the carers equally, and as such are modelled as a unit. We assume that the resulting fitness of offspring after both investment stages (b) is a function of both the mother's prebirth investment in offspring quality (q) and the total postbirth rearing investment (x_{com}), which is the sum of the rearing contributions of the female, male and all helpers:

$$x_{\mathrm{com}} = x_{\mathrm{f}} + x_{\mathrm{m}} + \sum_{i=1}^{H} x_{\mathrm{h}}^{i}$$

$$b(q, x_{\mathrm{com}}) = k_{\mathrm{b}} \cdot \Big(((1-v) \cdot x_{\mathrm{com}} + v \cdot k_{\mathrm{a}} \cdot q - x_{\min}) - ((1-v) \cdot x_{\mathrm{com}} + v \cdot k_{\mathrm{a}} \cdot q - x_{\min})^2 \Big) (1+q)^n$$

The parameters k_{a} and n together control whether prebirth investment conveys a ‘head start’ or a ‘silver spoon’ to offspring. When offspring receive a ‘head start’, investment is substitutable between pre- and postbirth development stages, and hence there are no ‘silver spoon’ effects present $(n = 0)$ and greater maternal investment reduces the need for rearing investment $(k_{\mathrm{a}} = 1)$. This represents (for example) offspring that are large at birth reaching a larger size more quickly (Quillfeldt & Peter, 2000), or those born smaller requiring greater rearing investment to reach independence (Russell et al., 2008). Conversely, when offspring receive a ‘silver spoon’, prebirth investment is not substitutable because it raises the benefit offspring receive if reared successfully $(n = 1)$. Under the ‘silver spoon’ paradigm, high prebirth investment may benefit offspring by substituting for postbirth investment $(k_{\mathrm{a}} = 1)$ for the same reasons given above, or may have no direct effect on postbirth investment needs $(k_{\mathrm{a}} = 0)$. Alternatively, if high-quality offspring are ‘primed’ for greater future investment and suffer under poor rearing conditions (Monaghan, 2008; Oksanen et al., 2003), or if high-quality offspring are larger with greater energetic needs (Klaassen & Bech, 1992), prebirth investment might increase postbirth demand $(k_{\mathrm{a}} = -1)$. Our aim in this study is to compare cases in which greater maternal prebirth investment either reduces or increases the marginal value of later investment during the rearing period, and consequently we focus on ‘silver spoon’ cases in which $k_{\mathrm{a}} = -1$, to more clearly contrast with the ‘head start’ case. The specific offspring benefit functions for the ‘head start’ (b_{HS}) and ‘silver spoon’ (b_{SS}) relationships are hence:

$$b_{\mathrm{HS}}(q, x_{\mathrm{com}}) = k_{\mathrm{b}} \cdot \Big(((1-v) \cdot x_{\mathrm{com}} + v \cdot q - x_{\min}) - ((1-v) \cdot x_{\mathrm{com}} + v \cdot q - x_{\min})^2 \Big)$$
$$b_{\mathrm{SS}}(q, x_{\mathrm{com}}) = k_{\mathrm{b}} \cdot \Big(((1-v) \cdot x_{\mathrm{com}} - v \cdot q - x_{\min}) - ((1-v) \cdot x_{\mathrm{com}} - v \cdot q - x_{\min})^2 \Big) \cdot (1+q)$$

Offspring are assumed to benefit from care only above a minimum level of investment $x_{\min}$. The first derivative of the offspring benefit function is assumed to be positive above this threshold, such that greater investment benefits offspring, while the second derivative is negative, implying diminishing returns on investment. For simplicity we use a quadratic function, weighted by benefit parameter k_{b}.

Three other parameters are needed to capture how investment influences outcomes for offspring: (1) the importance of prebirth investment relative to postbirth investment (i.e. how altricial or precocial the species is), termed v; (2) whether prebirth investment increases or decreases offspring demand postbirth, termed k_{a}; and (3) the strength of any prebirth ‘silver spoon’ effects (Grafen, 1988) that boost the value of later investment, termed n. The v parameter controls the relative benefit to the offspring of investment delivered pre- and postbirth, and is used to explore cases in which prebirth investment in initial offspring quality and investment during offspring rearing may not be equally valuable to offspring. The n parameter functions by multiplying the offspring benefit function by $(1+q)^n$, to represent a lasting positive effect on offspring reared successfully. To summarize, the generic offspring benefit function is:

To assist in visualizing the differences between the above ‘silver spoon’ and ‘head start’ functions, we generate a plot of how offspring benefit (b) changes with offspring quality (q) and total investment (x_{com}) under typical model parameters (Fig. 1).

To find optimal investment rules for all carers under these different benefit functions, we assume that each carer attempts to maximize a weighted sum of the benefit to the offspring (weighted by the relatedness of offspring to the carer), minus the carer's own costs of care, minus the costs borne by other related carers (again weighted by relatedness to those carers). These maximands are given by $w_{\mathrm{f}},\ w_{\mathrm{m}}$ and w_{h}^{i} for the breeding female, breeding male and ith helper, respectively:

$$w_{\mathrm{f}} = r_{\mathrm{fo}} \cdot b(q, x_{\mathrm{com}}) - c_{\mathrm{f}} - r_{\mathrm{fh}} \cdot \sum_{i=1}^{H} c_{\mathrm{h}}^{i}$$

$$w_{\mathrm{m}} = r_{\mathrm{mo}} \cdot b(q, x_{\mathrm{com}}) - c_{\mathrm{m}} - r_{\mathrm{mh}} \cdot \sum_{i=1}^{H} c_{\mathrm{h}}^{i}$$

$$w_{\mathrm{h}}^{i} = r_{\mathrm{ho}} \cdot b(q, x_{\mathrm{com}}) - c_{\mathrm{h}}^{i} - r_{\mathrm{fh}} \cdot c_{\mathrm{f}} - r_{\mathrm{mh}} \cdot c_{\mathrm{m}} - r_{\mathrm{hh}} \cdot \sum_{i=1}^{H-1} c_{\mathrm{h}}^{i}$$

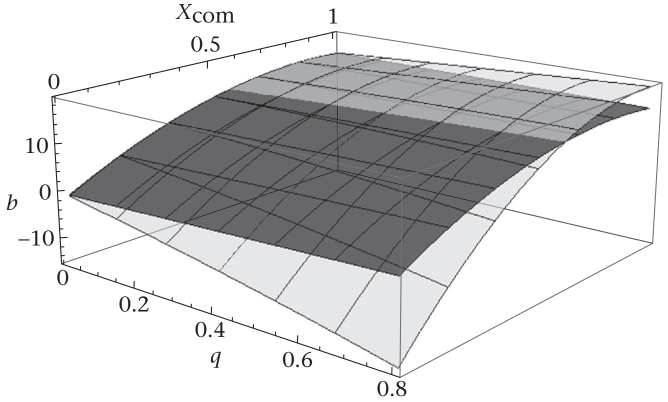

Figure 1. Plot of how offspring benefit (b) changes with differing levels of prebirth maternal investment (q) and total rearing investment (x_{com}) under the assumptions that maternal investment gives offspring either a 'head start' (dark grey surface) and is substitutable with rearing investment, or a 'silver spoon' that results in higher-quality offspring requiring more care but gaining greater fitness if successfully reared (light grey surface). Values of offspring benefit are arbitrary, and are relative to typical parameters plotted in the Results section.

Solving the Model

All carers make a simultaneous choice of investment level after the initial stage, based on the level of offspring quality q chosen by the female. At equilibrium no carers should be able to alter their maximands by changing their investment levels, i.e.:

$$\frac{\partial w_f}{\partial x_f} = \frac{\partial w_m}{\partial x_m} = \frac{\partial w_h^i}{\partial x_h^i} = 0$$

The resulting equilibrium investment rules are termed $\hat{x}_f$, $\hat{x}_m$ and $\hat{x}_h^i$ for the female, male and helpers, respectively; all helpers are assumed to behave identically as they all have the same cost and benefit functions. These investment rules depend only on the quality variable q and the model parameters, so at equilibrium:

$$x_f = \hat{x}_f(q),\ x_m = \hat{x}_m(q),\ x_h^i = \hat{x}_h(q)$$

Finally, we substitute the above equilibrium investment rules back into the female maximand to determine her optimum choice of offspring quality in the first step. At equilibrium the female should not be able to increase her maximand by altering q:

$$\frac{\partial w_f\left(\hat{x}_f(q), \hat{x}_m(q), \hat{x}_h(q)\right)}{\partial q} = 0$$

Solving the above gives us rules for q, x_f, x_m and x_h at equilibrium that depend only on the extrinsically specified cost, benefit and relatedness parameters.

RESULTS

Prebirth Investment as a 'Head Start'

We first consider cases in which initial female investment in offspring quality is both substitutable with later rearing investment and of similar value, so that it gives offspring an effective 'head start' towards a given level of total investment ($k_a = 1, n = 0, v = 0.5$). Under these circumstances, our model predicts that breeding females should reduce investment in offspring quality when greater numbers of helpers are present (Fig. 2a), as they are then able to reduce their personal costs without major negative effects to the offspring, thanks to compensation by other carers. Carers are all predicted to reduce their rearing-stage investment with increasing helper number, demonstrating 'load lightening' (Crick, 1992), with the decline being most noticeable with groups of full-sibling helpers because these invest the most when group size is small (Fig. 2b). The breeding male behaves similarly to a single full-sibling helper during the rearing period, although his presence or absence has a greater influence on maternal strategy than does a single full-sibling helper, because the mother avoids exploiting related carers to the same degree as those to whom she is unrelated.

The total amount of investment delivered by all carers during the rearing period increases with helper number (Fig. 2c), and is slightly greater for helpers related to offspring through the breeding male than for those related through the breeding female, owing to the female adopting a more exploitative prebirth investment strategy when helpers are unrelated to her. The increase in rearing investment with group size is largely masked by the reduction in prebirth investment by the female, leading to little change in total investment delivered to offspring (Fig. 2d). Together these results support the helper compensation hypothesis, which suggests that mothers should reduce early stage investment in offspring when in larger groups because helpers are able to compensate, and that this can conceal the positive effects of helpers on offspring when the rearing period is studied in isolation.

Effects of Altriciality/Precociality

Under 'head start' conditions ($k_a = 1, n = 0$), we can change the value parameter v to compare investment rules between systems in which prebirth investment or postbirth investment is relatively more valuable to the offspring. High values of v (≈ 0.9) represent either a sensitive period during early development that can only be effectively supported by prebirth maternal investment or a relatively unimportant rearing period (as might occur in a highly precocial species). Low values of v (≈ 0.1) represent cases in which early variation in investment is largely unimportant or offspring are altricial with a long development before independence, and hence are influenced far more by investment during the rearing period. An intermediate value of v (≈ 0.5) represents variation in investment during either stage being equally effective in altering the resulting offspring benefits. The relative effectiveness of investment between the two stages strongly influences the patterns of investment seen, with a female's investment in offspring quality predictably peaking when her early investment is highly valuable (Fig. 3a). Individual helpers invest more in small groups than in large groups, and as rearing investment becomes less effective helpers initially invest more (in order to continue delivering similar benefits to offspring), but eventually reduce investment when the meagre benefits to offspring can no longer offset the costs incurred by carers (Fig. 3b). Total rearing investment delivered to offspring peaks when rearing investment is only moderately effective, as the greater requirements of the offspring elicit greater contributions from the carers provided that the group is large enough to support them (Fig. 3c). Total investment in offspring across both breeding stages likewise peaks at intermediate levels of precociality, with group size having a clear effect only when rearing investment is less effective and hence more costly for small groups to provide in sufficient quantity (Fig. 3d).

Prebirth Investment as a 'Silver Spoon'

When higher-quality offspring require more investment during rearing, but do better in adulthood if their needs are met ($k_a = -1, n = 1$), breeding females increase their prebirth

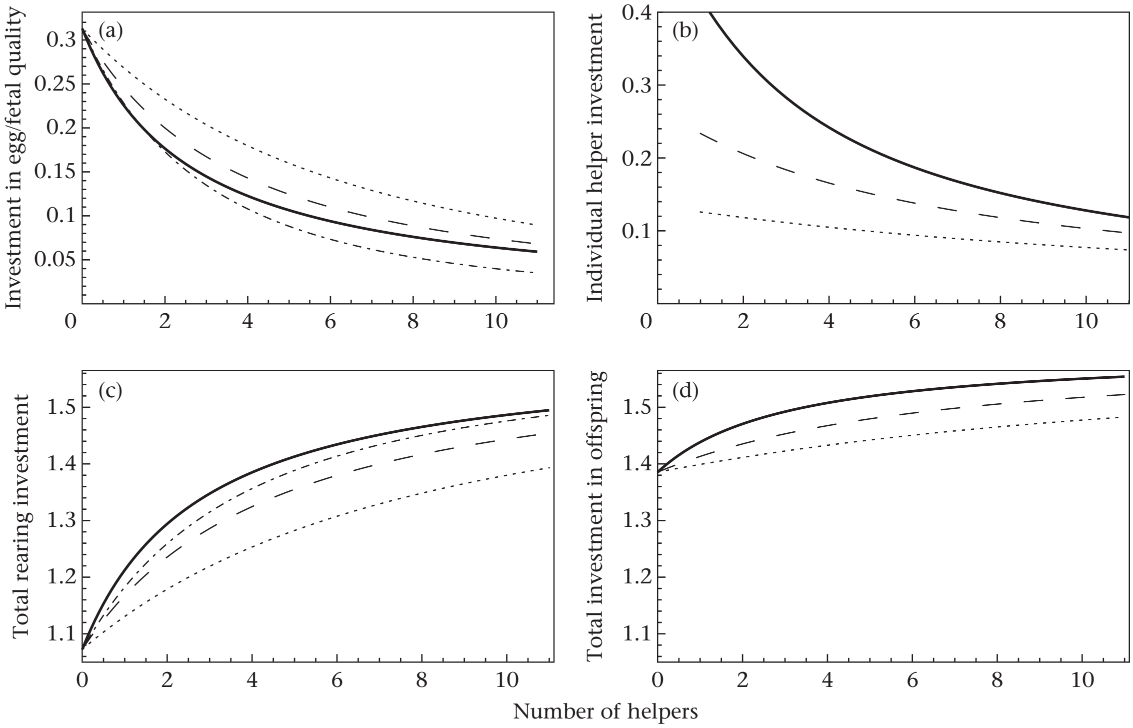

Figure 2. (a) Under 'head start' investment conditions, maternal prebirth investment decreases with increasing group size, as helpers are able to take on a greater proportion of the total investment required by offspring. Breeding females invest less with helpers that are full siblings to the offspring (solid line) than with half-sibs (dashed line = maternally related; dot-dashed line = paternally related) or cousins (dotted line), because closely related helpers are more willing to deliver more care later in the breeding attempt. (b) Individual helper rearing investment declines with group size as helpers 'load-lighten' each other; this decline is more obvious the more closely related helpers are to offspring as distantly related helpers always invest little and thus have little scope to reduce costs (in this plot the paternally related half-sib line is omitted for clarity, as it very closely overlaps maternally related half-sibs). (c) The total investment delivered to offspring during the rearing period increases with group size as helpers compensate for the lowered investment of the mother; full-sibling helpers lead to greater total investment than half-sibs or cousins. (d) Total investment in offspring over the breeding attempt (initial female investment + rearing investment) increases with group size regardless of the type of helper in the group, and despite the reduction in female investment, but the effect is very small as a proportion of total investment delivered and hence might be overlooked empirically. Values of investment levels are arbitrary.

investment in offspring quality as helper number increases (Fig. 4a). This effect occurs because more helpers can more easily feed larger, higher-quality offspring and hence take advantage of the greater potential benefit that arises when they are sufficiently provisioned. Higher investment in initial offspring quality leads to higher rearing investment to offset the hungrier offspring and to deliver the greater potential benefit of the 'silver spoon', and as a consequence maternal prebirth investment is highest when the care group comprises half-sibling helpers that are related to offspring through the breeding male, because the mother avoids taxing related carers with high costs (Fig. 4a).

As with 'head start' conditions, under 'silver spoon' conditions helpers of all types reduce their individual investment as group size increases ('load lightening'; Fig. 4b). This may, however, be a negligible reduction in groups with distantly related helpers. As a result, total rearing investment by the group still increases with group size, but in contrast to 'head start' conditions, groups comprising breeding-male-related half-sibs match or exceed the investment of full-sib helper groups (Fig. 4c). This effect arises because (1) helpers unrelated to the breeding female do not care if she pays high costs during the breeding attempt, and (2) under 'silver spoon' conditions high investment during the rearing stage is most valuable when paired with high initial investment by the mother, leading to her paying very high costs when there are many carers. Total investment in offspring increases more obviously with group size under 'silver spoon' than under 'head start' (Fig. 4d) conditions, because of the lack of maternal/helper compensation and greater potential benefits of high group size.

Recruiting Additional Helpers

The benefit accrued by offspring from adding another helper to the group varies depending on whether 'head start' or 'silver spoon' conditions apply. Under 'head start' the benefit is greater for small groups than for large groups, and greater when helpers are more closely related to offspring as they are more willing to provide care (Fig. 5a). The level of altriciality also has an influence: when rearing investment is less important to offspring (i.e. in more precocial species), the presence of an additional helper predictably conveys little benefit, as the new helper is unable to meaningfully change the effective investment received. However, offspring in highly altricial species benefit less from an additional helper than do offspring in moderately altricial species, because (1) small groups can deliver high benefits to offspring when rearing investment is highly valuable, leaving little scope for helper effects beyond load lightening, and (2) the female is unable to split her costs efficiently between both investment stages when her investment in offspring quality is essentially meaningless (Fig. 5b).

Under 'silver spoon' conditions (Fig. 5b), the benefits to offspring of recruiting an additional helper are much greater than under 'head start', as helpers can increase offspring benefit even in large groups. The extra available care during the rearing period can be directed (via increased maternal prebirth investment) towards larger, hungrier, but potentially more valuable offspring, rather than simply reducing the costs of other carers through load lightening. As with 'head start' conditions the benefits are greatest with small groups and with closely related helpers, but under 'silver

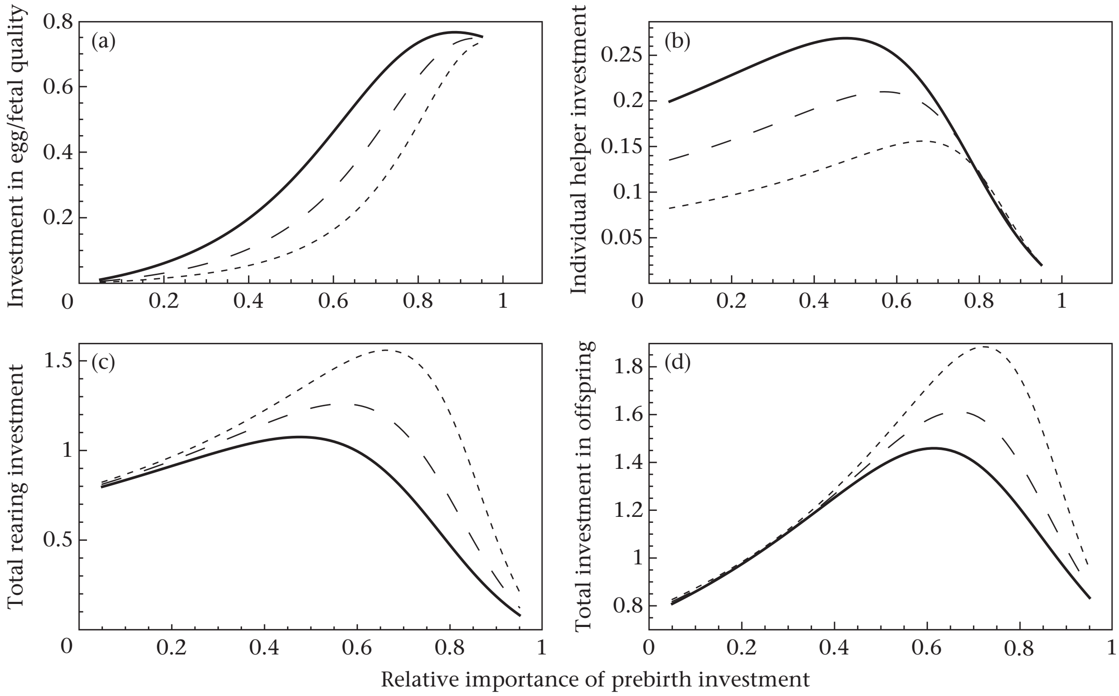

Figure 3. (a) Under ‘head start’ conditions, investment in offspring quality is generally greater when early stage maternal investment is more valuable to young (precocial species), but decreases with extremely important early investment as other carers struggle to deliver any benefits and the female cannot efficiently split her costs between the stages. Quality investment decreases with increasing group size (3 = solid line, 6 = large dashes, 9 = small dashes), but peaks when early investment is more valuable in larger groups. (b) Helper investment is greatest when investment is similarly valuable across the stages, and larger groups peak when rearing investment is less valuable. Helpers generally work harder in small groups (solid line) than intermediate (large dashed line) or large (small dashed line) groups, but only when rearing investment is similarly or more valuable than early investment: when early investment is critical and rearing investment unimportant more helpers have little effect. (c) Total rearing investment is lower in smaller groups than in larger groups, but diverges more and peaks at higher levels of precociality in larger groups: this is because large groups can support the high investment levels needed to benefit offspring meaningfully even when unit investment is of low value. (d) Total investment in offspring is largely invariant with group size when prebirth investment is unimportant, when maternal investment is highly valuable large groups deliver substantially more investment to offspring.

spoon’ conditions the difference between adding a closely or distantly related helper is reduced.

DISCUSSION

We find clear differences depending on whether maternal prebirth investment is substitutable (‘head start’) or complementary (‘silver spoon’) with postbirth offspring care, both in the investment strategies adopted by carers and in how offspring benefit. Mothers are expected to reduce prebirth investment under good rearing conditions when their investment gives offspring a ‘head start’, as this reduction can be compensated for later. In contrast, when prebirth investment provides a ‘silver spoon’ that leads to potentially greater offspring fitness if they are reared successfully, mothers should take advantage of good conditions by increasing prebirth investment.

Our results provide support for the concealed helper effects hypothesis (sensu Russell, Langmore, et al., 2007) when prebirth investment is substitutable with investment during the rearing period (the ‘head start’ condition). Mothers are predicted to reduce their investment in offspring quality at the production stage when more helpers are present, and helpers should respond by increasing their investment during offspring rearing, leading to the total amount of care delivered to offspring remaining similar across a range of group sizes (Russell et al., 2008). This female tactic raises the possibility that empirical studies focusing on the rearing period alone might erroneously conclude that large numbers of helpers can deliver additional investment to offspring without any positive effect, when in reality the helpers are greatly reducing the overall costs paid by the breeding female across the breeding attempt (Russell & Lummaa, 2009).

Concealed helper effects are predicted to arise whenever investment is substitutable between offspring investment stages, but in practice several aspects of ecology or life history may limit the scope for mothers to make this substitution. In particular, maternal tactics will be less important when group size or helper helpfulness is unpredictable at the time when the mother produces the offspring (i.e. there is an unknown supply of care), for example if helpers are failed breeders that arrive partway through the breeding attempt. Similarly, there is little scope for maternal tactics when the future conditions during the breeding attempt are unpredictable, making the costs of delivering care difficult to forecast. Furthermore, in some systems the final quality of offspring may be unaffected by early investment (e.g. Van De Pol, Bakker, Saaltink, & Verhulst, 2006), represented in our model by a very low *v*, and in others extra carers may only contribute by reducing predation or defending the territory (Burt & Peterson, 1993) rather than removing quantitative costs of care from the breeding pair; in both cases the female should theoretically produce the minimum viable quality of young. The opposite case, of maximal investment in offspring quality, should be expected when breeding females are highly unlikely to breed again, and hence benefit little from increasing their own survival probability beyond the current breeding season (Clutton-Brock, 1984). The contrasting predictions of ‘head start’ and ‘silver spoon’ prebirth investment will hence interact with maternal survival probability (and her likelihood of remaining dominant) to determine whether mothers match or compensate for current conditions. For example, a healthy mother secure in her breeding position has less incentive to invest heavily

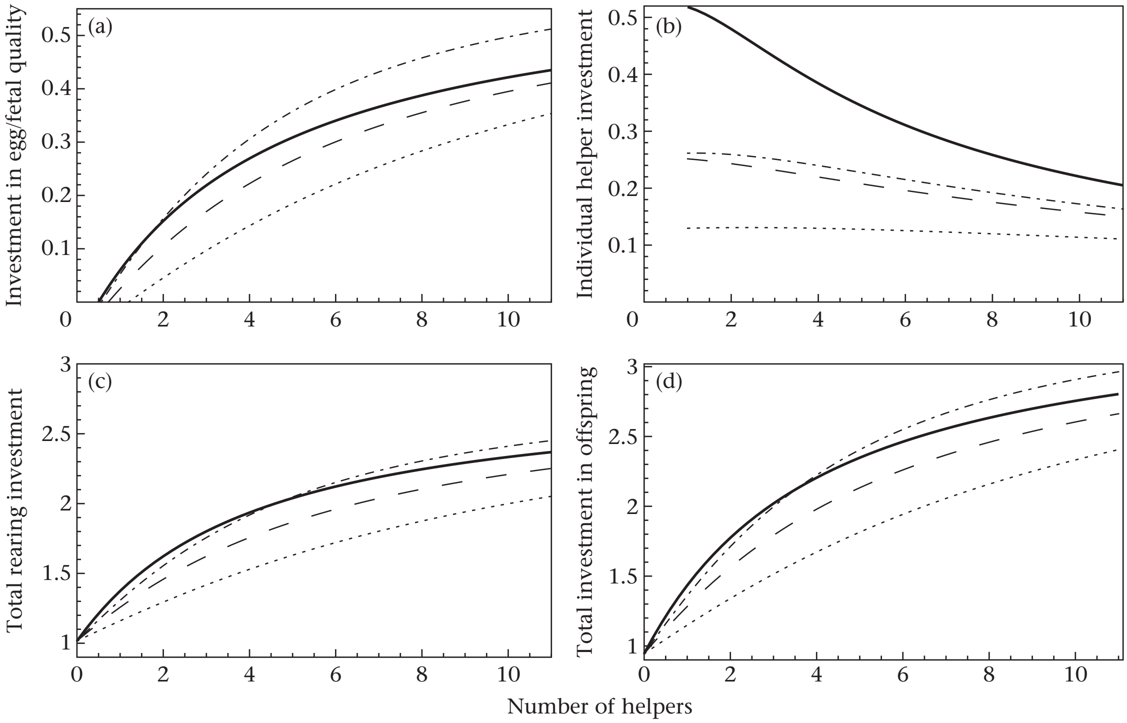

Figure 4. (a) When larger offspring require more food but gain greater benefits from investment (a 'silver spoon'), mothers increase investment in offspring quality as group size increases. The increase is largest when helpers are half-siblings to offspring and unrelated to the mother (dot-dashed line); however, mothers invest less with half-sib helpers related through her (dashed line) than with full-sib helpers (solid line). (b) All helpers load-lighten with increasing group size, with closely related helpers reducing the most. Groups with paternally related half-sibs contribute slightly more than those with maternally related half-sibs owing to the female adopting a more exploitative prebirth investment strategy. (c) Total rearing investment is lower in smaller groups than in larger groups, but diverges more and peaks at higher levels of precociality in larger groups: this is because large groups can support the high investment levels needed to benefit offspring meaningfully even when unit investment is of low value. (d) Total investment in offspring is largely invariant with group size when prebirth investment is unimportant, but when maternal investment is highly valuable large groups deliver substantially more investment to offspring.

in a 'silver spoon' for offspring, and hence should exhibit less matching than an equivalent mother with a lower confidence of future reproduction.

When mothers can provide a 'silver spoon' of lasting positive effects to their offspring, good breeding conditions instead lead to increased maternal investment in offspring because of the dynamic complementarity (sensu Heckman, 2007) between pre- and postbirth investment. Fundamentally, a 'silver spoon' effect occurs if rearing highly successful offspring is only feasible when offspring are born at high quality, as this incentivizes mothers to increase prebirth investment under good breeding conditions rather than to reduce their personal costs by compensating. For example, if adult size largely determines the likelihood of becoming a dominant breeder, and compensatory growth is difficult (Robinson, Sinclair, & McEvoy, 1999) or has negative consequences (Fisher, Nager, & Monaghan, 2006; Metcalfe & Monaghan, 2003), mothers should favour high prebirth investment even when it is costly to them and not valuable to offspring without follow-up investment by the care group. Conversely, if offspring that are low quality at birth have very low expectations of gaining fitness (even when reared successfully), there is little incentive for carers to invest in them during the rearing period (Montgomerie & Weatherhead, 1988; Thünken, Meuthen, Bakker, & Kullmann, 2010). The strength of any potential 'silver spoon' effect will hence depend partly on the breeding system of the species in question, as greater competition for breeding positions will increase the value of producing high-quality offspring that are strong competitors. Similarly, a stronger 'silver spoon' effect might occur when offspring must compete with other broods at an early age, for example in banded mongooses, *Mungos mungo*, in which heavier offspring outcompete lighter offspring for access to helper 'escorts' (Hodge et al., 2009). A 'silver spoon' effect cannot occur when early investment is unimportant (e.g. Van De Pol et al., 2006), but will apply in some form whenever investment at one stage alters the value of investment delivered in future stages.

The strength of any potential 'head start' or 'silver spoon' effect on offspring fitness will be determined partly by how important prebirth investment is to offspring, relative to postbirth investment. Highly altricial species have long periods after birth during which all carers can influence outcomes for offspring at independence, making this stage relatively more important than initial variation in offspring quality. In contrast, precocial offspring may receive little parental care, or fewer forms of care (e.g. only predator defence), making the mother's prebirth contribution relatively greater. Our results indicate that mothers should indeed invest heavily prebirth when offspring are precocial, but that postbirth care should also be high for moderately precocial young, especially in large groups. This is because many carers can collectively provide a large amount of postbirth investment without suffering high personal costs, and this investment is still slightly beneficial to offspring.

More theoretical work is needed on how tactical maternal investment can modify investment rules and outcomes for offspring in cooperative groups. Along with previous work on female manipulation of offspring number (Savage et al., 2013a, 2013b), we have shown that maternal investment in offspring quality can drastically alter investment rules in cooperative species. Mothers are expected to increase offspring number under good conditions (Savage et al., 2013b), but reduce prebirth investment if 'quality' conveys a 'head start' (this study). This implies that altering

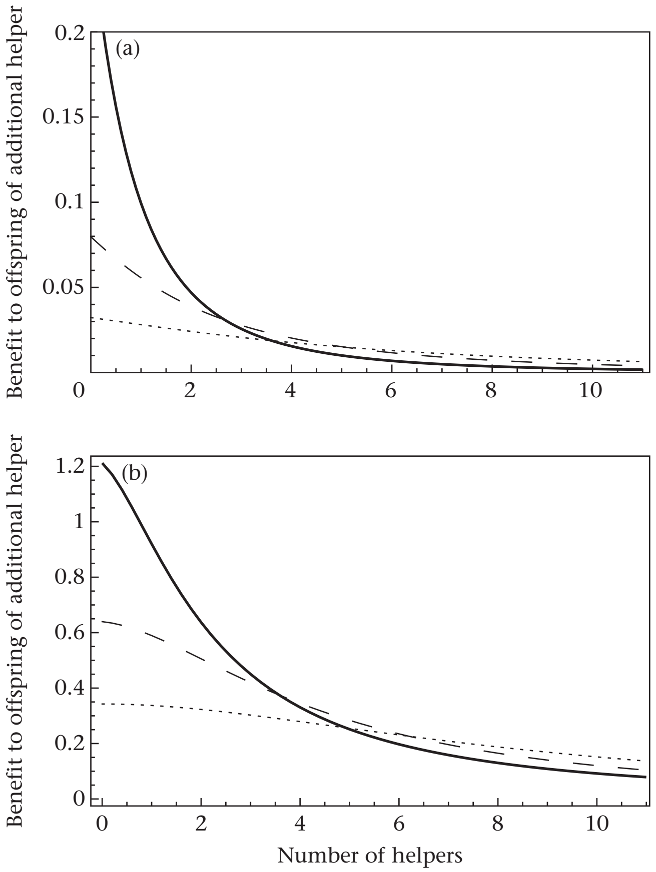

Figure 5. (a) Under 'head start' conditions, offspring benefit most from an additional helper when in small groups, but this effect is much stronger with full-sibling helpers (solid line) than it is with half-sib (dashed line) or cousin (dotted line) helpers. In large groups with less helpful helpers, offspring benefit more from the recruitment of an additional helper than when in similarly sized groups with full-sib helpers, as the current total investment in offspring is lower. (b) The benefit to offspring of adding an extra helper varies similarly under 'silver spoon' conditions as under 'head start' conditions, but is of greater magnitude owing to the multiplicative effect of the mother boosting offspring quality. However, the differences in offspring benefit between adding a full-sib helper (solid line) and adding a cousin helper (dotted line) are much smaller under 'silver spoon' than under 'head start', and substantial benefits to recruiting helpers persist even in large groups.

offspring number is more similar to giving a fixed number of offspring a 'silver spoon', as both circumstances lead to prebirth investment matching rather than compensating for breeding conditions. The similarity arises because the 'head start' case results in a lower limit on maximum offspring benefit (and hence female payoff), owing to the diminishing returns of high investment in individual offspring. When mothers control offspring number they can avoid this limit by producing more offspring, but each requires a minimum level of investment to be reared successfully; this is analogous to the 'silver spoon' case in which prebirth investment essentially raises the limit on maximum offspring benefit, but high-quality offspring can suffer after birth because of greater energetic needs.

It is difficult to predict the expected investment strategies when mothers can alter both offspring number and offspring quality simultaneously, even when assuming a simple trade-off between the two. Offspring size is often used as a proxy for offspring quality, but although size–number relationships have been widely explored across many taxa (Kaufman & Kaufman, 1987; Roff, 2002; Sinervo & Licht, 1991; Smith, Kallander, & Nilsson, 1989; Walker, Gurven, Burger, & Hamilton, 2008), changes in one factor may have complex effects on the other, making the assumption of simple size–number trade-offs unreliable (Brown & Shine, 2009; Lepage, Gauthier, & Desrochers, 1998). Most valuable as an addition to current theory would be a demographic approach to modelling a cooperative breeding system, incorporating maternal control of offspring size and/or number. This would facilitate cross-species comparisons of investment strategy by exploring intragroup relatedness, the costliness of different breeding stages and the effects of potential outside options on helper decisions within a more flexible model framework. In addition, dynamic complementarity effects between development stages require further attention as a potential explanation for the range of maternal investment tactics seen in nature; more work is needed to understand how investment at one stage of development influences its value during later stages.

Although our study focuses on group size to model differences in rearing conditions, our results generalize to other aspects of the environment that alter the costs of care. For example, in pair-breeding species in which males differ in their ability to provide care, mothers might be expected to reduce prebirth investment if better males simply provide more food (i.e. offspring need a 'head start' when females pair with poorer males). Alternatively, if high-quality males provide genetic benefits that boost offspring fitness (a 'silver spoon'), particularly if this benefit is only realized in offspring that are high quality at independence, mothers should invest more pre- and postbirth when paired with a higher-quality mate (Horváthová, Nakagawa, & Uller, 2012).

Acknowledgments

We thank Jan Lindström, Andrea Manica and two anonymous referees for their comments on the manuscript. Funding was provided by grants from the Natural Environment Research Council (PFAG/030) (studentship, J.L.S.; New Investigators, A.F.R.), and the Royal Society University Fellowship Scheme (A.F.R.).

References

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*, 707–715. http://dx.doi.org/10.1098/rspb.2008.1251.

Brown, G. P., & Shine, R. (2009). Beyond size-number trade-offs: clutch size as a maternal effect. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*, 1097–1106. http://dx.doi.org/10.1098/rstb.2008.0247.

Burgess, S. C., & Marshall, D. J. (2014). Adaptive parental effects: the importance of estimating environmental predictability and offspring fitness appropriately. *Oikos, 123*, 769–776. http://dx.doi.org/10.1111/oik.01235.

Burt, D. B., & Peterson, A. T. (1993). Biology of cooperative-breeding scrub jays (*Aphelocoma coerulescens*) of Oaxaca, Mexico. *The Auk, 110*, 207–214.

Canestrari, D., Marcos, J. M., & Baglione, V. (2011). Helpers at the nest compensate for reduced maternal investment in egg size in carrion crows. *Journal of Evolutionary Biology, 24*, 1870–1878. http://dx.doi.org/10.1111/j.1420-9101.2011.02313.x.

Clutton-Brock, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *American Naturalist, 123*, 212–229.

Clutton-Brock, T. H., Albon, S., & Guinness, F. (1985). Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature, 313*, 131–133.

Crick, H. (1992). Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis, 134*, 56–61.

Cunningham, E. J. A., & Russell, A. F. (2000). Egg investment is influenced by male attractiveness in the mallard. *Nature, 404*, 74–77.

Eising, C. M., Müller, W., & Groothuis, T. G. G. (2006). Avian mothers create different phenotypes by hormone deposition in their eggs. *Biology Letters, 2*, 20–22. http://dx.doi.org/10.1098/rsbl.2005.0391.

Fisher, M. O., Nager, R. G., & Monaghan, P. (2006). Compensatory growth impairs adult cognitive performance. *PLoS Biology, 4*, e251. http://dx.doi.org/10.1371/journal.pbio.0040251.

Fox, C., Thakar, M., & Mousseau, T. (1997). Egg size plasticity in a seed beetle: an adaptive maternal effect. *American Naturalist, 149*, 149–163.

Grafen, A. (1988). On the uses of data on lifetime reproductive success. In T. H. Clutton-Brock (Ed.), *Reproductive success* (pp. 454–471). Chicago, IL: University of Chicago Press.

Hatchwell, B. J. (1999). Investment strategies of breeders in avian cooperative breeding systems. *American Naturalist, 154*, 205–219. http://dx.doi.org/10.1086/303227.

Heckman, J. J. (2007). The economics, technology, and neuroscience of human capability formation. *Proceedings of the National Academy of Sciences of the United States of America, 104*, 13250–13255. http://dx.doi.org/10.1073/pnas.0701362104.

Hodge, S. J., Bell, M. B. V., Mwanguhya, F., Kyabulima, S., Waldick, R. C., & Russell, A. F. (2009). Maternal weight, offspring competitive ability, and the evolution of communal breeding. *Behavioral Ecology, 20*, 729–735.

Horváthová, T., Nakagawa, S., & Uller, T. (2012). Strategic female reproductive investment in response to male attractiveness in birds. *Proceedings of the Royal Society B: Biological Sciences, 279*, 163–170. http://dx.doi.org/10.1098/rspb.2011.0663.

Houston, A. I., & Davies, N. B. (1985). The evolution of cooperation and life history in the dunnock, Prunella modularis. In R. M. Sibly, & R. H. Smith (Eds.), *Behavioural ecology: Ecological consequences of adaptive behaviour* (pp. 471–487). Oxford, U.K.: Blackwell Scientific Publications.

Kaufman, D., & Kaufman, G. (1987). Reproduction by Peromyscus polionotus: number, size, and survival of offspring. *Journal of Mammalogy, 68*, 275–280.

Klaassen, M., & Bech, C. (1992). Resting and peak metabolic rates of Arctic Tern nestlings and their relations to growth rate. *Physiological Zoology, 65*, 803–814.

Koenig, W. D., Walters, E. L., & Haydock, J. (2009). Helpers and egg investment in the cooperatively breeding acorn woodpecker: testing the concealed helper effects hypothesis. *Behavioral Ecology and Sociobiology, 63*, 1659–1665. http://dx.doi.org/10.1007/s00265-009-0773-y.

Lack, D. (1947). The significance of clutch-size. *Ibis, 89*, 302–352.

Lepage, D., Gauthier, G., & Desrochers, A. (1998). Larger clutch size increases fledging success and offspring quality in a precocial species. *Journal of Animal Ecology, 67*, 210–216.

McNamara, J. M., Gasson, C. E., & Houston, A. I. (1999). Incorporating rules for responding into evolutionary games. *Nature, 401*, 368–371. http://dx.doi.org/10.1038/43869.

Metcalfe, N. B., & Monaghan, P. (2003). Growth versus lifespan: perspectives from evolutionary ecology. *Experimental Gerontology, 38*, 935–940. http://dx.doi.org/10.1016/S0531-5565(03)00159-1.

Monaghan, P. (2008). Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences, 363*, 1635–1645. http://dx.doi.org/10.1098/rstb.2007.0011.

Montgomerie, R. D., & Weatherhead, P. J. (1988). Risks and rewards of nest defence by parent birds. *Quarterly Review of Biology, 63*, 167–187.

Oksanen, T., Jokinen, I., Koskela, E., Mappes, T., & Vilpas, H. (2003). Manipulation of offspring number and size: benefits of large body size at birth depend upon the rearing environment. *Journal of Animal Ecology, 72*, 321–330.

Paquet, M., Covas, R., Chastel, O., Parenteau, C., & Doutrelant, C. (2013). Maternal effects in relation to helper presence in the cooperatively breeding sociable weaver. *PLoS One, 8*, e59336. http://dx.doi.org/10.1371/journal.pone.0059336.

Quillfeldt, P., & Peter, H.-U. (2000). Provisioning and growth in chicks of Wilson's storm-petrels (*Oceanites oceanicus*) on King George Island, South Shetland Islands. *Polar Biology, 23*, 817–824.

Robinson, J., Sinclair, K., & McEvoy, T. (1999). Nutritional effects on foetal growth. *Animal Science, 68*, 315–331.

Roff, D. A. (2002). *Life history evolution*. Sunderland, MA: Sinaeur Associates.

Royle, N. J., Lindström, J., & Metcalfe, N. B. (2005). A poor start in life negatively affects dominance status in adulthood independent of body size in green swordtails *Xiphophorus helleri*. *Proceedings of the Royal Society B: Biological Sciences, 272*, 1917–1922. http://dx.doi.org/10.1098/rspb.2005.3190.

Russell, A. F., Brotherton, P. N. M., McIlrath, G. M., Sharpe, L. L., & Clutton-Brock, T. H. (2003). Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behavioral Ecology, 14*, 486–492. http://dx.doi.org/10.1093/beheco/arg022.

Russell, A. F., Langmore, N. E., Cockburn, A., Astheimer, L. B., & Kilner, R. M. (2007). Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science, 317*, 941–944. http://dx.doi.org/10.1126/science.1146037.

Russell, A. F., Langmore, N. E., Gardner, J. L., & Kilner, R. M. (2008). Maternal investment tactics in superb fairy-wrens. *Proceedings of the Royal Society B: Biological Sciences, 275*, 29–36. http://dx.doi.org/10.1098/rspb.2007.0821.

Russell, A. F., & Lummaa, V. (2009). Maternal effects in cooperative breeders: from hymenopterans to humans. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*, 1143–1167. http://dx.doi.org/10.1098/rstb.2008.0298.

Russell, A. F., Young, A. J., Spong, G., Jordan, N. R., & Clutton-Brock, T. H. (2007). Helpers increase the reproductive potential of offspring in cooperative meerkats. *Proceedings of the Royal Society B: Biological Sciences, 274*, 513–520. http://dx.doi.org/10.1098/rspb.2006.3698.

Santos, E. S. A., & Macedo, R. H. (2011). Load lightening in southern lapwings: group-living mothers lay smaller eggs than pair-living mothers. *Ethology, 117*, 547–555. http://dx.doi.org/10.1111/j.1439-0310.2011.01905.x.

Savage, J. L., Russell, A. F., & Johnstone, R. A. (2013a). Intra-group relatedness affects parental and helper investment rules in offspring care. *Behavioral Ecology and Sociobiology, 67*, 1855–1865. http://dx.doi.org/10.1007/s00265-013-1595-5.

Savage, J. L., Russell, A. F., & Johnstone, R. A. (2013b). Maternal costs in offspring production affect investment rules in joint rearing. *Behavioral Ecology, 24*, 750–758. http://dx.doi.org/10.1093/beheco/ars203.

Sinervo, B., & Licht, P. (1991). Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. *Science, 252*, 1300–1302.

Smith, H., Kallander, H., & Nilsson, J.-Å. (1989). The trade-off between offspring number and quality in the great tit *Parus major*. *Journal of Animal Ecology, 58*, 383–401.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford, U.K.: Oxford University Press.

Strasser, R., & Schwabl, H. (2004). Yolk testosterone organizes behavior and male plumage coloration in house sparrows (*Passer domesticus*). *Behavioral Ecology and Sociobiology, 56*, 491–497. http://dx.doi.org/10.1007/s00265-004-0810-9.

Taborsky, B., Skubic, E., & Bruintjes, R. (2007). Mothers adjust egg size to helper number in a cooperatively breeding cichlid. *Behavioral Ecology, 18*, 652–657. http://dx.doi.org/10.1093/beheco/arm026.

Thünken, T., Meuthen, D., Bakker, T. C. M., & Kullmann, H. (2010). Parental investment in relation to offspring quality in the biparental cichlid fish *Pelvicachromis taeniatus*. *Animal Behaviour, 80*, 69–74. http://dx.doi.org/10.1016/j.anbehav.2010.04.001.

Van De Pol, M., Bakker, T., Saaltink, D.-J., & Verhulst, S. (2006). Rearing conditions determine offspring survival independent of egg quality: a cross-foster experiment with oystercatchers *Haematopus ostralegus*. *Ibis, 148*, 203–210. http://dx.doi.org/10.1111/j.1474-919X.2006.00479.x.

Verboven, N., Monaghan, P., Evans, D. M., Schwabl, H., Evans, N., Whitelaw, C., et al. (2003). Maternal condition, yolk androgens and offspring performance: a supplemental feeding experiment in the lesser black-backed gull (*Larus fuscus*). *Proceedings of the Royal Society B: Biological Sciences, 270*, 2223–2232. http://dx.doi.org/10.1098/rspb.2003.2496.

Walker, R. S., Gurven, M., Burger, O., & Hamilton, M. J. (2008). The trade-off between number and size of offspring in humans and other primates. *Proceedings of the Royal Society B: Biological Sciences, 275*, 827–833. http://dx.doi.org/10.1098/rspb.2007.1511.

Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist, 100*, 687–690.

Williams, T. D. (1994). Intraspecific variation in egg size and composition in birds: effects on offspring fitness. *Biological Reviews, 69*, 35–59. http://dx.doi.org/10.1111/j.1469-185X.1994.tb01485.x.

Williams, T. D. (2001). Experimental manipulation of female reproduction reveals an intraspecific egg size-clutch size trade-off. *Proceedings of the Royal Society B: Biological Sciences, 268*, 423–428. http://dx.doi.org/10.1098/rspb.2000.1374.