Reproductive investment when mate quality varies: differential allocation versus reproductive compensation

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Reproductive investment decisions form an integral part of life-history biology. Selection frequently favours plasticity in investment that can generate maternal effects on offspring development. For example, if females differentially allocate resources based on mate attractiveness or quality, this can create a non-genetic link between mate attractiveness and offspring fitness with potential consequences for ecological and evolutionary dynamics. It is therefore important to understand under what conditions differential investment into offspring in relation to male quality is expected to occur and the direction of the effect. Two opposite predictions, increased investment into offspring produced with high-quality mates (differential allocation (DA)) and increased investment with low-quality males (reproductive compensation (RC)) have been suggested but no formal theoretical treatment justifying the assumptions underlying these two hypotheses has been conducted to date. Here, we used a state-based approach to investigate the circumstances under which the variation in mate quality results in differential female investment into offspring and how this interacts with female energetic resource levels. We found that a pattern of increased investment when mating with high-quality mates (i.e. DA) was the most common optimal investment strategy for females in our model. By contrast, increased investment when mating with low-quality mates (i.e. RC) was predicted only when the relative impact of parental investment on offspring quality was low. Finally, we found that the specific pattern of investment in relation to male quality depends on female energetic state, the likelihood for future mating opportunities and the expected future distribution of mate quality. Thus, the female's age and body condition should be important factors mediating DA and RC, which may help to explain the equivocal results of empirical studies.

Keywords: dynamic program; differential allocation; compensation hypothesis; sexual selection; mate choice; maternal effects

1. INTRODUCTION

The traits governing patterns of investment into reproduction represent an important target for selection. Life-history theory provides a robust context in which the evolution of reproductive investment can be investigated (Roff 1992, 2002; Stearns 1992). This body of theory was formally initialized by Fisher (1930), who showed that the lifetime reproductive success should be estimated by taking into account how the current reproductive expenditure affects future reproductive success (Brommer 2000). Much evidence exists that organisms have been selected to allocate resources to reproduction over time in response to the costs and benefits of current and future reproductive opportunities (e.g. Houston & McNamara 1999).

Since life-history theory generally predicts that reproductive investment should be high when the expected returns in fitness are high, any factors that increase or decrease the expected returns on investment should have the potential to affect reproductive allocation decisions. This implies that there should, optimally, be facultative adjustment of reproductive investment in response to biotic and abiotic factors, which can generate maternal effects on offspring development. One important factor that potentially could influence returns on a given reproductive investment is mate quality. Indeed, selection on female choice based on male sexual traits implies that some males generate higher returns on investment than others (Andersson 1994), suggesting that differential reproductive investment in response to male quality should be widespread (Sheldon 2000). This idea was initially formulated by Burley (1986), who predicted that females should increase investment when paired with males of high quality as long as reproduction is costly, there is a tradeoff between current and future reproductive success and mate quality influences reproductive returns on investment (e.g. by increasing offspring

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survival, see Sheldon (2000)). Although Burley developed her argument based on a model species where both males and females care for the young (zebra finches: Burley 1986), the argument is general and can be made for any iteroparous organism that faces variation in mate quality (Sheldon 2000). Hence, females are expected to invest more when they are paired with mates of high quality, thereby generating a positive relationship between partner quality and reproductive investment (referred to as differential allocation, DA). However, this hypothesis has recently been challenged (Gowaty *et al.* 2003, 2007; Bluhm & Gowaty 2004; Gowaty 2008). Gowaty and colleagues have suggested that, rather than increasing investment when paired with a high-quality partner, females should exhibit reproductive compensation (RC) for poor-quality mates by increasing reproductive effort in order to counteract the negative effect that mate quality has on offspring fitness. Thus, the RC hypothesis specifically predicts that females should invest relatively more when they mate with males of low quality (Bluhm & Gowaty 2004; Gowaty *et al.* 2007). The two hypotheses therefore generate opposite predictions.

Differential investment in response to mate quality has implications that go beyond the study of optimal allocation of energetic resources to reproduction. Generally speaking, maternal effects can alter the rate and direction of evolution via indirect genetic effects (Kirkpatrick & Lande 1989; Cheverud & Moore 1994; Moore *et al.* 1997; Räsänen & Kruuk 2007), which is also true for maternal effects in relation to mate quality (Moore *et al.* 1997; Wolf *et al.* 1999b; Sheldon 2000). More specifically, increased or reduced allocation to offspring of high-quality males could increase or decrease differences in male fitness, thereby affecting the strength of sexual selection, in particular in the context of genetic quality or benefits (Sheldon 2000; Qvarnström & Price 2001). For example, because there is accumulating evidence that maternal effects influence the attractiveness of sons in adulthood (e.g. Lindström 1999; Kotiaho *et al.* 2003; Forstmeier *et al.* 2004; see Saino *et al.* (2007) for a comparative approach), DA can increase the similarity between fathers and sons caused by shared genes, even in species with no paternal resource investment, and thus lead to erroneous conclusions regarding the genetics of sexual traits (Sheldon 2000).

In order to be able to understand the importance of differential investment in relation to mate quality for the evolutionary dynamics of sexual traits, we need to be able to predict under what circumstances DA or RC is likely to occur. Empirical evidence is ambiguous; several studies in a diversity of taxa have found a positive correlation between female reproductive investment and indicators of male quality (e.g. birds: Petrie & Williams 1993; butterflies: Wedell 1996; frogs: Reyer *et al.* 1999; fish: Kolm 2001; mammals: Gowaty *et al.* 2003; lizards: Olsson *et al.* 2005; crickets: Head *et al.* 2006), however, other studies have found a pattern consistent with RC (e.g. Bluhm & Gowaty 2004; Gowaty *et al.* 2007), whereas, others have produced inconclusive or negative results (e.g. Oksanen *et al.* 1999; Mazuc *et al.* 2003; Rutstein *et al.* 2004; Galeotti *et al.* 2006; Nakagawa *et al.* 2007).

While the development of predictive theory underlying the DA and RC hypotheses is largely logical, several researchers have suggested different factors that may influence the generality of reproductive investment predictions based on mate quality. Sheldon (2000) suggested that the pattern of DA should be strongly affected by the expected quality of future partners, variance in the effect that mate quality has on offspring fitness and the effect that reproductive investment has on future reproduction. Alternatively, Gowaty *et al.* (2007) have suggested that RC is particularly probable when mate choice is constrained, e.g. when females cannot forego reproduction to secure a better mate. Thus, verbal arguments suggest that RC and DA are each predicted depending on the different biological factors, but to our knowledge, no formal theoretical treatment of the problem has yet been conducted.

Our goal here is to explore factors that may affect differential reproductive investment as a function of mate quality in a state-based approach using dynamic programming (Mangel & Clark 1989; Clark & Mangel 2000) and to identify major factors that may influence the pattern of RC or DA in a general framework. We begin by presenting a model of resource investment into offspring. Like the logical models discussed above, we assume that the reproductive investment is costly in terms of survival for females, that mate quality influences offspring fitness and that investment in current offspring is traded off against future reproductive opportunities. We also assume that some minimal investment of resources is required for reproduction but that females can facultatively adjust this investment by increasing it to improve offspring fitness. Below, we detail the biological rationale for the model, explore optimal patterns of investment as a function of mate quality, and then discuss the implications of our results by outlining suggestions for future theoretical and empirical work.

2. THE BASIC MODEL

We modelled reproductive investment by females using a state-based approach (Mangel & Clark 1989; Clark & Mangel 2000). State is defined as the energetic resources a female has at a given time to allocate towards reproduction or somatic maintenance. We assume females may facultatively allocate energetic resources towards offspring production at a given reproductive attempt and that these decisions may optimally maximize the expected lifetime reproductive success. We divide time during the reproductive lifetime into discrete intervals, each equal to the minimum time possible between subsequent reproductive attempts (the specific time period is dependent upon the life history of a given population or species). Thus, for simplicity, and because our focus here is on variation in the basic biological parameters that may predict DA or RC, we model an organism that may engage in several subsequent reproductive events over their lifetime but we do not specifically include, for example, differential survivorship between breeding seasons (although the model framework is general enough to accommodate such complex life-history patterns; see Mangel & Clark 1989; Clark & Mangel 2000). Given these assumptions,

we estimate fitness resulting from the set of reproductive allocation decisions that maximizes individual reproductive success during a single breeding season.

We assume that females have a finite, renewable amount of resources to use for reproduction during their life, denoted $X(t)$, where X is the female's energetic state at the beginning of time interval t . We assume that females adjust the amount of resources they invest into offspring production facultatively. Specifically, we assume the production of offspring incurs a baseline cost but that females may provide additional resources to offspring (e.g. by increasing yolk provisioning or providing post-hatching parental care). The model described below predicts the optimal reproductive investment by females: zero investment (i.e. foregoing reproduction), baseline minimal investment or investing 'extra' energetic resources in offspring at one of the three levels (low, medium or high). Thus, the amount of resources invested in reproduction is denoted by $D(t)$, where D is the amount of resources invested at time interval t . We assume females reproduce only when they find a mate, thus $D(t)=0$ when no mate is present. When females find a mate, they may choose to forego reproduction ($D(t)=0$), invest the baseline amount of resources into offspring ($D(t)=1$) or invest resources in excess of the minimum baseline ($D(t)=2, 3$ or 4), thus

$$D(t) = \begin{cases} \{0, 1, \dots, 4\} & \text{if } X(t) \geq 4, \\ \{0, 1, \dots, X(t)\} & \text{otherwise.} \end{cases} \quad (2.1)$$

We assume that an investment quantity of $D(t)$ directly results in an incremental increase in the fitness of offspring such that the time specific probability of offspring survival, ψ_t , increases by F_d . We assume that if two different reproductive decisions results in equal fitness gains, the optimal investment choice will be the lower energetic expenditure of the two (NB the unit of investment here is arbitrary, the exact quantity of which will be species or population specific). We note here that the specific mechanism of allocation to offspring will vary between populations or species. We model this investment such that investment incurs an energetic cost to females and confers a fitness gain to individual offspring, rather than increasing the number of offspring produced.

We define 'male quality' as the effect a particular male has on the fitness of his offspring in terms of survival, a well-documented empirical pattern (reviewed in Møller & Alatalo 1999; Møller & Jennions 2001). The effect of male quality on offspring fitness may be the result of different mechanisms depending on the biological characteristics of a particular species, such as conferring higher intrinsic (e.g. genetic) quality (reviewed in Jennions & Petrie 2000) or due to some direct benefit supplied by a male to his offspring (reviewed in Møller & Jennions 2001). Here, we assume the most general case as a first approximation, where male quality directly influences offspring fitness (regardless of the mechanism). We assume that the distribution of male quality is a population-specific parameter that may influence the optimal pattern of female reproductive allocation. Finally, we assume that females have perfect

information about the quality of their present mate and the distribution of mate quality in the future.

The increment in female fitness at time t is denoted by $W(d, x, m, t)$ when an investment decision towards reproduction, d , is made at energetic state $X(t)=x$ with a mate of quality m . Here, we assume mating with a mate of quality m increases the time-specific probability of offspring survival, ψ_t , by M_m . Thus, the energetic expenditure towards offspring is a decision to be optimized across different combinations of state, mate quality and time. In addition to impacting female energetic state, reproductive investment may also negatively affect female survivorship. The component of female fitness accrued during a given reproductive bout ('current fitness') is defined as

$$W_C(d, x, m, t) = \theta(\psi_t + F_d + M_m), \quad (2.2)$$

where θ is the average number of offspring produced and $0.0 \leq (\psi_t + F_d + M_m) \leq 1.0$. The future component of fitness is defined as

$$W_F(d, x, t) = (1 - \alpha_t - \varphi_D) \times \left(\sum_{m=0}^{N_m} P_m [W_C(D_M^*(x + \Delta x, t + 1), x + \Delta x, m, t + 1) + W_F(D_M^*(x + \Delta x, t + 1))] \right), \quad (2.3)$$

where N_m reflects the arbitrary number of categories describing the distribution of male quality at time $t + 1$; P_m is the probability of encountering a male of quality m ; Δx is the change in female state resulting from $D(t)$ (leading to state $x + \Delta x$ at time $t + 1$); $D_M^*(x + \Delta x, t + 1)$ denotes the optimal allocation of resources by females of state $x + \Delta x$ at time $t + 1$ as a function of male quality, m ; and $W_F(D_M^*(x + \Delta x, t + 1))$ represents the future reproductive success at time $t + 1$ (i.e. the asterisk, *, denotes the investment decision resulting in the highest current plus future fitness return for a particular combination of state, mate quality and time). Here, in essence, the fitness returns for all possible female investment decisions are calculated for each time period, female energetic state and male quality. Thus, the optimal allocation decision at time t , $D_M^*(x, t)$, is solved by choosing the decision that maximizes the sum of equations (2.2) and (2.3). Finally, φ_D is the reduction in survivorship probability as a consequence of reproductive investment and α_t is the baseline probability of mortality at time t .

(a) Forward simulation

The above described model generates a matrix of decisions with the number of dimensions equal to the number of state variables, i.e. a matrix of optimal female reproductive allocation decisions as a function of state, time and mate quality. However, this set of data does not provide insight into the net results of a sequence of decisions on the average expected state or decision expected through time. For this, we use a Monte-Carlo simulation approach (Clark & Mangel 2000) in order to explore the probability distribution of individual state variables on the sequence of decisions made by simulated populations of individuals (see below). This step allows a concise description of both the expected distribution of allocation decisions, given

the assumption of a particular set of state variables and also the expected distribution of states, given the assumption that a population adheres to the optimal decisions calculated about.

We initiate the beginning distribution of female states to seed the simulation. We define $P(x, m, t)$ as the probability that a focal female will have x energetic reserves with a male of m quality at time t . For the simulation described here, we simulated female reproductive state using a normal distribution with arbitrary parameters of $X_0 = X_{\max}/2$ and standard deviation of 2. That is, assuming that female state is normally distributed and 'seeding' the simulation with some probability of a female being at a particular energetic state, here we simulate the actual frequency of state-dependent decisions that may be predicted. Thus, at $t=0$

$$P(x, m, 0) = \begin{cases} >0 & \text{if } x \sim \text{Nor}(X_{\max}/2, 2), \\ 0 & \text{otherwise.} \end{cases} \quad (2.4)$$

(b) *Parametrization of the model*

For the basic model, we assume that females encounter males randomly each time period with respect to male quality. Specifically, we assume that there are three male types (low, intermediate and high-quality males; $m=0, 1$ or 2) and that $P_0=P_1=P_2$, unless and otherwise specified (see below). Male quality is quantified as the impact of a given male on offspring fitness. Here, we begin with parameters where quality has a null effect on offspring survivorship for intermediate males, and increases or decreases offspring survivorship for high and low males, respectively. There is a constant pressure of mortality, α_t , for all t from t_0 to $t_{\max}-1$. Finally, females may choose to invest in offspring incrementally at increasing cost to their energetic reserves (i.e. their state). Thus, females may choose to make the minimum reproductive investment (i.e. providing no extra investment; $D(x, m, t)=1$; $\Delta x = -1$; $F_d=0.0$) to produce a clutch decrementing their state by Δx , may forego reproduction incurring no energetic cost and a net gain in state ($D(x, m, t)=0$; $\Delta x = +1$), or may incrementally invest in offspring at increasing cost to state but increasing offspring survivorship. This facultative investment, $D(x, m, t)$, increases offspring survivorship, $F(x, m, t)$, respectively and influences female state change (Δx) concomitantly.

To initially parametrize our model, we used data extracted from the literature for the zebra finch, *Taeniopygia guttata* (Zann 1996), a model system that has been used extensively to study female investment in relation to male traits (Sheldon 2000). With this starting point, we created a set of baseline parameters representing a set of life-history parameters within the framework described above for which to explore how variation in parameter space influences the overall pattern of reproductive effort expended by females. We note here that the variation across different model systems remains interesting as both DA and RC have been reported empirically (e.g. Burley 1986; Cunningham & Russell 2001; Bluhm & Gowaty 2004; Rutstein *et al.* 2005; Gilbert *et al.* 2006) and that different assumptions (i.e. specific biological models building on our general approach here) may apply for different systems. The data used here should

therefore only be seen as an approximation and not an explicit model of existing zebra finch studies *per se*. The baseline model parameters were initialized as follows:

- (i) Offspring survivorship for all times, t ; $\psi_t=0.3$.
- (ii) Effect of female investment on offspring survivorship by female investment decision, d ; $F_d=\{0.0, 0.0, 0.05, 0.10, 0.15\}$.
- (iii) Paternal effect on offspring fitness by male quality, m ; $M_m=\{-0.25, 0.0, 0.25\}$.
- (iv) Expected distribution of male quality; $P_m=\{0.33, 0.34, 0.33\}$.
- (v) Decrement of female energetic state by female investment decision, d ; $\Delta x_d=\{1, -1, -2, -3, -4\}$.
- (vi) Baseline female mortality for all times t ; $\alpha_t=0.2$.
- (vii) Mortality incurred due to reproductive investment; $\phi_D=\{0.0, 0.1, 0.15, 0.2, 0.25\}$.

Baseline parameter values were systematically varied by up to ± 100 per cent in order to explore the sensitivity of model predictions to individual parameter values. For simplicity, here we present a subset of model runs that had a significant effect on the predicted pattern of female reproductive investment decisions. Below are the values of parameters for model runs that we discuss below. Unless and otherwise indicated, only one variable for each alternative model was varied relative to those of the standard baseline values:

- (viii) Costly reproduction; $\Delta x_d=\{2, -2, -4, -6, -8\}$.
- (ix) High maternal fitness effect; $F_d=\{0.0, 0.0, 0.10, 0.15, 0.20\}$.
- (x) Low paternal fitness effect; $M_m=\{-0.05, 0.0, 0.05\}$.
- (xi) Poor males late; $P_m=\{0.90, 0.05, 0.05\}$ (for all $t > [t/2]$).
- (xii) Good males late; $P_m=\{0.05, 0.05, 0.90\}$ (for all $t > [t/2]$).
- (xiii) Good offspring; $\psi_t=0.6$ (for all times, t).

3. RESULTS

The main predictions from the model with respect to how variation in parameters affects the patterns of facultative investment are summarized in table 1. Female reproductive investment predictions for a range of biological parameters (see above) are summarized in figure 1. DA (higher average investment in offspring with a high-quality mate) is a commonly predicted pattern over a range of parameter settings (figure 1a–f), while RC (higher investment in a low-quality mate) was only predicted when extra female investment yielded relatively small impacts on offspring fitness (figure 1g,h). Overall, the pattern of DA was robust to variation in the biological parameters we modelled. However, the level of female energetic reserves is predicted to strongly influence optimal investment and to interact with mate quality (figure 1a–h). High impact of female investment on offspring fitness resulted in relatively large increases in investment for high-quality males (figure 1b). Low impact of male quality on offspring fitness results

Table 1. Major female reproductive investment predictions arising from variation in key biological parameters.

factor	prediction
female energetic reserves (female state, X)	strong effect: females with low energetic reserves tend to invest more conservatively into reproduction independent of male quality and females with higher energetic reserves can maximize their fitness by investing more heavily in offspring in relation to male quality
time (t)	moderate effect: females tend to invest in reproduction conservatively early in their breeding season or lifetime when future reproductive opportunities exist; differential investment over time in relation to male quality
investment relative to offspring fitness (offspring baseline fitness, ψ)	strong effect: females tend to exhibit DA when their relative energetic investment has a strong effect on offspring fitness, and exhibit RC when their investment in offspring has a relatively low impact on offspring fitness
future mate availability and quality (male quality probability distribution, P_m)	moderate effect: females tend to invest conservatively when the availability of higher quality males as mates may increase for future mating opportunities; differential investment in relation to the frequency distribution of male quality
mate choice (predicted investment, D)	strong effect: females tend to exercise strong mate choice in the sense that they are predicted to forego reproduction with poor quality males when finding higher quality mates in the future is possible. RC is predicted when future opportunities are limited (and when female impact on offspring fitness is limited)

in an effect of male quality on female investment only for females in a poor energetic state (figure 1*d*). The expected distribution of mates had a relatively large effect on the average predicted level of female investment (figure 1*e,f*), with females investing relatively heavily when the future expected quality of mates is relatively low; however, the distribution of future mate quality has little effect on the overall predicted pattern that higher reproductive investment is favoured with high-quality males (i.e. DA).

While figure 1 shows the average predicted pattern of optimal female investment, figure 2 shows a typical example of how optimal individual investment varies across female state and the time of season. Here, decisions when female investment is high (the costly reproduction model corresponding to figure 1*c*) show that, for low-quality males, females should optimally forego reproduction until very late in the breeding season, when maximum investment is predicted (terminal reproductive investment). For intermediate and high-quality mates, baseline reproductive investment or higher investment is predicted depending on time during the breeding season and female energetic state.

Forward simulation results for two model runs with opposite predictions are shown in figure 3. Average expected female state declines during the breeding season in a similar way for the baseline model showing a DA pattern of reproductive investment; however, the good offspring model where offspring baseline survivorship is relatively high predicts a pattern of RC. Based on the average investment predictions for these models (figure 1*a,g*, respectively), females are predicted to behave quite differently with respect to the quality of their mate early in the season when they possess higher energetic reserves (figure 1*a,g*). However, late in the breeding season, most females in the populations are predicted to behave similarly regardless of mate quality because mean optimal investment and mean state predictions converge.

Figure 4 shows the average expected lifetime reproductive success for females following a facultative (i.e. optimal) reproductive investment strategy with mates of different quality. Alternative investment strategies are also shown when females always forego

reproduction, or invest the minimum, a low amount above the minimum or a high amount above the minimum into offspring. Figure 4*a–c* show expected fitness returns for females with a random expectation of future mate quality, while figure 4*d–f* show fitness returns for females when future male quality is expected to be high. The shape of the expected fitness curve for females with a random expectation of mate quality is relatively flat over time and the fitness ‘cost’ of a fixed investment strategy (the difference between the fitness return of the optimal predicted investment relative to each fixed strategy) is relatively small (figure 4*a–c*). Facultative adjustment of investment results in much higher reproductive gains relative to fixed investment for females that can predict future mate quality will be high (figure 4*d–f*).

Figure 5 shows the average expected lifetime reproductive success for females following a facultative (i.e. optimal) reproductive investment strategy for a pattern of reproductive investment predicting RC (in a model where offspring have relatively high survivorship, as shown in figure 1*g*); fixed investment strategies are also shown when females forego reproduction, or invest the minimum or a low amount above the minimum into offspring. Here, by definition, the facultative optimum results in the highest fitness regardless of male quality. Payoffs for the respective fixed strategies have a similar shape (but different heights) according to male quality. However, when females do not have the option to forego mating, mate quality becomes an important determinant of fitness. Investing even the minimum in offspring when paired with a male of low quality results in a large reduction in fitness on average compared to other strategies for females at most times during the breeding season, with a greater reduction in fitness coming earlier in time (figure 5*a*). This pattern holds until the very end of the breeding season when terminal reproductive investment should occur. The expected fitness return is different when females are paired with a male of medium quality, where investing the minimum is equal to or higher than forgoing reproduction at all times during the breeding season (figure 5*b*). When paired

Figure 1. Dynamic program results showing the optimal mean level of female investment (D^*) across reproductive opportunities during the breeding season. (a) Results for the finch baseline model; all other panels show results for runs relative to this baseline. (b) Results where reproductive investment is relatively costly. (c) Results where female investment has a relatively high fitness effect on offspring. (d) Results where male quality has a relatively low fitness effect on offspring. (e,f) Results where the distribution of male quality changes during the breeding season so that the average male quality is relatively poor later in the season or relatively good, respectively. (g) Results where offspring baseline survivorship is relatively high. (h) Results where male quality is relatively high late in the breeding season and offspring survivorship is relatively high. In general, (a–f) show a pattern of DA in female reproductive investment, where females invest relatively heavily in offspring of higher quality males. Here, females can have a relatively large impact on offspring fitness independent of the effect of mate quality on offspring fitness. (g,h) A clear pattern of RC, where females invest relatively more in offspring of lower quality males. Here, female reproductive returns are relatively low for higher investment and future mating opportunities are limited. Solid line, good; dashed line, medium; dotted line, poor female state.

with a high-quality male, female expected fitness returns are always higher when investing above the minimum (figure 5c).

4. DISCUSSION

Our findings suggest that DA, the pattern of high female reproductive investment with high male mate quality, is robust to variation across the range of biological parameters we modelled, thus confirming the heuristic arguments made by Burley (1986, 1988). This is consistent with the empirical observation of DA in a variety of organisms exhibiting a range of life-history variation (Sheldon 2000). By contrast, we found RC for low male quality predicted only under a restricted range of conditions. In particular, RC occurred only when the baseline offspring survivorship is relatively high or where the expectation of future mate quality was low (figure 1g,h). The reason for this may be that when the fitness return on a given quantity of reproductive investment for females is high, then the net fitness return for increased investment with high-quality males may be lower than the same investment with low-quality males. Thus, we found that RC was predicted only when the relative fitness impact of such increased investment was low. Empirical support for RC has been found in one study of the mallard (Bluhm & Gowaty 2004) but not by another, where the opposite pattern was found (Cunningham & Russell 2001). Gowaty and co-workers have suggested that RC should occur when females are forced to mate with non-preferred males (Bluhm & Gowaty 2004; Gowaty *et al.* 2007). This pattern was predicted in our model when the expected mate quality is relatively low and females cannot forego reproduction (as in figure 1h), lending some support to verbal arguments but also emphasizing their sensitivity to variation in other parameters. Furthermore, we emphasize here that changes in the basic model, such as explicitly incorporating mate choice, could influence the overall pattern of investment and may be included in future models.

In addition to showing that the DA should generally be more commonly observed than RC and indicating parameters likely to have the greatest impact on female reproductive investment decisions, our model suggests that there should be intra-individual variation in the extent to which females show differential investment in relation to male quality within a population or species. In fact, it is a quite general outcome of our simulations that while RC or DA occurs, the particular pattern should be strongly dependent upon factors such as female energetic state and time during the breeding season (i.e. the expected future reproductive gain offset by current reproductive investment). For example, while females with high energy reserves may exhibit RC when the relative impact of their investment is low, females in the same population at a low energetic state are predicted to invest in a pattern more closely resembling DA (figure 1g,h). Furthermore, time during the breeding season (or, for example, female age) is also expected to influence reproductive investment because of the impact of expected future reproductive success on lifetime reproductive success (figures 2 and 3). Thus, results from experimental studies may depend on the state and age (or perceived potential for future reproduction) of the individuals in a population. There is some empirical support for such effects. In a study of mallards, females that laid small eggs in control

Figure 2. Optimal female reproductive investment decisions (D^*) in relation to male quality (poor, intermediate and high). A typical optimal reproductive investment decision matrix from our model (shown here are the optimal decision matrices for our 'costly reproduction' model where reproductive investment by females for a given fitness increase in offspring requires a relatively higher energetic expenditure compared to the baseline finch model; see text for additional details). The three matrices each correspond to a different current mate quality, poor (a), intermediate (b) or high (c). Here, females are predicted to forego reproduction with a poor quality male irrespective of energetic state until quite late in the breeding season when terminal reproductive investment is predicted. The overall profile of investment predictions (0 is foregoing reproduction, 1 is minimal investment to produce offspring and 2, 3 and 4 are increasing levels of 'extra investment' to enhance offspring fitness) is similar for mates of intermediate and high quality, with low extra investment predicted at higher female energetic state, increasing towards the end of the breeding season. There is a weak interaction between female energetic state and mate quality, with female investment investing slightly more conservatively with intermediate-quality mates.

Figure 3. Forward simulation showing the change in population mean female state based on optimal reproductive decisions. Here, females begin the breeding season with an arbitrary distribution of energetic reserves and the overall pattern is decreasing reserves throughout the breeding season. The pattern of decline in condition is similar for a our baseline parameter set that predicts a DA pattern of investment and a 'good offspring' set (where offspring exhibit relatively high fitness independent of parental investment relative to the baseline finch model; see text for additional details) which predicts RC. Circles, baseline (DA); squares, good offspring (RC).

clutches had a greater increase in egg volume with highly attractive males (Cunningham & Russell 2000). This example is particularly interesting as another study of mallards found evidence for RC, but only in relatively older females (Bluhm & Gowaty 2004). Although there are alternative explanations and the fact that direct comparisons between studies are compromised by differences in methodology, these results support our finding that differences in female energetic state and age are important predictors of the extent to which they invest differently in relation to

male quality and that these should explicitly be considered in empirical studies. Importantly, the effects of perceived future reproductive potential and female state also provides a framework in which to test the outcome of the model presented herein using experimental approaches.

DA has been suggested to have important implications for sexual selection (Sheldon 2000; Qvarnström & Price 2001; Kotiaho *et al.* 2003; Uller *et al.* 2005). For example, if females allocate more resources to the offspring when paired with attractive males, any intrinsic differences in offspring quality resulting from the direct effect of male quality will be enhanced. Consequently, DA may reinforce the response to selection. Such effects are particularly important if the reproductive investment has effects on sexual traits of the offspring in adulthood, which has been documented in several species (Lindström 1999; Qvarnström & Price 2001). Seven years ago, Qvarnström & Price (2001) made a call for theoretical studies that explicitly address how parental effects influence evolution of sexual traits. Only a few such attempts have been made (e.g. Moore *et al.* 1997; Wolf *et al.* 1999a,b) but we argue that the fact that DA and RC are both empirically and theoretically supported should provide further impetus to develop models that attempt to clarify the evolutionary implications of differential investment in relation to mate quality.

We can see several potentially important developments. First, the modelling framework presented here can be used to incorporate the individual complexity of different model systems (see above) and thereby increase predictive power in an experimental setting. For example, in species with bi-parental care, investment by one partner may lead to reduced investment by the other partner which may affect the optimal reproductive investment. Such interactions between partners and the sexual conflict that it may involve must

Figure 4. Fitness return curves are shown here for the finch baseline model (*a–c*), where females have a random expectation of future mate quality, and the good males late model (*d–f*), where expected future mate quality is high (see text for additional details). Rows correspond to predictions for different current mate qualities (i.e. low, intermediate or high). Lines on each panel show the average fitness return for a fixed investment with the current mate. Fitness return curves are relatively flat over time and the cost of fixed reproductive investment (the difference in height between fixed strategies and the optimum facultative strategy) is relatively small when the expectation of future mate quality is random (*a–c*) compared to when future mate quality is predictably good (*d–f*). (*a,d*) poor male; (*b,e*) medium male; (*c,f*) good male. Solid line, optimum; dotted line, minimum; long-dashed line, low; short-dashed line, high female investment.

be addressed using a game theoretic approach in which the negotiation process can explicitly be implemented (Houston *et al.* 2005). Indeed, as suggested by the simple model presented here, specific predictions from models will depend on the particular biological characteristics of a given system (e.g. the mechanisms and degree to which females are capable of facultatively adjusting energetic investment in offspring to increase their fitness), which suggests that a detailed understanding of empirical systems is invaluable in order to be able to generate biologically realistic models that can be accurately tested. Also, our model assumes that females have complete and perfect information about the quality of their current mate (as well as the distribution of mate quality in the future). The introduction of imperfect information about male quality, stochasticity in future mate quality or the impact of assessing relative mate quality through

Figure 5. Fitness return curves for fixed strategies for a model exhibiting RC. Results are shown here for the good offspring model, where the baseline survivorship of offspring is higher relative to our baseline finch model (see text for additional details). The reduction in fitness for females that do not have the option of foregoing reproduction with males (as opposed to a facultative strategy or fixed investment) is moderate for females mating with males of low or intermediate quality (the height difference between dotted and short dashed lines) relative to a high-quality mate. (*a*) Poor; (*b*) medium; (*c*) good males. Solid line, optimum female investment; dotted line, no reproduction; long-dashed line, minimum; short-dashed line, low female investment.

learning could affect the predicted pattern of optimal reproductive investment (and can be incorporated into the modelling framework here; see Clark & Mangel 2000). The details of such complexities will also have potential ramifications for the direct and indirect effects of investment and male quality on offspring phenotype, including survival. This was realized by Burley (1986), who suggested that DA is an evolved female strategy that generates an incentive for high-quality males to stay with their partners that could be adaptive even if males reduced their own effort in response to increased female investment. Second, rather than providing increased investment into each offspring, females may produce more offspring when paired with attractive males. Both increased egg investment and increased clutch size has been shown to be female responses to male attractiveness (e.g. Petrie & Williams 1993; Cunningham & Russell 2001), but their implications

for the transmission of phenotypic traits across generations are likely to differ. For example, if females increase offspring number rather than offspring size, attractive fathers in good condition will not necessarily give rise to attractive offspring in good condition. Third, from an evolutionary point of view, understanding the sources of phenotypic variation in target trait(s) resulting from differential reproductive investment may require an experimental approach that incorporates selection arising from the genetic environment in which selection occurs (e.g. Cheverud & Moore 1994; Moore *et al.* 1997; Wolf *et al.* 1997, 1999a,b). This applies to the evolution of indicator traits of genetic quality as well as traits involved in reproductive investment. Combining studies of reproductive investment in relation to sexual traits of partners with studies of its consequences for evolutionary dynamics (e.g. responses to selection) may provide a link between optimality and quantitative genetic approaches, and therefore may allow stronger inference regarding the evolutionary implications of maternal effects (Cheverud & Moore 1994). Finally, the importance of differential maternal investment for models of indicator traits of genetic quality in sexual selection and the maintenance of genetic variation have just begun to be explored (e.g. Miller & Moore 2007). Thus, we suggest that greater theoretical and empirical consideration of plasticity in reproductive investment can help in further our current understanding of the evolution of sexual traits in both sexes.

In conclusion, using a state-based optimality approach, we show that the basic predictions of the DA hypothesis are sound. By contrast, RC occurs only at highly specific parameter combinations, suggesting that it is unlikely to be common in natural populations. However, the outcome is sensitive to the state and age of females, which may explain conflicting results in the empirical literature. We suggest that the strongest test of our predictions can be achieved in systems where partner quality, female state and the strength of the male effect on offspring fitness can be simultaneously manipulated. Such systems should exist among both invertebrates and vertebrates, making the scope of the present model quite general. However, it should be noted that both DA and RC rely upon an ability of females to adjust their investment at the time for, or subsequent to, assessment of mate quality. Thus, there may be important biological constraints operating in a particular system dictating patterns of investment that must be considered in future studies of reproductive investment in relation to mate quality. For example, greater plasticity in behavioural traits relative to physiological traits may mean that both DA and RC will be more common in species with post-hatching parental care compared with capital breeders without post-ovulation parental care. To what extent repeated and mutual negotiation over care between males and females and associated conflicts (Houston *et al.* 2005) will affect the outcome remains to be theoretically and empirically addressed. Furthermore, theoretical and empirical considerations of differential maternal investment in relation to sexual traits combined with studies of its consequences for responses to selection could

clarify the evolutionary dynamics of both maternal effects and sexually-selected traits.

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