

RESEARCH ARTICLE

Can low-quality parents exploit their high-quality partners to gain higher fitness?

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Abstract

An individual's optimal investment in parental care potentially depends on many variables, including its future fitness prospects, the expected costs of providing care and its partner's expected or observed parental behaviour. Previous models suggested that low-quality parents could evolve to exploit their high-quality partners by reducing care, leading to the paradoxical prediction that low-quality parents could have higher fitness than their high-quality partners. However, these studies lacked a complete and consistent life-history model. Here, we challenge this result, developing a consistent analytical model of parental care strategies given individual variation in quality, and checking our results using agent-based simulations. In contrast to previous models, we predict that high-quality individuals always outcompete low-quality individuals in fitness terms. However, care effort may differ between high- and low-quality parents in either direction: low-quality individuals care more than high-quality individuals if their baseline mortality is higher, but less if their mortality increases more steeply with increasing care. We also highlight the ambiguity of the term 'quality' and stress the need for 'genealogical consistency' in evolutionary models.

KEYWORDS

adaptive dynamics, consistency, evolutionary theory, parental care, sexual conflict

1 | INTRODUCTION

Parental care, alongside mating and fertilization, is one of the most intimate interactions between the sexes and provides fertile soil for sexual conflict. Trivers (1972) first identified that parents' fitness interests are not as closely aligned as once thought (see also Arnqvist & Rowe, 2005). This is because the fitness benefits of parental care accrue to both parents, whereas the costs (e.g. via mortality or future fecundity) are typically paid by the individual providing the care. Consequently, except under strict lifelong monogamy, both parents would generally benefit from increased parental effort by their

partners, even when this increased effort reduces the partner's own fitness (Lessells, 2006).

The recognition of conflict between coparents opened the door to game-theoretic studies of parental behaviour (Fromhage et al., 2007; Maynard Smith, 1977; McNamara et al., 2000; Webb et al., 1999; Yamamura & Tsuji, 1993). The predictions of such models are often sensitive to pre-existing differences between coparents, including asymmetries in caring abilities and future fitness prospects (Barta et al., 2002; Kokko & Jennions, 2008; McNamara & Wolf, 2015; Ramsey, 2010). Many such differences are described as (aspects of) individual 'quality'. For example, the perception of

a partner's genetic quality is an important feature in many models in which parents differentially allocate care effort to offspring from different partners (Iwasa & Pomiankowski, 1999; Møller & Thornhill, 1998). Other studies focus on quality in the context of parenting itself, by assuming that it is costlier for a low-quality parent to provide a given level of care than it is for a high-quality parent (Alonzo, 2012; Lessells & McNamara, 2012).

Lessells and McNamara (2012) produced a game-theoretic model in which low- and high-quality individuals are paired with each other. Each parent provides care for the joint offspring over multiple bouts. In each bout, a parent chooses the amount of care they will provide, which may depend on the care their partner provided in the previous bout. The authors concluded that when parental effort differs between coparents, the higher-investing parent will have lower fitness than their partner. They further predicted that high-quality parents should invest more in care than low-quality parents. As a consequence, low-quality parents could exploit the parental effort of their high-quality partners, yielding the surprising result that low-quality individuals had higher fitness than high-quality individuals. This result is restated more explicitly in the recent book by McNamara and Leimar (2020, section 3.4).

This interesting result has yet to receive support from empirical studies of parental care. Surprisingly, many such studies (García-Navas et al., 2012; Mariette et al., 2011; Ringsby et al., 2009; Williams & Fowler, 2015) have found no association between within-pair differences in provisioning rates and fitness measures (but see Santos & Nakagawa, 2012). Experiments with burying beetles (Kilner et al., 2015) showed that high-quality parents paired with low-quality partners subsequently had higher mortality rates than if paired with high-quality partners. However, the mortality rates of low-quality parents were even higher. Kilner et al. (2015) also constructed a theoretical model, which predicts that high-quality parents should have higher fitness than low-quality parents, in contrast to the prediction of Lessells and McNamara (2012).

Here, we further challenge this prediction by developing a consistent model of the evolution of parental care effort in a population with individual variation in quality. Contrary to Lessells and McNamara (2012) and McNamara and Leimar (2020), our model predicts that an individual's fitness correlates positively with their quality as a parent. However, the relationship between quality and care effort may be more complicated.

We begin by introducing the concept of 'consistency' in evolutionary models and highlighting the potential shortcomings of inconsistent models. This will help frame the comparison between our model and that of Lessells and McNamara (2012).

1.1 | Model consistency

The importance of consistency in evolutionary models was recognized relatively late in the development of the field (Houston & McNamara, 2005). Multiple ground-breaking models (e.g., Kokko & Jennions, 2008; Parker et al., 1996) were shown to be inconsistent by subsequent studies (respectively, by Fromhage & Jennions, 2016; Parker & Ball, 2005); even Maynard-Smith was not exempt

(Maynard-Smith 1977, as discussed by Wade & Shuster, 2002). 'Consistency' as a modelling concept has consequently been highlighted in textbooks dedicated to evolutionary game theory and evolutionary dynamics (Kokko, 2007; McNamara & Leimar, 2020). The Fisher condition, in particular, has emerged as an essential check of consistency: the total reproductive output must be equal for both sexes in a population so long as each offspring has a mother and a father (Houston & McNamara, 2005; Jennions & Fromhage, 2017).

The term 'consistent' most frequently refers to embedded life-history games, in which fitness is an emergent property of an explicit life-history model (Figure 1; see also section 9.1 of McNamara

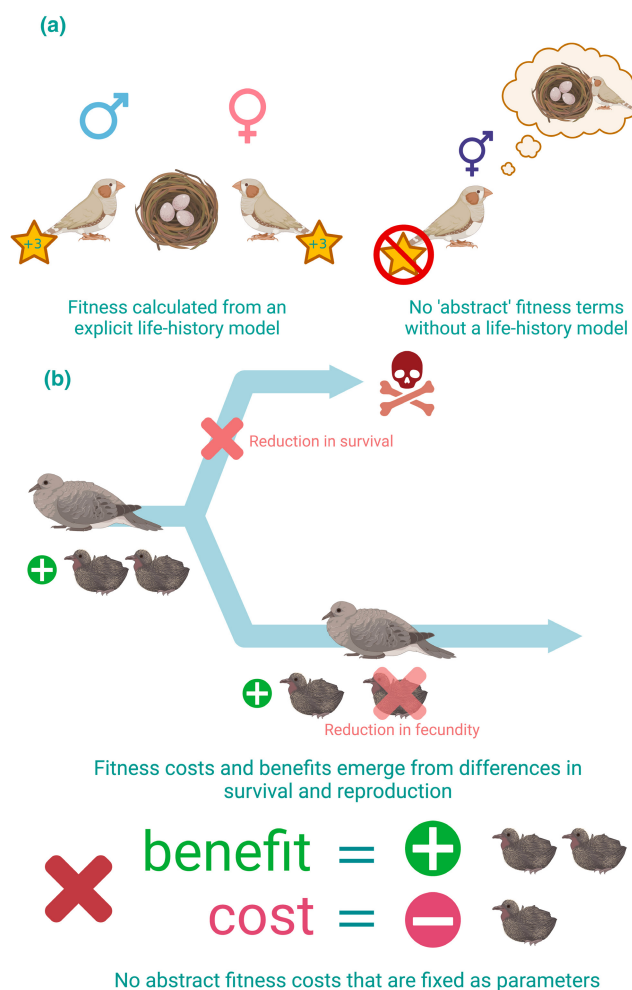


FIGURE 1 (a) Genealogical consistency demands that fitness be calculated from an explicit model of reproduction and mortality over the entire lifespan. In particular, there should be no 'abstract' fitness terms that are not grounded in an explicit life-history model. Fitness should be allocated equally to both biological parents of an offspring to satisfy the Fisher condition. (b) Fitness costs and benefits should similarly emerge naturally from the life-history model. In the upper part of panel b, we see fitness costs emerging via two distinct mechanisms: a reduction in the probability of survival and a reduction in fecundity at a specific time point. Time moves from left to right, as indicated by the blue arrows. Fitness costs and benefits should not be modelled as abstract terms without an underlying life-history model. [Created with BioRender.com]

& Leimar, 2020). In particular, such models are 'genealogically consistent', meaning that any offspring produced can be traced back to a specific reproductive event involving specific parent individuals of the appropriate sexes. Fitness associated with such offspring is attributed to all biological parents, ensuring that the Fisher condition is met. Furthermore, ecological conditions and individual behaviour impact the members of a population in a coherent manner. In short, consistent models represent an internally coherent biology and ecology (hence the alternative term 'self-consistency': see Chapter 7 of Kokko, 2007).

In a consistent model, the fitness costs and benefits of one strategy, relative to another, can be analyzed explicitly in terms of changes in survival and reproduction during specific episodes of an organism's life, rather than being modelled via abstract terms. In particular, fitness benefits and costs cannot simply be added to or subtracted from an abstract 'baseline fitness'. Instead, they must emerge naturally from the life-history model (e.g. due to changes in mortality, mating success or fecundity at specified time points: Figure 1). While the above discussion is framed in terms of individual-level selection, it can be applied equally to models in which alleles are the unit of selection, by replacing 'offspring' with 'allele copies'.

McNamara and Leimar (2020) view consistency as significant but optional. From this perspective, exogenous methods of assigning fitness payoffs (i.e. fitness payoffs that do not arise from a complete model of the organism's life history) result in less complex models that can nonetheless make reliable predictions. One interpretation of this view is that models with exogenous fitness payoffs are useful heuristics that should be considered biologically meaningful until shown otherwise. Given the frequency with which consistent models have overturned the predictions of related inconsistent models, this point of view is not without risk. Despite the additional complexity, we believe that it is essential to base evolutionary models on a detailed life-history account of how fitness arises.

We now outline the parental care model of Lessells and McNamara (2012) before introducing our own model.

2 | ANALYTICAL MODEL

Houston and Davies (1985) outlined a simple model to predict how much parents should invest in caring for their offspring. The fitness benefit of biparental care is shared by both parents and is a function of the sum of parental care efforts by both parents. The cost of care for each parent is a function of its own effort.

Lessells and McNamara (2012) added two new ingredients to the Houston–Davies model: variation in parental quality and the possibility of multiple bouts of care during a single breeding season. Parental quality moderates the costs of providing care: a lower-quality individual suffers higher costs for a given care effort than a higher-quality individual. The introduction of multiple care bouts allows a parent's care strategy to depend on the actions of its coparent in the previous bout. Here, we will consider variation in parental quality but restrict ourselves to the case of a single care bout. We

begin by summarizing the Lessells–McNamara model for the case of a single care bout.

2.1 | The Lessells–McNamara model

Consider a pair of coparents with sexes i and j that invest c_i and c_j , respectively, in caring for their joint offspring. The fitness benefit to each parent arising from these joint offspring is an increasing function $b(c_i + c_j)$ of the sum of their care efforts, while the fitness costs of caring are $k(c_i)$ and $k(c_j)$, respectively. These costs are assumed to offset each parent's *residual* fitness (denoted by v_i and v_j respectively), which is the fitness they would gain in the future if they provided no care for the current brood. The net fitness of parent i is then:

$$w_i = b(c_i + c_j) + v_i - k(c_i) \quad (1)$$

It is important to note that 'residual fitness' v_i in equation (1) is not anchored to any explicit model of a parent's future survival and reproduction (Henshaw, 2021). Instead, it is assumed to be a fixed constant that does not depend on an individual's quality or care strategy. The 'cost' of parental effort is simply subtracted from this residual fitness.

On the surface, this conceptualization seems acceptable. However, by modelling future fitness as a fixed, exogenously determined term, the model fails to account for how this fitness arises, violating genealogical consistency (see Section 1.1 above). Low- and high-quality individuals do not have the same life-history options, and their future fitness may differ. A consistent model, such as the one we provide below, is needed to consider such potential differences.

In particular, we note that this model is Fisher inconsistent, since an individual's future fitness ($v_i - k(c_i)$) is not linked to that of future mating partners. This inconsistency is particularly problematic when paired with another key assumption of Lessells and McNamara (2012): namely that all pairings involve one low-quality and one high-quality individual (which might occur, for instance, if one sex is consistently better at parenting than the other). Suppose, for instance, that low-quality individuals reduce their care effort, thereby increasing their future fitness. By the Fisher condition, this future fitness should be shared with future high-quality partners, but the model has no mechanism to achieve this. As a result, the fitness of high-quality individuals is underestimated in this scenario.

2.2 | Outline of our analytical model

We now construct a genealogically consistent model based on those of Houston and Davies (1985) and Lessells and McNamara (2012). We will use this model to derive the evolutionarily stable care strategies of high- and low-quality individuals engaged in biparental care, as well as their resulting fitness. For simplicity, we assume that only

one bout of care occurs and there is no negotiation between parents about the amount of care provided (i.e. this is a 'sealed bid' model: Houston & McNamara, 2005). We also assume that an individual's care strategy can depend on its own quality, but not on the quality of its partner (but we relax this assumption later). Nonetheless, on an evolutionary timescale, the optimal care strategy for an individual of a given quality may depend on the care strategies of its potential mating partners. It is assumed that males and females do not differ in their care strategies.

In our model, overlapping generations of individuals reproduce in a series of discrete breeding seasons. In each breeding season, individuals are paired at random. As in the earlier models, the expected number of a pair's joint viable offspring is an increasing function of the sum of their care efforts. In particular, the benefit associated with higher effort in care is a saturating function: as care effort increases, the marginal benefit of increasing care diminishes. Parents either die after caring or remain alive for the next breeding season. Increasing effort in care reduces the probability that the carer survives. The absolute fitness of an individual is given by the sum of all offspring it produces in its lifetime. The surviving offspring mature to breed in the next breeding season. Quality is determined environmentally, with each individual assigned at random to one of two quality levels: 'low-quality' or 'high-quality'. The quality of an individual influences its probability of dying after each breeding season, such that low-quality individuals have higher mortality than high-quality individuals for the same individual care effort. An individual's quality is fixed and does not change over the individual's lifetime.

We use adaptive dynamics to determine the evolutionarily stable care effort of high- and low-quality individuals. To do this, we consider a population where all residents use the strategy (c_H, c_L) . We then introduce a rare mutant using strategy (\hat{c}_H, \hat{c}_L) into the population and calculate its fitness.

2.3 | Mortality as a function of individual care effort

We write $m_H(c)$ and $m_L(c)$ for the probability that a high- or low-quality individual, respectively, dies after investing c in care in the previous breeding season. An individual's probability of mortality $m_Q(c_Q)$ depends both on its quality $Q \in \{H, L\}$ and also in a quality-dependent manner on its care strategy c_Q . We write this as follows:

$$m_Q(c_Q) = m_{\text{base},Q} + m_{\text{care},Q}(c_Q) \quad (2)$$

The baseline mortality $m_{\text{base},Q}$ represents the probability that an individual of quality Q dies after providing no care in the current breeding season. Thus, this parameter represents mortality due to causes unrelated to parental care. The care-induced mortality $m_{\text{care},Q}(c_Q)$ is an increasing function of care provided c_Q such that $m_{\text{care},Q}(0) = 0$. By increasing care effort, an individual thus reduces its chances of surviving to the next breeding season.

We allow the mortality functions of high- and low-quality individuals to differ in two ways. First, low-quality individuals may have higher baseline mortality (i.e. $m_{\text{base},L} > m_{\text{base},H}$). Second, mortality may increase more steeply with increasing care for low-quality individuals than for high-quality individuals (i.e. $\frac{d}{dc} m_{\text{care},L}(c) > \frac{d}{dc} m_{\text{care},H}(c)$). For our model, we used the function $m_{\text{care},Q}(c) = g_Q c^2$ where g_Q is a quality-dependent constant such that $g_H < g_L$.

2.4 | Demographic equilibrium

Suppose the population is of size N and consists of N_H high-quality individuals and N_L low-quality individuals. The expected number of deaths after each breeding season is then:

$$M_{\text{total}} = N_H m_H(c_H) + N_L m_L(c_L) \quad (3)$$

We assume that each deceased individual is replaced by a recruit from among the offspring of the previous breeding season, such that the size of the population remains constant. We write p_H for the proportion of high-quality new recruits (a fixed parameter). At demographic equilibrium for large N , the number of deaths of high-quality individuals must be equal to the number of new high-quality recruits:

$$p_H M_{\text{total}} = N_H m_H(c_H) \quad (4)$$

Solving this equation simultaneously with the constraint that $N_H + N_L = N$ yields:

$$N_H = \left(\frac{p_H m_L(c_L)}{p_H m_L(c_L) + (1 - p_H) m_H(c_H)} \right) N \quad (5.1)$$

$$N_L = \left(\frac{(1 - p_H) m_H(c_H)}{p_H m_L(c_L) + (1 - p_H) m_H(c_H)} \right) N \quad (5.2)$$

These equations represent the structure of the population at demographic equilibrium when the resident strategies are c_H and c_L .

2.5 | Offspring survival as a function of joint care effort

We write $b(c_{Q_1}; c_{Q_2})$ for the fitness benefit gained by the coparents via their shared progeny, where c_{Q_1} and c_{Q_2} are the quality-dependent care strategies adopted by each parent. This benefit is assumed to be proportional to a sigmoidal function of the total care:

$$b(c_{Q_1}; c_{Q_2}) \propto \exp\left(\frac{-1}{c_{Q_1} + c_{Q_2}}\right) \quad (6)$$

The constant of proportionality may differ over time to ensure that mean relative fitness always equals one. However, for the

adaptive-dynamics approach, it is only necessary to compare fitness between rare mutants and residents at demographic equilibrium and so we can ignore the constant of proportionality. Note that, in what follows, two care variables separated by a comma will always represent the two inherited care strategies of a single individual (i.e. one for each quality level). Care variables separated by a semi-colon, on the contrary, denote the care strategies played by each parent in a pair.

2.6 | Determining evolutionarily stable strategies

Consider a mutant individual (which can be either high or low quality) that pairs up with high-quality individuals and low-quality individuals with probabilities equal to their respective frequencies in the population (i.e. we assume that parental quality is not visible to potential mates and there is no mate choice for quality). Pairings with low-quality and high-quality partners bring about different fitness benefits. Hence, the expected fitness gain to a mutant in a single breeding season is the sum of the two conditional expectations given each partner quality, weighted by their respective probabilities. Denoting the care strategy of a mutant with quality $Q \in \{H, L\}$ by \hat{c}_Q , the fitness gains of low- and high-quality mutants from a single breeding season are given respectively by:

$$w_L(\hat{c}_L) = \frac{N_H}{N} b(\hat{c}_L; c_H) + \frac{N_L}{N} b(\hat{c}_L; c_L) \quad (7.1)$$

and

$$w_H(\hat{c}_H) = \frac{N_H}{N} b(\hat{c}_H; c_H) + \frac{N_L}{N} b(\hat{c}_H; c_L) \quad (7.2)$$

These equations represent the expected fitness gain to mutants in each breeding season that they are alive to participate in.

After any given breeding season, the probability that a mutant survives is given by $1 - m_Q(\hat{c}_Q)$. The total fitness of a mutant with quality Q is therefore given by the geometric series:

$$W_Q(\hat{c}_Q) = w_Q(\hat{c}_Q) + (1 - m_Q(\hat{c}_Q))w_Q(\hat{c}_Q) + (1 - m_Q(\hat{c}_Q))^2 w_Q(\hat{c}_Q) + \dots = \frac{w_Q(\hat{c}_Q)}{m_Q(\hat{c}_Q)} \quad (8)$$

Weighted by the probabilities of the mutant being high or low quality, the expected fitness of a mutant with strategies (\hat{c}_H, \hat{c}_L) is then:

$$W(\hat{c}_H, \hat{c}_L) = p_H W_H(\hat{c}_H) + (1 - p_H) W_L(\hat{c}_L) \quad (9)$$

Selection gradients on the care strategies of high- and low-quality mutants are given by:

$$s_H = \left. \frac{\partial W(\hat{c}_H, \hat{c}_L)}{\partial \hat{c}_H} \right|_{\hat{c}_H=c_H, \hat{c}_L=c_L} \quad (10.1)$$

and

$$s_L = \left. \frac{\partial W(\hat{c}_H, \hat{c}_L)}{\partial \hat{c}_L} \right|_{\hat{c}_H=c_H, \hat{c}_L=c_L} \quad (10.2)$$

We calculated evolutionarily stable strategies (ESS) for care effort given fixed parameter values by solving the following simultaneous equation numerically using Wolfram Mathematica:

$$s_H = s_L = 0 \quad (11)$$

In addition to the base analytical model, we also constructed a modified model in which an individual can perceive its partner's quality after choosing a mate but before deciding how much care to provide. Individuals can consequently base their care effort on both their own and their partner's quality in this modified model (see Appendix S1 for methods and corresponding simulation results; analytical results of the modified model are presented in the main text below).

3 | SIMULATION MODEL

To check the results of the base analytical model, we performed individual-based simulations with a similar structure. We simulated a population of individuals with overlapping generations. Each individual was randomly assigned a quality (high or low) at birth. Each individual carried genes for two traits: care effort when high-quality and care effort when low-quality. Our simulation consisted of a series of 'breeding seasons' with the following structure:

1. Individuals are paired randomly. Each individual can only be paired once in a breeding season.
2. Each pair produces offspring, with the total fitness value of offspring determined by the total care they receive from both parents.
3. Some individuals die. An individual's probability of mortality is a function of both its quality and the care it provided in the current breeding season (high-quality individuals have lower death rates than low-quality individuals for the same amount of care provided).
4. Dead individuals are replaced with new recruits chosen from among the offspring of the current breeding season. Offspring of a given pair are chosen with probability proportional to their total fitness value from step 2.

For simplicity, we simulated a population with sexual reproduction but no sexes (i.e. any individual can breed with any other). A population with sexes but without sexual dimorphism (as in the analytical model above) would behave similarly. As in the analytical model, we assume that parental care is provided in a single bout, with no room for behavioral updates to the caring strategy. Furthermore, parents are unaware of the care strategies of their

coparents. Parental mortality and offspring fitness were calculated using the same functions as the analytical model above.

3.1 | Genetics of care strategies

For simplicity, we assume a haploid genetic system. Each care strategy is determined by a single allele represented by a positive real number (a 'continuum of alleles' model). Although each individual carries genes for both quality-dependent care strategies, only the strategy corresponding to an individual's own quality is expressed. Initially, each individual's alleles are chosen randomly from a normal distribution with mean μ_{initial} and standard deviation σ_{initial} .

New recruits inherit alleles for each care strategy (c_L and c_H) from their mother or father with equal probability. Inheritance at each locus is assumed independent (i.e. recombination is perfect). With a probability of π_{mut} per allele per generation, alleles were subject to small random mutations, simulated by adding a random number chosen from a normal distribution (with mean 0 and variance σ_{mut}) to the current allele value.

4 | RESULTS

We studied how mortality differences between high- and low-quality individuals impacted the ESS care efforts and the average fitness at equilibrium for individuals of both quality levels. Lessells and McNamara (2012) define 'quality' in terms of differences in mortality; hence, the mortality of high-quality individuals will necessarily be lower than that of low-quality individuals for a given care effort. To explore the impact of mortality differences on quality-specific care effort and fitness, we varied the mortality parameters for low-quality individuals while keeping the values for high-quality individuals constant.

The plots in the left column of Figure 2 show the equilibrium care effort for individuals of each quality level against variation in (i) g_L , which determines how steeply the mortality of low-quality individuals increases with their parental effort (Figure 2a), or (ii) the baseline mortality $m_{\text{base},L}$ of low-quality individuals (Figure 2b,c). The plots in the right column show the mean lifetime fitness of individuals of each quality level for the same scenarios.

Predicted care efforts in the analytical model and the simulations were in close agreement, with minor deviations attributed to stochastic effects due to random choice of surviving offspring.

4.1 | Higher quality always means higher fitness

The results of both the analytical model and the simulations indicate that high-quality parents always had higher mean fitness than low-quality parents. This was true regardless of whether high- and low-quality individuals differed in baseline or care-induced mortality

(or both) and regardless of which quality level invested more heavily in offspring (see below). Similarly, when an individual's care effort could depend on its partner's quality in addition to its own, the fitness of high-quality individuals consistently exceeded that of low-quality individuals (Figure 3b,d,f).

4.2 | Care effort varies predictably across different scenarios

High-quality parents invested relatively more in care when care-induced (but not baseline) mortality differed between quality levels. This result is intuitive: when increasing care was costlier for low-quality than for high-quality individuals, low-quality individuals evolved to invest less in care.

In contrast, when baseline (but not care-induced) mortality was higher for low-quality individuals, these individuals cared more than high-quality individuals (Figure 2b). This is because, with a higher probability of dying before the next breeding season, it is beneficial to invest more in caring for current offspring (i.e. terminal investment: Clutton-Brock, 1984). Increases in care-induced mortality led to higher care effort for lower-quality individuals, regardless of whether baseline mortality was equal for both quality types (Figure 2b) or higher in low-quality individuals (Figure 2c).

Qualitatively similar results were obtained when care effort could depend on both individual and partner quality (Figure 3a,c,e). Low-quality individuals invested less in care than high-quality individuals when their care-induced mortality was higher (Figure 3a), whereas elevated baseline mortality caused low-quality individuals to provide more care (Figure 3c), as in the base model. Individuals additionally adjusted their care effort to partially offset variation in the expected effort of their partner. Thus, for parameter settings where high-quality individuals provided more care, individuals of both quality levels provided less care when partnered with a high-quality than with a low-quality individual (Figure 3a,e). Conversely, when high-quality individuals cared less, their partners increased care effort relative to pairings with low-quality partners (Figure 3c,e).

5 | DISCUSSION

We constructed adaptive-dynamics models and an agent-based simulation to study the evolutionarily stable parental care strategies of low- and high-quality parents. In our models, quality is constructed as a binary trait rather than a continuum and is environmentally fixed at birth. Contrary to the results of Lessells and McNamara (2012) and McNamara and Leimar (2020), our models predict that high-quality parents consistently outperform low-quality parents in fitness terms. Evolutionarily stable care effort may differ between high- and low-quality parents in either direction: low-quality individuals care more than high-quality individuals if their baseline mortality is higher, but less if their mortality increases more steeply with increasing care.

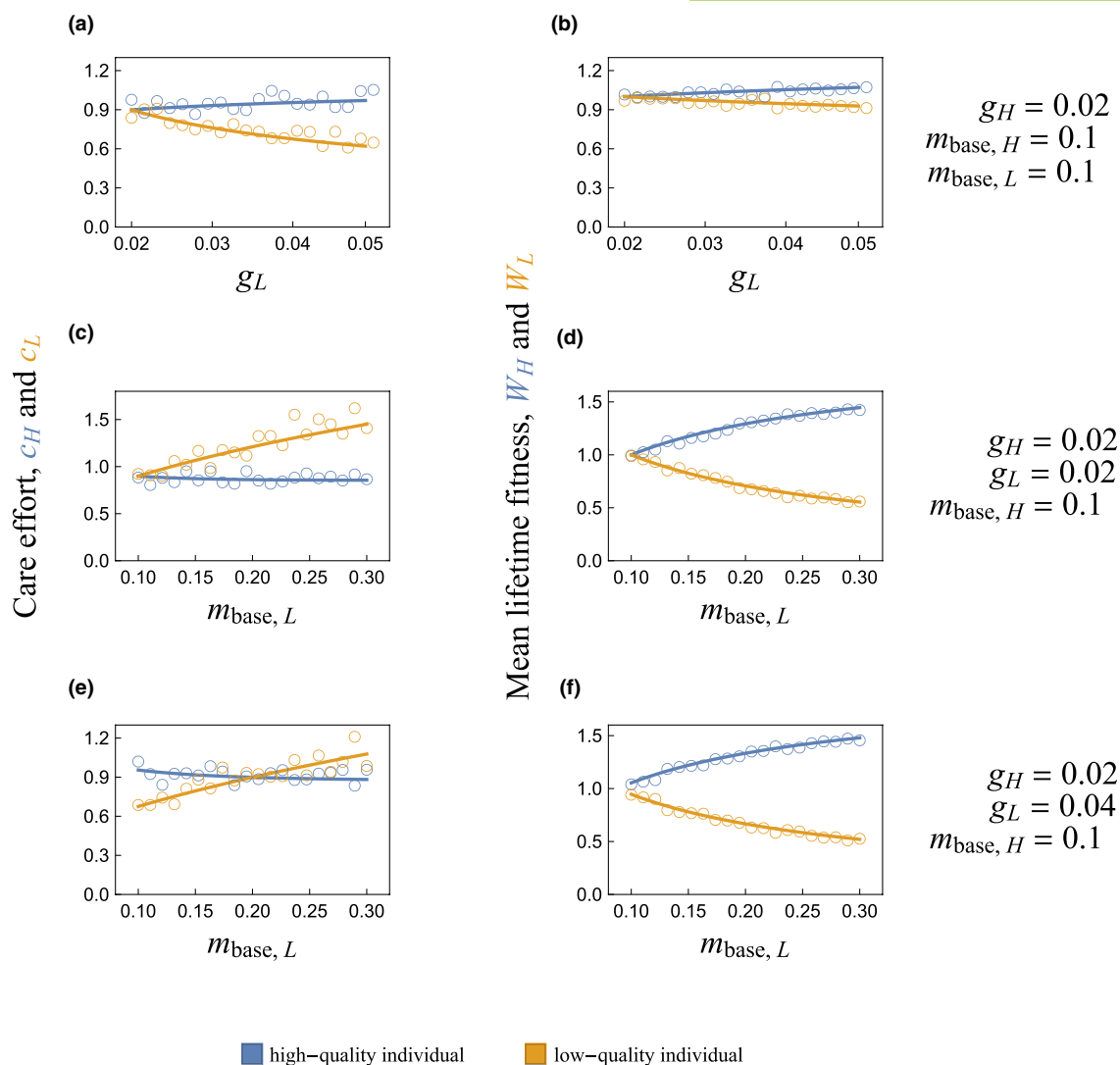


FIGURE 2 Evolutionarily stable care strategies and lifetime fitness for low- and high-quality individuals, based on the base analytical model (solid lines) and simulations (circles). $m_{\text{base},Q}$ represents the baseline mortality of an individual with quality $Q \in \{H, L\}$ (H: high-quality, L: low-quality), whereas g_Q represents how steeply such an individual's mortality increases with its care effort (see figure panels for values). Blue/orange lines and circles indicate the care effort (panels a, c and e) and mean lifetime fitness (panels b, d and f) of high/low-quality individuals, respectively. Each circle represents the mean fitness and care effort of the last 1000 individuals of that quality that died before the simulation run was terminated. A proportion $p_H = 0.5$ of new recruits was assigned to be high-quality. In the simulations, a population of 1000 individuals evolved for 100000 breeding seasons. Individual care effort strategies for both quality levels were chosen initially from a normal distribution with $\mu_{\text{initial}} = 1$ and $\sigma_{\text{initial}} = 0.05$. Mutations occurred with a probability of $\pi_{\text{mut}} = 0.1$ per allele per generation and mutational effects had a standard deviation of $\sigma_{\text{mut}} = 0.05$.

5.1 | The ambiguity of 'quality'

The concept of individual 'quality' is frequently invoked in evolutionary biology, but its exact meaning and implications vary considerably between authors. 'Quality' may be considered in the context of particular traits (e.g. parenting ability, as here) or it may be closely linked to fitness itself (as in 'good genes' models of sexual selection, where 'quality' often represents breeding values for fitness or fitness components: Henshaw et al., 2022). The sources of individual variation in quality may be environmental, genetic or both. This plurality in meaning can make it challenging to compare hypotheses and models that differ in their conception of 'quality'.

Wilson and Nussey (2010) address the ambiguity of the term 'individual quality' and propose several definitions. One of their definitions is that quality is an axis of phenotypic heterogeneity that is positively correlated with fitness. Under this definition, 'high-quality' individuals are fitter on average by definition. This definition of quality is inconsistent with the results of Lessells and McNamara (2012), who predict that low-quality individuals have higher fitness than high-quality individuals. Indeed, from the perspective of Wilson and Nussey (2010), high caring ability would correspond to low rather than high quality in the Lessells–McNamara model. Regardless of how we describe variation in caring ability, the prediction of Lessells and McNamara (2012) is surprising, but, we

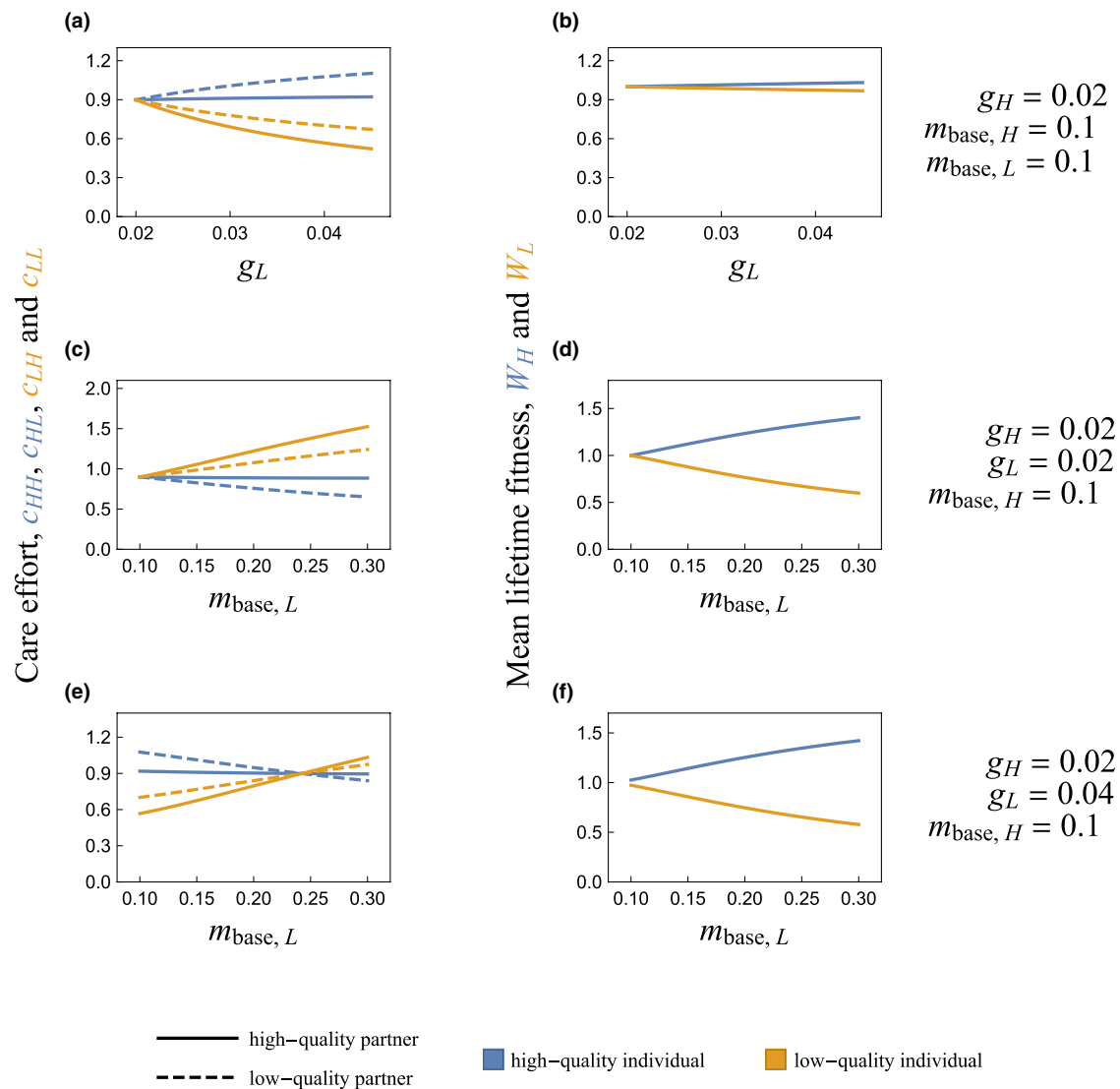


FIGURE 3 Evolutionarily stable care strategies and lifetime fitness for low- and high-quality individuals when an individual's care effort can depend on both its own quality and the quality of its partner (see Appendix S1 for model details and simulation results). Blue/orange lines indicate the care effort (panels a, c, e) and mean lifetime fitness (panels b, d, f) of high/low-quality individuals, respectively. Solid/dashed lines indicate the care effort of individuals with high/low-quality partners, respectively (panels a, c, e). $m_{base, Q}$ represents the baseline mortality of an individual with quality $Q \in \{H, L\}$, whereas g_Q represents how steeply such an individual's mortality increases with its care effort (see figure panel for values). A proportion $p_H = 0.5$ of new recruits was assigned to be high-quality.

hope to have shown here, results from an artefact of the model construction (see Section 2.1 above).

5.2 | Variation in parental quality within and between the sexes

In our model, the sexes are assumed alike in their distribution of parental quality. In the absence of mate choice for quality, this means that all individuals pair with partners of low- or high-quality in proportion to their population frequencies. If the sexes differ consistently in parental quality, however, then low-quality parents (of one sex) might routinely pair with high-quality parents (of the other) (cf.

McNamara & Wolf, 2015). In this case, the Fisher condition tightly constrains fitness differences between high- and low-quality individuals, as the total fitness of males and females must be equal (see Section 2.1 above).

5.3 | Mate assessment and signals of quality

Both our models also assume that potential partners cannot gauge an individual's parental quality in advance. If, on the contrary, there are reliable cues of parental quality, then we might expect assortative mating for quality in systems with biparental care (Johnstone, 1997). The fitness of high-quality individuals might

then exceed that of low-quality individuals by a greater margin than is predicted by our model. Individuals might also try to manipulate their own quality cues to influence the mate-choice behaviour of potential mates.

In our second model, we considered ESS care effort when individuals can adjust their care effort based on their partner's quality (Figure 3; methods in Appendix S1). Intriguingly, both high- and low-quality individuals can elicit increased care effort from their partners under some circumstances, which depend on the relationship between parental quality and mortality. When individuals evolve to reduce care in response to cues of high partner quality (see Figure 3a), we might expect that high-quality individuals should attempt to mask their quality from their partners. However, such deception can be expected only in the absence of assortative mating on the basis of quality, since assortative mating should select for high-quality individuals to reveal their quality. Moreover, widespread deception will reduce the reliability of quality cues, potentially selecting for care strategies that disregard such cues entirely. Similar considerations apply when cues of low-quality partners elicit reduced care, except that it may be more difficult for low-quality individuals to appear high-quality than vice versa. These dynamics become more complex still if care is modelled in bouts as in the Lessells–McNamara model. Further modelling would be necessary to understand the delicate coevolutionary interplay between quality, signals of quality and parental investment.

Future empirical work could attempt to manipulate cues of quality independently of quality itself (e.g. by manipulating apparent body size or providing supplementary food during periods of courtship feeding but not during parental investment). Furthermore, it would be interesting to disentangle selection acting on cues of quality into components arising via assortative mating, differential parental investment by partners and parental quality itself (e.g. using a causal approach: Henshaw et al., 2020).

AUTHOR CONTRIBUTIONS

Kartikey Awasthi: Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); software (equal); visualization (equal); writing – original draft (lead). **Jonathan Henshaw:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); supervision (lead); visualization (equal); writing – review and editing (lead).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/jeb.14174>.

DATA AVAILABILITY STATEMENT

The simulation code used for the two models is available on Zenodo at <https://doi.org/10.5281/zenodo.7757254>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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