

# Differential Allocation Revisited: When Should Mate Quality Affect Parental Investment?

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**ABSTRACT:** Differential allocation (DA) is the adaptive adjustment of reproductive investment (up or down) according to partner quality. A lack of theoretical treatments has led to some confusion in the interpretation of DA in the empirical literature. We present a formal framework for DA that highlights the nature of reproductive benefits versus costs for females mated to males of different quality. Contrary to popular belief, analytical and stochastic dynamic models both show that additive benefits of male quality on offspring fitness have no effect on optimal levels of female investment and thus cannot produce DA. Instead, if offspring fitness is affected multiplicatively by male quality, or male quality affects the female cost function, DA is expected because of changes in the marginal benefits or costs of extra investment. Additive male quality effects on the female cost function can cause a novel form of weak DA, because reduced costs can slightly favor current over future reproduction. Combinations of these distinct effects in more realistic model scenarios can explain various patterns of positive and negative DA reported for different species and mating systems. Our model therefore sheds new light on the diversity of empirical results by providing a strong conceptual framework for the DA hypothesis.

**Keywords:** reproductive compensation, sexual selection, parental investment, state-dependent model, maternal effect, paternal effect.

## Introduction

Differential allocation (DA) is usually described as the strategy of a parent adjusting its investment in the current reproductive attempt according to the perceived attractiveness or general quality of its mate. This idea was first presented by Burley (1986, 1988), who demonstrated the

phenomenon in posthatching parental care in captive zebra finches (*Taeniopygia guttata*). Experimental work demonstrating DA has since been carried out across a wide range of species, mating systems, and patterns of parental care (reviewed in Sheldon 2000; Ratikainen and Kokko 2010; Horvathova et al. 2012).

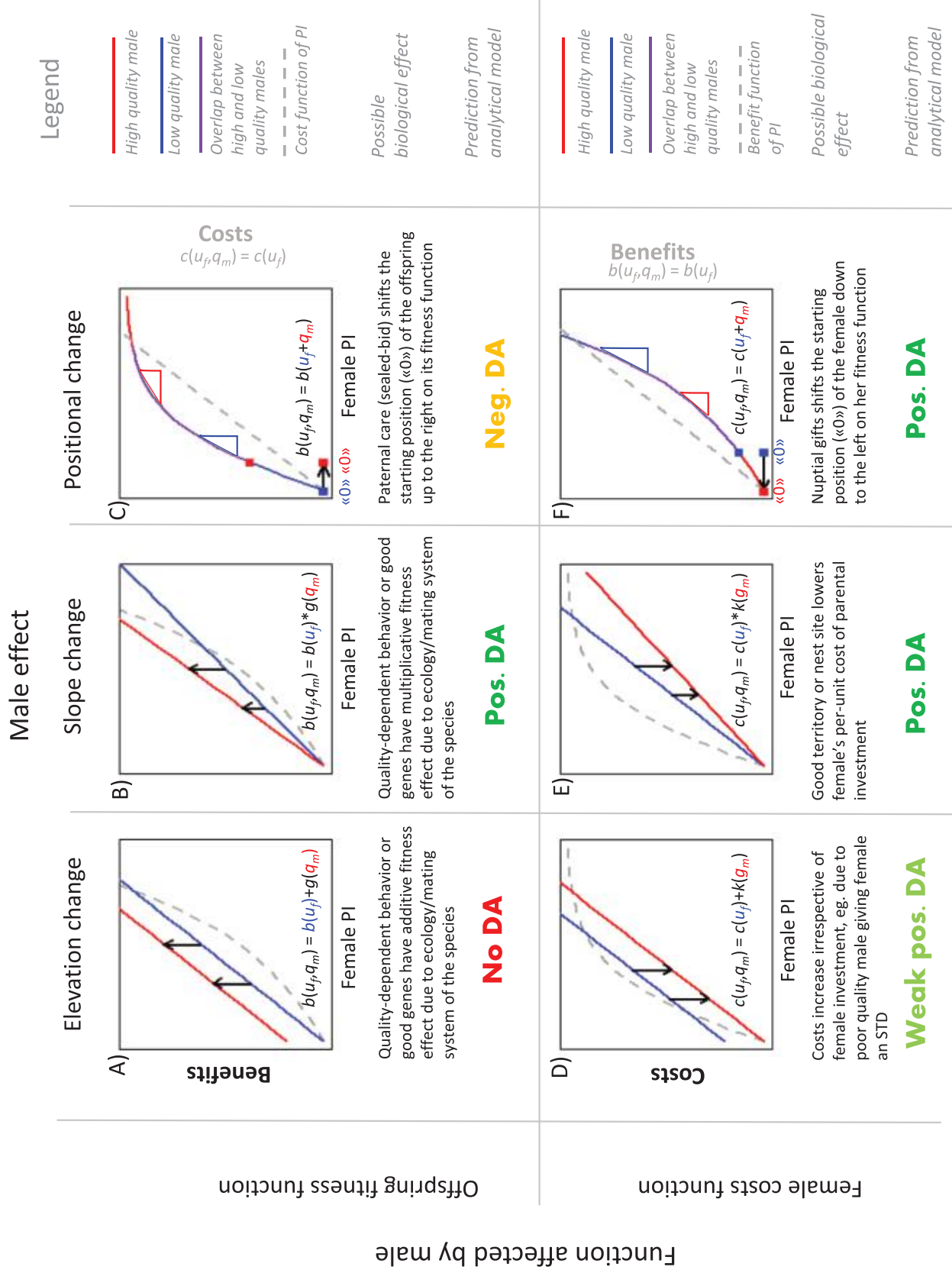
DA has traditionally been considered to imply an increase in parental investment (PI) with increasing mate quality, but several studies have shown a decrease in PI with increasing mate quality (Bluhm and Gowaty 2004; Byers and Waits 2006; Bolund et al. 2009), a pattern initially viewed as in direct conflict with DA. This has become known as reproductive compensation (RC; Gowaty et al. 2007; Gowaty 2008), but the more recent viewpoint has been that DA and RC simply represent the ends of a continuum of investment patterns across mate qualities (Harris and Uller 2009; Ratikainen and Kokko 2010; Kindsvater et al. 2013). We therefore employ here the terms “positive DA” and “negative DA,” to represent an increase and a decrease in PI with increasing mate quality, respectively. Although it is important to recognize that adaptive DA can be carried out by both male and female parents in various forms of parental and reproductive investments, for convenience we discuss the more common situation here of male mate quality effects on female reproductive investment, but most arguments can easily be turned around to understand how female quality should affect male reproductive investment.

Empirical work on DA has for a long time lacked a formal theoretical framework within which to place any results, and only recently have mathematical models started to emerge. Harris and Uller (2009) presented a dynamic state-based model showing that different parameterizations, representing different life-history scenarios, could produce either positive DA or negative DA when maximizing lifetime fitness. They focused on the life-history trade-off between current and future female investment. This trade-off arises due to having only a finite amount of resources (“energy”) available for

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lifetime reproduction and is a key to understanding why DA appears in the first place (Sheldon 2000). However, Ratikainen and Kokko (2010) point out several shortcomings of the model, the most severe of which was using an overly simplistic linear increase in offspring survival with greater female investment and increasing mate quality. This equates to a scenario where the slope of the offspring's fitness function is the same for all male qualities and only elevation changes (fig. 1A; but see "Discussion"). One of the fundamental assumptions of the DA hypothesis is that mate quality influences the optimal level of investment (Sheldon 2000), and we show here that this is only the case when offspring fitness benefits are multiplicative (mate quality affects the slope of the fitness function; fig. 1B), not when they are purely additive (mate quality affects only fitness function elevation; fig. 1A). We would argue that a much stronger focus on exactly how the partner affects the shapes of the cost and benefit functions is needed in order to understand when to predict positive and negative DA. Still, the model by Harris and Uller (2009) provides a very important first step, and the stochastic dynamic modeling approach taken was entirely appropriate considering the state-dependent nature of the DA hypothesis (McNamara and Houston 1996).

A more recent model by Kindsvater and Alonzo (2014) shifted the focus to effects of different types of male quality, ranging from purely genetic benefits to nuptial gifts and different forms of paternal care, such as nest defense or offspring provisioning. Differing patterns of DA are expected depending on which of these benefits male attractiveness conveys to females, a point first made by Møller and Thornhill (1998; see also Krist and Munclinger 2015). Furthermore, Kindsvater and Alonzo (2014) emphasize the effect of male quality on the shape of the offspring growth (i.e., benefit; fig. 1A–1C) curve, and their model allows female reproductive allocation responses to vary with regard to both the size and the quantity of offspring. This issue of different types of male quality and their potentially different effects on female DA may explain the contrasting results seen in various experimental studies (e.g., Bolund et al. 2009; López-Rull and Gil 2009; Uusi-Heikkilä et al. 2012), and this model therefore provides a useful meeting point for empiricists and theoreticians. However, Kindsvater and Alonzo (2014) do not directly address what has become the central question concerning the DA hypothesis: how the total amount of resources

invested in a reproductive attempt should vary according to mate quality in a given reproductive attempt, considering the quality of the current partner and the expected quality of future partners (Sheldon 2000). In the Kindsvater and Alonzo (2014) model, mate quality never changes over the course of a female's lifetime. Despite this, the Kindsvater and Alonzo (2014) model still represents a valuable addition to DA theory, and we use it here as inspiration for a more detailed consideration of possible male quality effects on female reproductive decisions.

The wide range of systems in which DA has been observed (Sheldon 2000; Horvathova et al. 2012) suggests a general evolutionary advantage to DA. However, we still lack a convincingly general conceptual framework for DA based on a formal theoretical model. We present here an analytical model as well as a more biologically realistic stochastic dynamic model and in this way examine adaptive variation in female reproductive investment in response to all the different types of possible effects of male quality in this context.

#### Classification of Male Quality Effects

For male quality or attractiveness to affect female reproductive decisions, the male must affect either the benefit function or the cost function of female reproduction (fig. 1A–1C and 1D–1F, respectively) or both. Both of these could be affected in three conceptually distinct ways: mate quality changing additive effects via the elevation (fig. 1A, 1D), multiplicative effects via the slope (fig. 1B, 1E) or the horizontal position of the function (fig. 1C, 1F), or some combination of these. The benefits here are offspring fitness as a function of PI, which can be affected in a number of ways, as pointed out by Kindsvater and Alonzo (2014). The effect of male quality on the offspring fitness function can work through expected differences in levels of paternal care (e.g., offspring provisioning or nest defense), or it can be due to effects of heritable differences in offspring quality ("good genes") or attractiveness (e.g., benefits in any Fisherian runaway process; see fig. 1). The female cost function can also change according to male quality via a range of male effects, such as quality-dependent nuptial gift sizes, nest site or territory qualities (affecting the per capita costs of female care), or male social dominance and protection from harassment

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**Figure 1:** Classification of male quality effects on offspring fitness benefits (A–C) and female fitness costs (D–F) as functions of female parental investment (PI), with biological examples and predictions informed by the analytical model. Equations in the boxes show the interpretation of male quality effects in the analytical model. A, Male quality increases the elevation of the offspring fitness function. B, Male quality increases the slope of the offspring fitness function. C, Male quality shifts the female's starting position (blue point) on the X-axis of the offspring fitness function to the right (red point), thus starting the red line at a higher value than the blue line. D, Male quality lowers the elevation of the female cost function. E, Male quality lowers the slope of the female cost function. F, Male quality shifts the female's starting position (blue point) on the X-axis of her cost function to the left (red point), thus starting the red line at a lower value than the blue line. DA = differential allocation; STD = sexually transmitted disease.

by other males and the prevalence of sexually transmitted diseases (see fig. 1). Therefore, male quality effects on female DA can appear in a variety of natural systems, even those with no obvious male contribution to offspring production beyond providing a gamete.

For both benefits and costs, any change to the function can be seen as a change in either the additive effects of the elevation (fig. 1A, 1D) or the multiplicative effects of the slope (fig. 1B, 1E) or a combination of the two, depending on the biological scenario being represented. Offspring fitness is realistically assumed to be a positive decelerating function of PI. Female fitness costs are assumed to be a positive accelerating function of reproductive investment. However, it is conceptually useful to first use linear functions in order to disentangle the effects of changing separately either only the elevation or only the slope. For example, male “good genes” for immunity against certain pathogens could act generally to increase the elevation of the offspring benefit function, irrespective of the level of maternal care. Alternatively, male “good genes” concerning digestive efficiency could improve the offspring’s ability to benefit from maternal care, thereby increasing the slope (but not the elevation) of the offspring benefit function. Likewise, poor-quality males with sexually transmitted diseases might increase the elevation of the female cost function, whereas good-quality males providing higher-quality territories might decrease the slope of the female cost function (i.e., the per capita cost of providing care). Since at least one of the benefit or cost functions needs to be curvilinear in order for an intermediate optimum level of investment to exist, in each case we let the focal function (the one being affected by male quality) be linear and the background function (not being affected by male quality) be curved. After this examination of linear function elevations versus slopes, we then continue on to more biologically realistic scenarios, with greater insight into the effects of curvilinear benefit and cost functions.

In figure 1C, 1F we illustrate the third possible effect of male quality shifting the horizontal position of the female on the PI  $X$ -axis of the offspring benefit and female cost functions. This shift to the right on the offspring benefit function (the starting position of the red line is farther along the  $X$ -axis than the starting position of the blue line in fig. 1C) emulates the effect of the male helping with parental care, in that the shape and position of the curve remain unchanged, but the offspring is effectively moved up its fitness function by a certain distance. This is different conceptually from genetic effects of male quality that may change the slope and/or elevation of the function itself (although a combination of both effects can be envisioned). Note, however, that the conceptualization of biparental investment in figure 1C involves the male making his decision before the female, so it is essentially a “sealed-bid” model with a strict order and no behavioral dynamics in the form of biparental negotiation (Houston and Davies 1985; McNamara

et al. 1999). The interesting point here is that for a curved benefit function (as in fig. 1C), a greater shift to the right caused by a higher-quality male also causes a decrease in the slope and thus the marginal (multiplicative) benefits per capita of investment by females (colored triangles in fig. 1C). For the female cost function, an effect of improved male quality, such as a nuptial gift of a larger size, could similarly shift the horizontal position of the female to the left on her cost curve (fig. 1F), but again this would not involve a change in the shape of the function itself. In this case, a higher-quality male would shift the female down her cost curve, reducing the slope experienced initially and allowing her the opportunity to initially invest more at a lower per capita cost before reaching the steeper parts of the function.

It is crucial in DA theory to conceptually divide the effects of male quality into these separate effects either on the elevations or slopes of the offspring benefit or parental cost functions of female PI or on the starting positions along these functions. This is because these different effects most often arise from different origins and field researchers may have an intuition or data to suggest which type of male quality effect(s) the females in their system are likely to be experiencing. Depending on the ecology of the species in question, male brood defense may, for example, affect the elevation of the offspring fitness function (fig. 1A) if it increases the probability of offspring survival equally regardless of how much maternal investment each offspring receives. Alternatively, male brood defense may affect the slope (fig. 1B) if offspring receiving more maternal investment are more likely to benefit from the quality of their father’s brood defense. Male quality effects on the female cost curve (fig. 1D–1F) are most likely social in origin. For example, a high-quality male providing a resource-rich territory may lower the female’s per-unit cost of offspring provisioning, thereby affecting the slope of the cost curve. Alternatively, a high-quality male may prevent harassment from other males, affecting the elevation of the female cost curve. Furthermore, male quality effects on the female cost curve are going to have more direct consequences for future female reproduction, as compared to effects on the offspring fitness function. This is because offspring benefit effects affect future investment only through the lowering of energetic reserves according to the level of current investment, which ultimately is decided by the female. Therefore, it is important to appreciate that costs and benefits of female reproduction do not entirely represent the same life-history currency. We feel that the conceptual classification of male quality effects shown in figure 1 is essential for sorting out the different processes, and possibly opposing selection pressures, that mate quality could have on adaptive DA.

In this article, we will first show how these basic slope/elevation/PI and benefit/cost distinctions can be represented mathematically, and we derive some fitness results from a

simple analytical model that can inform predictions regarding DA in the different scenarios. Then we present a stochastic dynamic state-based model of DA using these basic scenarios, as well as some more biologically realistic scenarios to properly explore the effects on DA within this framework. This modeling is aimed at clarifying much of the confusion surrounding this topic and providing robust predictions for empiricists regarding level and direction of DA expected in different systems.

### A General Mathematical Model

The scenarios outlined in figure 1 can be described mathematically where we investigate whether and how optimal female investment in the first of two breeding seasons depends on male quality. Let us write  $u_f$  for her own current investment and  $q_m$  for the quality of her current mate. As mentioned before, we assume that an increase in male quality positively affects the number of surviving offspring in a female's brood. Female benefits,  $b$ , in terms of offspring fitness at time steps  $t$  and  $t + 1$  are then

$$b_t(u_f, q_m),$$

$$b_{t+1}(\tilde{u}_f, \tilde{q}_{m,i}, c(u_f, q_m)),$$

for current and future fecundity, respectively, where  $\tilde{u}_f$  represents the female's investment at  $t + 1$  (which may be different than  $u_f$ ) and  $\tilde{q}_{m,i}$  is the effect of a future male of quality  $i$ . The cost function  $c(u_f, q_m)$  (see fig. 1D–1F) is added to the expression for future fecundity, because we assume that the female's current investment, as well as her current male's quality, changes the amount of resources she can allocate to her future fecundity. However, in appendix, part A, section A3 (appendix pts. A, B available online), we show that our results generalize to scenarios where costs affect survival rather than future fecundity. Hence, the female's fitness function is given by her current fecundity plus her future fecundity devalued by her probability  $\alpha$  of surviving until the next breeding season:

$$W = b_t(u_f, q_m) + \alpha \sum_{i=1}^{N_m} [p_i b_{t+1}(\tilde{u}_f, \tilde{q}_{m,i}, c(u_f, q_m))] \quad (1)$$

so that the optimal level of female investment  $u_f^*$  can be found by solving the equation

$$\frac{\partial W}{\partial u_f} = \frac{\partial b(u_f, q_m)}{\partial u_f} + \alpha \frac{\partial c(u_f, q_m)}{\partial u_f} \frac{\partial \bar{b}_{t+1}(\tilde{u}_f, c(u_f, q_m))}{\partial c} = 0. \quad (2)$$

The bar in  $\partial \bar{b}_{t+1} / \partial c$  denotes that a female's future benefits are averaged over all  $N_m$  possible qualities  $\tilde{q}_{m,i}$  of a female's future partners (see appendix, pt. A). While the quality  $\tilde{q}_{m,i}$  of any future male may well affect a female's future invest-

ment  $\tilde{u}_f$ , it does not affect a female's investment in response to her current partner's quality  $q_m$ , so  $\tilde{q}_{m,i}$  can be treated as a constant. Note that this assumes that the probabilities ( $p_i$ ) of mating with different-quality males in the future are not affected by the female's current investment or mate quality.

### Analytical Model Results

*Absence or Presence of DA.* We see that the absence or presence of DA depends on whether the female's optimality criterion (eq. [2]) depends on  $q_m$  and calculate whether this is the case for each scenario in fig. 1 (see appendix, pt. A, sec. A1).

This analysis shows that in the benefit-elevation scenario (figure 1A), female investment  $u_f^*$  does not depend on male quality  $q_m$ . Hence, when male quality contributes additively to female fecundity, we do not expect DA to arise. In the benefit-slope scenario (fig. 1B), however, male quality and female investment determine offspring fitness in a multiplicative fashion, so that  $u_f^*$  depends on  $u_m$ . Here, we expect females to show DA. A similar multiplicative relationship between male quality and female investment holds for the benefit-position scenario (fig. 1C), and again we expect DA to arise.

In the cost-elevation scenario (fig. 1D), male quality affects female costs additively. Whether this scenario produces DA depends on the shape of the future benefit function  $b_{t+1}$ . Although the marginal costs of investment are unaffected by male quality, DA may still appear if the derivative  $b'_{t+1}$  in equation (2) depends on  $q_m$ . This will be the case if  $b_{t+1}$  is nonlinear, whereas if  $b_{t+1}$  is linear, the dependency of  $b'_{t+1}$  on  $q_m$  disappears (see appendix, pt. A, sec. A1). The future fecundity function may be interpreted in different ways, but it is not implausible to assume at least a somewhat nonlinear function (as in the stochastic dynamic model below), so we predict that some weak DA will occur. For the other cost scenarios (fig. 1E, 1F),  $u_f^*$  always depends on  $q_m$ , so we expect DA to occur in both of these cases.

*Direction of DA.* For those scenarios in which female investment  $u_f$  depends on the current male's quality  $q_m$ , we write female investment as a female's best response  $u_f \equiv r(q_m)$  to the current male's quality (e.g., see McNamara et al. 2003). We can then assess the direction of DA (positive or negative) by evaluating the slope of the female's best response function, the sign of  $r'(q_m)$ : if females decrease investment with increasing male quality (negative DA), we have  $r'(q_m) < 0$ , while positive DA results in  $r'(q_m) > 0$ . To obtain an expression for  $r'(q_m)$ , we substitute for  $u_f \equiv r(q_m)$  in equation (2) and then take the derivative with respect to  $q_m$ , after which we solve for  $r'(q_m)$  and evaluate whether positive or negative DA is expected. The expressions are shown in appendix,

part A, section A2, and evaluated for all the scenarios in panels B–F in figure 1 (the first case, benefit-elevation, does not yield any DA).

The key result of this best-response analysis is that positive DA is expected to be the norm, occurring in all but one scenario (benefit-position). Positive DA is selectively favored in the benefit-slope scenario because an increase in male quality increases a female's marginal returns  $b'_i$  on current investment (i.e.,  $\partial^2 b_i / \partial q_m \partial u_i > 0$ ; see fig. 1B). Similarly, positive DA evolves in all cost scenarios, because an increase in male quality always decreases the cost of a female's current investment (i.e.,  $\partial c / \partial q_m < 0$ ; see fig. 1D–1F), favoring greater female investment. This effect is amplified in both the cost-slope and cost-position scenarios, where increasing male quality also reduces a female's marginal costs  $c'(u_i)$  of investment (i.e.,  $\partial^2 c / \partial q_m \partial u_i < 0$ ; see fig. 1E, 1F), resulting in stronger positive DA relative to the cost-elevation scenario.

The exception is the benefit-position scenario, where negative DA is expected. Here, an increase in male quality decreases a female's marginal returns  $b'_i$  on current investment (i.e.,  $\partial^2 b_i / \partial q_m \partial u_i < 0$ ; see fig. 1C). Hence, in the face of lower marginal returns when mated to a high-quality male, females should decrease investment.

## Stochastic Dynamic Model

### Model Description

To verify the results of the simple analytical treatment of DA, we also created a more realistic state-based stochastic dynamic model (Houston and McNamara 1999; Clark and Mangel 2000). This approach has the advantage of allowing the female multiple breeding opportunities during her lifetime, where she can make state-dependent choices. Each time step she meets a male of random quality  $q_m$  and may choose how large a reproductive investment  $u_i$  she makes in a single offspring. The female gains fitness benefits in terms of offspring fitness  $b_i(u_i, q_m)$ , which may depend on male quality. The costs of reproduction,  $c(u_i, q_m)$ , may also depend on male quality and have the explicit effect of lowering the female's condition or energetic state  $x$ , thus affecting how large an investment she is able to make in future time steps.

Females have a fixed probability ( $\alpha$ ) of surviving until the next breeding opportunity and a probability ( $\lambda$ ) of foraging success, which increases their energetic state by  $d$  units before the next breeding opportunity. Adding state-dependent survival ( $\alpha$  as a function of energetic state,  $\alpha(x)$ ) does not alter the results qualitatively and was thus excluded from the model for simplicity. The model begins at end time  $T$  and iterates backward to find the optimal investment,  $u_i^*$ , and fitness value given the optimal investment,  $W^*(u_i^*, x, q_m, t)$ , for every combination of state, mate quality, and time step. At each

combination, the fitness values are calculated for all investments by

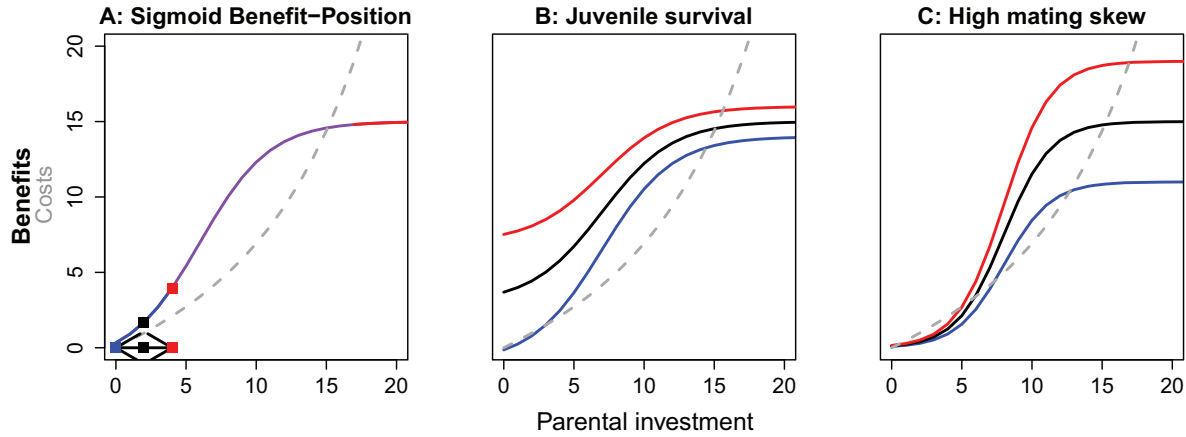
$$W(u_i, x, q_m, t) = b_i(u_i, q_m) + \alpha \left[ \sum_{i=1}^{N_m} p_i \{ \lambda W^*(x - c(u_i, q_m) + d, q_i, t + 1) + (1 - \lambda) W^*(x - c(u_i, q_m), q_i, t + 1) \} \right] \quad (3)$$

and the program maximizes over all possible investments. Parameter values and further variable descriptions are given in table A1 (tables A1, A2 available online). Details of the stochastic dynamic modeling and equation (3) are discussed further in appendix, part B. In addition, we examined lifetime trajectories for individual females by running forward simulations using the Markov chain Monte Carlo method (Clark and Mangel 2000), based on the optimal investments from the model output.

### Scenarios

As with the analytical model, the stochastic dynamic model was used to test the same baseline scenarios shown in figure 1. We also create some additional scenarios based on more flexible and realistic sigmoid benefit functions, where each class of males provides a different set of parameters and thus differently shaped benefit functions (fig. 2). Function expressions are presented in appendix, part B, and parameters descriptions and values are given in table A1. All scenarios are summarized in table A2.

For the additional scenarios, we first demonstrate the effect of a positional shift on the now sigmoid offspring fitness function (sigmoid benefit-position; fig. 2A), which is similar to benefit-position in that the fitness function itself does not change with male quality, only the female's starting position on it. Then we have two scenarios where different-quality males offer different shapes of offspring fitness functions. The juvenile survival scenario (fig. 2B) illustrates a situation where the main effect of higher-quality males is to ensure higher offspring fitness at lower levels of female investment (by increasing the lower asymptote of the function), similar to the good offspring scenario in Harris and Uller (2009). This then also captures the potentially relevant effect of offspring of poor-quality males having lower elevations but steeper slopes in their fitness function and offspring of good-quality males having higher but less steep fitness functions. In contrast, the high mating skew scenario (fig. 2C) illustrates a mating system where offspring of poor-quality males provide females with little absolute fitness, while good-quality offspring may potentially provide very large fitness returns if they receive high levels of care. This is



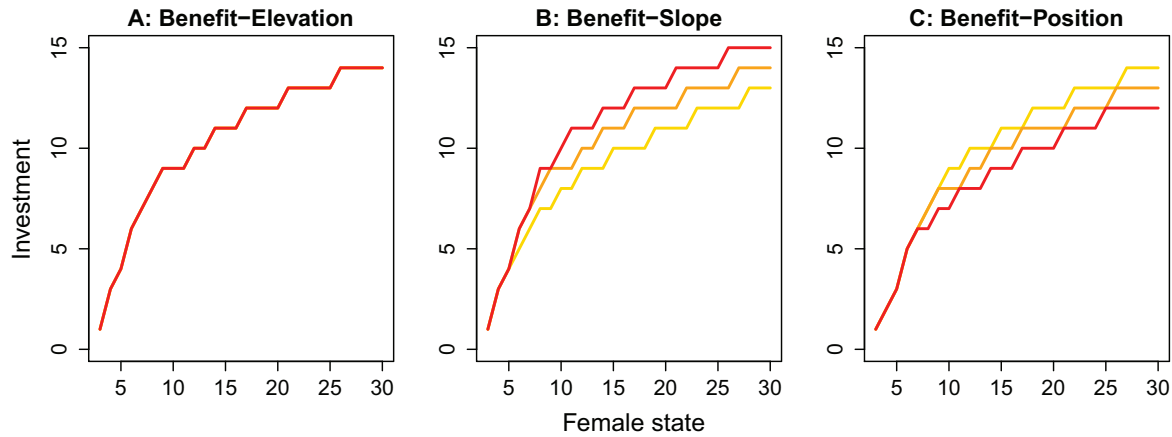
**Figure 2:** Additional scenarios with sigmoid offspring fitness benefits (solid lines) and accelerating female fitness costs (dashed lines) as functions of female parental investment (PI). Red lines are with good-quality males, black lines are with intermediate-quality males, and blue lines are with poor-quality males. The purple line in A indicates that red and blue lines overlap. A, Male quality (e.g., in the form of greater paternal care) shifts the female’s starting position (black point = medium male) on the X-axis of the offspring fitness function to the left (blue point = poor male) or right (red point = good male), thus starting the red line at a higher value than the blue line. B, Male quality has a strong effect on offspring fitness for low levels of female PI (e.g., because of good genes or predator defense). C, Male quality has a strong effect on offspring maximum attainable fitness (e.g., because of the “sexy son” effect).

captured by increasing the inflection point and upper asymptote of the offspring fitness function with increasing male quality. All scenarios and parameter values used are listed in table A1.

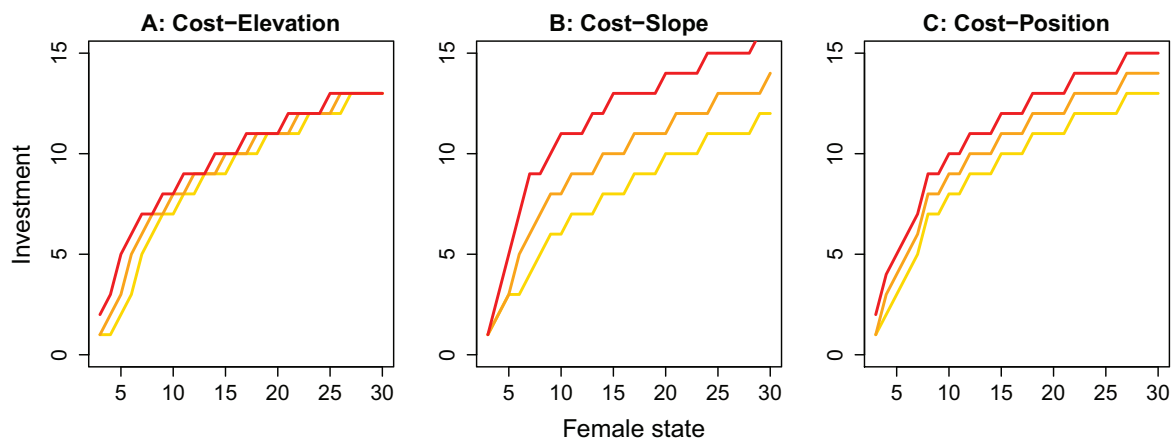
*Stochastic Dynamic Model Results*

The results of the stochastic dynamic optimizations are shown in figures 3 (benefit scenarios), 4 (cost scenarios), and 5 (sigmoid scenarios). All investments stabilized with

respect to time (see appendix, pt. B), and therefore only the optimal investments for all states during the first time step are shown, with one line for each male quality. In figures 3–5, any difference in the elevation of the lines for males of different qualities represents DA for females in that state (i.e., positive DA if the lines for the higher-quality males [red] are uppermost, negative DA if the lines for the poorer-quality males [yellow] are uppermost). Note that there is often strong state dependence, not only in the absolute levels of female reproductive investment



**Figure 3:** Optimization results from benefit scenarios. A, Benefit-elevation, no DA; B, benefit-slope, positive DA; C, benefit-position, negative DA (see table A1, available online, for details). Optimal female reproductive investment is shown against female energetic state at  $t = 1$ , with good-quality (red line), intermediate-quality (orange line), and poor-quality (yellow line) males. Where lines overlap, the line color for the highest male quality is shown.



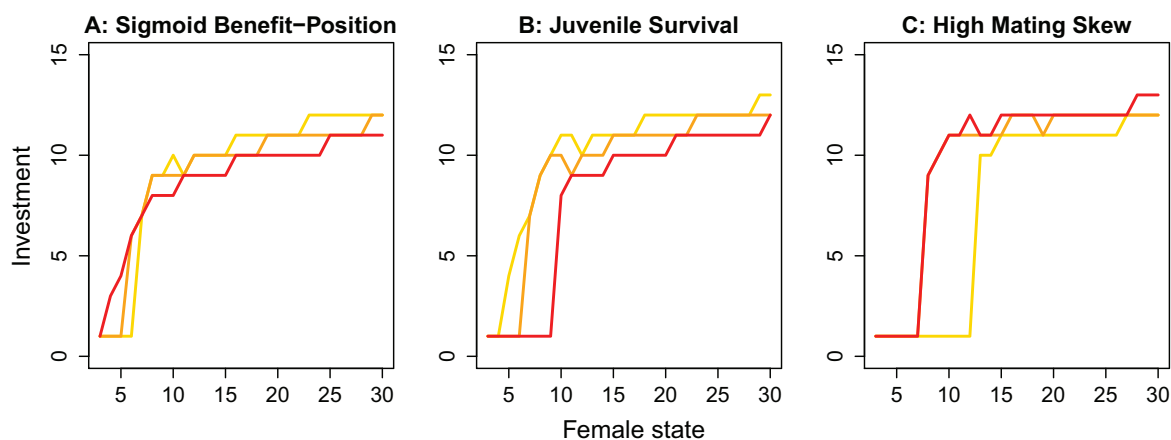
**Figure 4:** Optimization results from cost scenarios. A, Cost-elevation, weak positive DA; B, cost-slope, positive DA; C, cost-position, positive DA (see table A1, available online, for details). Optimal female reproductive investment is shown against female state at  $t = 1$  with good-quality (red line), intermediate-quality (orange line), and poor-quality (yellow line) males. Where lines overlap, the line color for the highest male quality is shown.

but also in the strength of DA and occasionally in the direction of DA (e.g., fig. 5A, with positive DA at low states and negative DA at higher states). Results from the forward simulations for all scenarios are shown in the supplementary material (available online). We now discuss each of the main results in more detail for the simplified and then the more realistic scenarios.

*Baseline Scenarios.* Contrasting the benefit-elevation and benefit-slope scenarios confirms the analytical model result (appendix, pt. A, sec. A1) that only the multiplicative effect

of the slope of the offspring fitness function, not the additive effect of the elevation, matters in terms of generating DA. Benefit-elevation thus acts as a control, demonstrating that any DA we see in benefit-slope (or any other scenario with male quality effects on the offspring fitness function) must be coming from the changes in slope, since changes in the elevation alone clearly do not produce DA. DA occurs because of changes in the multiplicative marginal fitness benefits per unit of PI, not the additive absolute benefits.

The levels of investment, as well as the amount of DA, in the benefit scenarios (fig. 3) depend strongly on the



**Figure 5:** Optimization results from the additional scenarios. A, Sigmoid benefit-position, positive and negative DA; B, juvenile survival, variable negative DA; C, high mating skew, variable positive DA (see table A1, available online, for details). Optimal female reproductive investment is shown against female state at  $t = 1$  with good-quality (red line), intermediate-quality (orange line), and poor-quality (yellow line) males. Where lines overlap, the line color for the highest male quality is shown.



female's energetic state, suggesting that females in low state might not always have the resources to be able to fully benefit from a strategy of DA. This state-dependent effect on the scale of DA is less obvious in the cost scenarios (fig. 4), with male quality effects on the female cost function influencing investment strategies for even the females in the lowest states. The weak positive DA in cost-elevation (fig. 4A) lends support to the analytical results in this regard, and it appears to be relatively robust since it persists across a range of different life-history parameter values and shapes of cost and benefit functions. This form of DA arises since the state-dependent trade-off between current and future investments is nonlinear, as in the analytical model, and it also persists if the cost function is curved and the benefit function is linear (the opposite of fig. 1D). The effect all but disappears when females are in high states, since the marginal benefit of this one extra unit of current investment declines with increasing investments (figs. 4A, 1D).

Due to this weak DA in the cost-elevation scenario, we are not entirely able to separate elevation effects from slope effects on the cost function in the same way as we could for the benefit function. And because the female cost functions in cost-slope all pass through the origin, increasing the slope also inevitably increases the elevation for a given investment. However, the DA seen in cost-slope (fig. 4B) is much stronger than in cost-elevation and is more pronounced at high states, indicating an effect of change in slope that is separate from that of change in elevation. Therefore, the male quality effects on the slope of the female cost function in figure 4B mirror the effects on the slope of the offspring benefit function in figure 3B and confirm that positive DA in these cases arises due to changes in the marginal costs or benefits of care.

For the position scenarios, where male quality shifts the female position on the  $X$ -axis of either the offspring benefit function (benefit-position) or the female cost function (cost-position), the focal function is curved and the background function linear (see fig. 1C, 1F). When moving right up the decelerating curve of the offspring benefit function in benefit-position, the offspring fitness increases and the slope decreases. As expected from scenarios benefit-elevation and benefit-slope (above), increasing male quality in benefit-position therefore produces negative DA, due to the decreasing marginal benefits of PI further up the function and irrespective of an increase in the absolute benefits (fig. 3C). The analogous positional shift to the left down the cost function, due to increasing male quality in the scenario cost-position, thus produces positive DA as a result of both the weak effect of a decrease in elevation (cost-elevation) and the stronger effect of a decrease in slope (cost-slope). Our analytical results for direction of DA support this negative DA in benefit-position and positive DA in cost-position.

*Additional Scenarios.* Including a more realistic sigmoid offspring benefit function (see fig. 2 and description above in "Scenarios") produces different investment patterns from those seen in the simplified scenarios. Because of the small marginal benefits from low levels of initial investment, the sigmoid offspring benefit function means that females avoid investing until they know that they can get onto a steeper part of the function. This produces more abrupt increases in female investment with state, depending of course on how male quality affects the offspring benefit function. The result of this can be seen in the patterns of DA in figure 5B, 5C, which appear as if they are nearly "all-or-nothing" investment decisions.

Interestingly, for the sigmoid benefit-position scenario, where male quality equates to greater paternal investment, we would predict positive DA for females in low states and negative DA in high states (fig. 5A). In this scenario, females in medium to high states can invest enough for their offspring to reach levels above the inflection point of the sigmoid offspring benefit function. These females then experience decelerating fitness returns from any additional investment they provide on top of that provided by good-quality males. This therefore has the effect of producing negative DA in these females in a high state, as in the benefit-position scenario above (see figs. 1C, 3C). In contrast, females in a low state tend to be investing while in the accelerating part of the sigmoid offspring benefit function, and so any positional shift caused by increased PI by good-quality males moves them onto a steeper part of the benefit function. This then increases the marginal benefits of any additional female reproductive investment and produces positive DA for females in the lowest states (fig. 5A). Knowledge of female condition or energetic state may therefore be crucial for empirical tests of DA under such a scenario.

The juvenile survival scenario (fig. 5B) provides another important finding by illustrating a case of strong negative DA that is not the result of any strategic reduction in female investment due to higher levels of paternal care from good-quality males (as in benefit-position). In this scenario, although the elevation of the benefit function is lowest for the offspring of poor-quality males, it has a much steeper slope (due to a greater difference between the upper and lower asymptotes, i.e., minimum and maximum offspring fitness; see fig. 2B). Therefore, investment in offspring of poorer-quality males provides females with greater marginal benefits—an effect purely of differences in the benefit slope but in the opposite direction than in the scenario benefit-slope above. This favors greater investment from females when caring for offspring of poor-quality males (fig. 5B). The magnitude of this negative DA effect decreases for females in a high state, due to the marginal benefits of investment decreasing in all types of offspring as their benefit functions reach their asymptotes. However, the forward simulations show that females are unlikely to stay in these high states for very long

during their lives (see fig. S8 in supplementary material; figs. S1–S9 available online), and so this differential juvenile survival scenario suggests a viable alternative explanation for findings of negative DA.

The high mating skew scenario results in the most pronounced all-or-nothing investment pattern, with a strong step-up in investment levels with increasing female state and large sudden DA effects due to differences in male quality (fig. 5C). This result echoes the “invest versus do not invest” patterns of female care seen in various empirical studies of DA (e.g., Drickamer et al. 2000; Uusi-Heikkilä et al. 2012). In this scenario, investment in offspring of poor-quality males rarely pays off, because of the prohibitively high female PI required to get them onto the steep part of their fitness benefit function, and even then the increase in offspring fitness is barely enough to outweigh the costs of such high investment by the female (see fig. 2C). It is therefore only females in high states that invest at all in offspring from poor-quality males. Indeed, females below a certain state (around  $x = 12$ ) will even forgo breeding when faced with a poor-quality male partner in order to postpone any reproductive investment until the next time step (possibly finding food and increasing in state in the meantime) where they may then hope to meet a better-quality male.

### Discussion

Our two models of DA succeed in showing that there are, in fact, three different effects of male quality that can produce DA. The most obvious of these is (i) multiplicative change in the offspring benefit function (slope), but there is also (ii) multiplicative change in the female cost function (slope) that has the equivalent effect via the marginal fitness payoffs per female investment. Our results also show that (iii) additive change in the female cost function (elevation) can also cause weak DA. Contrary to suggestions in some of the DA literature, the last possibility here, (iv) additive change in the offspring benefit function (elevation), cannot produce DA.

These distinctions therefore help clarify the results shown by Harris and Uller (2009), where a change in the offspring fitness function (i.e., the benefit function) is included explicitly as an effect of male quality. In their model, however, male quality always affects both the elevation and the slope of the offspring fitness function. We therefore clarify their conclusions about the necessary conditions for positive and negative DA. We would not expect that high baseline offspring survivorship or low relative offspring fitness effects of PI are necessarily associated with negative DA. Instead, we would predict negative DA from differences in the offspring benefit function whenever the offspring of poor-quality males have a steeper slope to their fitness function (and thus provide greater marginal fitness

benefits to investing females), as compared to offspring from good-quality males (i.e., the juvenile survival scenario that we model here).

### Comparisons to Empirical Studies

The analytical results and the dynamic model results with simple linear functions enable us to identify and categorize the different types of DA that can arise in natural systems. The next step is to apply this framework to the wide range of empirical results on DA, since the main insight from these models is the general conceptual framework they provide to classify the possible mechanisms behind DA in each case. Therefore, we briefly mention here the findings of several empirical DA studies that are illuminated by the results of our models. We stress that these studies are not meant to serve as evidence that our model is correct; rather, they provide real examples of the different kinds of effects we discuss and illustrate how our model framework can be applied in empirical work.

Both our analytical and stochastic dynamic model results show unambiguously that when male quality changes nothing but the elevation of the offspring fitness function, then there is no DA (fig. 3A). This was exactly as we expected (see also Krist and Munclinger 2015) and may well be the theoretical explanation for why many tests of DA have shown null results, such as the Oksanen et al. (1999) cross-fostering experiment with bank voles (*Clethrionomys glareolus*). This study found male mating success to be significantly heritable, indicating that there were indeed genetic benefits to the offspring of good-quality males, but females did not adjust maternal effort according to the genetic quality of their offspring. According to Oksanen et al. (1999), separate experiments showed that weaning mass did not affect mating success of offspring. Maternal care in this system thus seems to be primarily related to the basic requirements of growth/survival, and females cannot especially improve the attractiveness and reproductive success of sexy sons through additional increases in maternal effort. In other words, the overall elevation of the offspring fitness function increases with male genetic quality, but the marginal increase or slope in offspring fitness with increasing maternal care does not—a benefit-elevation rather than a benefit-slope scenario. Considering the possibility of publication bias, null results such as these may well be underrepresented in the literature.

Negative DA mainly came from two sources in our model: (1) the benefit-position-type compensation reactions within sealed-bid biparental care and (2) the benefit-slope effect in the juvenile survival scenario, where offspring of poor-quality males had lower overall fitness but were more responsive to marginal increases in maternal investment. Several empirical examples of negative DA can likely be attributed to one of these two sources. In the broad-nosed pipefish (*Syngnathus*

*typhle*), the female inserts eggs into the male's brood pouch for brooding. Goncalves et al. (2010) found that females laid eggs with higher protein content for small males, a finding of negative DA. Male brooding ability is physiologically constrained by body length, which is also a measure of attractiveness or quality as ranked by female mating preference, so the scenario here is very similar to our benefit-position. Since there is no room for negotiation over levels of paternal care, mothers presumably increased their investment in egg nutrients when experimentally paired with small males because of the larger marginal benefits involved when such female investments are experienced by offspring lower down on their benefit curve, whereas females paired with good-quality males experienced smaller marginal benefits due to stronger diminishing returns from their investment in offspring higher up the benefit curve when on top of more substantial levels of paternal investment.

A particularly clear example of our juvenile survival scenario comes from the RC hypothesis, which focuses on additional maternal investment in offspring from matings with nonpreferred mates in order to make up for likely offspring viability deficits (Gowaty et al. 2007; Gowaty 2008). This is thus a case where a benefit-slope effect produces negative DA due to larger marginal benefits of extra investment in offspring from poor-quality mates (i.e., when there are "constrained" matings). Many empirical examples appear to be neatly explained by this scenario, such as female pronghorns (*Antilocapra americana*) mated with less attractive males increasing milk delivery to suckling young, in a period where suckling is completely under maternal control (Byers and Waits 2006), or female mallards (*Anas platyrhynchos*) laying larger eggs for nonpreferred than for preferred males when offspring viability was shown to be lower in constrained matings (Bluhm and Gowaty 2004).

However, not all results align as well with our framework, and there are some less easy to explain cases both of null results and of positive and negative DA. For instance, Bolund et al.'s (2009) result of negative DA in zebra finches seems initially counterintuitive. It could have been explained similarly by the juvenile survival scenario, were it not occurring in the very species most famous for positive DA (Burley 1988). The experimental setup was very different, though: male attractiveness in this study was determined by extrapair mating success. An explanation for the contrasting result could be that the females expect more parental care from high-quality partners and therefore reduce their investment, as in our benefit-position scenario (figs. 1C, 3C), but if it is the unattractive males that provide more care, since they by definition are less likely to be out pursuing extrapair matings, then the increased female investment with unattractive males must be seen as positive DA. This would go against our model result (fig. 3C). However, demonstrating this requires data on feeding rates of

each sex during the chick-rearing stage and of differences between attractive and nonattractive males. In addition, cross-fostering or even hand-rearing chicks of attractive and nonattractive males and quantifying offspring fitness as a function of per capita PI would reveal the nature of any genetic effects driving DA.

Some of the best demonstrations of DA come, not surprisingly, from the insect world. Several systems involve good-quality males providing larger, more nutritious seminal products that the female uses for somatic maintenance as well as reproductive investment (Vahed 1998; Simmons and Kotiaho 2002). This is therefore a good example of our nuptial gifts scenario (cost-position), which we have shown can produce positive DA in the form of increased female investment even without good genes (as in benefit-slope). Positive DA has indeed been reported in species like this, such as in female comma butterflies (*Polygonia c-album*) that invest more in reproduction when mated with males raised on a higher-quality diet (Wedell 1996). Female dung beetles (*Onthophagus taurus*) have also been shown to construct larger brood balls when mated with large-horned males (Kotiaho et al. 2003), and while there may be benefit-elevation-type genetic benefits here (i.e., there were significant heritabilities for male horn length, body size, and ejaculate size; Kotiaho et al. 2003), our model suggests that this is unlikely to be driving DA in this case. DA in these dung beetles should therefore be driven by benefit-slope-type good-genes effects and/or a cost-position effect from good males providing females with more nutritious seminal fluids. Experimental tests could distinguish between these two alternatives, for example, by transferring dung beetle eggs from large- or small-horned sires to brood balls of alternative sizes. Under the benefit-slope scenario, offspring of large-horned males are expected to perform even better than offspring of small-horned males on larger brood balls compared to small brood balls. If not, and the offspring benefit slopes have been shown to be the same for all types of offspring, then the positive DA pattern must come from the cost-position effect of paternal investment in nuptial gifts moderating female costs. Experimental manipulations like this based on our model framework could therefore potentially identify which properties of the offspring fitness function and female cost function are responsible for any DA detected.

The results from the high mating skew scenario are somewhat harder to put into context in terms of specific examples of DA within the empirical literature. However, they do suggest a close link to the adjacent field of sexual selection, because the contrasting shapes of the offspring fitness functions from different-quality males in this scenario are caused by extreme differences in expected offspring mating success. We show that extreme positive DA in the high mating skew scenario should result in mothers

in poor state not even bothering to invest in offspring from poor-quality males, which itself would feedback and intensify the high mating skew in such populations. The closest example of such an effect would perhaps be the classic study on red deer (*Cervus elaphus*) by Clutton-Brock et al. (1981), showing that mothers in very poor condition forgo any reproduction that year, while only mothers in the highest state bother to try to produce sons that could then go on to realistically compete for matings in such a highly polygynous mating system. Mothers in intermediate state compromise and produce daughters, because the fitness of female offspring is not so heavily dependent on levels of maternal investment (or perhaps paternal genes) as it is in the high skew scenario. Our model does not include the complications of adaptive sex ratio adjustments or sex-biased PI, and so its predictive power is limited in this case. However, it does confirm an unexplored role for DA in such systems and in life-history theory where parental care and sexual selection meet (see Kokko and Jennions 2008).

#### *Conclusions and Future Directions*

In general, DA of the strength we record in the realistic scenarios presented here is expected to have evolutionary implications simply through modifying the reproductive outcomes for the different parental phenotypes. Increased female investment in response to already sexually preferred male phenotypes (e.g., secondary sexual traits and other signals of good genes and thus indirect benefits) exaggerates the transfer of these traits to the next generation beyond that caused by sexual selection and assortative mating (Sheldon 2000; Kotiaho et al. 2003; Uller et al. 2005). The scenarios that produce positive DA in our model will further increase the fitness of any sexually selected traits if they are also used by females as indicators of male quality in their DA decisions. Conversely, negative DA in the form of increased investment in offspring of poor-quality males carrying nonpreferred traits will oppose evolutionary change in male phenotypes due to sexual selection. DA therefore has the potential to have significant evolutionary consequences in areas such as sexual selection (Sheldon 2000; Qvarnström and Price 2001; Uller 2012). Sheldon (2000) argued that it would be difficult to prove that DA is an adaptive parental effect, but theoretical work since then has at least demonstrated its potential adaptive role (Harris and Uller 2009; Kindsvater and Alonzo 2014). Kotiaho et al. (2003) emphasize the importance of controlling for DA in quantitative genetics studies, and ever since Burley (1988) the potential complications arising from DA in studies of parental care have been well known. However, we have yet to see a full model of the evolution of sexually selected signals used in both mate choice and DA. Such a model would certainly be of great interest to both fields, be-

cause it is currently unclear how positive or negative DA as we describe here will modify any runaway effects of mate choice or how sexual selection might constrain or enhance the possibility of adaptive DA.

Our model here does not allow any direct comparisons with the results from Kindsvater and Alonzo (2014), since it does not include several offspring in each brood. However, we are currently expanding our model to include this feature (I. I. Ratikainen, T. R. Haaland, and J. Wright, unpublished manuscript), which allows various interesting comparisons. With that we will be able to more effectively interpret the vast literature of empirical work on DA and RC to provide a much clearer understanding of what drives the observed patterns of mate-quality-dependent levels of reproductive investment.

The models we present here represent a significant step forward in our understanding of DA (and hence RC). All the effects of male quality are explicitly modeled as effects on either the elevation or the slope of the benefit or cost functions or the female's position on those functions. As a result, we have been able to identify the specific scenarios that lead to positive or negative DA and how they are created by each of these effects separately or in combination. Future empirical studies on DA should aim to quantify offspring fitness functions or female cost functions when mated with different-quality males and use this to inform predictions regarding DA. These models and the findings we present should therefore provide a general and potentially very useful conceptual framework for the understanding of DA, its future theoretical development, and a clearer, more informed interpretation of the results of empirical studies in this area.

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