Parental investment with a superior alien in the brood

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Abstract

When a parent's parentage differs across breeding attempts, established theory predicts that the parent should invest more in a brood when perceived parentage is high. We present a model of parental investment in which offspring unrelated to the parent have a competitive advantage over the parent's own offspring and take a larger share of investment. We show that this can weaken or, if the competitive advantage is great, reverse the predicted relationship between perceived parentage and parental investment. A moderate competitive advantage of extra-pair young over within-pair young could partly explain the lack of any clear relationship between paternal care and paternity in many studies, and could easily arise if females choose extra-pair partners for good genes. Our results are also relevant to interspecific avian brood parasitism. As parasites reared together with host offspring are often superior competitors, their hosts could benefit from increasing investment in response to suspected parasitism.

Introduction

Parental investment is *any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring* (Trivers, 1972). A parent that increases its parental investment in the current brood will by definition have lower expected success in another breeding attempt. As long as there is some variation across breeding attempts in the parent's perceived parentage, or paternity (*sensu* Houston & McNamara, 2002), it should (all other things being equal) invest less in a brood in which it perceives parentage to be low (Winkler, 1987; Whittingham *et al.*, 1992; Westneat & Sherman, 1993; Houston, 1995; Houston & McNamara, 2002). Much of the empirical effort directed towards testing parental investment theory has focused on birds (but see Neff, 2003; Rios-Cardenas & Webster, 2005). Although male birds seem unable to recognize their own offspring directly, they may employ cues such as their partner's behaviour and

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absence in her fertile period as indicators of whether she has sought extra-pair copulations, and thus of parentage (Kempenaers & Sheldon, 1996; Lifjeld *et al.*, 1998). Field studies and experimental tests of whether investment decreases with reduced paternity have, however, produced mixed results (e.g. Dixon *et al.*, 1994; Kempenaers *et al.*, 1998; Lifjeld *et al.*, 1998; Sheldon & Ellegren, 1998; Dickinson, 2003; Bouwman *et al.*, 2005).

One implicit assumption made by standard models of parental investment in response to perceived parentage is that within-pair young and extra-pair young obtain equal expected shares of the total investment. Yet, intriguingly, one of the major explanations for why females should engage in extra-pair copulations in the first place is that they obtain genetic benefits for their offspring (reviewed by Jennions & Petrie, 2000; Griffith *et al.*, 2002), either because the extra-pair males are genetically superior to their social males (i.e. 'good genes') or because they are more genetically compatible. If extra-pair young as a consequence are more vigorous than within-pair young, it seems likely that they also could enjoy a competitive advantage. Some of the key evidence for genetic benefits are from studies showing that extra-pair young fledge with a higher probability than within-pair young (Kempenaers *et al.*, 1997; Charmantier *et al.*, 2004). Enhanced immunocompetence in

extra-pair young (Johnsen *et al.*, 2000) could conceivably confer a competitive advantage in the presence of pathogens. On a more speculative note, if extra-pair offspring are genetically superior, females could also benefit from provisioning extra-pair eggs with more resources than within-pair eggs (Sheldon, 2000; Griffith *et al.*, 2002; Krist *et al.*, 2005). There are also nongenetic mechanisms that conceivably may render extra-pair young more competitive: for instance, extra-pair young may be laid in earlier eggs and hatch earlier than within-pair young (Cordero *et al.*, 1999; Krist *et al.*, 2005). Moreover, if extra-pair young have access to any cues that inform them about their extra-pair status, we would expect them to compete harder and beg more simply because they are less related to the within-pair offspring and to the cuckolded male. Any advantage enjoyed by extra-pair young will alter the marginal benefits of parental investment in a way that is not addressed in the standard models.

Hosts of nonevicting avian brood parasites raise parasite nestlings along with their own, thus facing a challenge similar to the one facing cuckolded males. It has been shown that host parents can use observations of adult brood parasites near their nest (Davies & Brooke, 1988; Moksnes *et al.*, 1993; Bártol *et al.*, 2002; Davies *et al.*, 2003) or prior observations of odd eggs (Hauber *et al.*, 2006) as indicators of a higher than average risk of parasitism, and use this information in egg rejection decisions. Rejection or discrimination of parasite nestlings is a relatively rare phenomenon (reviewed by Grim, 2006). However, even if a host parent is unable to recognize parasite nestlings and thus to directly disfavour or reject them, it can always adjust the effort it puts into providing parental investment to the brood, and we may expect it to modify this effort according to its assessment of the risk of parasitism. Parasite nestlings are unrestricted by kinship to their host and often superior competitors for food (Soler *et al.*, 1995; Kattan, 1996; Dearborn, 1998; Lichtenstein & Sealy, 1998; Soler *et al.*, 1999), and are thus likely to reduce the fitness of their nestmates significantly. Consequently, standard models of parental investment may not predict how a host should respond to a potential act of parasitism.

Current theory predicts a positive relationship between parental investment and paternity across successive breeding attempts of the same male (assuming that paternity in the current attempt is not correlated with paternity in subsequent events – see Houston & McNamara, 2002). We propose that when offspring unrelated to the parent are more competitive than the parent's own offspring, this relation may be weakened, or even reversed. We show this formally, first by using a relatively simple two-offspring model of parental investment, and then by modifying a standard multiple-offspring model. The results are discussed in relation to brood parasitism and extra-pair paternity in birds.

The models

A two-offspring model

Consider a parent that must decide what amount of resources to invest in a brood of size two, in which one of the offspring may be an alien unrelated to the parent. The parent is unable to preferentially allocate its investment to its own offspring, but can respond to the perceived presence of an alien by changing total parental investment. We make the standard assumption that the fitness B of an own offspring is a strictly increasing, decelerating (concave) function of parental investment, reflecting diminishing returns on investment. Let x be the total parental investment. If the brood consists of two of the parent's own offspring, we assume that investment will be shared equally, making the brood worth $V_{own}(x) = 2B(x/2)$ to the parent, a function that will be concave and strictly increasing with x. Mixed broods contain one own and one alien offspring. The value to the parent of a mixed brood in which investment is shared equally is $1/2 V_{own}(x)$. If, however, the alien is a stronger competitor, then it will take more than half of the investment, which will depress the value of the brood below $1/2 V_{own}(x)$. A reasonable assumption is that the depression will be stronger when parental investment is low than when it is high, as the alien may satiate and leave a greater share of total investment to the parent's own offspring in the latter case. Let $G(x)$ denote the fraction of the investment taken by the alien. We assume that as the total parental investment increases, the alien offspring takes an increasing amount of the available investment in absolute terms (i.e. $xG(x)$ is strictly increasing), but a decreasing fraction of it (i.e. $G(x)$ is strictly decreasing), due to the satiation effect. The value to the parent of a brood in which the alien is a stronger competitor is then $V_{mixed}(x) = B(x[1-G(x)])$. Finally, investment in the current brood carries a cost $C(x)$ to the parent, as it reduces the ability to invest in other, future broods. This cost depends implicitly on expected future paternity, but not on current paternity. We assume that $C(x)$ is strictly increasing in an accelerating (convex) or linear fashion. An illustrative example is provided in Fig. 1.

We first consider the case where the parent is certain whether an alien offspring is present in the current brood or not. The payoff to the parent equals the value of the brood minus the cost of parental investment. As long as the brood value function is higher than the cost function for some range of parental investment, the optimal level of investment x^* is then simply the one that maximizes the distance from the brood value function down to the cost function (Fig. 1). From the first-order condition for the optimum, it is clear that the slope of the brood value function must equal the slope of the cost function at x^*. It follows that in the absence of any competitive advantage for the alien, the parent
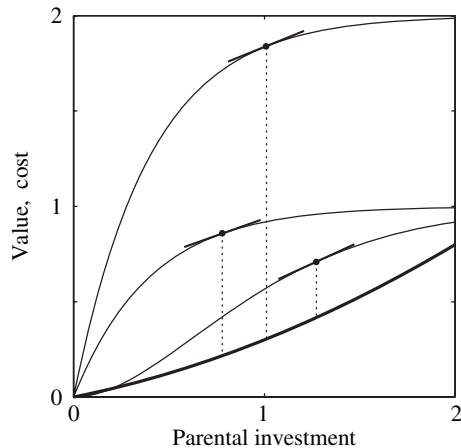
Fig. 1 The two-offspring model: the value to the parent of a brood as a function of parental investment, in the case of a fully own brood (V_{own}, top thin line), a mixed brood in which the alien lacks any competitive advantage ($V_{\text{own}}/2$, middle thin line) and a mixed brood in which the alien has a competitive advantage (V_{mixed}, bottom thin line). Parental investment has a cost in terms of reduced reproductive success in other broods (thick curved line). At the optimal level of investment, the distance between the value and cost function is maximized (illustrated by dotted lines), and their slopes are equal (illustrated by thick tangent lines). In this example, we use a second-order cost function $C(x) = bx + dx^2$. The shapes of V_{own} and V_{mixed} are generated using the functional form $G(x) = 1/2 + 1/(2+x)$ to describe the fraction of the investment taken by the alien, and a standard functional form for offspring fitness, $B(x) = 1-e^{-kx}$ (e.g. Mock & Parker, 1997), where k is a positive constant determining how quickly offspring fitness increases with investment. See main text for further explanation. Parameters $k = 5$, $b = 0.2$, $d = 0.1$.

should always respond to loss of parentage by investing less. This can be seen from the fact that for all functional forms $V_{\text{own}}(x)$ and $C(x)$ that satisfy our assumptions, the x-value at which $(1/2)V'_{\text{own}}(x) = C'(x)$ holds must necessarily be lower than the x-value at which $V'_{\text{own}}(x) = C'(x)$ holds (the prime denotes a derivative). On the other hand, in a mixed brood in which the alien takes a larger share of the resources than does the parent's own offspring, optimal parental investment may well be higher than in a brood of two of the parent's own offspring, despite the fact that a mixed brood has lower value to the parent. The reason is that a superior alien may depress the brood value curve in such a way that the point of the brood value curve at which the slope equals the slope of the cost function is displaced towards higher levels of investment (Fig. 1). Note that a loss of parentage will only lead to higher investment if the cost of investment is sufficiently low; if the cost of investment $C(x)$ is higher than $V_{\text{mixed}}(x)$ for all x, the optimal investment is zero, in which case loss of parentage will lead to brood rejection.

Now consider the case where the parent only has partial information about whether an alien is present. If

the probability that there is an alien in the current brood equals p, the expected value of a brood is given by

$$V(x,p) = (1-p)V_{\text{own}}(x) + pV_{\text{mixed}}(x).$$

The parent's payoff is

$$w(x,p) = V(x,p) - C(x) \tag{1}$$

Suppose that the parent observes an informative cue, which leads to a marginal increase in the perceived risk p that an alien is present in the current brood. What is the effect on the locally optimal parental investment x^* (assuming that future paternity, and hence the cost of current investment, is independent of current cues)? A nonzero optimal investment x^* must satisfy $\partial w/\partial x = 0$. Using the implicit function theorem on this equation, and noting that $\partial^2 w/\partial x^2 < 0$ holds at any maximum x^*, we can show that $\partial x^*/\partial p$ must have the same sign as

$$\left.\frac{\partial^2 w}{\partial p \partial x}\right|_{x=x^*} = V'_{\text{mixed}}(x^*) - V'_{\text{own}}(x^*). \tag{2}$$

This is a simple result: a marginal increase in the perceived risk of having an alien in the brood, p, leads to an increase in the locally optimal level of parental investment x^* if and only if $V_{\text{mixed}}(x)$ is steeper than $V_{\text{own}}(x)$ at x^*. (When predicting the effect of small changes in p on the globally optimal investment, however, it is also necessary to check whether the globally optimal investment may fall to zero in a discontinuous fashion.)

In Fig. 2, we illustrate how the optimal level of investment may increase with p, using the brood value curves V_{own} and V_{mixed} from Fig. 1. The optimal level of investment increases with p when the cost of investment is low. This makes sense, as V_{mixed} is steeper than V_{own} only when the investment x is high (Fig. 1), and high levels of investment are generally favoured by low costs of investment. Note that if the alien and the own offspring had shared investment equally, as assumed in earlier models, the optimal parental investment would always decrease as parentage decreases, as $(1/2)V_{\text{own}}(x)$ is less steep than $V_{\text{own}}(x)$ for all x.

A multiple-offspring model

We now consider broods of size n, in which there may be anywhere between 0 and n alien offspring. We are interested in the optimal level of investment in relation to the parent's perceived parentage in the brood under consideration, which is defined (cf. Houston, 1995) as one minus the probability p that any randomly selected member of the current brood is an alien unrelated to the parent (note that p now has a slightly different interpretation than in the two-offspring model). It follows that the number of alien offspring in the brood, M, is a
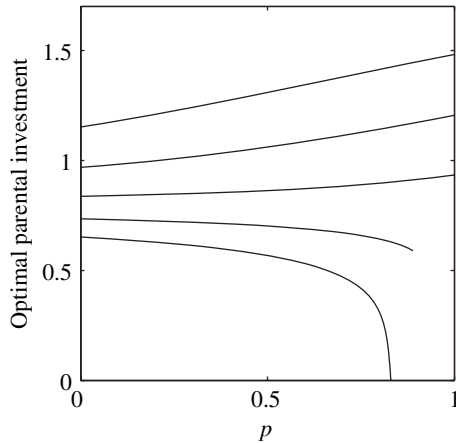
Fig. 2 The two-offspring model: the optimal level of parental investment in a brood as a function of the probability p that one of the offspring is an alien. To the right of the broken line, the optimal investment is zero. The cost of investment increases from the top line to the bottom line. The shapes of V_{own} and V_{mixed} are exactly as in Fig. 1, and the same second-order form is used for $C(x)$, with parameter values $d = 0.1$, and (from top to bottom) $b = 0.05, 0.25, 0.45, 0.65$ and 0.85.

binomially distributed random variable with mean np and variance $np(1 - p)$. In this model, we assume that because of competitive superiority or because they are unrestricted by kinship in begging, each alien offspring obtains $(1 + c)$ times the resources obtained by one of the parent's own offspring, where c is a non-negative constant. Thus, each of the parent's own offspring obtains a fraction $1/(n + Mc)$ of the resources provided, and attains the fitness $B(x/(n + Mc))$. The brood contains in total $n - M$ own offspring, and its value to the parent is therefore $V(x) = E\{(n - M)B[x/(n + Mc)]\}$, where E denotes expectation. Note that $V(x)$ is an increasing, concave function of x, as sums of increasing concave functions are themselves increasing and concave. As before, we assume that the cost function $C(x)$ increases in a convex or linear fashion. The optimal investment x^* thus maximizes the fitness function

$$w(x) = V(x) - C(x) = E\{(n-M)B[x/(n+Mc)]\} - C(x). \quad (3)$$

If the value of the brood is lower than the cost of investment for all levels of investment, then the optimal level of investment equals zero and the parent should reject the brood. Otherwise, the optimal investment x^* will satisfy $w'(x^*) = 0$, and the slope of the brood value function will equal the slope of the cost function at x^*.

If $c = 0$, we may put the fitness function in the form $w(x) = (1 - p)\beta(x) - C(x)$, where $\beta(x)$ denote the value of a 100% own brood, i.e. $\beta(x) \equiv nB(x/n)$. This is equivalent to a standard model in the literature (cf. Houston, 1995). The first-order condition is then $(1 - p)\beta'(x) = C'(x)$. If we assume that perceived parentage varies from one breeding attempt to another for a

given parent, and that current parentage is independent of future parentage, it follows that optimal parental investment always increases when current perceived parentage increases (Houston, 1995; Houston & McNamara, 2002).

Analytical results are harder to obtain for the general case when $c > 0$, so we proceed using numerical exploration. As in Fig. 1, we will use the standard functional form $B(x) = 1 - e^{-kx}$, but for simplicity, we will now use a linear cost $C(x) = bx$. As M is binomially distributed with mean np and variance $np(1 - p)$, the probability that $M = m$ is equal to

$$\binom{n}{m}p^m(1 - p)^{n-m}.$$

We may thus rewrite eqn (3) as

$$w(x) = \sum_{m=0}^{n}\left\{\binom{n}{m}p^m(1 - p)^{n-m}(n - m)\left[1 - \exp\left(\frac{-kx}{n + mc}\right)\right]\right\} - bx, \quad (4)$$

in which the first term is the expected value of the brood to the parent. This expression is used to plot the illustrative example in Fig. 3, which confirms our finding from the first model, namely that the optimal parental
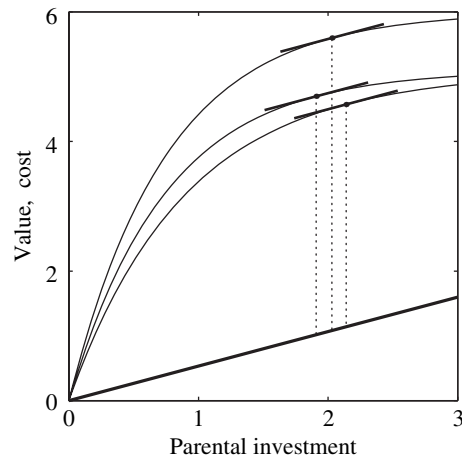

Fig. 3 The multi-offspring model: the expected value to the parent of a brood as a function of parental investment (curved lines). For any level of investment, the value of the brood is highest when there are no offspring unrelated to the parent present (top curved line, $p = 0$). When perceived parentage is less than one, the expected value decreases with the competitive advantage, c, of offspring unrelated to the parent (middle curved line, $p = 0.15$, $c = 0$; bottom curved line, $p = 0.15$, $c = 2$). Parental investment has a cost in terms of reduced reproductive success in other broods (thick straight line). At the optimal level of investment, the distance between the value and cost function is maximized (illustrated by dotted lines), and their slopes are equal (illustrated by thick tangent lines). Parameters: $n = 6$, $b = 8/15$, $k = 8$.

investment may increase when parentage decreases if the alien offspring are competitively superior. Differentiating expression (4) with respect to x, we obtain the first-order condition

$$\frac{\partial}{\partial x} w(x,p) = \sum_{m=0}^{n} \left[\binom{n}{m} p^m (1-p)^{n-m} \frac{n-m}{n+mc} k \right.$$
$$\left. exp\left(-\frac{kx}{n+mc}\right) \right] - b = 0. \qquad (5)$$

The properties of B and C ensure that there is a unique solution x^* to this first-order condition. If this solution is positive, it is the globally optimal level of investment; if it is negative, the globally optimal level of investment equals zero. Using the implicit function theorem on eqn (5), it is clear that $\partial x^*/\partial p$ equals $-(\partial^2 w/\partial p \partial x)/(\partial^2 w \partial x^2)$ evaluated at x^*. Taking the left-hand side of eqn (5) and differentiating with respect to p yields

$$\frac{\partial^2 w}{\partial p \partial x} = \sum_{m=1}^{n-1} \left[\binom{n}{m} p^{m-1}(1-p)^{n-m-1}[m-np]\frac{n-m}{n+mc} k \right.$$
$$\left. exp\left(-\frac{kx}{n+mc}\right) \right] - n(1-p)^{(n-1)} k\, e^{-kx/n}, \qquad (6a)$$

whereas differentiating with respect to x yields

$$\frac{\partial^2 w}{\partial x^2} = -\sum_{m=0}^{n} \left[\binom{n}{m} p^m (1-p)^{n-m} \frac{n-m}{(n+mc)^2} k^2 \exp\left(\frac{-kx}{n+mc}\right) \right]. \qquad (6b)$$

Equation (5) can now be solved numerically to determine the locally optimal level of investment x^*. If x^* is positive, x^* is a global maximum. We then determine $\partial x^*/\partial p$ by evaluating expression $-(\partial^2 w/\partial p \partial x)/(\partial^2 w/\partial x^2)$ at x^*, using eqns (6a) and (6b).

In the numerical explorations, it is possible to reduce the number of parameters by one: note that if both b and k are increased by the same factor r, the optimal investment simply decrease by a factor $1/r$. (This can be seen from the fact that the solution obtained when substituting kr and br for k and b in expression (4) must be the same as the one obtained when scaling x with a factor $1/r$.) Thus, the sign of $\partial x^*/\partial p$, and its magnitude relative to the case where $c = 0$, are determined by p, c, n and the aggregated parameter k/b. One may interpret a high value of k/b as meaning that a small investment will have a large effect on the reproductive success of the current brood but only a small detrimental effect on the ability to invest in other broods.

Numerical explorations confirm that marginal decreases in perceived parentage leads to increases in the optimal investment when perceived parentage and the competitive advantage of alien offspring are both high (Fig. 4). (Note that the effect may disappear if the competitive advantage becomes extreme; not shown.) The range of c and p over which marginal decreases in

perceived parentage lead to increases in the optimal investment is wider when clutch size n is high and when k/b is high (Fig. 4). For small competitive advantages, the relationship between optimal investment and perceived parentage is positive, but the strength of this relationship may be weaker (when p is low) or stronger (when p is high) than obtained in the standard model in which the competitive advantage is zero (Fig. 4).

The multi-offspring model thus gives further support to the idea that it sometimes should be optimal to increase parental investment when paternity decreases. It should be noted, however, that the model is constructed by modifying the standard model in the simplest way we find meaningful, i.e. by assuming that the ratio of investment obtained by each alien offspring to that obtained by each of the parent's own offspring is constant. In a more realistic (but less mathematically tractable) model, the alien offspring would be likely to satiate when investment gets high, as in our two-offspring model; thus, leaving more investment for the own offspring. It seems likely to us that this would be an extra incitement for the parent to increase investment. It should also be noted that we for simplicity have used a linear cost function in our numerical explorations. An accelerating cost function may be more realistic. Results qualitatively similar to those in Figs 3 and 4 have been obtained using a weakly accelerating cost function (not shown).

Discussion

The theoretical literature suggests that across repeated breeding attempts by the same individual, there should be a positive relationship between perceived parentage and parental investment (e.g. Winkler, 1987; Whittingham *et al.*, 1992; Westneat & Sherman, 1993; Houston, 1995; Houston & McNamara, 2002). Empirical support for this is mixed (e.g. Dixon *et al.*, 1994; Kempenaers *et al.*, 1998; Lifjeld *et al.*, 1998; Sheldon & Ellegren, 1998; Dickinson, 2003; Bouwman *et al.*, 2005). Our results show that the expected positive relationship between perceived parentage and parental investment may be weakened, or even become reversed, when offspring unrelated to the parent take a larger share of parental investment. A negative relationship between parental investment and perceived parentage is more likely if the alien offspring has a relatively high competitive advantage. In the absence of any competitive advantage, parental investment should increase with perceived parentage, consistent with earlier findings. Our results also show that a negative relationship is more likely when the costs of parental investment are low. The costs of parental investment may include reduced parental survival, reduced ability to invest in later broods or opportunity costs, such as reduced chances of re-nesting or obtaining extra-pair copulations.
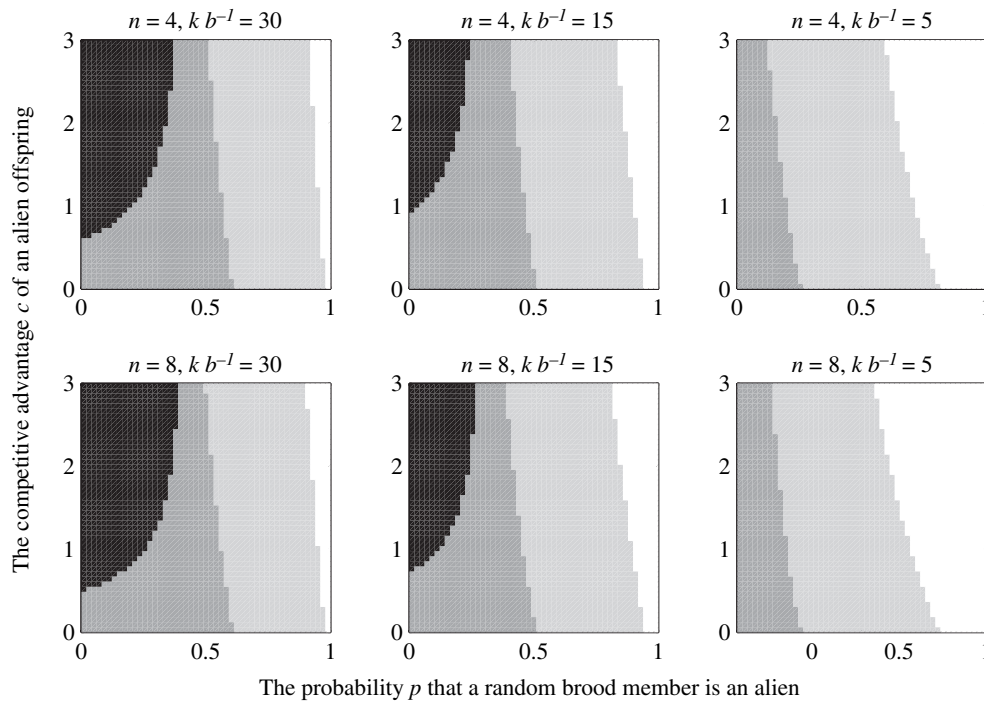
Fig. 4 The multi-offspring model: the effect on optimal parental investment (PI) from a marginal change in the probability p that a random member of the current brood is an alien. *Black*: optimal PI increases as p increases. *Dark grey*: optimal PI decreases as p increases, but less steeply than in the absence of any competitive advantage. *Light grey*: optimal PI decreases as p increases, and more steeply than in the absence of any competitive advantage. *White*: optimal PI is zero; parent should reject brood.

When these costs are low, the parent may compensate for its own offspring's competitive inferiority by increasing the total investment in the brood relatively cheaply.

We are uncertain about how strong any competitive advantages experienced by extra-pair young are likely to be, and suspect that a weakening of the positive relationship between paternal investment and perceived parentage may be a more common outcome than an outright reversal. It is important to note, however, that the effect could potentially differ between males of different qualities: male parents lacking 'good genes' or being less compatible with their mates may father low-quality offspring that are particularly likely to face tough competition from extra-pair young, and may thus be the most likely candidates for investing more in broods of lower parentage. Of course, a male lacking 'good genes' may have few extra-pair mating opportunities, and his parental investment is therefore also more likely to entail lower opportunity costs, which would also facilitate a weaker or reversed relationship between paternal investment and paternity certainty (see Houston & McNamara, 2002). An explicit model of paternal investment in relation to quality would therefore require a more detailed treatment of how both intra-pair and extra-pair paternity vary across males of different qualities (Houston & McNamara, 2002). Other types of investment costs

(e.g. increased mortality) could be higher for a low-quality male, and may also be considered in such a model. If a negative relationship between paternal investment and paternity certainty does occur, it is not clear whether females should try to hide their attempts to commit extra-pair copulations; a moderate amount of extra-pair paternity may cause the male to invest more.

It should be noted that our models are restricted to the interaction between a single parent and its brood. The male and female parents will view a mixed brood differently, and the male's response to his loss of paternity could in theory depend on the female's investment in the mixed brood. Parents might in principle either compensate for or match changes in their partner's investment (Johnstone & Hinde, 2006), and this could influence how total investment should change with paternity certainty in the biparental case.

Turning to the effect of brood parasitism on parental investment, obligate avian brood parasites are often very strong competitors for resources in the nest. In addition, the two host parents have clearly aligned interests regarding the presence of parasite nestlings. If costs of investment are low, hosts of nonevicting brood parasites could therefore well benefit from investing more in broods that are more likely to have been parasitized. Suppose that a parasite has bypassed the defences of a host and successfully parasitized it, and that this host

species is unable to reject the parasite egg or to disfavour the parasite nestling. It follows that the parasite and the host could both be better off if the parasite could inform the host that it had slipped an egg into the clutch. The parasite could do this by, for instance, staying in close proximity to the nest after laying, or by making a display. There is good empirical evidence that hosts use external cues during egg recognition (Davies & Brooke, 1988; Moksnes *et al.*, 1993; Bártol *et al.*, 2002; Davies *et al.*, 2003), but to our knowledge, no one has yet investigated whether parental investment is influenced by such cues. Although many avian brood parasites sneak into the host territory to lay their egg unseen by the host, several parasites whose offspring are raised together with host young have egg-laying tactics that seem unlikely to go unnoticed: in the great spotted cuckoo (*Clamator glandarius*), the male cuckoo flies around the host nest while calling loudly to distract the hosts away, so that the female may sneak in and lay her egg (Arias-de-Reyna, 1998; Davies, 2000). Similar male distraction displays are used during egg laying in the Jacobin cuckoo (*Clamator jacobinus*), Levaillant's cuckoo (*Clamator levaillantii*) and the Asian koel (*Eudynamys scolopacea*) (Arias-de-Reyna, 1998; Davies, 2000). In the great spotted cuckoo, the female also calls loudly when flying away after laying (Arias-de-Reyna, 1998). Other examples are the screaming cowbird *Molothrus rufoaxillaris*, which is typically noisy and conspicuous when visiting host nests (Fraga, 1998), and some parasitic *Vidua* finches that seem to be allowed to lay their egg in plain view of their estrildid hosts (Skead, 1975; Davies, 2000). Although the egg-laying tactics may have evolved for reasons completely unrelated to parental investment, they may nevertheless provide hosts with informative cues about the risk of having been parasitized and allow them to invest optimally in the brood, to the mutual benefit of host and parasite. The parasite's laying behaviour may then subsequently come under selection to further increase the probability of being noticed by the hosts.

If hosts invest more when parasitized, but are unable to disfavour the parasite offspring directly during feeding, a parasite nestling may also potentially benefit from informing the host of its presence. This may be exploited by the parent's own offspring. The theory of parent–offspring conflict predicts that offspring typically should be selected to take more resources from their parents than it is in the parents' interest to give (Trivers, 1974). In an unparasitized nest, a host offspring may therefore potentially benefit from manipulating its parent into believing that there is a parasite present, as that would favour greater investment by the parent. This may give rise to a paradoxical evolutionary arms race, in which host offspring are selected to mimic the appearance of parasite offspring, and parasite offspring are selected to use honest signals that the host offspring have difficulties copying (e.g. supernormal calls). A slightly different but not mutually exclusive reason why host offspring should

mimic parasite offspring have been offered by Hauber & Kilner (2007).

In conclusion, we have shown that unequal competitive abilities of within-pair young and extra-pair young in a brood may weaken or reverse the expected positive relationship between parental investment and perceived parentage across breeding attempts. We have assumed that parentage in the current reproductive attempt is not correlated with parentage in subsequent events; the incorporation of such correlations in the model framework would be an interesting future extension. We suggest that the competitive strengths of within-pair and extra-pair young should be quantified in empirical studies that attempt to determine the relationship between parental investment and paternity.

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