A General Stochastic Dynamic Model of the Differential Allocation Hypothesis

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Abstract

Differential allocation (DA), adjusting reproductive investment according to the quality of the current mate, is an area of evolutionary behavioral ecology that is subject to much confusion, with vague terminology, apparently contradictory empirical results, and a shortage of theoretical work. I have created a state-based stochastic dynamic model of the differential allocation hypothesis in which females are mated with different quality males throughout their lifetime, and male quality affects either the nature of the costs or the benefits of the female's reproductive effort, or both, in various ways. I show that male quality induced variation in the elevation of the benefit function (offspring fitness function) has no effect on the optimal level of female investment, and thus cannot produce DA, contrary to popular belief until now. On the other hand, male quality induced changes in the slope of the benefit function as well as the cost function shift the optimal level of investment in ways expected from true DA by changing the marginal benefits or costs of extra investment. Male quality effects on the elevation of the cost function can also cause a weak type of DA, but only for females in low states investing all they can when optimal levels of investment cannot be achieved. Having identified and teased apart these distinct effects, I produce some more further model runs which aim at explaining certain patterns of DA seen in different species and mating systems. My model therefore sheds new light on many confusing results in the field, and a natural next step in order to capture the wide variety of observed DA patterns is to expand the model to include several offspring per brood.

Sammendrag

Differential allocation (DA), å justere reproduktiv investering etter kvaliteten på den nåværende maken, er et felt innen evolusjonær atferdsøkologi der det har vært mye forvirring, med uklar terminologi, tilsynelatende motstridende empiriske resultater, og en mangel på formelle teoretiske arbeider. Jeg modellerer DA-hypotesen med en 'state-based stochastic dynamic model', hvori hunner møter hanner av ulik kvalitet gjennom livet, og makekvalitet påvirker enten avkommets fitnessfunksjon eller hunnens kostnadsfunksjon av reproduktiv investering, eller begge to, på ulike måter. Jeg demonsterer at det kun er hvis effekten av makekvalitet på avkommets fitnessfunksjon avhenger av hunnens investering at investeringen vil endres. Dersom makens kvalitet gir hunnen samme fordel uavhengig av henens investering, vil ikke hunnen endre sin investering. Når makekvalitet påvirker hunnens kostnadsfunksjon, derimot, vil både investeringsavhengige og -uavhengige fordeler kunne føre til at hun endrer investering, selv om de forskjellige effektene påvirker hunner med ulikt energinivå og på ulike tider i livet. Etter å ha identifisert og skilt disse effektene fra hverandre, lager jeg noen videre modellscenarioer som tar sikte på å forklare enkelte DA-mønstre som er observert i ulike arter og parringssystemer. Jeg diskuterer resultatene mine i lys av eksisterende empirisk og teoretisk litteratur. Jeg kan konkludere med at modellen har kastet lys på mange forvirrende resultater innen feltet, og et naturlig neste steg for å fange hele variasjonen i DA-mønstre vi observerer i naturen er å utvide modellen til å inkludere flere avkom per kull.

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1 Introduction

1.1 Background

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 Nancy Burley (1986), who demonstrated the phenomenon by experimentally altering zebra finch (*Taenopygia guttata*) male attractiveness with colored leg rings. Since the leg rings did not change any fitness aspect for the bearer, Burley hypothesized that the observed increase in reproductive success for red-ringed males must have arisen from heightened parental investment (PI) by their female partners, an effect that she later confirmed in separate experiments (Burley 1988). Since then the field has expanded, and DA has been demonstrated for a variety of different species and mating systems, ranging from waterfrogs (*Rana* spp., Reyer *et al.* 1999) to hermaphrodite earthworms (*Eisenia andrei*, Domínguez and Velando 2013), but mostly in various species of birds and fish (e.g. Cunningham and Russell 2000; Kolm 2001; López-Rull and Gil 2009; Mahr *et al.* 2012; Uusi-Heikkilä *et al.* 2012). Discussions on DA apply equally well to male reproductive decisions, but the majority of systems studied in a DA context involve female investment. The language here will therefore focus on female investment in response to male quality, but this does not preclude applications for male investment in response to female quality.

Many studies have shown a pattern initially viewed as in direct conflict with DA, such as a pattern of increased female PI when paired with lower quality males (e.g. Michl *et al.* 2004; Bluhm and Gowaty 2004; Byers and Waits 2006; Goncalves *et al.* 2010). This has become known either as 'reproductive compensation' (RC) (Gowaty *et al.* 2007; Gowaty 2008) or 'compensatory investment' (CI), as preferred by others (Bolund *et al.* 2009). Many studies have also shown null results, (e.g. Oksanen *et al.* 1999; Mazuc *et al.* 2003; Grana *et al.* 2012), and considering the possibility of publication bias such results may well be underrepresented in the literature. Despite the large number of empirical tests years, the field of DA/RC has become rather cluttered and confused, and has not reached any real resolution. This seems to be largely due to two main reasons.

Firstly, differential allocation and reproductive compensation / compensatory investment are not mutually exclusive. RC should rather be seen as a form of DA where the allocation is increased to compensate for poor mate quality, rather than to reap the benefits of good mate quality, since both involve adjusting reproductive investment according to the quality of the current mate. Ratikainen and Kokko (2010) address the terminological confusion and suggest 'negative DA' for the RC pattern, and 'positive DA' for Burley's original unidirectional concept, a solution we will also adopt. Sheldon (2000)'s influential review mentions that none of the assumptions in the DA hypothesis excludes either of these directional effects. Furthermore, the research in the two fields, which have been rather separated, should be unified to a larger extent than has previously been achieved (see Horvathova

et al. 2012; Sheldon 2000). Depending on the experimental design and the mating system under study, finding that females provide less care with high-quality males may simply reflect that females normally expect higher levels of care from high-quality partners. This may be an evolutionarily stable strategy to directly benefit from having a partner doing a larger share of the required total parental investment (see Houston and Davies 1985; McNamara *et al.* 1999; Harrison *et al.* 2009), and such compensatory negative DA does not necessarily exclude the possibility of other positive DA effects in the same system. Similarly, concluding positive DA to be the case when females paired with attractive males increase their secondary reproductive effort, would be equally erroneous if the increase is due to attractive males normally providing less care, for example if they are engaging in more extra-pair activity (Ratikainen and Kokko 2010). These negative or positive compensatory effects within biparental care systems are a distinctly different process, and it is therefore important to emphasize that the original DA hypothesis explicitly focuses on the conditional allocation of resources to reproduction depending on the differences in the marginal fitness benefits of extra investment in offspring due to difference in offspring quality, rather than some of these other effects of differences in male quality on female reproductive investment (Sheldon 2000).

Secondly, there has been alarmingly little formal theoretical work carried out on DA. The growing body of empirical work with its apparently contrasting conclusions has had little by way of a firm theoretical framework within which any results can be placed, and therefore much of the subsequent confusion seems somewhat inevitable. The first mathematical treatment was a dynamic state-based model by Harris and Uller (2009), which indeed showed that for different parameterizations, simulating different life history scenarios, both positive and negative DA can arise when maximizing fitness accrued in current and future reproductive bouts. The model focuses on the trade-off between current and future investment for different probabilities of acquiring mates of different qualities, and wisely left out complications such as the game-theoretic considerations of conflict over biparental investment mentioned above (Houston and Davies 1985; McNamara *et al.* 1999; Harrison *et al.* 2009), although given the number of biparental systems under study here it might be interesting to examine this as part of a much more complex DA model. However, Ratikainen and Kokko (2010) pointed out several other shortcomings of the Harris and Uller (2009) model, the most severe of which was using an overly simplistic linear increase in offspring survival for higher mate quality and female investment (Fig. 1a). Considering offspring fitness as a function of maternal investment, this appears to involve a scenario where the slope of the function is the same for all mate qualities, and only the elevation changes (Fig. 1a, but see section 4.3). One of the fundamental assumptions of the DA hypothesis is that the quality of the mate influences the optimal level of investment (Sheldon 2000), and we imagine that the greatest benefits to allocating differentially will arise when mate quality affects the slope of the offspring fitness function (i.e. the marginal benefits, Fig. 1b) and not necessarily the elevation (Møller and Thornhill 1998). Therefore, the Harris and Uller (2009) model does not appear as general in identifying the causes of DA as one could hope.
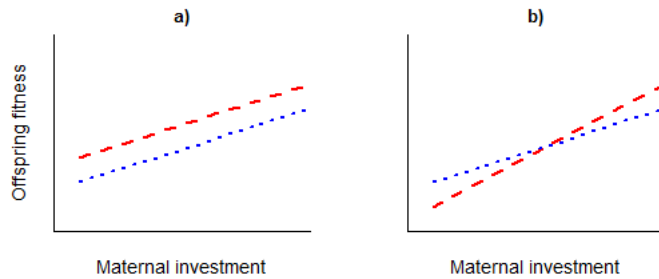
Figure 1: Offspring fitness as a function of cumulative maternal investment for offspring of a good quality (red, dashed line) and poor quality (blue, dotted line) male. In a) mate quality affects the elevation of the offspring's function but not the slope, while in b) mate quality affects the slope but not the elevation (average fitness remains the same). Differential allocation should increase the mother's optimal investment in offspring of high quality males only in scenario b).

A recent model by Kindsvater and Alonzo (2014), on the other hand, has examined the effects of different types of male benefits, ranging from purely genetic benefits (males provide no parental care), to nuptial gifts, to diverse forms of paternal care such as nest defense or feeding. Differing patterns of DA will appear depending on which of these benefits male attractiveness conveys, a point first made by Møller and Thornhill (1998). Furthermore, Kindsvater and Alonzo (2014) emphasize the male's effect on the shape of the offspring growth curve, and their model considers female allocation responses with regard to both offspring size and quantity. This focus on different effects of males on females may explain contrasting results in various experimental studies (e.g. López-Rull and Gil 2009; Bolund *et al.* 2009; Uusi-Heikkilä *et al.* 2012), and the model is a useful meeting point for empiricists and theoreticians. However, it does not directly address the central question of the differential allocation hypothesis: how the total amount of resources invested in a reproductive attempt should be varied according to mate quality in that given attempt, considering the expected quality of future partners (Sheldon 2000). Kindsvater and Alonzo (2014) model the lifespan of monogamous females mated for life with same mate; there is never a chance of mate quality changing. Besides, total investment (I) is partitioned into the number (n) and size (s) of offspring, but while changes in n and s are examined in detail, the overall effect on I is largely ignored. While the variation in investment according to offspring size and number depending on different male benefits is both interesting and illuminating, it is not at the heart of the differential allocation hypothesis. Quite the contrary: if all proposed findings of DA could be explained by this trade-off alone, and no variation in total investment depending on mate quality was found, then the DA hypothesis would bear little weight. Secondary PI (investment in offspring after birth, such as nestling feeding rate in Burley's original experiments) and other ways of taking advantage of current mate quality (Poisbleau *et al.* 2013) may be equally relevant measures of DA, and the wide range of observed forms of investment seems to imply a general evolutionary advantage to DA, beyond adjusting the offspring
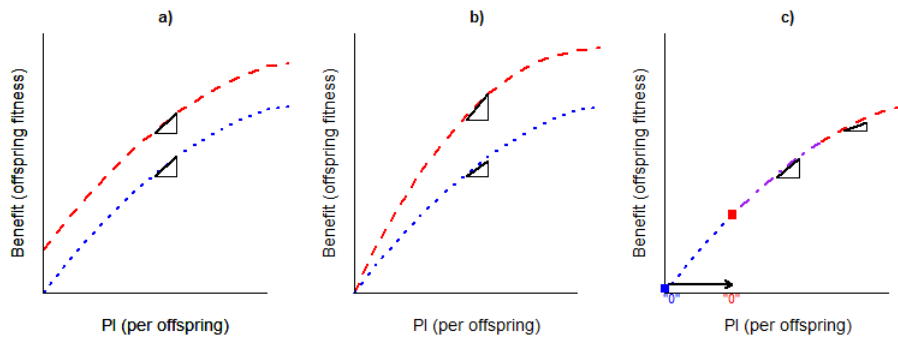
Figure 2: Offspring fitness as a function of cumulative maternal per-offspring investment, which is affected by male quality either by a change in (a) elevation, (b) slope, or (c) the mother's starting position on the x-axis. Red, dashed line: Offspring of good quality male. Blue, dotted line: Offspring of poor quality male. Purple: Red and blue overlap.

quality-quantity trade-off according to male benefits. Still Kindsvater and Alonzo (2014) represents a valuable addition to the theoretical work on DA, paving the way for a more detailed way of considering possible male effects on the female's reproductive decision.

1.2 Classification of male effects

Much of the confusion regarding the theory behind DA, which neither of the afore-mentioned models explain comprehensively, comes from the different ways in which male quality could potentially affect the shapes of the offspring fitness function (Fig. 2) and/or the female's cost function (Fig. 3). Both of these could be affected in one of three conceptually distinct ways: mate quality changing the elevation, slope or horizontal position of the female on the investment axis, or a combination of these effects.

The simplest case, and that most often implied in discussions of DA historically is a change in the overall elevation of the offspring fitness function due to genetic quality (Fig. 2a). This should not change the marginal benefits of extra investment in each offspring, and therefore not directly cause DA (see also Fig. 1a). Much of the confusion in the literature perhaps results from this basic misunderstanding, and many of the convincing results observed in specific studies are due to one or more of the other associated categories of effects shown in Figs. 2 and 3. The mother should be selected to optimize her investment in each offspring in order to maximize her net fitness benefits (benefits minus costs), and if the shape of the offspring fitness function (and thus the marginal benefit of increased investment) remains unchanged, a change of elevation will not shift this optimum in terms of per-offspring PI.

Male genetic quality may equally well change the slope of the offspring fitness function, and in these cases the mother's benefits from adjusting her investment
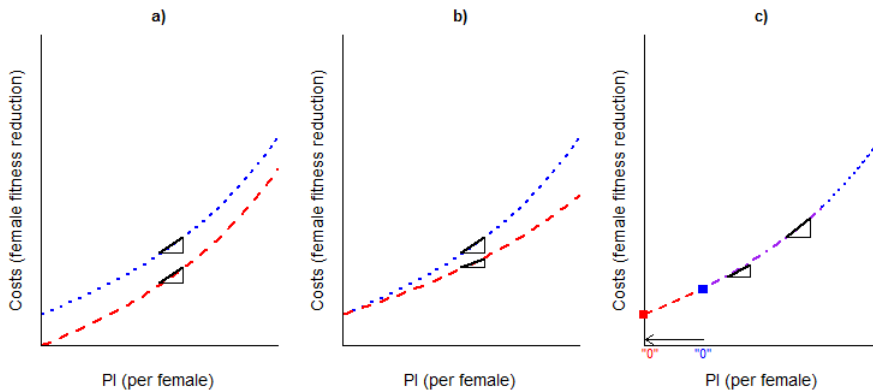
Figure 3: Maternal cumulative cost curves as a function of maternal investment, which is affected by male quality either by a change in (a) elevation, (b) slope, or (c) the mother's starting position on the x-axis. Red, dashed line: Female mated to a good quality male. Blue, dotted line: Female mated to a poor quality male. Purple: Red and blue overlap.

according to mate quality are evident, since the marginal fitness returns per unit of investment change (Fig. 2b). One of the most obvious ways that mate quality could affect the shape of the benefit curve in this way is in the genetic quality of the offspring. Depending on how mate quality affects the slope of the offspring fitness function, we may see positive or negative DA, because it is these marginal (per capita) fitness returns per unit of maternal investment that determine whether the optimal investment for offspring of high quality males is at a higher or lower level than for offspring of low quality males. This is likely to be the main process we see driving DA. It is also likely to be common since it can appear in all systems, including those with no paternal care or male investment in female's reproduction.

In cases where males also provide parental care, the point of the start of maternal investment is 'shifted' a certain amount further to the right along the offspring fitness function (Fig. 2c). To the female, the whole function is essentially shifted towards the left by the amount of expected male care (depending on male phenotypic quality), and with any curvilinear offspring fitness functions the optimal amount of maternal PI will be changed (i.e. lowered if the function more quickly reaches an upper asymptote due to the normally assumed diminishing returns, resulting in a pattern of negative DA). The offspring fitness function itself remains unchanged, but the female needs to invest less in order to get each offspring to its optimum level of total investment, or rather obtains lower marginal fitness benefits from investing further in such offspring of higher quality males. Note that this conceptualization of biparental investment has the male making his decision before the female makes hers, so it is essentially a "sealed-bid" model with no behavioral dynamics in the form of negotiation (see Houston and Davies 1985; McNamara *et al.* 1999).

It is then useful to consider the same division of male effects for the mother's fitness costs function as well (Fig. 3), especially considering its expected non-linearity

(accelerating costs for high levels of PI). This is because male quality effects on the female investment cost curve are likely to be phenotypic and varied in their social origin (see below), as compared to the mostly indirect genetic effects of male quality on offspring benefit curves (see above). In addition, any male quality effects on the cost function are going to have more direct consequences for future female reproduction, as compared to changes to the offspring benefit function. So, it is conceptually useful to separate between the potentially contrasting effects of different aspects of male quality on the female cost versus offspring benefit functions.

While an elevation change (Fig. 3a, an overall shift in female cost regardless of the level of maternal PI), might not be a very biologically relevant scenario, effects such as poor quality mates giving females sexually transmitted diseases (STDs) can be envisioned. Again, under the classic conceptualization of DA, the optimal level of maternal investment shouldn't change. In contrast, changing the slope of the cost function (Fig. 3b) emulates the male effects relevant to DA, because it changes the per capita cost of investment for the female, such as a high quality male providing and defending a better quality feeding territory or nest site. These curves will have different slopes, but the same points of origin at the y-intercept (no fitness cost with no PI), so the slope change also entails a change in elevation in this case. Though in a different way than originally envisioned (since male effect on offspring quality is not the main point), this will result in a DA pattern of maternal investment, since decreased marginal costs favour increased investment in offspring of higher quality males. And finally, a male effect such as a nuptial gift will shift the mother's position on the cost curve to the left, but does not change the curve itself (Fig. 3c). Then females can invest more before reaching the part of their cost curve where marginal costs get too large, so this could also lead to increased maternal investment. However, conceptually this is more similar to the compensatory reductions in maternal investment within biparental care (Fig. 2c) than to positive DA.

Incorporating this conceptual division of male effects is therefore very useful for sorting out the different effects and possibly opposing selection pressures that mate quality could have on DA. Various combinations of effects of the two curves can also be envisioned, and we aim to create more biologically relevant scenarios and explore these within this framework, using a new and more general stochastic dynamic state-based model of maternal PI, in the hope of clarifying the predictions regarding level and direction of DA.

2 Model description

The state-based stochastic dynamic model (Houston and McNamara 1999; Clark and Mangel 2000) follows a female with a maximum of t' breeding opportunities during her lifespan. Each time step in the model is one breeding season or breeding opportunity, at which the female may choose how large a reproductive investment, i, she makes. Investing in reproduction produces offspring, whose fitnesses f depend on the size of i with a certain relationship, $F(i)$. Reproductive investment also comes at a cost to the female, in that it lowers her energetic state, X, with the function $G(i)$, and thus also her survival probability, $\alpha(x)$. X spans from x_{min} to x_{max}, and reproductive investments cannot lower her state to below x_{min}.

There are 3 classes of male qualities, m, in the population, and at each reproductive event the male type the female meets is chosen at random, following a specified probability distribution. The effect of male quality is that each class of males offers the female a specific cost function, $G_m(i)$, which maps i to X (determines how much her state is lowered from a given investment), or a specific offspring fitness function, $F_m(i)$, which determines her benefits of reproduction. In the first set of scenarios we model, illustrating the conceptually different effects described in subsection 1.2, we for simplicity use a completely linear $F(i)$ or $G(i)$ with slope 1, and a monotonically curved $G(i)$ (1-scenarios) or $F(i)$ (2-scenarios) in the background.

When we then progress on to some more realistic scenarios, we chose the generalized logistic function

$$F(i) = a + \frac{k - a}{(1 + qe^{-b(i-p)})^{\frac{1}{v}}}, \tag{1}$$

as the offspring fitness function. Tweaking the different parameters (Table 1) can emulate a fuller and more realistic range of different male benefits on offspring fitness (e.g. upper and lower asymptote, growth rate, near which asymptote fastest growth occurs, at which x-axis point fastest growth occurs). The cost function increases exponentially,

$$G(i) = si + r^{si}, \tag{2}$$

with two shape parameters (s and r, see Table 1). With these, the stochastic dynamic model iterates backwards over the female's lifetime by choosing an optimal investment for each combination of energetic state and male quality and time, $i^*(x, m, t)$, trading off the varying benefits and costs of reproduction with each male type, and the varying value of her future self at different times in life. Coding of the backwards iteration is heavily inspired by Roff (2010), and entails the biological assumption that females are fully aware of the quality of males they may meet in the future, and the probability of meeting them.

2.1 Optimization

The backwards iteration produces three matrices of optimal investments, $i^*(x, m, t)$, and three matrices of fitness values given optimal investment, $W(x, m, t)$, one of

each for the three male qualities. The fitness values W are made up of a current and a future fitness component. The current fitness component is the offspring produced in that reproductive event, $F_m(i)$, and the future fitness component is the expected fitness the female is able to gain in the rest of her lifetime if she acts optimally. It is calculated iteratively, meaning that first the fitness values of the optimal choices for each state and mate type at time step t', $W^*(x, m, t')$, are calculated, and these are then used in the calculations at time step $t' - 1$.

The future component of fitness is thus the state-dependent probability of survival until the next time step, $\alpha(x)$, times the sum of fitness values $W^*(x, m, t)$ of each state that can be reached in the next time step, multiplied by the probabilities of getting to each of those states. This also depends on whether or not the female finds food, which increases her state by y, and happens with a fixed probability λ. Thus, at each time step fitness values V_i are calculated for each investment $I = i$:

$$V_i(x, t, m) = F_m(i) +$$

$$\alpha(x)[\sum_{m=1}^{n} P_m \{\lambda W(x - G_m(i) + y, t+1) + (1 - \lambda)W(x - G_m(i)), t+1)\}] \quad (3)$$

the dynamic programming equation (Houston and McNamara 1999; Clark and Mangel 2000) determines W^*:

$$W^*(x, m, t) = max_i \{V_i(x, m, t)\}, \quad (4)$$

and the i producing the highest V_i is saved as $i^*(x, m, t)$ in the matrices of optimal investments.

2.2 Monte Carlo forward simulation

The matrices produced by the backwards iteration described above say nothing about which female behaviors or states we are most likely to observe, simply what the optimal behaviors are once the female is in a given state. For example, we might never observe a female in high state late in her life, but with this model we still know what her optimal investment and maximum attainable fitness would be if the case was to occur. However, we can use this output to simulate lifetime trajectories of sequences of investment decisions for individual females, using random number generation to determine outcomes in the probabilistic events, such as foraging success, mortality and which male quality the female meets (Clark and Mangel 2000). This is known as the Markov Chain Monte Carlo method (MCMC). Running these simulations for a large number of females provides insight into what different states and behaviors we can expect to observe in a large population, given the model assumptions.

We use simulations of 1000 individual lifespans and record how much they invest at each time step, which state they are in and which type of male they meet. The states at the beginning of the simulation are normally distributed with

Table 1: Description and values of parameters used in the model

X	Female energetic state, with $x_{max} = 15$ and $x_{min} = 3$ and increments of 1. Female dies if $x < x_{min}$.
I	Possible reproductive investments, ranging from 0 to x_{max} with increments of 1.
$\alpha(x)$	Survival probability. Set to $0.85 + 0.005 * x$ in baseline model runs.
λ	Probability of finding food, stable at 0.9.
y	Energetic value of food, set to 2 (baseline) or 1.
m	Male qualities. $m = 1$ is a poor male, $m = 2$ is medium, $m = 3$ is good.
P_m	Probability distribution of meeting the three male types. We examined $P_m = \{0.3, 0.4, 0.3\}$ (baseline), $P_m = \{0.6, 0.2, 0.2\}$ and $P_m = \{0.1, 0.6, 0.3\}$.
r_m	Cost function shape parameter. Constant at 1.7.
s_m	Cost function slope parameter. Baseline 0.2.
k_m	Offspring fitness function upper asymptote. Baseline 10.
a_m	Offspring fitness function lower asymptote. Baseline 0.
q, v	Offspring fitness function shape parameters. Baseline 0.4.
b_m	Offspring fitness function growth rate. Baseline 0.5
p_m	Offspring fitness function inflection point. Baseline 3.
T	Maximum life span, set to 20.

$\mu = x_{max}/1.5$ and $\sigma = 1$; a lower distribution of starting states only lowers reproductive investments the first few time steps (thus lets us observe less of the state space), whereafter the simulations follow similar trajectories. Through following the average state and investments of the females as time progresses, we can observe how they trade off reproduction and lifespan. By running the full model with different ecological scenarios (see below), we get different sets of optimization results that we can use for forward simulations, so these can reveal how the aforementioned trade-offs are affected by for example different male benefits ($F(i), G(i)$), the survival probability between each breeding attempt ($\alpha(x)$), the potential increase in state between each breeding attempt ('value of food', y) and the distribution of males in the population (P_m).

2.3 Model scenarios

We used the model described above to first test a sequence of basic male effects, before proceeding to more complex scenarios with combinations of male effects, representing some biologically realistic settings. This first step was in order to clearly separate the effects of changing the elevation and slope of the benefits ($F(i)$) or costs ($G(i)$) function. We used completely linear functions for these, which varied with different male qualities, while keeping a monotonous accelerating (costs, while examining effects of changing the linear benefits function) or decelerating (benefits, while examining effects of changing the linear costs function) curve unchanged in the background. These curves are cubic, in order to ensure a constant rate of change in the slope. We refer to the scenarios where male quality affects the benefit function as scenario 1 a, b and c (Fig. 2 a, b and c, respectively) and those where it affects the cost function as scenario 2 a, b and c (Fig. 3 a, b and c respectively), see Table 2.

The a and c scenarios (respectively elevation and positional shift, see subsection 1.2) are in the linear case mathematically equivalent, since the only thing affected by shifting the function a certain distance in either direction is the elevation. The same effect could be gained by changing its elevation by the relevant amount directly. The c-scenarios (x-axis positional shifts) only become mathematically relevant when we use curved functions, for which a positional shift will change not only the elevation, but also the slope. To illustrate this effect we ran the 1c and 2c versions of the model with curved focal functions (monotonically accelerating $F(i)$ and monotonically decelerating $G(i)$) and a completely linear function with slope 1 in the background, only adding or subtracting from the realized level of investment i (1c and 2c, Table 2).

To illustrate some biologically relevant scenarios, and provide connections with previous modelling efforts (Harris and Uller 2009; Kindsvater and Alonzo 2014), we applied our aforementioned sigmoid offspring fitness function (equation 1) and accelerating female costs function (equation 2). We ran this model with some interesting combinations of male effects (1c & 2b, 1b & 2c) and some scenarios where different male qualities provided different sets of $F(i)$ or $G(i)$ parameter

values (Table 1, Fig. 4). Both these 'combination scenarios' and 'reparametrized scenarios' are intended to represent some often encountered ecological situations and clarify some of the confusion in the empirical literature, and are listed in Table 2.

For the combination scenarios, 1c & 2b is meant to illustrate the common scenario of territorial passerine birds with biparental care, where the main effects of male quality would be a good territory lowering the female's costs per unit investment, as well as the male's capacity to help with parental care. 1b & 2c may represent insects, where the advantages of an attractive mate are mainly genetic quality and nuptial gifts, rather than paternal parental investment (Vahed 1998).

The 'juvenile survival' scenario (Fig. 4a) illustrates a setting where the main effect of higher quality males is to ensure higher offspring fitness at low levels of female investment, similar to Harris and Uller (2009)'s 'good offspring' scenario. This then also captures the potentially relevant effect of low quality male offspring having a lower elevation but steeper slope in the offspring fitness function, and high quality male offspring having a higher but less steep function. 'High mating skew' (Fig. 4b) illustrates an ecological setting where poor quality offspring (offspring of poor quality males and/or offspring receiving little investment) get little absolute fitness, while good quality offspring may potentially get very large fitness returns.
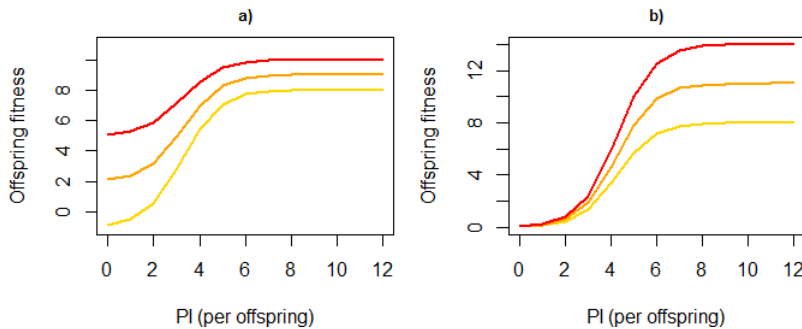

Figure 4: Offspring fitness as a function of maternal per-offspring investment with poor (yellow), medium (orange) or good (red) quality males in reparametrized scenarios. a) Juvenile survival scenario. b) High mating skew scenario.

Table 2: Description of model scenarios

Scenario	Model representation
Simple scenarios with one linear and one monotonically curved function	
Linear focal function and monotonically curved background function	
1a	-1 or +1 added to linear $F(i)$ for poor and good males, respectively
1b	Slope of linear $F(i)$ changed from 1 to 0.8 and 1.2 for poor and good males, respectively
2a	+1 or -1 added to linear $G(i)$ for poor and good males, respectively
2b	Slope of linear $G(i)$ changed from 1 to 1.2 and 0.8 for poor and good males, respectively
Monotonically curved focal function and linear background function	
1c	Investment i gives benefits of $F(i-1)$ and $F(i+1)$ for poor and good males, respectively
2c	Investment i gives costs of $G(i+1)$ and $G(i-1)$ for poor and good males, respectively
Complex scenarios with sigmoid $F(i)$ and accelerating $G(i)$	
Combination effects scenarios	
1c & 2b	$s_m = \{0.25, 0.20, 0.15\}$, 1c as described above
1b & 2c	$b_m = \{0.3, 0.5, 0.7\}$, 2c as described above
Reparametrized scenarios	
Juvenile survival	$a_m = \{-1, 2, 5\}, k_m = \{8, 9, 10\}$
High mating skew	$k_m = \{8, 11, 14\}, p = 5$

The entire model was created in R Version 2.15.1 (R Core Team 2012), and the coding uses the additional packages abind (Plate and Heiberger 2011) and RColorBrewer (Neuwirth 2011).

3 Results

3.1 Linear scenarios

The results from the simple model runs with linear benefit or cost scenarios (1a-c, 2a-c, Table 2) are summarized in Table 3. Note that in these results we use the term 'DA' to include any change in PI across male qualities, regardless of the process creating it.

Table 3: Results from simple model runs

Scenario	Results
1-scenarios (offspring fitness function affected)	
1a	No DA. The $i^*(x, t, m)$ are identical for all male qualities. Forward simulation shows identical investments regardless of male quality, except at the end of the simulation (when sample sizes get very small). Average lifespan is 7.78, $\sigma = 5.77$.
1b	Strong positive DA for females in high states, little DA for females in lower states. Forward simulation shows positive DA from poor to medium quality males, and a weaker difference between medium and good quality males. Average lifespan is 7.90, $\sigma = 5.79$.
1c	Clear negative DA in high states, weaker relationship in low states. Average lifespan is 6.77, $\sigma = 4.84$.
2-scenarios (female costs function affected)	
2a	Weak positive DA for low states, no DA for high states. Forward simulation shows females staying in low enough state for most of their lives so the DA effect is well pronounced. Average lifespan is 7.10, $\sigma = 5.10$.
2b	Strong positive DA for females in high states, weak or no DA in low states. Forward simulation shows positive DA from poor to medium quality males, and less difference between medium and good quality males. Average lifespan is 6.02, $\sigma = 4.44$.
2c	Clear positive DA for all states, optimal investment decreased or increased by 1. Average lifespan is 7.57, $\sigma = 5.73$.

Figure 5 is an example of the results from the optimization, with the optimal investment matrices $i^*(x, t, m)$, shown for each male quality in scenario 1b. Figure 6 shows the same data with the matrices subtracted from each other, in order to emphasise the direction and magnitude of DA. Results from the forward simulation of the same scenario are shown in Figure 7. These three figures are shown in order for all scenarios in appendix A.1.
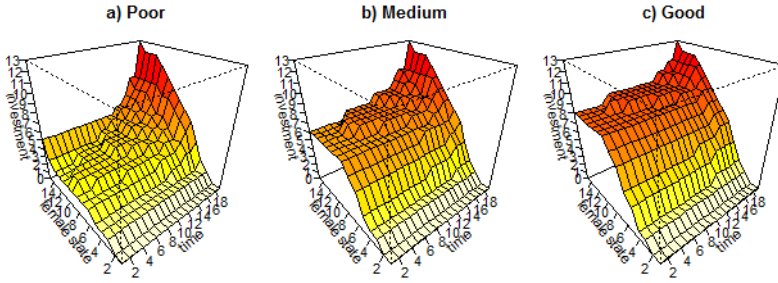
Figure 5: Optimization results from scenario 1b, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.
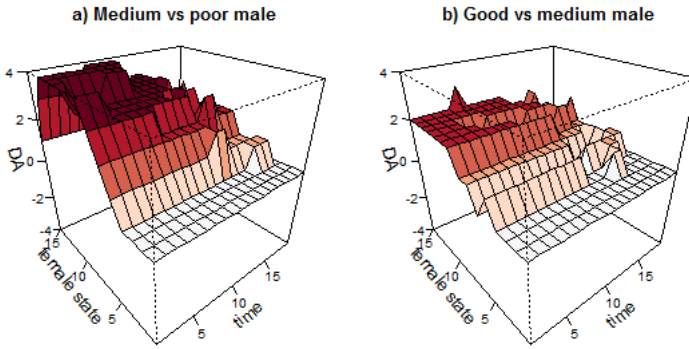

Figure 6: Optimization results from scenario 1b, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).

Although results from our model are completely dependent on the particular cost and benefit functions we feed into it, every effect we may get can be described as a combination of the scenarios above, which is why a complete understanding of each of these separately is the only way we can fully understand any results we get.

The 1a and 1b scenarios confirm that only the slope of the offspring fitness function, not the elevation, matters in terms of DA. 1a acts as a control that demonstrates that any DA we see in 1b, or any other scenario manipulating the offspring fitness function, must be coming from the slope change, since the elevation change alone clearly does not affect DA.

The isolated effect of changing the slope of the offspring fitness function is in shifting the level of investment that maximizes the net benefits. This compares the slope of the offspring fitness function to the steadily accelerating slope of the costs function. In our scenario 1b, a slope of 0.8 puts the net benefits maximum around 2-3 for poor quality males, 6-7 for medium quality males, and 8-9 for good
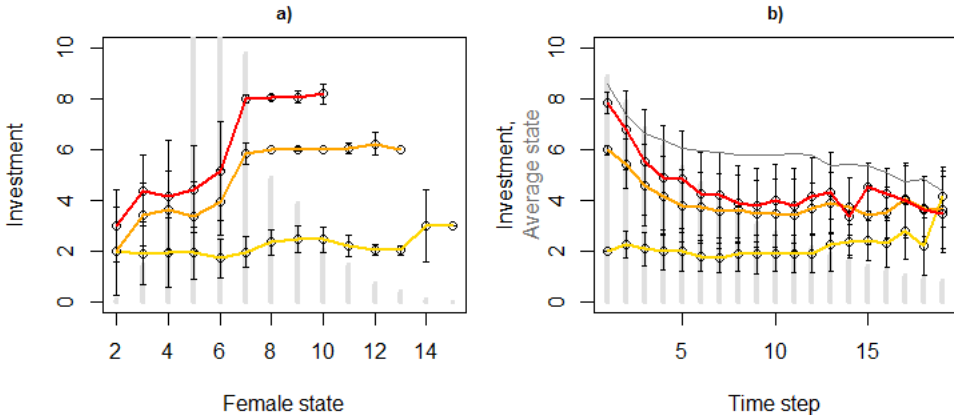
Figure 7: Forward simulation results from scenario 1b, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100 (i.e. there were just under 600 matings with females in state 8). The dark gray line in (b) shows the average state of all females at each time step.

quality males (Fig. 5a–c). As Fig. 7a therefore shows, the DA effect is strongest when females are in highest state, i.e. are able to invest enough to reach this optimum without reaching x_{min}, and Fig. 7b shows that this will be mostly early in life. The difference between good and medium quality males (red and orange line) become small as average state decreases to around six. At this point females can invest enough that we are able to discriminate between the optima for poor and medium/good males, but not between medium and good.

The 2b scenario shifts that optimum in a similar manner to the 1b scenario, from 2-3 for poor quality males, to 4-5 for medium quality males, to 6-7 for good quality males (Fig. A.13, appendix A.1), and the forward simulation also acts similarly (Fig. 8).

On the other hand, 2a, which like 1a was expected to not have any effect on DA, shows a weak positive DA effect. This cannot arise from a shift of the net benefits optimum as described in the b-scenarios, since the offspring benefit and female cost slopes are unchanged. Though initially puzzling, this effect persisted through numerous model runs with different life history parameter values ($\alpha(x)$, y, x_{max}) and cost/benefit functions. It is clear when comparing the optimization results and the forward simulation results that the DA effect in this case arises from females being in such a low state that they can not reach the net benefits optimum, which is around 4-5. The forward simulation shows that females that are in high enough state to reach that optimal investment — regardless of how their mate affects their cost curve — show no DA at all (Fig. 9a), indicating that it is not beneficial to invest more even though you can, due to diminishing returns in the benefit curve.
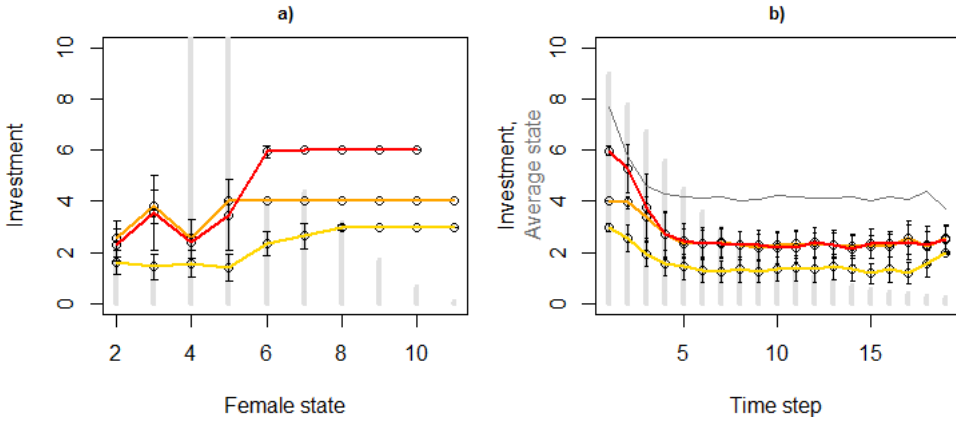
Figure 8: Forward simulation results from scenario 2b, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.

But as Fig. 9b shows, state rapidly declines to such low levels that the females cannot reach that optimal investment, and are thus still in the section of the graph *before* diminishing benefits returns prevent extra investment. Therefore, simply by manipulating cost function elevation, male quality will indeed produce a DA effect in lower female states, since females with a good quality male will be able to invest more before she reaches x_{min} (which is 3), and females with a poor male are able to invest less. The females are in effect moving up and down the slope in the beginning of their $i^*(x, t, m)$ matrix (Fig. A.10a, b; the slope before the plateau at 4-5), which is different for different males (Fig. 10c; a ridge of positive DA in the area of the state space where the aforementioned slopes lie). Although similar, it is not exactly terminal investment (that would be the 'wall' in the back right of the 3d-graphs of the optimizations), since our model does not allow females to invest so much in reproduction that they die with certainty, but it is equivalent in effect to the poker strategy of an 'all in' bet. Every extra investment is bringing more benefits than costs, so it is paying low-state females to invest as much as possible given their mate quality, and therefore a DA effect is produced in these states. It could be argued that this DA effect reflects that between-breeding mortality was not sufficiently state dependent, as that would make it less tempting to go 'all in'. However, the effect persisted over a range of different $\alpha(x)$ functions, where other model features broke down long before this one.

Due to this weak DA in the 2a scenario, we are not entirely able to separate elevation effects from slope effects on the cost function. As the cost functions with poor, medium and good males in scenario 2b all pass through the origin, there is inevitably a direct positive elevation-slope covariance at any given investment. Still, it is clear that the slope effect (which shifts the net benefits optimum) is only
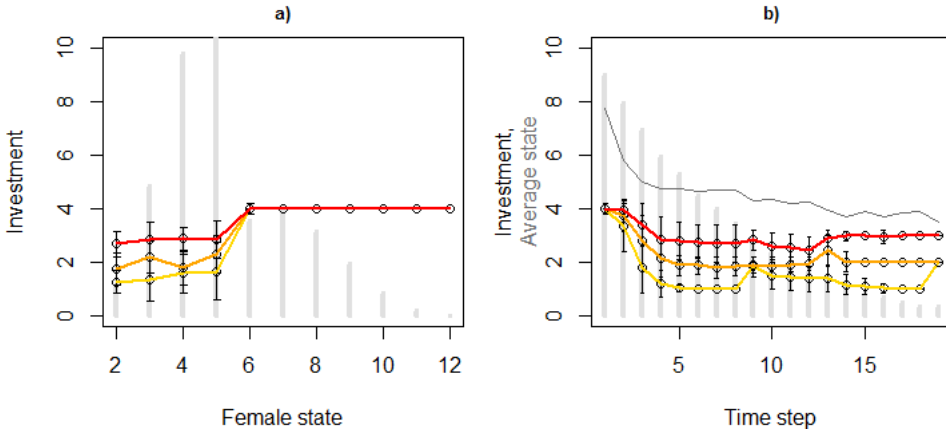
Figure 9: Forward simulation results from scenario 2a, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.
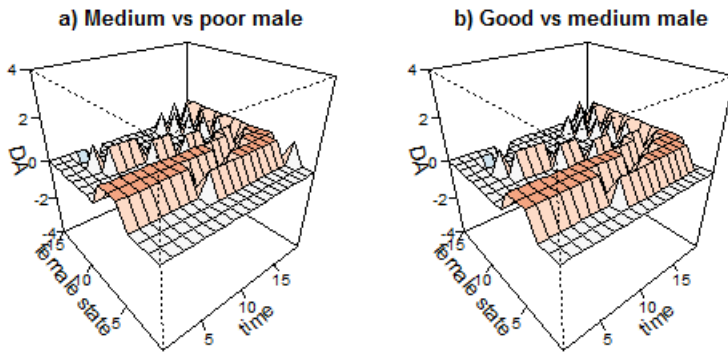

Figure 10: Optimization results from scenario 2a, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).

relevant when females are in high enough state to reach the optimum investment, and the elevation effect (which shifts how much the female can invest before reaching x_{min}) is only relevant when females are in low enough state that they can't reach the optimum investment (Fig. 8).

For the c-scenarios, where male quality shifts the female's position on the x-axis of either the offspring fitness function (1c) or the cost function (2c), we made the focal function curved monotonically curved and the background function linear. As discussed above (section 3.1), any DA effect in scenario 1 is due to a slope change,
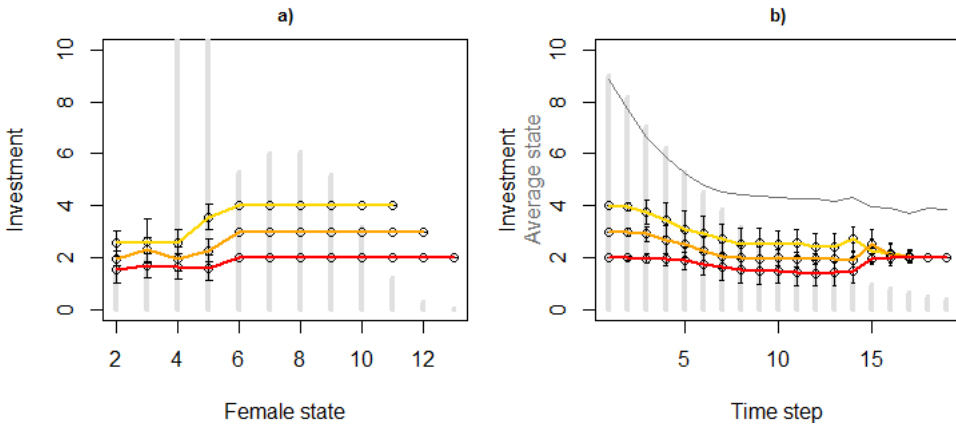
Figure 11: Forward simulation results from scenario 1c, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.

Figure 12: Forward simulation results from scenario 2c, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.
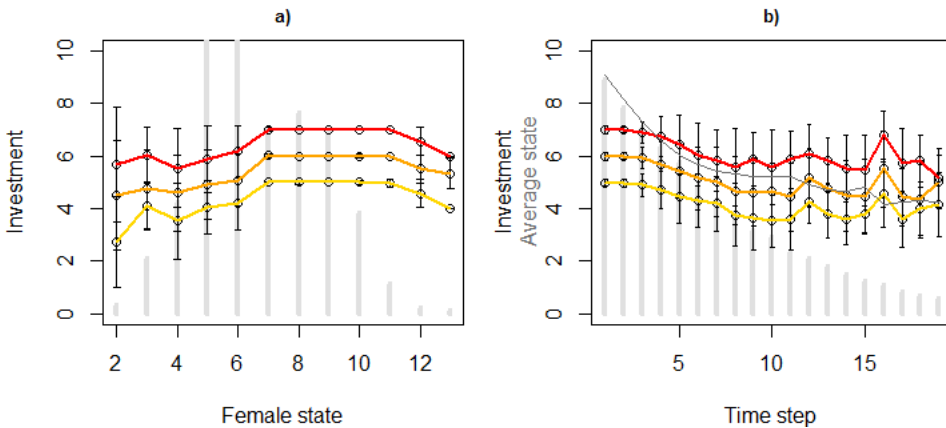
not an elevation change. The steadily diminishing returns of the curved offspring fitness function determines the female's net benefit maximum, and male quality then increases (poor quality males) or decreases (good quality males) the amount the female needs to invest in order to get to this maximum, shifting the optimal investment in this scenario from 3 to 4 or 2, respectively (Fig. 11). In scenario 2c, we cannot as easily determine whether the positive DA arising from a positional

shift is due to the slope change or the elevation change that the shift entails, but Fig. 12, clearly resembles Fig. 8 more than Fig. 9.

3.2   Complex scenarios

Results from the more complex model runs with a sigmoid offspring fitness function and curved female costs function are summarized briefly in Table 4, and complete sets of figures are provided in appendix A.2 and A.3.

Table 4: Results from complex model runs

Scenario	Results
Combination effects scenarios	
1c & 2b	Mostly negative DA in high states, and no DA or weak positive DA in low and medium states. Forward simulation shows negative DA in the first 3 time steps, thereafter positive DA especially from poor to medium males. Average lifespan is 7.67, $\sigma = 5.73$.
1b & 2c	Positive DA mostly in intermediate states, no DA in highest or lowest states. Forward simulation shows clear positive DA for all except the first time step, but less towards the end of the simulation as average state declines. Average lifespan is 7.32, $\sigma = 5.49$.
Reparametrized scenarios	
Juvenile survival	Optimum plateau at 6 is unchanged for different male qualities, but strong negative DA in how and when the shift between levels of investment occurs. No DA in lowest states; in high states DA only from medium to good males. Forward simulation shows intermediate states and thus strong negative DA throughout the lifetime. Average lifespan is 7.94, $\sigma = 5.62$.
High mating skew	'All-or-nothing' investment, which leads to no DA in most state-times, but very strong positive DA where mate quality affects how and when the shift between levels of investment occurs. Forward simulation shows strong positive DA from poor to medium males for all times, but from medium to good males only in middle life (approx. age 3-11). Average lifespan is 7.65, $\sigma = 5.64$.

Combination effects scenarios

In scenario 1c & 2b, the 1c effect that creates negative DA (cf. Fig. 11) dominates, by shifting the optimum 1 up or down if the female is in high enough state to invest to the level of the net benefits optimum (Fig. 13a). But this is moderated or even outweighed by the 2b effect that creates positive DA (cf. Fig. 8), especially when

the female is in low state (Fig. 13a). We also note that the DA between poor and medium quality males is much greater than the DA between medium and good quality males, an effect that becomes very pronounced in the forward simulation (Fig. 13b).

Scenario 1b & 2c produces positive DA, but it only occurs in part of the parameter space (Fig. 14). This is due to the benefits curve now being sigmoid rather than linear or monotonically curved. Increasing the growth rate of a sigmoid function
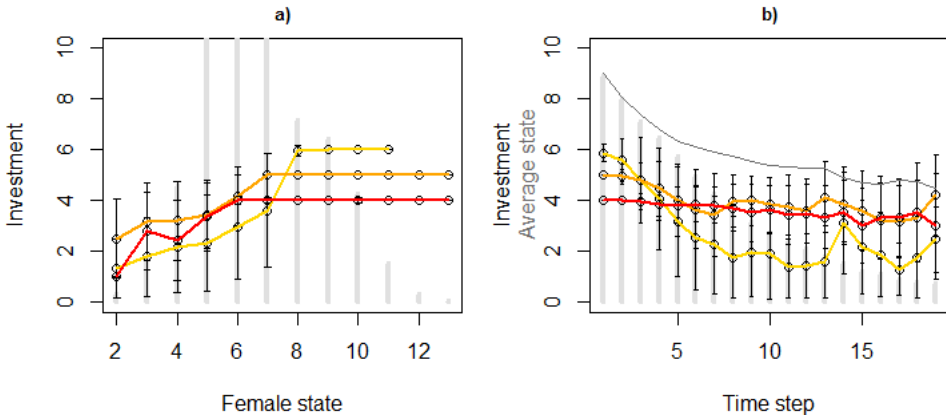

Figure 13: Forward simulation results from scenario 1c & 2b, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.
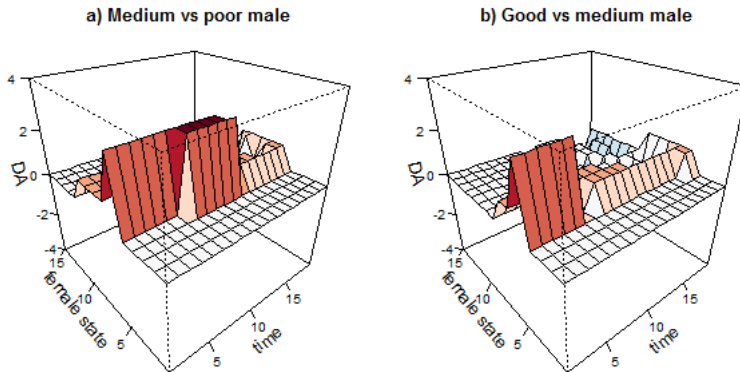

Figure 14: Optimization results from scenario 1b & 2c, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).

has the strongest effect at and near the inflection point, while increasing the slope of a linear function, as we did in 1b, affects the entire function. At high investments the sigmoid curve is flat due to diminishing returns, which explains why there is no DA in very high states — even though the female could invest much more, she has no reason to (compare top left corners of Figs. 6 and 14). The benefit function being sigmoid is also the reason why 2c does not give straightforward +1 or -1 investment here, as it did in Fig. 12. For the monotonically curving benefits function, slope was steepest at the beginning of the function, and every extra investment the female could afford due to the cost-elevation effect was worthwhile. In this scenario, though, marginal returns are very poor at the beginning of the function, so investing doesn't begin to pay off unless intermediate investments can be reached. Put together, then, this scenario produces strong DA for intermediate states. The flat upper asymptote of the benefit function prohibits DA at high states, and the flat lower asymptote prohibits DA at low states.

Reparametrized scenarios

The juvenile survival scenario provides an important finding, illustrating a case producing strong negative DA without any 1c-effect (strategic reduction in biparental care). Although the elevation of the benefit function is highest for good quality males for all investments, it has a less steep slope, simply due to the difference between the upper and lower asymptote being smaller (Fig. 4a). Poorer quality males thus have benefit functions with lower elevation but steeper slopes, favoring strongly increased female investment for offspring of these males, in all but the lowest female states, a pure 1b-effect. In high states early in life there is no DA from poor to medium males, since diminishing returns prohibit continuing investment, but the negative DA trend from medium to good males is pronounced during the entire simulations (Fig. 15).

In the high mating skew scenario we see an all-or-nothing investment pattern, with the interesting part being the section of the shift between the two. DA is mostly in moderately high states, which again is due to the flat sections at the beginning and end of the benefit function (Fig. 4b). Investment in offspring of poor quality males rarely pays off (high investment is needed in order to get to the steep part of the benefit curve in this case, and even then it is only barely steep enough to outweigh the costs of such high investment), and it is therefore only seen in the highest states in the optimization (Fig. 16a), and only as terminal investment in the forward simulation (Fig. A.30b).
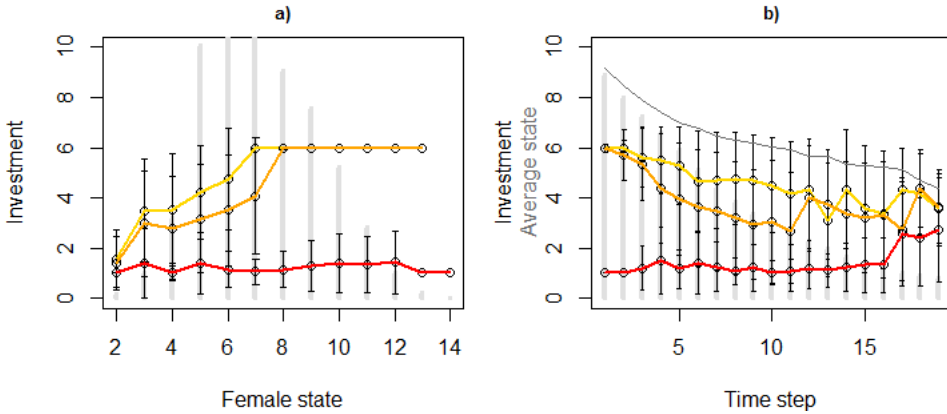
Figure 15: Forward simulation results from juvenile survival scenario, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.
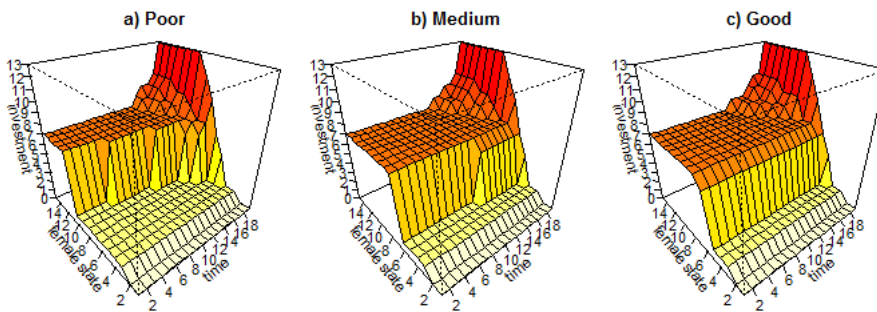

Figure 16: Optimization results from high mating skew scenario, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.

4 Discussion

4.1 Model interpretation

The simple model runs with linear focal functions have enabled us to identify and categorize the different types of DA that can arise. A next major step is being able to apply this framework to empirical studies of natural systems, since the insights from the model now allows us to see the mechanisms behind DA, which empirical researchers were previously unable to know about. The best way to explain the implications of these findings is by explaining empirically what tests would be needed to critically test the predictions of the model. Distinguishing between the different male effects of elevation, slope and positional changes on the benefit function (1a-, 1b- and 1c-effects, respectively) and cost function (2a-, 2b- and 2c-effects, respectively) often requires additional experimental manipulation beyond what existing papers have provided, and I will highlight these tests throughout the discussion.

While heritable genetic effects are a very likely effect of male quality, our model predicts that only the slope of the offspring fitness function generates DA—the elevation itself does not, contrary to popular belief. In order to verify this prediction empirically, one would have to experimentally assess the shape of the offspring fitness function. Cross-fostering experiments are useful in identifying genetic effects, and if the amount of investment per offspring is measured, one could additionally reveal differential fitness effects per investment in offspring of different genetic make-up (good- or bad-quality sire). In species with more limited parental care, for example mass provisioning insects such as Kotiaho *et al.* (2003)'s dung beetles (see below), experimenters may raise offspring of both genetic make-ups on several progressive 'amounts' of parental investment, and thus get a picture of the marginal increases in fitness with each additional bit of investment. Just measuring some fitness proxy at the end of the parental care period does not help us in this regard, since it as mentioned above could be a 1a-effect, where offspring of good genetic quality are fitter regardless of per capita PI.

Teasing apart the effects of benefits and costs also requires additional experimental manipulation. Changing the slope of either the benefit or cost functions (1b or 2b) changes the optimal net benefit investment, and produces strong positive DA in our model when the other function is monotonically curved. These effects are qualitatively very similar in their results, both producing strongest DA when the female is in high enough state to invest to the optimum, and determining which of the effects is responsible for any DA seen in an experimental test would require additional evidence. A 1b-effect could again be demonstrated in cross-fostering experiments where the amount of investment per offspring is measured, by recording different effects of investment on offspring with different genetic quality. A 2b-effect would be revealed by manipulating the female's workload, and thus learning how the female cost function looks. This could be done either by exposing females with different quality males (on different quality nest sites / territories)

to brood size manipulations, and/or (in cases of biparental care) by temporarily removing or handicapping the male during chick feeding, as was done by Wright and Cuthill (1990). Females experiencing a less steep cost curve would then be able to increase their workload more than would females with a steeper cost curve exposed to the same manipulation. An alternative procedure would be to simply eliminate the effect of the cost curve, by providing ad libitum food, which could be more convenient for recording cost curve effects on primary investment (egg size and contests).

The compensatory 1c-scenario producing negative DA does so through altering the marginal benefits of each unit of investment, i.e. a 1b-effect, but must be separated from genetic 1b-effects that do not involve levels of male PI. In biparentally caring birds, the possibility of continuous compensatory reactions to the partner's care level complicate any experimental manipulation of provisioning or attractiveness. This could be avoided by hand-rearing chicks sired by different quality males. If they do not respond differently, that would indicate a 1c rather than a 1b-scenario, but the relationship between male attractiveness and care levels independent of female investment must be determined in separate experiments.

There is an additional source of DA in our model which to our knowledge is not discussed anywhere else in the literature, which arises from male quality affecting the elevation of the cost function. As discussed in section 3.1), females go strategically 'all-in' when they are in so low state that they can not reach the net benefits optimum investment. This effect itself does not produce DA, but when male quality affects the elevation of the cost function, the all-in effect produces a DA pattern. If a good male figuratively gives the female a few extra poker chips, her all-in bid will be larger than that of a female who had a few chips taken from her. Once the female has enough chips to bid as she desires, giving her a few extra chips will not change her desired bid, and so the DA pattern disappears at higher female states. Thus, 2a only produces DA in females in low states, through changes in the size of the all-in investment. However, both 2b and 2c inherently also involve a bit of this 2a effect (a slope or positional change entails an elevation change as well), and it is difficult to think of any realistic male effect on the female's cost function that would only affect elevation and not slope (e.g. any nuptial gift of increase in the quality of the feeding territory could potentially affect both). Therefore, although the cost curve theoretically has two distinct process that can produce DA, in practice it may be possible to only separate between benefit and cost curve effects.

I will now work through our model results and compare them to empirical studies, highlighting patterns that can be explained by our model, and which experimental manipulations that would be needed in order to demonstrate our findings in the different systems. This should pave the way for a more logical and theoretically sound way of studying DA than has previously been seen.

4.2   Comparisons to empirical studies

Null results

The results from the simple scenarios with a linear focal function and monotonically curved background function are clear in their descriptions of different DA effects. When changing nothing but the elevation of the offspring fitness function (scenario 1a), no DA appears (figs. A.1, A.2, A.3). This very unambiguous result is exactly as predicted, and may well be the mathematical explanation for why many tests of DA have shown null results, such as Oksanen *et al.* (1999)'s cross-fostering experiment with bank voles (*Clethrionomys glareolus*). This study examined the males' genetic background and found mating success to be significantly heritable, indicating that there were indeed genetic benefits, but females did not adjust maternal effort according to the genetic quality of their offspring. Male bank voles provide no material resources to the female or offspring, which should eliminate 1c as well as any cost function effects. In systems where these male benefits are present, a null result such as this would be more surprising, but in light of our model this result is indeed the most reasonable. Oksanen *et al.* (1999) conclude that females gain significant genetic benefits from mating with attractive males, whereas they cannot improve their reproductive success further by increasing maternal effort. This is indicated in separate experiments where weaning mass was shown not to affect mating success of offspring. Maternal care thus seems to be primarily related to growth/survival, which is largely independent of attractiveness. In other words, the overall elevation of the offspring's fitness function increases with male genetic quality, but the marginal increase in fitness with increasing maternal care does not—a 1a rather than a 1b scenario.

Other results of no DA are less easily explained. House sparrows (*Passer domesticus*), where good males provide good nest sites and help with parental care, seem like a species in which DA certainly would have an adaptive role (Mazuc *et al.* 2003), but multiple studies have shown null results in tests of female DA in this species (Mazuc *et al.* 2003; Nakagawa *et al.* 2007). Both studies used the badge of status as a measure of male quality, and found no correlation with any maternal investment trait. In our model run illustrating this typical system of passerine birds with biparental care and territorial males (scenario 1c & 2b) the positive DA arising from the cost function benefit of good territory or (in the house sparrows' case) nest site holders (scenario 2b, table 3; Figs. A.13, A.14, 8) partly outweighs the reduction in maternal secondary investment expected if good quality fathers provide more care (scenario 1c, table 4; Figs. A.7, A.8, 11), at least in the low energetic states that we expect to see in natural populations (Figs. A.19, A.20, 13). This could appear to explain the observed lack of DA, but a problem with this line of thought is that male testosterone levels correlate strongly with badge size and hue, and males with high levels of testosterone provision chicks less (Mazuc *et al.* 2003), so the direction of DA with regard to attractiveness should in fact be opposite during chick provisioning (Houston and Davies 1985). Thus the two effects (1c and 2b) should cause even stronger positive DA, in theory.

Mazuc *et al.* (2003) did not alter badge size, but treated experimental males with crystalline testosterone implants, which lowered provisioning. Females did not increase their provisioning in response, and fledgling rate suffered as a result. In the Nakagawa *et al.* (2007) study, badge size was manipulated with dye, which did not affect testosterone levels or chick provisioning, so here the females should not be showing 1c-like negative DA masking any other positive DA. Both studies performed manipulations well before the onset of the breeding season and pair-bond formation, allowing females to presumably perceive 2b-type benefits. In Nakagawa *et al.* (2007) this is assuming that badge size *per se*, in addition to testosterone levels, affects the male dominance hierarchy and distribution of nest sites, something their data indicates it does. Assessing separately whether the experimental manipulation has affected the females' perception of male quality in the way intended is crucial in these experiments (Grana *et al.* 2012). If DA is the only outcome used to determine whether the manipulation was successful, a null result could either mean the female perceived the change and chose *not* to change her investment, or that the manipulation was unsuccessful in changing her perception in the first place. This would make DA an irrefutable hypothesis, in that null results are essentially uninterpretable, rather like studies of certainty of paternity on paternal care (Wright 1998). However, if manipulation is shown to have been effective in itself, then a null result in terms of the levels of female care is more telling. An experiment that could reveal whether badge size manipulation created a 2b-effect in Nakagawa *et al.* (2007) would be giving the females food supplementation or their nests additional shelter. If badge size actually did affect the distribution of nest sites, and this distribution played a role for the female's cost curve, this experiment would help females in poor nests more than females in good nests, and allow them to increase their provisioning more. Alternatively, extra eggs could be added, and the females in good nests may be able to increase their provisioning more. If not, there might not be a strong effect of male quality on the slope of the cost function in this system.

The focus on cost function and 1c-effects here rather than DA-driving genetic effects perhaps needs justification. Female house sparrows are known to exhibit potentially high levels of extra-pair copulations (Anderson 2006), and there is much uncertainty in to what extent badge size is heritable (Griffith *et al.* 1999). Both of the DA-papers discussed here mention this point, and although emphasizing that they have not examined it in their studies, point out that performing DA with respect to the badge size of her social partner may not be the best way for the female to increase her reproductive success. Cross-fostering experiments could reveal whether or not father's badge size has an effect on the offspring's fitness function, but measuring mean relatedness of offspring to the female's social partner would be necessary in order to find out whether DA could be advantageous in the first place.

Negative DA

1c-type 'compensation' leads to a pattern of negative DA

Examining the empirical studies showing negative DA ('reproductive compensation'/'compensatory investment') I note that most of these results are fully in line with my model, to the same extent that the positive DA results are. Although the terminology is questionable, negative DA is reported in broad-nosed pipefish (*Syngnathus typhle*), where 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. Male attractiveness (body length) correlates positively with brooding ability (offspring size at birth) despite both small and large females mating with both small and large males (Berglund *et al.* 1988), a scenario exactly akin to our sealed-bid paternal care scenario (1c), and without the behaviorally dynamic confusion of the simultaneously biparental birds like house sparrows. There is perhaps little opportunity for genetic effects on DA (1b) to evolve here, since females spread their eggs over a large number of males, and each male brood generally contains eggs from several different females (Berglund *et al.* 1988), and the male can probably not differentiate between them. In addition, Goncalves *et al.* (2010) point out that osmoregulation and transfer of nutrients and oxygen through the brood pouch gives ample opportunities for phenotypic differences in quality of male care to arise, so since brooding ability is physiologically determined by male size and there is no negotiation over care, the mother thus increases her investment in egg nutrients when experimentally paired with a small male in order to increase offspring fitness, and lowers it when with a good males due to (presumably) diminishing offspring fitness returns.

The paternally mouthbrooding Banggai cardinal fish (*Pterapogon kauderni*) shows clear positive DA in a very similar setting (Kolm 2001). Though lacking a specialized organ for paternal care such as the pipefish's brood pouch, quality of brooding (clutch weight on the day after spawning) is determined by the size of the male, independent of the size of the clutch's mother (Kolm 2001, 2002). Therefore we might have expected a 1c-like effet producing negative DA like in the pipefish discussed above. However, there is an important difference in the two species' mating systems. Banggai cardinal fish form temporary pairs before mating and a female spawns her entire clutch with only one male (Kolm 2002). Size is a strong determinant of fitness in the Banggai cardinal fish, which lay relatively few and large eggs and whose larvae have no pelagic phase (Kolm 2002). Therefore there is good reason to expect strong 1b-effects in this species, causing females to invest more with a large partner, who provide a steeper offspring fitness function, through good genes, paternal care, or both.

An offspring fitness function with low elevation but steep slope for poor quality males leads to negative DA

Gowaty's reproductive compensation hypothesis, focusing on extra investment in offspring of matings with non-preferred mates in order to make up for likely off-

spring viability deficits, largely in relation to pathogen resistance (Gowaty *et al.* 2007; Gowaty 2008), has unfortunately been kept quite separate from the DA hypothesis. However, it is completely compatible with the type of DA effects discussed here; the hypothesis is explicitly about effects on offspring fitness. It represents a particularly clear example of a 1b effect producing negative DA, where the marginal benefits of extra investment are large when with poor quality mates ('constrained' matings). This case is treated in our 'juvenile survival', where the absolute benefits from the offspring of poor quality males are never as large as for offspring of good quality males, but the marginal benefits are larger, and therefore there is negative DA. Many empirical examples of negative DA appear to be neatly explained by this scenario. Studying sexual selection in pronghorns (*Antilocapra americana*), Byers and Waits (2006) found a strong female preference for attractive males, and females mating with these had higher lifetime reproductive success and better offspring survival until weaning. However, females mating with less attractive mates increased their delivery rate of milk to suckling young in a period where suckling is completely under maternal control. This result of negative DA may well be an example of a scenario where attractive males provide an offspring fitness function that is higher in elevation but has a less steep slope, while unattractive males provide a function with lower elevation but steeper slope, but showing this to be the case would require offspring growth per amount of milk delivered to be measured continuously.

Working on mallards, (*Anas platyrhynchos*), Bluhm and Gowaty (2004) reported that second-year mothers laid heavier eggs for non-preferred than for preferred males. As they had previously shown that offspring viability was lower when mothers mated with non-preferred males, this may be another example of low quality males providing a lower but steeper offspring fitness function, like our juvenile survival scenario and the pronghorn example above. The fact that second-year mothers were heavier than first-year mothers (Bluhm and Gowaty 2004, Fig. 1a), who did not show negative DA, corresponds well with our results from this scenario: Fig. 15 reveals that only females in high state should show negative DA.

Bolund *et al.* (2009)'s zebra finches laying larger and more nutritious eggs for less attractive males, are an intriguing case of negative DA. It could have been explained similarly by the juvenile survival scenario, were it not occurring in the very species that is most famous for positive DA (Burley 1988). The experimental setup was very different though: male attractiveness in this study was determined by extra-pair mating success. An alternative explanation for the contrasting result could have been that the females expect more parental care from high-quality (attractive) partners and therefore reduce their investment, as in our 1c-scenario (Fig. A.8), but if it like here is the unattractive males that provide more care, since they by definition are less likely to be out on extra-pair matings, the increased investment for unattractive males must be seen as positive DA, which goes against our model result (Fig. A.8). However, demonstrating this requires data on feeding rates of each sex during the chick rearing stage, and of differences between attractive and non-attractive males. In addition, cross-fostering or even hand-rearing chicks of

attractive and non-attractive males and quantifying offspring fitness as a function of per capita PI would reveal the nature of any genetic effects driving DA.

The majority of results showing negative DA patterns involve mother birds adjusting egg yolk contents such as androgens, carotenoids and antioxidants or other immuno-enhancing compounds (e.g. Michl *et al.* 2004; Navara *et al.* 2006; Bolund *et al.* 2009), but other studies on yolk compounds have shown positive DA (Gil *et al.* 1999; Loyau and Lacroix 2010). The negative DA patterns (more of the given yolk compound is invested into eggs of less attractive males) are most easily explained by the effect from our juvenile survival scenario, favoring increased investment in offspring from lower quality males that might be expected to have lower elevation but steeper slopes to their benefit funtions, but the case may not be as simple as that. Horvathova *et al.* (2012) argue that studies on yolk compounds do not fit as neatly into theoretical discussion of DA, both since there may not be a cost to the mother of adding the small amounts of compounds measured in these studies, and since it is not as obvious that more is better, especially regarding hormones. For example, Gil *et al.* (1999) discuss that their result of higher testosterone deposition by the female in eggs of attractive males may just be an adaptation to testosterone being harmful to development or immune function in chicks of poor genetic quality. So all these cases of apparent DA, positive or negative, involve male quality changing the optimal level of yolk compounds for the offspring, but may not necessarily fit neatly inside the DA framework, since they may not concern the mother's current-versus-future trade-off and/or represent directional 'increases' and 'decreases' in investment. An interesting perspective, though, would be that the mother sets up different offspring fitness function scenarios (our 1a-b and/or 2a-b) by adjusting amounts of the different yolk compounds depending on the anticipated patterns of male and female PI, as well as the mating system (brood relatedness). For example, testosterone decreases growth per unit of investment, but increases begging and sibling competition (Gil *et al.* 1999). Carotenoids may increase the elevation and/or the slope of the offspring fitness function, antioxidants and other immuno-enhancing compounds may level out the left hand side of the offspring fitness function, as in our juvenile survival scenario, while yolk mass itself is maternal investment. These different effects are all captured by the model, and may provide a new, DA-tinged perspective on yolk investment.

Positive DA

Biparentally caring birds: 'Good genes'-type 1b or 'handicapping'-type 1c?

In cases with biparental care and sexual selection, where male sexiness lowers parental investment, for example because of increased extra-pair activity or handicapping through costly secondary sexual characteristics, the verbal arguments of female 'compensation' due to the male's lower parental investment (Houston and Davies 1985), and positive DA due to 'good genes', are difficult to tease apart. In barn swallows (*Hirundo rustica*), long tail feathers are a costly secondary sexual trait for males, and de Lope and Møller (1993) showed that females increased their

reproductive investment for males with experimentally elongated tails, but struggle to prove whether this is due to 'good genes' DA or compensation for the males' lowered provisioning ability (Witte 1995). Note here that both the 'compensation' term and the 'good genes' DA give the same qualitative pattern of positive DA, and it seems rather futile to debate whether or not this difference in 'motivation' for DA should be of relevance for which terminology to use. The former effect here is only marginally different from the effect seen in Wright and Cuthill (1989), where attaching weights to the tail feathers of either sex in the biparentally caring European starlings (*Sturnus vulgaris*) resulted in partial compensation by the partner—the only difference being whether the handicap is sexually selected or not. To determine whether there is an additional 1b-like DA effect on top of this in the barn swallows, one would have to handicap one group of swallows with un-sexy long tail feathers (e.g. painted white in order to be harder for females to see), and another group with similarly handicapping sexy tail feathers, and see whether the females increased their investment *more* in the latter group. If they did, it would imply that the females were perceiving a marginal benefits increase causing DA, but if they increased their investment as much in both groups, the females would only be compensating for the similar effects of the male handicap in both experimental groups. Again, DA-driving genetic benefits could be demonstrated by cross-fostering offspring of different genetic quality and measuring whether there were differences in response per unit of PI received.

On a similar note we have several studies showing positive DA in male parental care in response to non-handicapping manipulations of perceived clutch quality (Mahr *et al.* 2012; Walters *et al.* 2014). Walters *et al.* (2014) added brightly or darkly colored artificial eggs to house wren (*Troglodytes aedon*) clutches during incubation. Males responded to brighter eggs, which is a signal of higher egg quality, by increasing their feeding rate (a positive DA result), while females did not change their provisioning significantly. Mahr *et al.* (2012) manipulated the UV reflectance of female blue tits' (*Cyanistes caeruleus*) crown ornaments, and found that males lowered their feeding rate for females with experimentally UV-reduced crowns (i.e. poorer quality females received less help - a positive DA result). Females were not able to increase their feeding rate in response, possibly because unusually averse weather conditions already were making the females work at maximum effort in this wild population. Both egg color and crown coloration could plausibly have been interpreted by the males as indicators of female provisioning capacity (poor phenotype signalling less provisioning capacity), but the fact that the males responded with positive DA rather than a compensatory 1c tactic (expeting lower female care) indicates that they used these traits to determine fitness returns of the current clutch, i.e. a 1b-effect. Cross-fostering would, again, reveal whether offspring of females with these attractive traits indeed grow faster per unit of PI than offspring of less strongly signalling females.

In spotless starlings (*Sturnus unicolor*), males bring green plant material to the nests during as a courtship display, which is thought to act as a reliable signal of genetic quality (Veiga *et al.* 2006). López-Rull and Gil (2009) manipulated

male attractiveness by adding more green plant material to some nests, and found that females increased their clutch size for experimental males. This is not an increase in per-offspring investment, on the contrary, one would expect per-offspring investment to become lower in a large clutch due to maternal provisioning costs, since the males providing a lot of green plant material are often more polygynous and do not help much with parental care (Veiga *et al.* 2006). If so, it may be another case of the juvenile survival scenario, where offspring of attractive males have a higher offspring fitness function elevation but less steep slope. However, information on the subsequent maternal provisioning and offspring performance would be necessary in order to verify this, but this information was not recorded. An alternative explanation from our model could be that the added green plant material in the nest lowers the slope and/or elevation of the female cost curve, which could explain the change in egg number rather than quality, but hypotheses about greenery acting as protection against ectoparasites or for health benefits (which could have provided an elevation effect) are quite disputed, especially since females routinely cover or even remove the greenery. Cross-fostering experiments recording growth per unit of PI, survival and subsequent mating success would thus be the best way to identify the effects in action here. Especially a finding of lower survival at low care levels for poor than for good genetic quality offspring would indicate that male quality is flattening out the left part of the offspring fitness function—i.e. producing negative per-offspring DA through the 1b-effect encaptured in the juvenile survival scenario, rather than positive DA as the paper reports.

Nuptial gifts and other insect cases

Some of the best demonstrations of positive DA come, not surprisingly, from the insect world. Although our model is less suitable for insects than for birds and fish, with 20 breeding opportunities during a lifetime and high between-breeding survival, it is still interesting to view results from DA experiments on insects in light of our model. Kotiaho *et al.* (2003) found that female dung beetles (*Ontophagus taurus*) mated with large-horned males (for life) constructed larger brood balls, but also live longer than females mated with short-horned males. They are therefore wary of calling their result DA, since their increased investment with good males doesn't come at a cost of future reproduction. Still, larger-horned males providing females with larger and more nutritious seminal products, that are used for somatic maintenance as well as reproductive investment (Vahed 1998; Simmons and Kotiaho 2002), seem a good example of a 2c scenario, which I have shown can produce increased investment even without DA-driving genetic benefits (1b). Kotiaho *et al.* (2003) also found significant heritabilities for male horn length, body size and ejaculate size, but whether this only increases the elevation of the offspring fitness function or also increases the mother's marginal gains per unit of investment, causing an additional 1b-effect, is not clear. Demonstrating this could involve transferring eggs of similar genetic make-up (large- or small-horned sire) to brood balls of different sizes, and seeing whether offspring of different genetic make-ups had different responses (in terms of survival, adult horn length or body

size) to increasing brood ball size. Offspring are expected to perform better on larger brood balls, and offspring of large-horned males are expected to perform better than offspring of small-horned males, but if the slope of offspring performance across brood ball sizes is the same for offspring of large- and small-horned males (i.e. offspring of large-horned males perform equally much better for all brood ball sizes), there is only a 1a genetic effect, not a DA-driving 1b genetic effect, and thus the DA pattern must come from the cost function.

The previous result is reminiscent of Wedell (1996), in which female comma butterflies (*Polygonia c-album*) invest more in reproduction when mated with a high quality male (raised on stinging nettles) than a low quality male (raised on sallow), while still living longer. Radioactive markers in the nutritious male spermatophores were shown to be used both for female somatic maintenance and reproduction, but the females also increased their own relative reproductive investment when receiving more nutritious spermatophores. Wedell (1996) points out that the result shows that 'good genes need not necessarily be invoked to explain increased investment by females'. As I have shown, a nuptial gifts scenario that moves the female lower down on her cost curve produces positive DA, especially when costs are accelerating (Figs. A.17, 12), without invoking the benefit curve. However, the experimental setup may not have excluded genetic effects entirely, since genetically good quality males might be the only ones that gain competitive access to nettles in nature, and females could thus be expecting a genetic 1b-effect from the per capita fitness increases in offspring from their nettle-raised mates. Determining whether this is the case would require gathering eggs from nettles and sallow in the field, then raising offspring on their natal or the different plant in the laboratory, and recording whether there are differences in performance—preferably for more than one generation, to control for the very DA-effect we are discussing having occurred on the eggs gathered in the field.

In a study on house crickets (*Acheta domesticus*), Head *et al.* (2006) found that females mated sooner and laid more eggs for large males, despite direct costs to the females that they had already demonstrated (Head *et al.* 2005). Therefore, there was a clear trade-off in this case between current and future reproductive investment. There was a strong cross-generational link in sire phenotype and daughter preference, indicating genetic benefits of positive DA outweighing the costs (and also providing potential for co-evolution between male attractiveness and female DA). The DA was strongest in large females (only these increased clutch size when mating with preferred males), which the authors attribute to 'costs decreasing with increasing female size', but if size is an indicator of female state, it is fully in line with our result from scenario 1b, which shows little DA in low states and strong positive DA in high states (Figs. 6, 7).

4.3   Consequences and future directions

The model has succeeded in showing that the three effects that can produce DA is benefit function slope change, cost function slope change and cost function elevation

change. The last of the quartet, benefit function elevation change, cannot. In Harris and Uller (2009), only the offspring fitness function (i.e. benefit function) elevation change is included explicitly as an effect of male quality, yet the model does show some DA. This does not appear to stem from the source they propose (male quality changing benefit function elevation), but is an unintended by-product of the non-linearity of both the benefit and cost functions. It is possible within the model presented here to reproduce the Harris and Uller (2009) results, and also to produce results of no DA, when modifying the benefit and costs functions to remove this unintentional non-linearity.

Our model 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 plan to expand our model to include this feature, after which there should be potential for interesting comparisons. We also imagine that the several-offspring feature will enlighten another key difference between our 1- and 2-scenarios, namely that male benefits affecting the offspring fitness function work on a per-offspring basis, while male benefits affecting the female cost function affect the whole brood. This can be easily incorporated into our model, and is the natural next step in attempting to explain the large variation in DA patterns seen in the empirical literature, as I have already touched upon in the discussion of López-Rull and Gil (2009) above. The distinction between effects on the costs and benefits is still useful in our model, though, since costs affect female future fitness in ways that the benefits can't, and thus 2a produces weak positive DA, while 1a does not.

Regardless of the quality-quantity trade-off in modelling multiple offspring per brood, DA of the strength we record in some of the scenaria presented here has evolutionary implications simply in the varying reproductive success of different parental phenotypes. Increased investment in response to already preferred phenotypes in the partner (including extended phenotypes in the form of ornaments and other signals of quality, good nest sites, territories or nuptial gifts) exaggerates the transfer of these traits to the next generation beyond that caused by assortative mating (Sheldon 2000; Kotiaho *et al.* 2003; Uller *et al.* 2005). Imagine a novel mutation enhancing a secondary sexual male trait. It is selected for because females prefer to mate with males expressing this trait, and its frequency in the next generation thus increases relative to the wild type because its male carriers obtained more matings. Now, female DA with regards to this trait can increase its success *additionally*, since not only do carriers obtain more matings, their offspring also receive greater investment from their partner. Conversely, increased investment in response to non-preferred traits (i.e. negative DA) promotes evolution against the direction of selection: Despite the abovementioned mutation's success in obtaining matings, its offspring are receiving less maternal PI than wild-type offspring, and its spread is therefore slowed. DA is thus a parental effect which potentially can have especially large 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 adaptive role

(Harris and Uller 2009; Kindsvater and Alonzo 2014; this thesis). 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.

Conclusion

I have created a state-based stochastic dynamic model of the differential allocation hypothesis, performing first a sequence of simple model runs to explore the effect of slope and elevation on the female's cost and benefit functions. These show that the elevation of the benefit function (offspring fitness function) has no effect on the optimal level of investment, and thus cannot produce DA, contrary to popular belief until now. On the other hand, the slope of the benefit function as well as both the elevation and the slope of the cost function can shift the optimal levels of investment, though the different effects do so at different female states and times throughout life. Specifically, the slope of the benefit and cost functions affect the optimum level of maternal investment, while the cost function elevation does not affect this optimum at all, but if investments lower than this are increasingly beneficial, so that the female invests as much as she can (goes 'all-in'), the cost function elevation affects how much the female is able to invest. Therefore, scenarios where male quality affects slope will produce DA mostly when females are in high enough states to reach this preferred investment, while scenarios where male quality affects cost function elevation will produce DA only when state is so low that they cannot.

A compensational reaction in response to the male providing parental care shifts the female's position on the x-axis of the offspring fitness function. While the function itself is unchanged, the marginal benefits of the female's investment changes, and may therefore change her optimum level of investment in patterns appearing as positive or negative DA, depending on how the slope of the offspring fitness function changed. Similarly, a nutritious nuptial gift from the male may shift the female's position on the x-axis of her own cost function. Both the marginal and the absolute costs of the female's investment changes, and in this case either or both of these (depending on the female's state) may change the optimum level of investment.

With these distinct effects teased apart, the model was used to combine different effects and use a larger set of parameters in order to emulate the biology of certain animal taxa, ecological settings or mating systems. I show how patterns of negative DA (higher investment for poor quality mates) can arise either from a strategic reduction in investment when the partner invests a lot, or from a scenario where offspring of good quality males do quite well regardless of female investment, while offspring of poor quality males, albeit with lower fitness, have a steeper benefit curve slope with increasing female investment, and are therefore favored. I have discussed empirical and previous theoretical results in light of our model, finding little discord and largely being able to explain earlier results in light of my model. In general, the findings of the model are easiest to observe in systems where benefits and costs are obviously separated or can be controlled for by experimental manipulation. Additionally, empirically assessing the shape of the fitness functions of different

quality offspring, by measuring fitness (growth/survival) at different levels of PI, could demonstrate the importance of the model's elevation/slope distinction.

My model shows why the existing theoretical framework of DA and RC is flawed and has led to so much confusion, and points instead to where empirical studies need to look in order to understand the observed DA patterns. All effects of male quality are on either the elevation or the slope of the benefit or cost functions, or the female's position on them, and we have now have identified the DA, or lack of such, that each of these effects can create. When an empiricist knows which of these effects an experimental manipulation is creating and to which the female is responding, and has established this in separate experiments, DA should appear a lot less confusing.

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Appendix A   Results

A.1   Simple scenarios

1a
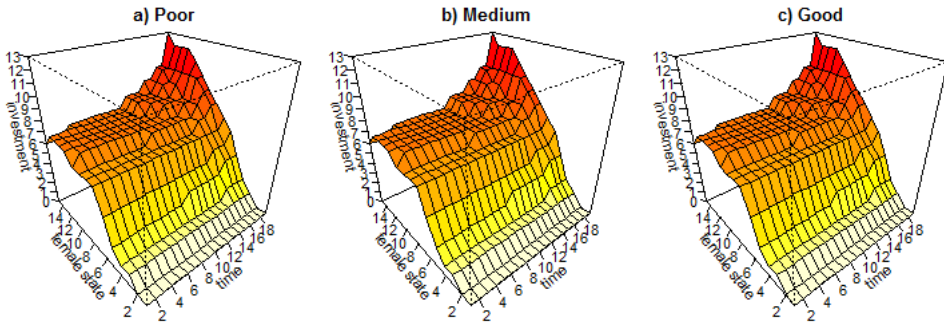
Figure A.1: Optimization results from scenario 1a, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.
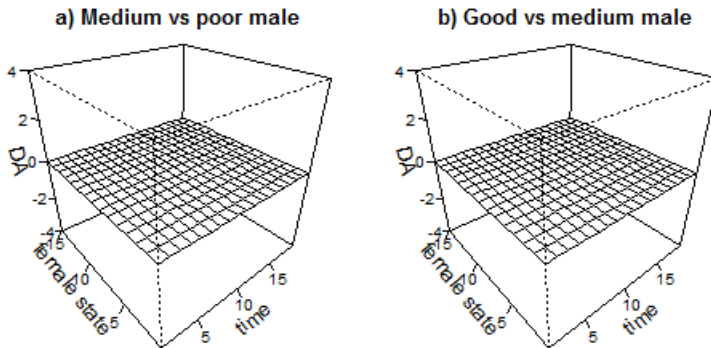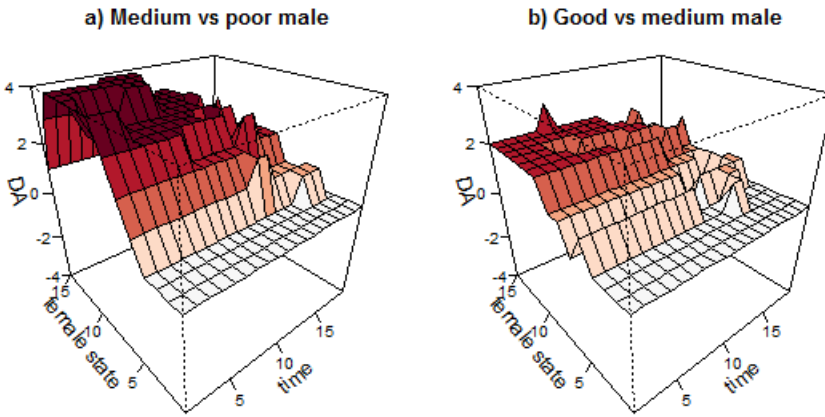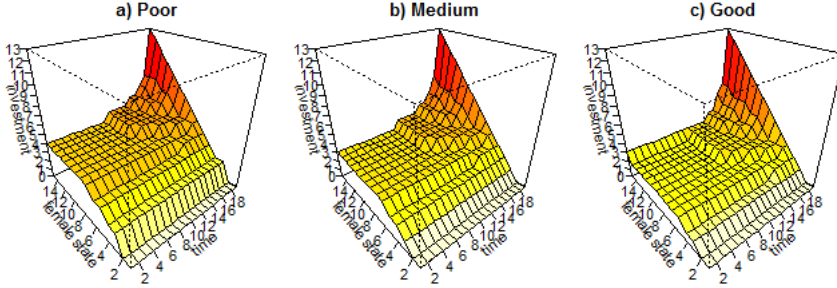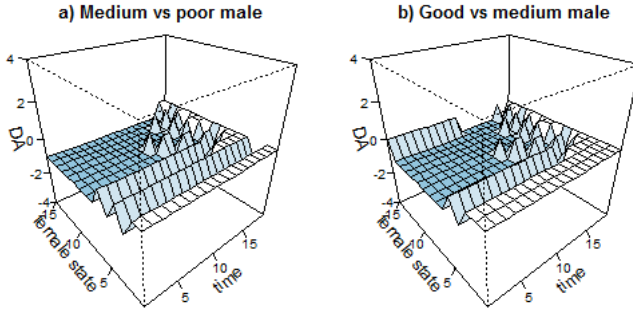

Figure A.2: Optimization results from scenario 1a, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).
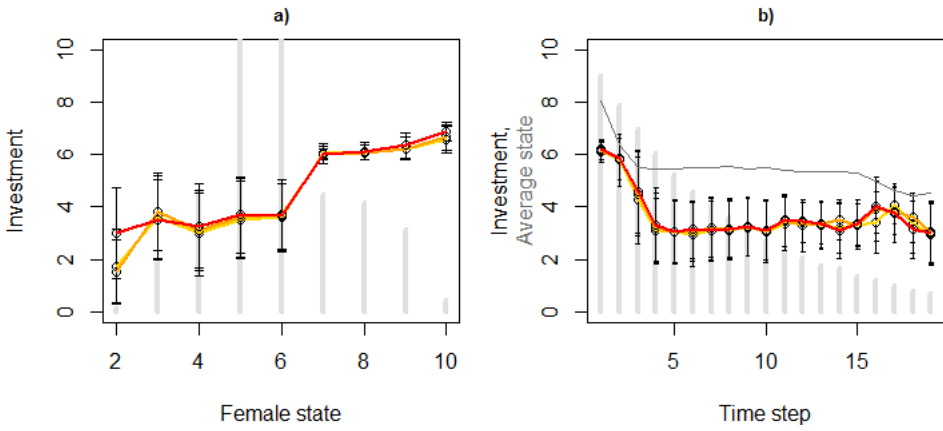
Figure A.3: Forward simulation results from scenario 1a, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.
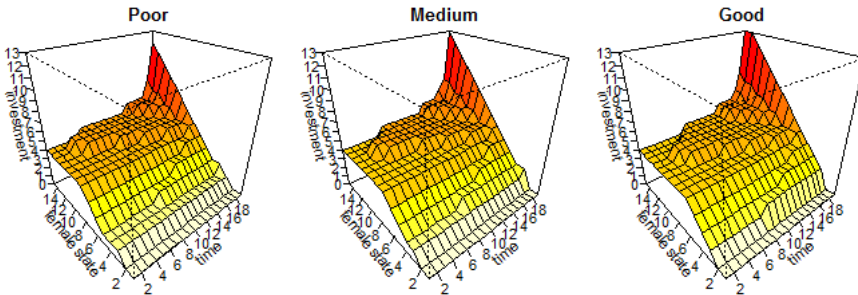
1b
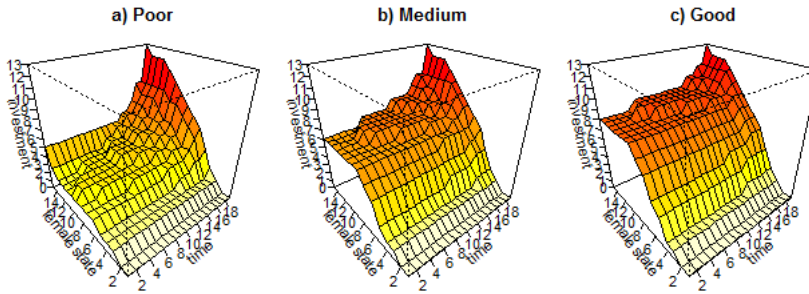
Figure A.4: Optimization results from scenario 1b, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.
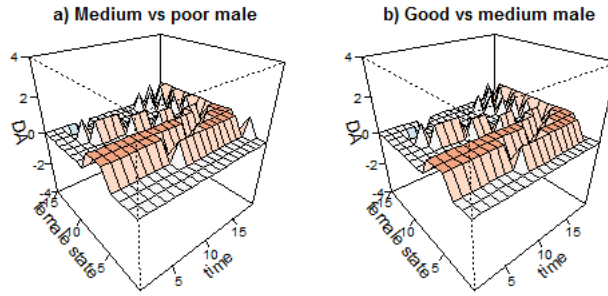
Figure A.5: Optimization results from scenario 1b, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).
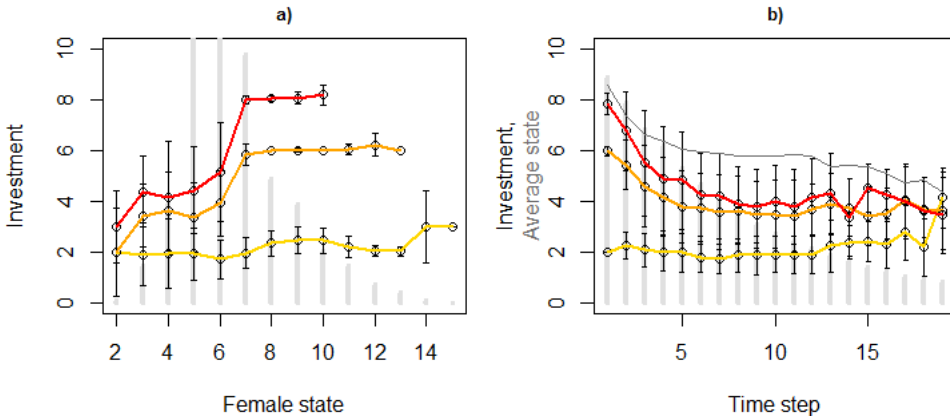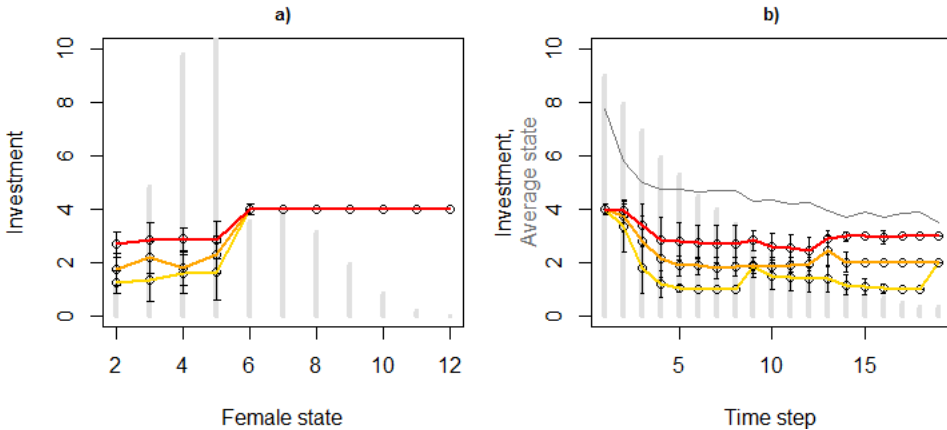

Figure A.6: Forward simulation results from scenario 1b, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100 (i.e. there were just under 600 matings with females in state 8). The dark gray line in (b) shows the average state of all females at each time step.

1c

The offspring fitness function in this scenario is $f(I) = 4.5708 * log(I + 1)$, while the female costs function is $g(I) = I$.

Figure A.7: Optimization results from scenario 1c, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.
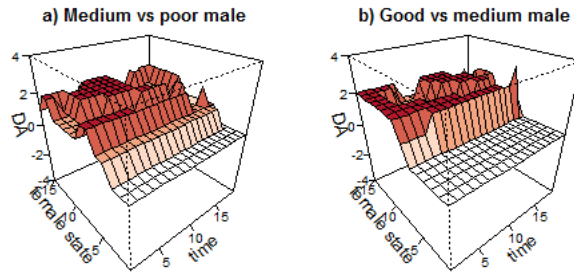

Figure A.8: Optimization results from scenario 1c, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).
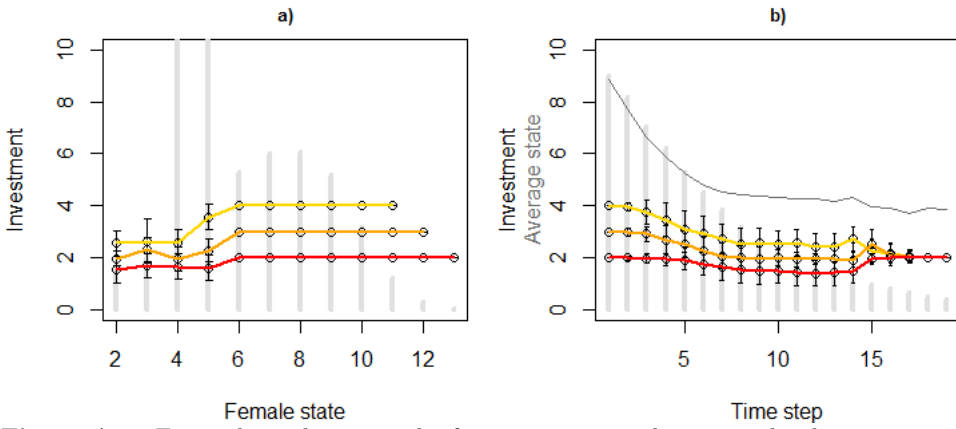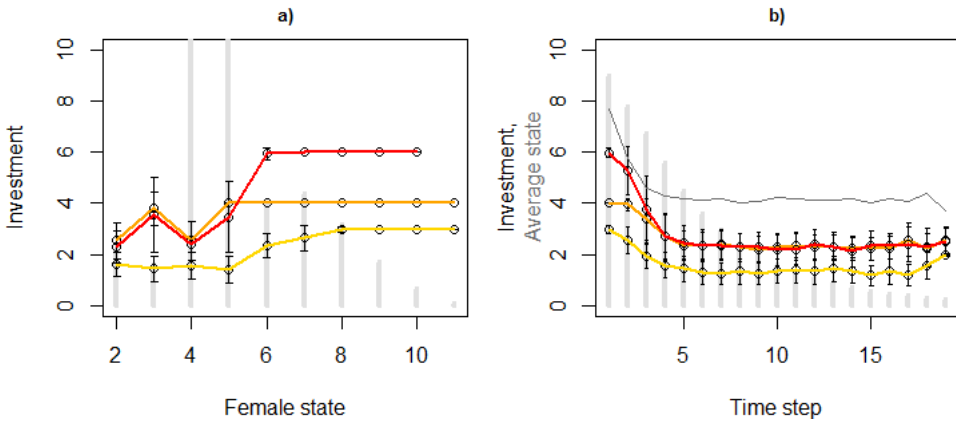
Figure A.9: Forward simulation results from scenario 1c, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.
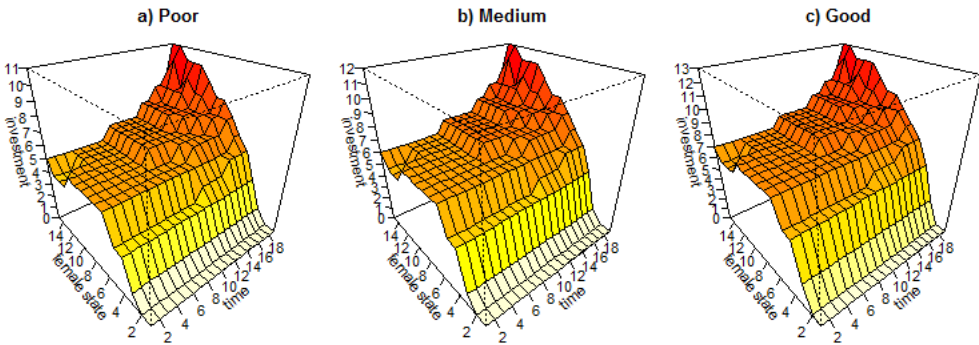
2a

Figure A.10: Optimization results from scenario 2a, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.
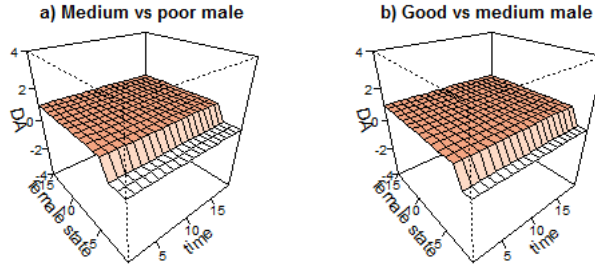
Figure A.11: Optimization results from scenario 2a, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).
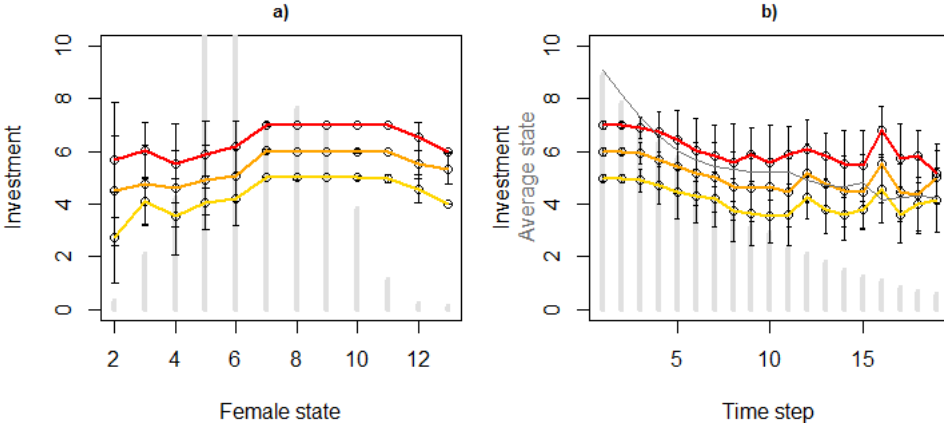

Figure A.12: Forward simulation results from scenario 2a, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.

2b
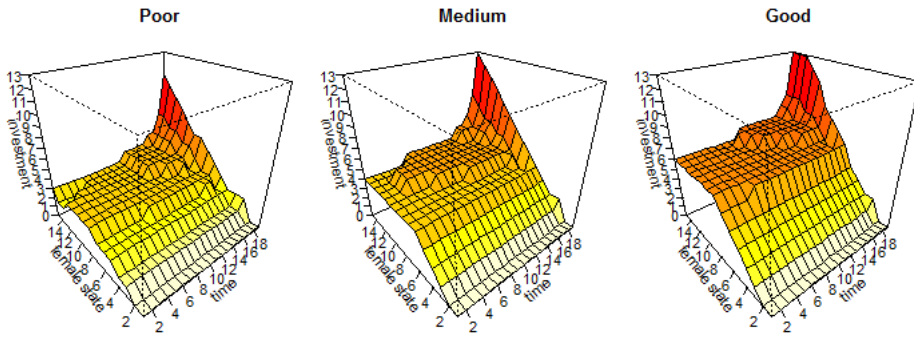
Figure A.13: Optimization results from scenario 2b, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.

Figure A.14: Optimization results from scenario 2b, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).

Figure A.15: Forward simulation results from scenario 2b, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.

2c

The female cost function in this scenario is $g(I) = 1.2^{1.2*I} - 1$, while the offspring fitness function is $f(I) = I$.
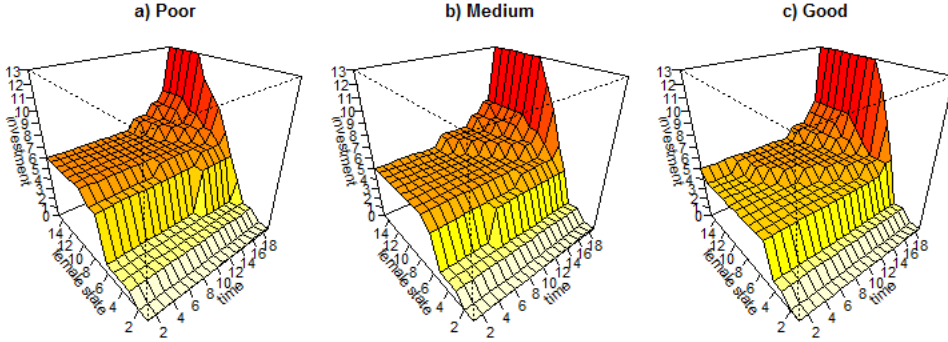

Figure A.16: Optimization results from scenario 2c, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.
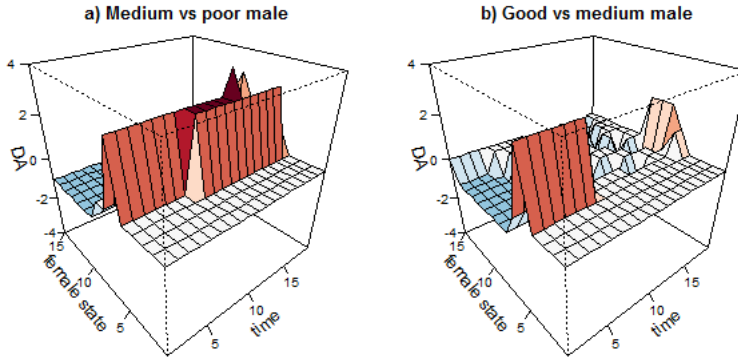
Figure A.17: Optimization results from scenario 2c, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).
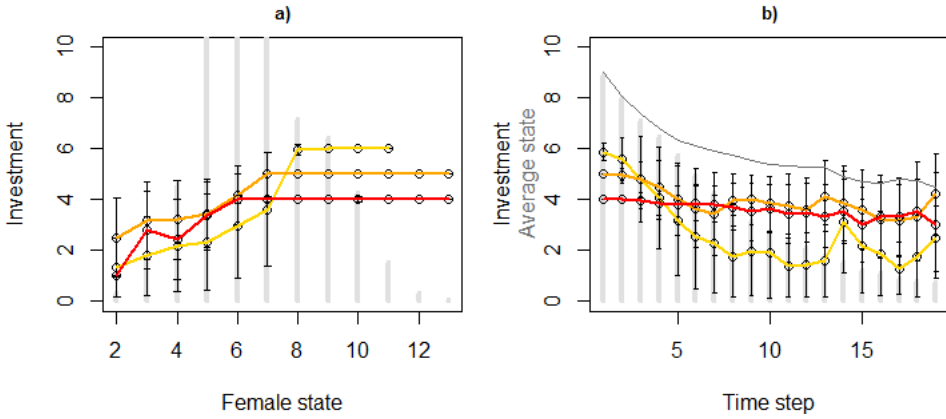

Figure A.18: Forward simulation results from scenario 2c, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.

Male quality distribution $P_m = \{0.6, 0.2, 0.2\}$ gave slightly higher investments for medium quality males when the female is in low state early in life. This exaggerates the positive DA in the first half of the forward simulation ($t < 10$), which becomes less pronounced in the second half, but still persists due to good males receiving more investment. Life span unaffected (mean age at death 7.34, $\sigma = 5.30$). For $P_m = \{0.1, 0.6, 0.3\}$ the results are much more similar to the baseline run, and life span is still unchanged (mean age at death 7.55, $\sigma = 5.66$).

A.2   Combination effects scenarios

1c & 2b

Figure A.19: Optimization results from scenario 1c & 2b, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.
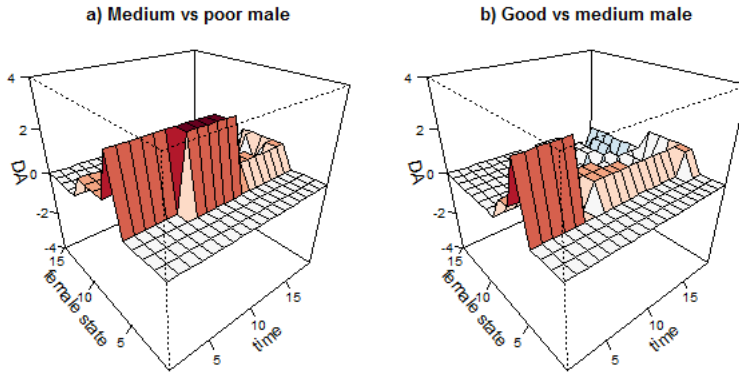

Figure A.20: Optimization results from scenario 1c & 2b, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).
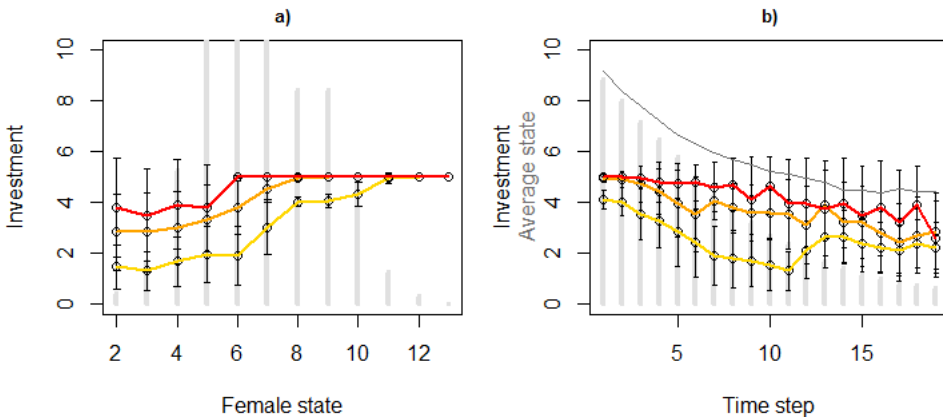
Figure A.21: Forward simulation results from scenario 1c & 2b, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.

1b & 2c
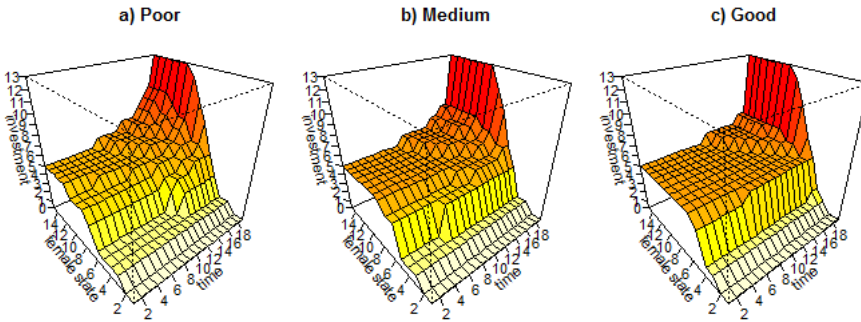
Figure A.22: Optimization results from scenario 1b & 2c, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.

Figure A.23: Optimization results from scenario 1b & 2c, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).

Figure A.24: Forward simulation results from scenario 1b & 2c, showing realized invest-ments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.

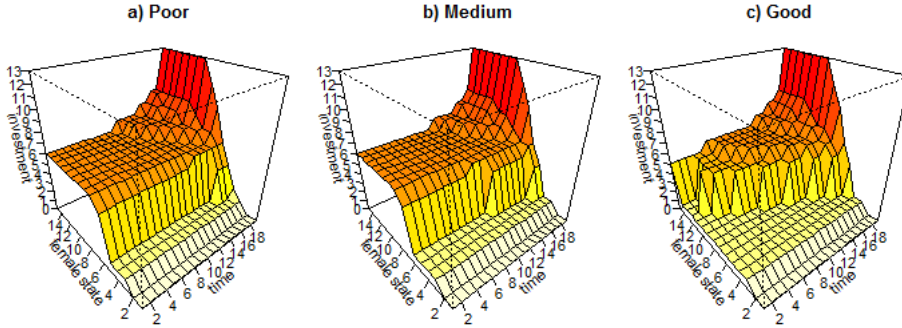## A.3   Reparametrized scenarios

Juvenile survival

Figure A.25: Optimization results from juvenile survival scenario, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.
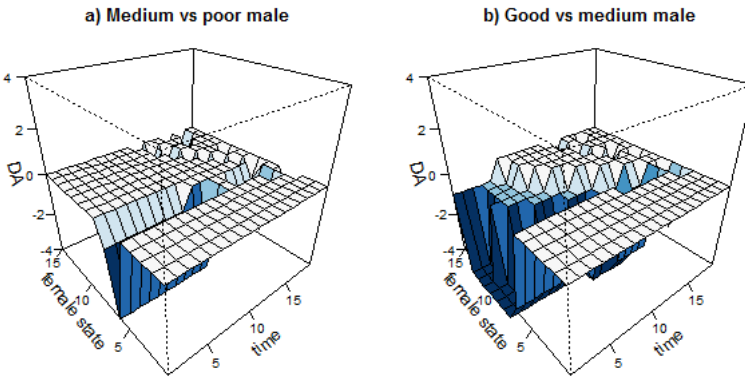

Figure A.26: Optimization results from juvenile survival scenario, showing the direction and magnitude of DA, defined as the difference between $i^*(x, t, 2)$ and $i^*(x, t, 1)$ (a) and $i^*(x, t, 3)$ and $i^*(x, t, 2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).
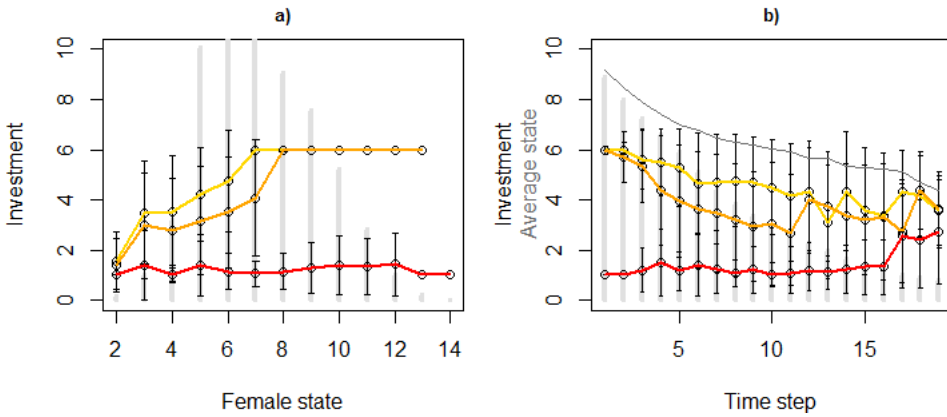
Figure A.27: Forward simulation results from juvenile survival scenario, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.
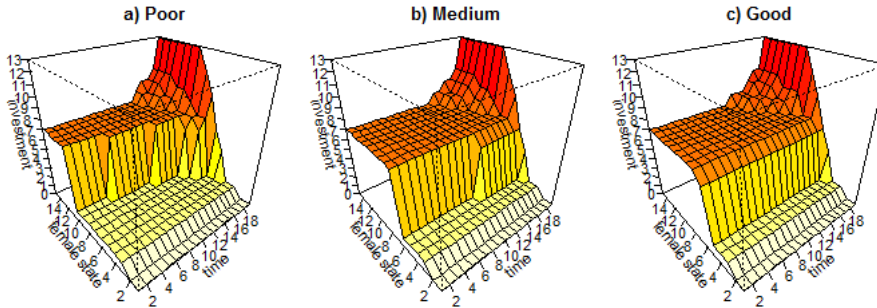
High mating skew

Figure A.28: Optimization results from high mating skew scenario, showing the optimal investment matrices $i^*(x, t, m)$ graphically. a) $m = 1$, b) $m = 2$, c) $m = 3$.
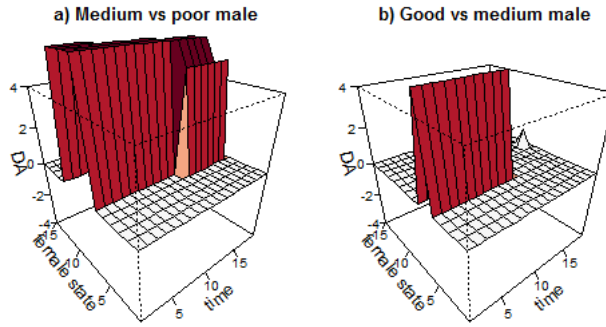
Figure A.29: Optimization results from high mating skew scenario, showing the direction and magnitude of DA, defined as the difference between $i^*(x,t,2)$ and $i^*(x,t,1)$ (a) and $i^*(x,t,3)$ and $i^*(x,t,2)$ (b). Red hues indicate differences greater than 0 (positive DA), blue hues indicate differences smaller than 0 (negative DA).
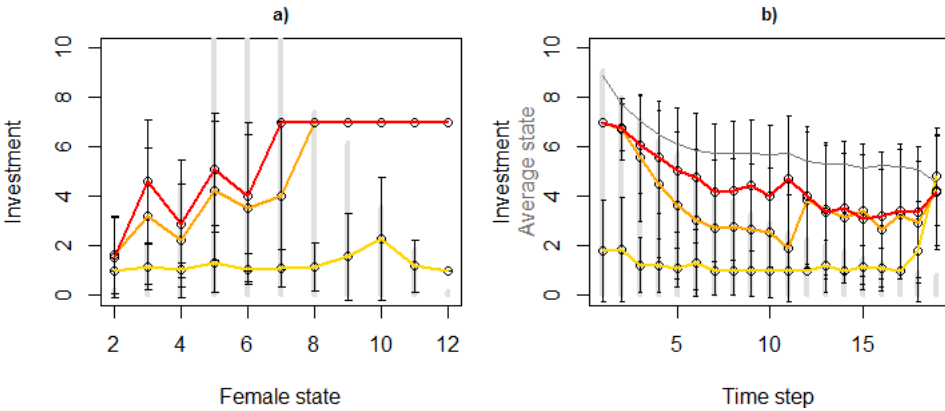

Figure A.30: Forward simulation results from high mating skew scenario, showing realized investments with poor (yellow line), medium (orange line) and good (red line) quality males, for females in different states (a) and different time steps (b). Lines show means for each state or time step, with error bars of 1 standard deviation. Gray bars in the background show how many instances of each mating occurred in 1000 simulations, divided by 100.