

Maternal costs in offspring production affect investment rules in joint rearing

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Published in: *Behavioral Ecology* **24**(3), 750-758

Link: <http://www.behco.oxfordjournals.org/cgi/doi/10.1093/behco/ars203>

Abstract

When multiple individuals contribute to rearing the same offspring, conflict is expected to occur over the relative amounts invested by each carer. Existing models of biparental care suggest that this conflict should be resolved by partially compensating for changes by co-investors, but this has yet to be explicitly modeled in cooperative breeders over a range of carer numbers. In addition, existing models of biparental and cooperative care ignore potential variation in both the relative costs of offspring production to mothers and in maternal allocation decisions. If mothers experience particularly high costs during offspring production, this might be expected to affect their investment strategies during later offspring care. Here we show using a game-theoretical model that a range of investment tactics can result depending on the number of carers and the relative costs to the mother of the different stages within the breeding attempt. Additional carers result in no change in investment by individuals when production costs are low, as mothers can take advantage of the greater potential investment by increasing offspring number; however this tactic ultimately results in a decrease in care delivered to each offspring. Conversely, when production costs prevent the mother from increasing offspring number, our model predicts that other individuals should partially compensate for additional carers and hence offspring should each receive a greater amount of care. Our results reinforce the importance of considering investment across all stages in a breeding attempt, and provide some explanatory power for the variation in investment rules observed across cooperative species.

Keywords: *bi-parental care, cooperative breeding, game theory, incomplete compensation, maternal effects, sealed-bid*

Introduction

Whenever an animal invests in a reproductive attempt, the amount invested represents a trade-off between the benefits accrued to the current brood of offspring and the costs to the investor in terms of survival and future reproductive potential (Williams 1966). In breeding systems where multiple individuals contribute jointly to offspring care, carers additionally should benefit when the other(s) contribute a greater share of the total investment (Trivers 1972). In such systems, the lifetime fitness consequences for each individual investing in a breeding attempt will depend significantly on the amount invested, with the optimum amount emerging as a function of the probability of success of the attempt, the individual's relatedness to the offspring, the possibilities of current and future direct fitness gains, and by the behaviour of the other partner(s) contributing to care. The predictability of this investment by others, their likely relative contributions, and the point during the breeding attempt at which they invest will all influence an individual's investment decisions. Without understanding these varied influences on investment behaviour, the causes and consequences of caring can easily be misinterpreted, and the adaptive benefit to individuals forming a social pair or group to raise offspring will remain obscured.

Joint contribution to offspring care can arise either through biparental care, where both parents contribute to raising offspring, or through cooperative care, where at least one parent and non-parent contribute. Biparental and cooperative care systems are fundamentally similar in that they divide offspring care between individuals that benefit from caring, but in cooperative systems both the number of carers and their average relatedness to each other are typically greater. In both systems the breeding female gains a potential tactical advantage in the conflict over care through her ability to choose offspring size and number, but also often pays a greater cost because she must invest in offspring before other carers. The extent to which she can capitalize on her advantage will depend in part on these personal costs, as well as on the number and predictability of additional carers available (Russell & Lummaa 2009). Despite many theoretical analyses of investment in offspring, little attention has been given to the effects on carer investment rules of maternal tactics prior to the joint rearing period, and likewise the possible effects of multiple and variable numbers of carers has remained relatively unexplored.

Most models of biparental systems (e.g. Houston & Davies 1985; McNamara et al. 1999) suggest that the conflict over care should be resolved by each parent investing less than if raising the brood of young alone, and by responding to changes in their partner's investment with incomplete (partial) compensation, such that a change in investment by one partner (or the presence/absence of a partner) leads to a change by the other of smaller magnitude and in the opposite direction (but see Jones et al. 2002; Johnstone & Hinde 2006). This prediction has received considerable empirical support (e.g. Bart & Tornes 1989; Raadik et al. 1990; Wright & Cuthill 1990; Whittingham et al. 1994; Markman et al. 1995; Royle et al. 2002; Hinde 2005; reviewed in Harrison et al. 2009), and recent theoretical work has shown that incomplete compensation should also stabilize negotiations involving three carers (Johnstone 2011). However, support for incomplete compensation in biparental care is by no means ubiquitous (Johnstone & Hinde 2006; Harrison et al. 2009), and empirical studies investigating the effect of additional carers on individual investment levels in

cooperative systems have found an even wider range of carer investment strategies. These range from carers completely compensating for the additional helper, such that there is no net increase in investment by the group as a whole (Brown et al. 1978; Legge 2000), through the expected incomplete compensation (Hatchwell & Davies 1990; Wright 1998a) to no compensation, where individual investment remains steady (Mumme & Koenig 1990; Emlen & Wrege 1991), or even an increase in individual investment (Valencia et al. 2006). In addition, within a given species, individuals can show a range of response reactions depending on their status (breeder *vs.* non-breeder) and/or the number of other carers in the group (Hatchwell 1999; Clutton-Brock et al. 2004; Gilchrist & Russell 2007; Browning et al. 2012b). This variation in carer responses is poorly understood, but has been suggested to reflect variation in the probability of offspring starvation: where starvation is likely, partial or no compensation is expected so that additional helpers have some positive effect on brood provisioning frequency (Hatchwell 1999). Nevertheless, it is unclear why apparent evidence for both complete and no compensation is relatively common in cooperative breeders (Cockburn 1998; Heinsohn 2004) when theoretical work generally predicts incomplete compensation. One possibility is that complete compensation arises in conjunction with a non-zero relatedness value between carers, such that additional individuals can improve the survival of related carers after brood demand is satiated. Another possibility is that the level of compensation varies depending on the costs to the breeding female of producing offspring, providing she is able to predict the number of potential helpers and adjust offspring number accordingly (Russell et al. 2008). To our knowledge, no previous model has explored the consequences of tactical investment in offspring production by mothers, or the consequences of having variable numbers of other carers on the optimal investment strategies for each individual during offspring rearing.

As with simpler single-stage models of offspring care, when considering the influence of production costs on investment behaviour one would expect the precise amounts invested to depend upon the relative costs and benefits of care (Chase 1980; Winkler 1987), and these in turn to depend upon the number of offspring in the brood (Smith & Härdling 2000). The integration of models of optimal clutch size with those of investment in care has been largely overlooked (but see Smith & Härdling 2000), primarily because existing work suggests that females should produce a size and number of offspring that maximizes their return per unit investment regardless of the total amount invested (Smith & Fretwell 1974; Winkler & Wallin 1987). However this conclusion is based on an analysis of the tactics of a single parent, and one cannot assume that investment in offspring production and in subsequent care will be independent if other individuals can also contribute. Different numbers of offspring will elicit different levels of investment from other carers, and hence the individual choosing offspring number can potentially 'manipulate' the investment levels of others. If a breeding female is assisted by one or more individuals in raising offspring, and can adjust the number of offspring she produces in response to the presence of these helpers (e.g. Russell et al. 2003; Woxvold 2005), one must consider the evolution of offspring number and individual investment together in a single model. Smith and Härdling (2000) demonstrate the importance of considering this joint evolution and show that it can affect the stability of the mating system, however they do not address the specific investment levels or strategies that are expected under different cost parameters or numbers of carers.

The need for further theoretical work on reproductive investment is supported by the lack of consistent empirical results showing incomplete compensation (particularly in studies on cooperative breeders), which suggest that some underlying assumptions of current models need to be re-evaluated. Primary amongst these is that female investment in offspring size and number is independent of the subsequent investment by all carers, particularly given the work already linking them (Smith & Härdling 2000). Breeding females occupy a unique position in many care systems, as they are often capable of altering initial offspring size and number, and the idea that females can tactically invest in offspring in response to the number of carers has support from empirical studies (e.g. Davies & Hatchwell 1992; Taborsky et al. 2007; Russell et al. 2007; Santos & Macedo 2011; Canestrari et al. 2011). The breeding female also may pay a greater cost than other carers, as she invests time and energy producing and caring for young before other carers are able to invest. High costs to the breeding female at this initial production stage can have significant effects on her survival or later fecundity (Heaney & Monaghan 1995; Visser & Lessells 2001), leading to a trade-off for the female between the amount invested in the pre- and post-helper stages. While females are still expected to maximize their return per unit investment in offspring care, the number of helpers and relative costs of the two stages (pre- vs. post-birth/hatching) will affect how the female should optimally divide her investment. Any complete model of investment in offspring must consider both the number of carers and the relative costs of these different stages of investment to fully understand the trade-offs involved in breeding, in addition to resolving the familiar conflict between individuals over investment. The benefits different carers gain from raising the offspring are also critically important when considering investment in a cooperative system.

The model that we introduce is a game-theoretical model of investment with variable numbers of carers (2-12) and choice of offspring number by the breeding female. Investment is divided into two stages: in the first stage (offspring production) the female pays a cost to produce her chosen number of offspring, then in the second stage (offspring rearing), she and all other carers invest in offspring care. The relative costs of the two stages are modified to explore the consequences of breeding systems in which offspring production costs are dominant compared to those in which rearing costs are dominant, i.e. in which a greater or lesser proportion of the costs incurred by the breeding female fall before or after the point at which helpers are able to invest. The relative costs of investment between the female and other carers are also manipulated to determine their effects on investment. We evaluate our results in terms of the effects of helper number and timing of costs on the numbers of offspring produced, the individual investment rules of group members, and the amount of care delivered to each offspring.

The Model

Description

Our aim is to explore the outcome in terms of productivity, total investment per offspring, and response to additional carers when the female is able to alter the number of offspring based on the number of other carers (hereafter helpers) in the group. For simplicity we assume that the breeding male, if present, has a similar payoff function to the helpers (see discussion) and hence can be grouped with them in the model. Our model is a sequential game of two steps, similar to that developed by Smith and Härdling (2000). The female first chooses the number of offspring n , with knowledge of the number of helpers in the group z , and pays a cost derived from the number of offspring produced. Following this all carers play a simultaneous game to determine their individual investment levels. The choice of level of investment in the second step is assumed to be simultaneous and independent by all individuals, a 'sealed-bid' interaction following Houston and Davies (1985), rather than a 'negotiation' in which carers repeatedly interact in behavioral time to reach a stable investment level (as in McNamara et al. 1999, 2003; Johnstone & Hinde 2006). In general sealed-bid and negotiation models generate qualitatively similar results: for analogous models the results from sealed-bid approaches are reproduced in negotiations where individuals are inflexible in their response to each other's bids (McNamara et al. 1999). In our model we used a sealed-bid rather than negotiation approach because this allowed us to obtain analytical solutions for all numbers of carers, however individuals are assumed to be able to adjust their investment bid in the second step in response to the size of the brood set in the first step.

We first calculate the response of a breeding female and z 'helpers', (including the breeding male, if present) to a given brood size n . Breeding females choose an amount x_f to invest, and simultaneously all helpers choose an amount, termed x_h^i for the i^{th} individual. The vector of other carer investment amounts is \mathbf{x}_h where $\mathbf{x}_h = (x_h^1, x_h^2, x_h^3, \dots, x_h^{z-1}, x_h^z)$. Investment in offspring influences their survival and future reproduction, and we assume all offspring benefit equally and regardless of the particular individuals contributing. The benefit b to the brood of offspring depends on n and the total investment all individuals provide x_{tot} , where $x_{tot} = x_f + \sum_{i=1}^z x_h^i$. We assume that there is some constant minimum level of investment per offspring x_{min} below which individual offspring gain no benefit from being helped, such that the response of b to investment is a function of $x_{tot} / n - x_{min}$.

We include a constant k_b to scale benefit as appropriate with our cost functions. We assume that the first derivative of the benefit function (b') is positive, such that increasing investment leads to increasing benefit to the offspring, but that the second derivative (b'') is negative, such that increasing investment leads to diminishing returns. Given these assumptions, for illustrative purposes we use a quadratic function that yields analytical solutions:

$$b = k_b \cdot \left(\left(\frac{x_{tot}}{n} - x_{min} \right) - \left(\frac{x_{tot}}{n} - x_{min} \right)^2 \right)$$

Reproduction is costly (Williams 1966), as it requires the investment of resources such as time or effort that otherwise would have a positive effect on future fitness. The total cost to the female c_f depends on the number of offspring she produces n , and her investment in rearing the brood x_f as well as two constants: the relative cost of offspring production k_p (which acts on n), and the relative cost of offspring rearing k_r (which acts on x_f). The total cost to the female is calculated from the sum of the costs of the two steps, an approach supported by studies demonstrating a trade-off between investment in producing and rearing broods (e.g. Heaney and Monaghan 1995). We assume that for all individuals the first derivative of the cost function (c_f) is positive, such that increasing investment leads to increasing costs, and that the second derivative (c_f) is also positive, such that costs accelerate with greater investment. Similarly, for the i^{th} other carer the cost c_h^i depends on that individual's investment level x_h^i and the relative cost of offspring rearing (k_s to allow for differences from the female's rearing costs). Unlike the female's cost function it does not depend on n as the other carers do not produce offspring themselves. As before, for simplicity we choose a quadratic function for both cost functions:

$$c_f = k_p \cdot n^2 + k_r \cdot x_f^2$$

$$c_h^i = k_s \cdot (x_h^i)^2$$

Optimization of investment levels in a given brood requires trading off the benefit an individual receives from current reproduction against the costs from reducing survival probably or future reproductive success, and must also account for the relatedness between the investing individuals. Inclusive payoff functions for the female and helpers (respectively w_f and w_h^i for the i^{th} helper) are generated by taking the benefit individuals receive from helping and subtracting the costs individuals pay as a result of investment by themselves and by related individuals (weighted by their relatedness to the focal individual). For simplicity we assume that all other carers are equally related to the offspring, and that all individuals receive a benefit directly proportional to their relatedness to the brood (r_{fb} or r_{hb}). The breeding female and other carers are also all related equally (female-helper r_{fh} , helper-helper r_{hh}). To summarize, the inclusive payoffs are given by:

$$w_f = r_{fb} \cdot b - c_f - r_{fh} \cdot \sum_{i=1}^z c_h^i$$

$$w_h^i = r_{hb} \cdot b - c_h^i - r_{hh} \cdot \sum_{i=1}^z c_h^i$$

Solving the model

At equilibrium, neither the female nor any helper should be able to increase their payoff by altering their investment levels. Formally:

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

There are no differences between helpers aside from their investment decisions, so the same response to investment by the rest of the group will be made by all helpers, and at equilibrium x_h^i will be identical for all i . Solving the above produces rules for x_f and x_h^i in terms of n and z at equilibrium, which are termed \hat{x}_f and \hat{x}_h respectively.

We can now calculate the optimal strategy for the female to play in the first step. The female should choose a value of n such that it maximizes her payoff w_f given that $x_f = \hat{x}_f$ and $x_h^i = \hat{x}_h$ at equilibrium. For simplicity we assume that n is large, and thus approximately continuous. Formally:

$$\frac{\partial w_f}{\partial n} = 0$$

After solving this we have rules for x_f , x_h^i and n at equilibrium that depend only on helper number z and the extrinsically specified parameters.

Comparison of analogous breeding attempts

From these rules we can plot expected investment levels by females and helpers across a range of carer numbers, and substitute them back into the original payoff equations to determine the equilibrium payoff. However, although the above results can elucidates the costs of the two stages will affect investment decisions (by manipulation of k_r and k_s versus k_p), we need a way of equating the costs of the two stages before we can meaningfully examine the effects of different cost parameters on breeding attempts. To do this, we consider the simple case of a lone female investing in offspring.

As before, we calculate the optimal investment levels by maximizing the payoff equation w_f , but this time ignoring any investment by helpers ($z = 0$, $x_h^i = 0$). With no individuals other than the female, the game simplifies and is functionally single-step; the female must simply maximize her payoff (for this simplified case relabeled w_f^0) with respect to both her investment x_f^0 and the brood size n^0 . Formally:

$$\frac{\partial w_f^0}{\partial x_f^0} = \frac{\partial w_f^0}{\partial n^0} = 0$$

Solving this equation for x_f^0 and n^0 generates equilibrium values \hat{x}_f^0 and \hat{n}^0 which can then be substituted into w_f^0 to yield an equation for female payoff that depends only on the constants of the system. Plotting production cost k_p against rearing cost k_r (Fig. 2.1) then gives us contours of equal female fitness that each represent a set of analogous breeding attempts differing only in the “balance” between the production and rearing costs. We can now alter k_p and k_r to produce conditions where the breeding attempts are dominated either by production-stage or rearing-stage costs, but where the total payoff for the attempts are the same; this allows us to make comparisons between the two kinds of breeding attempt under conditions where they are analogous.

To generate results, we chose three pairs of values for k_p and k_r that fell along a typical payoff contour. The three pairs represent a low, moderate, and high production cost respectively, and correspond to values of k_p that differ by a factor of five. The values of the other constants (see supplementary material) were chosen either for approximation to real cooperative systems (e.g. in the case of relatedness values), or so that the resulting numbers of offspring fell within a normal range for a terrestrial vertebrate. Unless otherwise specified, we assume that females and helpers have the same cost constant during the rearing stage ($k_r = k_s$), and that relatedness values are 0.25 between the helpers and offspring, helper and other helpers, and helpers and the breeding female. Throughout, 'carers' refers to all individuals including the breeding female, while 'helpers' refers to every individual except the breeding female.

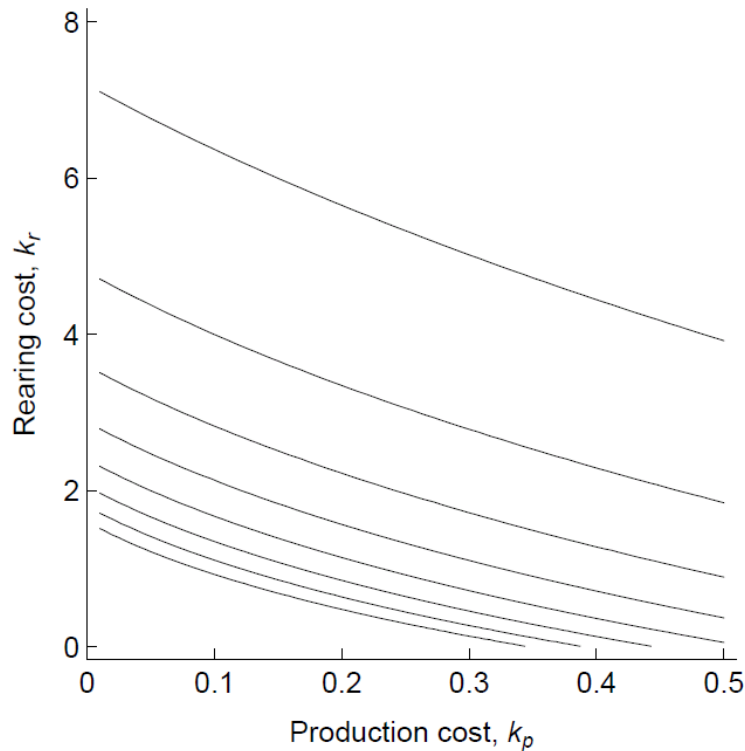
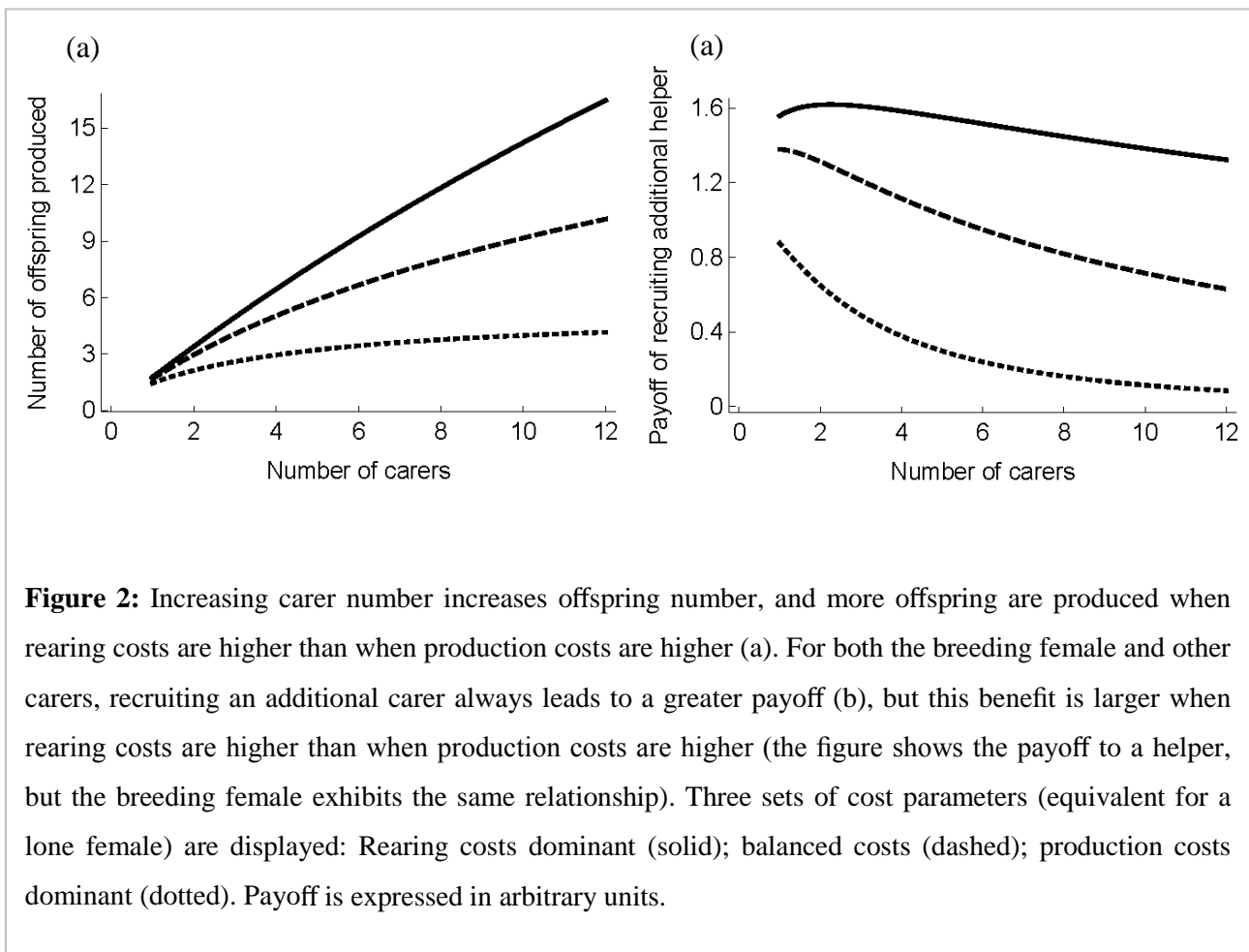


Figure 1: Contours of equal lone female payoff w_f^0 under varying values of production cost k_p and rearing cost k_r . Along these contours, paired values of k_p and k_r give the same payoff for a female raising a brood alone.

Results

(i) Productivity

Females produce more offspring as helper number increases (Fig. 2a). When the majority of costs fall in the rearing stage, offspring number and fitness are nearly linearly related to helper number, as helpers are able to contribute more effectively to the breeding attempt. In contrast, when the costs at the production stage are higher the positive effect on the payoff of having additional helpers plateaus quickly. This effect arises because the female rapidly reaches a level of initial investment in offspring that is extremely costly, and so is unable to capitalize on the presence of additional helpers by producing more offspring. This limitation on offspring production leads to a reduction in the benefit of acquiring additional helpers (to both the breeding female and existing helpers) as the number of helpers increases (Fig. 2b). This decrease is far more rapid, and the benefit to recruiting more helpers far lower, when production costs are relatively higher than rearing costs.



(ii) Investment levels

Investment levels have a more complicated dependence on helper number and the timing of costs. When there are few helpers the addition of another helper can lead to 'superadditive' investment, where all carers (helpers and breeding female) increase their individual investment in the brood (as in Valencia et al. 2006). As the number of helpers increases this positive effect on individual investment decreases, leading first to 'no compensation' (all carers maintain their individual investment, as in Wright et al. 1999) and then to compensatory care ('load-lightening'; all carers reduce their individual investment) (Fig.3a). The type of care received affects the amount of investment per offspring: when it is superadditive each offspring receives less investment as more helpers are added, but under compensatory care each receives more (Fig.3b). This apparent contradiction, whereby an increase in individual carer investment leads to lower per-offspring investment received (and *vice-versa*) is due to the greater number of offspring produced by the female in the production stage. The timing of costs is also crucial, as when rearing costs are dominant superadditive care and no compensation appear over a larger range of helper numbers, whereas dominant production costs favor compensatory care. In all cases the total amount of investment delivered to the brood by all carers increases as the number of carers goes up, but this total is higher when rearing costs are dominant.

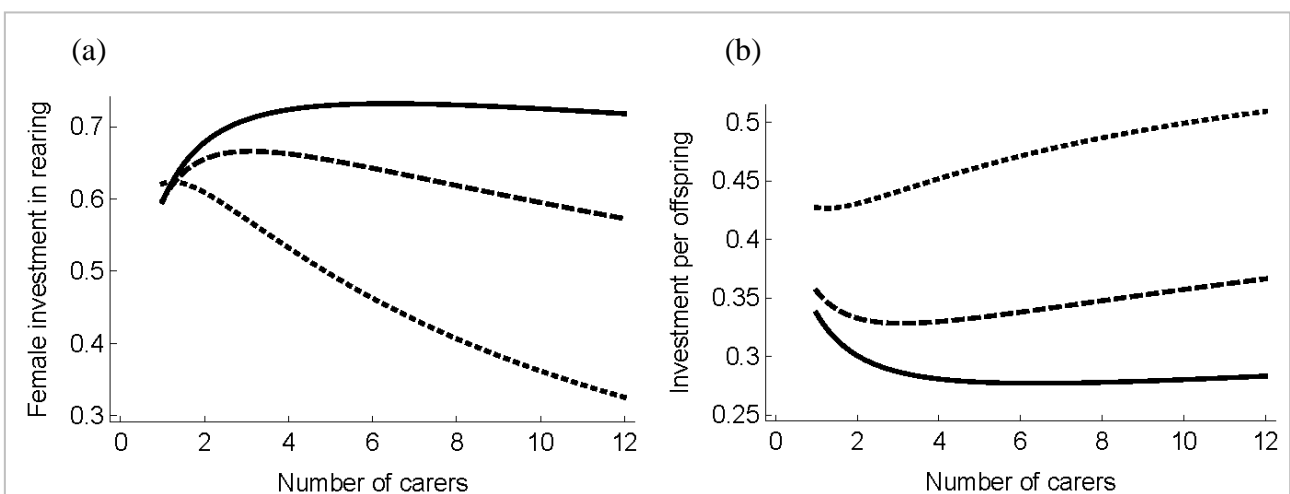


Figure 3: Additional carers reduce the effort expended by all individuals when production costs are high (incomplete compensation), and increase or maintain the effort (superadditive care or no compensation respectively) when rearing costs are high (a). In general, increasing carer number leads ultimately to load-lightening for any set of cost parameters. Individual offspring receive a greater amount of investment each when care is compensatory, but when it is superadditive they receive a lesser amount (b). The same sets of cost parameters are plotted: Rearing costs dominant (solid); balanced costs (dashed); production costs dominant (dotted). Investment is expressed in arbitrary units.

(iii) Variable rearing costs

We have generally assumed above that rearing costs are the same for identical levels of investment across breeding females and helpers. This assumption will often be violated in natural systems, as helpers are frequently found to differ from breeders in their foraging ability (e.g. Heinsohn 1991; Clutton-Brock et al. 2002), and young helpers may be poorer foragers than older helpers (e.g. Heinsohn and Cockburn 1994). Breeding females may also pay a unique cost when the offspring are young (but after other individuals are able to invest), for example from brooding the young before they can self-regulate their temperature. Taking this variation into account, we see that load-lightening by the female starts at larger numbers of helpers the greater the cost to helpers relative to the female (Fig. 4a). As expected helpers invest far less when their costs are higher, but they too show load-lightening at greater helper numbers when their costs are higher than those of the female (Fig. 4b). This relationship is fairly simply explained: the poorer the ability of helpers to provide investment, the more helpers are needed to reach the female's constraint on investment at the production stage. This of course assumes that the overall 'quality' of the helpers is predictable by the female at the time offspring are produced.

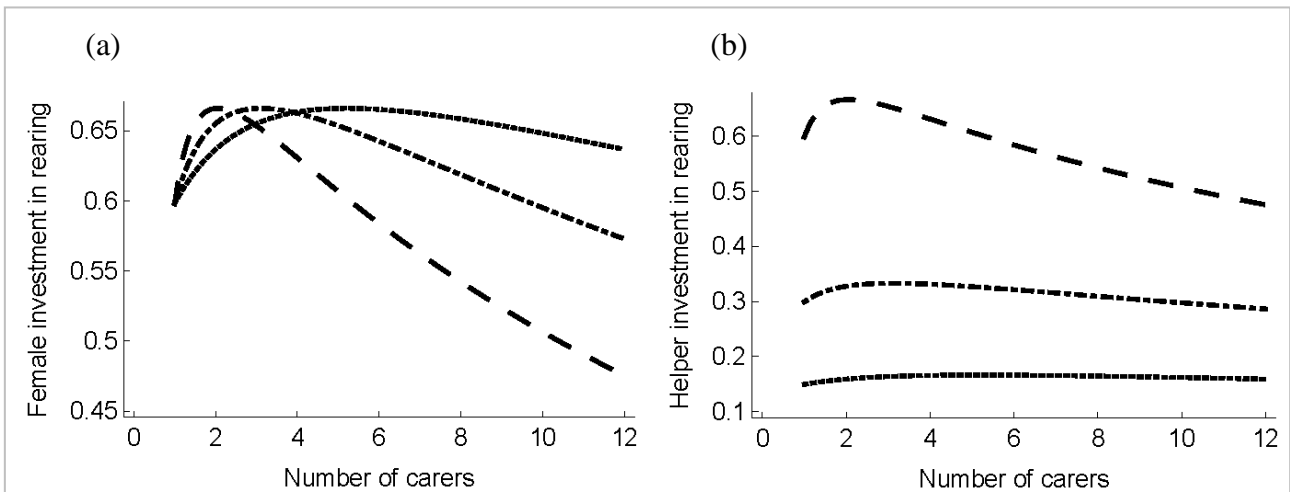


Figure 4: Differences between females and other carers in the cost of investment during the rearing stage alter whether compensatory care is expected from the female across different numbers of helpers (a). Compensatory care begins at smaller helper numbers when helper costs are lower than female costs, and the female is able to reduce her investment faster as helper number increases. Investment by other carers shows a similar relationship (b), but changing their cost parameter has a stronger effect on their total investment. Plots show costs to other carers half those of the breeding female ($k_s = k_r/2$) (dashed); equal costs ($k_s = k_r$) (dot-dashed); other carer costs double those of females ($k_s = 2k_r$) (dotted).

Discussion

Our results suggest that when rearing costs (rather than production costs) are dominant, females are expected to produce many offspring to capitalize on the presence of helpers. As the number of other carers in the system increases, all individuals will work harder and invest more in the brood both individually and as a group (superadditive care). However this increase in investment only partially compensates for the greater number of offspring initially produced, such that each individual offspring will have less invested in it than it would have had in a smaller brood with fewer helpers. The opposite pattern is predicted when production costs are dominant. In this case females still produce more offspring with additional helpers, but to a lesser extent. Each additional helper reduces the levels of investment of all carers (load-lightening), and each individual offspring has a greater amount invested in it when there are more helpers in the system. Whichever stage of costs is dominant, 'no compensation' or 'superadditive care' is more likely to be observed when helper costs are greater than female costs. Larger groups of carers are biased towards load-lightening, as the female will always eventually be constrained by her initial investment. Our finding that investment rules are symptomatic of particular cost parameters may help to explain some of the inconsistency in empirical studies of investment, as we would not expect the same investment rules across species that differ in factors of breeding biology or life history that restrict flexibility in offspring number, predictability of helpers, or the subsequent costs of incubating, provisioning or protecting the offspring until independence.

Existing analyses (e.g. Houston & Davies 1985) predict that in biparental systems each carer should respond to the investment of the other by incompletely compensating, and thus escape part of the costs of care (load-lightening). This result holds in general for both sealed-bid and negotiation analyses (though see Jones et al. 2002; McNamara et al. 2003; Johnstone & Hinde 2006), and recent work extending negotiation to three individuals suggests it also holds for three carers (Johnstone 2011). Our analysis, however, demonstrates that these predictions hold only for a fixed brood size. They are thus relevant when predicting the response of a female to experimental removal or manipulation of her mate after offspring have been produced (e.g. Bart & Tornes 1989; Raadik et al. 1990; Duckworth 1992; Fetherston et al. 1994; Markman et al. 1995; Itzkowitz et al. 2001), but not when comparing (either within or between species) the behaviour of females who can anticipate the number of helpers at the time of offspring production. The critical assumptions of our model are that individuals show systematic variation and respond to changes in offspring number in behavioral time, but these assumptions are supported by recent work showing tactical female investment during offspring production according to the number of carers available (Russell et al. 2003; Russell et al. 2007; Taborsky et al. 2007; Russell and Lummaa 2009; Canestrari et al. 2011; Santos and Macedo 2011). Similarly, examples from both observational studies (Magrath & Elgar 1997) and experiments (Sanz & Tinbergen 1999; Komdeur et al. 2002) show that breeding males are capable of responding to greater clutch sizes by increasing parental investment.

Inflexible brood sizes across different numbers of carers can be seen as a special case that occurs when production costs to the breeding female are very high, there is a biological constraint, or when it is very difficult to predict the amount of future help at the time of offspring production. Inflexible brood sizes lead

to the female and helpers escaping more of the costs of care as carer number increases, and offspring individually doing better; this follows the pattern one would expect if extrapolating from uni- and biparental systems. However, when the female is able to modify brood size in response to a predictable number of helpers a different pattern of investment can appear. When production costs are cheap relative to those of the rearing period, our model suggests that the breeding female should take advantage of the helpers' anticipated contributions by producing more offspring (as in Davies & Hatchwell 1992; Russell et al. 2003; Woxvold 2005), rather than by fully reducing her own level of investment. Under these circumstances, producing a larger brood/litter can be viewed as a means of 'manipulation': rather than simply anticipating the care that her group will provide, a female can induce the helpers to invest more than they otherwise would have by producing more offspring. Even though she too must invest more to raise these extra offspring, she gains a net benefit due to the extra total contribution she elicits from the other carers as the size of the group increases. This female 'manipulation' is not necessarily harmful to the other carers, but this will depend on the similarity of their current and future fitness functions to those of the female; in some shorebirds, polyandrous females 'manipulate' more males to care for their offspring in a similar way, by producing additional clutches sequentially (Lank et al. 1985). From the viewpoint of the helpers, they should always respond to additional offspring by increasing investment, because they always benefit from additional offspring being reared; combined with the response of the female to predictable help this leads to a close positive relationship between group size, offspring number, and total amount of investment by the group.

In species with less flexible brood sizes, another way for the breeding female to alter initial investment would be by manipulating the amount invested in each individual offspring at the production stage according to the number of helpers, an effect shown by Russell et al. (2007), Canestrari et al. (2011), and Santos and Macedo (2011). This tactic should be expected in species that produce small numbers of offspring, as the female will be more heavily constrained by the necessity of producing a discrete number of offspring. For example, in a species that normally produces four offspring, the minimum increase (to produce a single extra offspring) represents a 25% increase in production investment, whereas a species producing twenty offspring is capable of producing an additional one and only raising its costs by 5%.

In our model, low production costs can lead to individual offspring each receiving less investment when helpers are present than they would from a lone female, reproducing a theoretical result found in the biparental case by McNamara et al. (2003). In these cases the increase in helper investment only partially compensates for the greater number of offspring produced by the female to take advantage of the available help. Following this result, we predict that a positive effect of helpers on individual offspring survival and success should be more often seen when care is compensatory, but that helpers should cause females to increase the number of offspring she produces regardless of the cost parameters.

We treat all individuals other than the breeding female as equivalent in our model, but in real systems these carers will vary in their ability or willingness to deliver care due to factors such as age (and hence experience) (Heinsohn & Cockburn 1994; Langen 1996) or relatedness to the brood (leading to different indirect benefits) (Emlen & Wrege 1991; Nam et al. 2011; Browning et al. 2012a). Lowering relatedness

between helpers and offspring should decrease helper investment if indirect benefits are important, and less experienced helpers will likely pay higher costs, also leading to reduced investment. However in most systems there will be an inverse relationship between relatedness and experience as older individuals are more likely to have lived through a change in the breeding pair; this will lead to similarity in the payoff functions of helpers as the effects on investment work in opposite directions. The breeding male is a potential exception to the above rule as he will normally possess both high relatedness to the brood and significant experience, however studies typically indicate that breeding males do follow the same investment patterns as non-breeders during offspring rearing (Wright 1998b; McDonald et al. 2009). In our model the term that governs how individual payoff is affected by the costs incurred by other group members is referred to as 'relatedness', but could equally well represent any direct benefit where an individual's fitness is linked to the fitness or survival of other group members.

Our results suggest that cooperation should evolve more easily when a greater proportion of the costs of reproduction can be removed from the breeding female, as this allows more carers to invest effectively in offspring. As we have seen, when the female's costs are higher in the production stage the effect of additional carers on productivity quickly plateaus, whereas when they are lower the number of offspring produced is nearly linear with carer number, at least over the ranges considered. Conversely, the more potential carers that are available, the greater the advantage to shifting the earliest point that carers can invest towards the beginning of the breeding attempt, thus biasing the 'balance' of the attempt towards rearing costs. This could be achieved (for example) by producing young that are smaller and less well developed (assuming they can be fed by any individual), by developing mechanisms for other carers to share the costs of guarding or caring for eggs, or by provisioning the female during incubation or gestation to transfer away some of her production-stage costs.

Given that the effect of additional carers on female payoff is always positive, help should never be refused by the breeding female unless additional factors such as resource competition become important. This means that group size is likely to be driven by the relative values of the alternative options available to the other carers, especially when ecological factors are not acting to reduce the fitness of larger groups. In many systems we would expect there to be a certain payoff below which one or more alternative options (e.g. dispersal, floating, or challenging for breeding) becomes favourable, causing the helper to leave the system. Further theoretical work incorporating group formation and outside options would be needed to determine stable group sizes in a mixed population of breeders and helpers with varying relatedness. Although our model is framed in terms of helpers gaining indirect fitness benefits from offspring, the abstract relationship between offspring benefit and helper benefit equally well describes helpers accruing direct fitness benefits, provided that these direct benefits are contingent on the success of the breeding attempt in the same way indirect benefits would be. For example, the outcomes expected when helpers accrue fitness through augmenting group size fit well with our model, as this relies on offspring surviving and contributing to the future fitness of the helper. By contrast, our model is less useful for systems where selection for helping is based largely on 'help-for-experience' (Selander 1964); 'pay-to-stay' (Gaston 1978) or 'social prestige' (Zahavi 1995), because in such systems helper benefits are based on the act (rather than consequences) of

helping.

Future empirical studies in pair- and cooperatively-breeding species would benefit from considering the mounting evidence that maternal investment can vary significantly according to partner quality (Krist 2011; Horváthová et al. 2012) and/or group size (Russell & Lummaa 2009). As with any multi-stage investment system, focusing on decisions within individual stages in isolation may produce confusing or contradictory results if individuals can shift investment between stages as parameters change, or in response to the behaviour of others (Russell et al. 2008). Further theoretical work is needed to understand the effects on investment levels of restricted (but non-zero) investment by helpers at early stages. While we have focused here on effects of maternal variation in offspring number, one might also expect aspects such as offspring size, sex ratio, hatching synchrony and timing of reproduction to influence investment decisions in a cooperative group (Russell & Lummaa 2009).

Acknowledgements

We thank the editor and two anonymous referees for their constructive comments on the manuscript. This work was supported by a Natural Environment Research Council studentship to JLS, and by a Royal Society University Research Fellowship to AFR.

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