Evolution and Human Behavior 34 (2013) 405–411

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

The evolution of parent–offspring conflict over mate choice

Pieter van den Berg [a,b], Tim W. Fawcett [a,b,c], Abraham P. Buunk [b,d], Franz J. Weissing [a,*]

[a] Theoretical Biology Group, University of Groningen, 9747 AG Groningen, the Netherlands
[b] Evolutionary Social Psychology Group, University of Groningen, 9747 AG Groningen, the Netherlands
[c] Modelling Animal Decisions Group, University of Bristol, United Kingdom
[d] Royal Netherlands Academy of Arts and Sciences, the Netherlands

ARTICLE INFO

Article history:
Initial receipt 23 May 2013
Final revision received 30 July 2013

Keywords:
Intergenerational conflict
Sexual selection
Parental resource distribution
Theoretical model
Direct versus indirect benefits
Mate preference evolution
Arranged marriage
Good parent

ABSTRACT

In human societies, parents often have a strong influence on the mate choice of their offspring. Moreover, empirical studies show that conflict over mate choice between parents and offspring is widespread across human cultures. Here we provide the first theoretical investigation into this conflict, showing that it may result from an underlying evolutionary conflict over parental resource distribution. We present a series of evolutionary simulations in which we gradually expand a standard model of sexual selection by the stepwise addition of elements of parental involvement. In our model, females obtain resources enhancing their fecundity from both their chosen mate and their parents. Potential mates differ in their ability to provide resources and may signal this ability. Both females and their parents can develop a preference for the signal, with both preferences influencing the realized mate choice of the female. Parents may differentially allocate resources among their daughters depending on the resource-provisioning abilities of their sons-in-law. When fecundity returns on investment are diminishing, we find that parents invest most in daughters whose mates provide few resources. Subsequently, the daughters evolve to exploit this allocation rule through their mate choice, which is not in the parents' best interests. This results in a conflict over mate choice between parents and their offspring, manifested as an on-going divergence of offspring and parental preferences. We predict that the conflict should be most pronounced when fathers, as opposed to mothers, control resource allocation.

1. Introduction

Existing models of sexual selection focus on the coevolution of an exaggerated trait in one sex and a preference for that trait in the other sex (Andersson, 1994; Kokko, Jennions, & Brooks, 2006; Kuijper, Pen, & Weissing, 2012). These models assume that mate choice is influenced only by the choosing individuals and their prospective partners. Although this approach may be instructive for most organisms, it disregards the involvement of parents in their offspring's mating decisions—a salient feature of mate choice in humans (Apostolou, 2007a).

Parental influence on mate choice is commonly observed across human cultures (Minturn, Grosse, & Haider, 1969; Apostolou, 2007a). The degree of parental influence varies strongly between cultures (Apostolou, 2010a,b), from limited influence in much of Western Europe to almost complete influence in some Hindu and Islamic societies, and, in general, in collectivistic societies (Buunk, Park, & Duncan, 2010). For instance, near the end of the 20th century, about half of the marriages of Indian immigrants in the United States were arranged by the married couple's parents (Menon, 1989). Among present-day hunter–gatherer societies, there is some degree of parental influence on mate choice in 96% of 190 investigated societies (Apostolou, 2007a). Overall, evidence suggests that parental involvement in offspring mating decisions is the norm, rather than the exception, across cultures and throughout history (Apostolou, 2010a, b, 2012; Buunk et al., 2010). This suggests that parental influence on mate choice probably played an important role in the human ancestral environment, and may therefore have been an important force in the course of human evolution.

Parental influence on mate choice would be of little consequence if parental and offspring preferences were in complete agreement. However, recent research has revealed considerable conflict between parents and offspring over the latter's choice of a partner. Specifically, parents show a stronger preference than their offspring for attributes such as social class, family background, ethnic background and educational level, whereas offspring show a stronger preference than their parents for qualities such as physical attractiveness, smell, sense of humor and creativity (Apostolou, 2008a,b, 2011; Buunk, Park, & Dubbs, 2008; Dubbs & Buunk, 2010; Perilloux, Fleischman, & Buss, 2011). These results hold across a number of different sample groups, including Dutch and American students, as well as Kurdish people and young Argentinean people (Buunk & Castro Solano, 2010), and are found both when parents and offspring are questioned (Dubbs & Buunk, 2010). Evidence suggests that it is more often fathers than mothers that exercise influence over mate choice, and that daughters are more strongly influenced than sons (Apostolou, 2007a, 2010a, 2012).

---

* Corresponding author. Tel.: +31 50 363 2131.
E-mail address: f.j.weissing@rug.nl (F.J. Weissing).

1090-5138/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.evolhumbehav.2013.07.004

In his famous paper on parent–offspring conflict, Trivers (1974) already alluded to the possibility of a parent–offspring conflict over mate choice. Although the evolutionary interests of parents and offspring overlap to a great extent, they do not coincide. Several authors (Apostolou, 2007a, 2008a,b, 2011, 2012; Buunk et al., 2008; Perilloux et al., 2011) have suggested that parent–offspring conflict over mate choice is a consequence of differences in genetic relatedness to the grandoffspring. Because of the diluting effect of meiosis, a human being (like any other diploid, sexually reproducing organism) is twice as closely related to its child (relatedness coefficient $r = 0.5$) as to its grandchild ($r = 0.25$). This difference in genetic relatedness, it has been argued, implies that traits indicating genetic quality should be more highly valued in a spouse than in a son- or daughter-in-law (Apostolou, 2007a, 2008a,b, 2011, 2012).

Although this verbal argument is intuitively appealing, we doubt whether the difference in genetic relatedness is sufficient to explain parent–offspring conflict over mate choice. The relatedness difference means that non-heritable quality is also more important in a spouse than in a son- or daughter-in-law, so on this basis alone there is no reason why parents and offspring would differ in their preferences. The situation might change, however, if offspring compete for access to parental resources. Parents are equally related to all their offspring, but offspring are more related to themselves than to their siblings. As Trivers (1974) recognized, this leads to a fundamental evolutionary conflict, in which offspring are expected to prioritize their own reproductive success over that of their siblings. Offspring should try to secure more parental resources for themselves than for their siblings, whereas parents should favor a more equal distribution.

We hypothesize that the parent–offspring conflict over mate choice is rooted in this parent–offspring conflict over resource distribution. In humans, parents continue to invest resources in their descendent kin long after they have stopped reproducing (Hawkes, O'Connell, Jones, Alvarez, & Charnov, 1998; Sear, Mace, & McGregor, 2000; Lahdenpera, Lummaa, Helle, Tremblay, & Russell, 2004), often beyond the point at which their offspring are sexually mature (Coall & Hertwig, 2010). Thus the intergenerational conflict over resources may impact on various aspects of adult behavior, including mate choice.

We explain the basic logic of this idea by considering a simple scenario, in which a female can receive resources both from her parents and from her chosen mate, and the total amount of resources she receives determines her fecundity. For clarity, we refer hereafter to the female who is choosing a mate as the focal female. The focal female may also be referred to as a daughter, and she and her siblings may be referred to as offspring. The parents of the focal female will be referred to as the parents, and her offspring will be referred to as the grandoffspring.

We assume that males vary in their provisioning ability, in terms of the amount of resources they provide to their mate. If parents have more than one mated daughter, these daughters may differ in the amount of resources they receive from their mates. In that case, depending on the specific relationship between resources and fecundity, it may pay parents to distribute their resources unequally between their daughters (Whyte, 1978). This, in turn, provides an incentive for the daughters to adjust their mate preferences in an attempt to exploit the investment patterns of their parents. The daughters' mate choice may then be suboptimal from the parents' point of view—creating an evolutionary conflict between parents and offspring over mate choice.

To investigate this formally, we built an individual-based model of sexual selection that incorporates the possibility for parents to influence the mate choice of their offspring. To the best of our knowledge, this is the first theoretical study to consider the direct involvement of parents in the mate-choice process (but see Welbergen and Quader (2006) for a model of mate choice influenced by the chooser's offspring). To explore how this might influence the coevolution of male traits and female preferences, we built up our model in four steps, gradually adding different components of parental involvement. We took as our starting point the "good parent" model of sexual selection (Iwasa & Pomiankowski, 1999), which is closely related to the more familiar "good genes" models of sexual selection (Zahavi, 1975; Grafen, 1990a; Grafen, 1990b; Iwasa, Pomiankowski, & Nee, 1991). In good-parent models of sexual selection, males vary in the direct fitness benefits they provide to their mates. Males signal the amount of resources they can provide (their provisioning ability) using a costly, condition-dependent indicator trait. Females express varying degrees of (costly) preference for this trait; those with stronger preferences tend to mate with males showing greater trait expression. In this first step of our model, the focal female's parents have no influence on her mate choice.

In the second step, we incorporate a parental preference for the potential mate of the focal female (i.e. for their son-in-law). Parents are still assumed not to invest any resources, however, so the parental preference for the potential mate of the focal female should coincide with the focal female's own preference. That is, we expect no conflict between parents and daughters over mate choice.

In the third step, we allow parents to invest resources in their daughters, but impose a fixed pattern of resource allocation. We investigate three allocation patterns: (a) parents invest equally in all daughters (equal allocation); (b) parents invest more in daughters that receive fewer resources from their mate (compensatory allocation); and (c) parents invest more in daughters that receive more resources from their mate (augmenting allocation). Under equal allocation (a), similar to the situation with no parental investment, we expect no conflict over mate choice. Under compensatory allocation (b), daughters with a weaker preference than their sisters will tend to choose mates who invest less, and as a result will receive relatively more resources from their parents. Therefore, we expect that female preference will decrease over evolutionary time to "exploit" the investment pattern of their parents. Parents, in turn, should be selected to counteract the reduced preference of their daughters by strengthening their parental preference, resulting in parent–offspring conflict over mate choice. Under augmenting allocation (c), we expect females to exploit parental investment patterns in the opposite direction, by increasing their preference for males who invest heavily. This should be counteracted by a reduction in the parental preference, again leading to parent–offspring conflict over mate choice.

In the fourth and final step, we allow the parental resource-allocation strategy to evolve. We assume that fecundity returns on investment are diminishing (for alternative functions, see Supplementary Information, available on the journal's Web site at www.ehbonline.org). Under these conditions, parents maximize the total fecundity of their daughters by using a compensatory allocation strategy, giving more resources to daughters with low-investing partners (Fawcett, Van den Berg, Weissing, Park, & Buunk, 2010). Therefore, as in the fixed pattern of compensatory allocation imposed in (b) above, we expect daughters to develop weaker preferences for males who invest heavily, resulting in parent–offspring conflict over mate choice.

The logic of our hypothesis would also apply to male mate preferences, where parents allocate resources to their sons and influence his choice of a female partner (i.e. their daughter-in-law), but we do not investigate this scenario here.

2. The model

We created a model with discrete and overlapping generations, with two generations present in the population at any one time, hereafter referred to as the "parent generation" and the "offspring generation." Each individual in the offspring generation experiences the following sequence of events: fitness costs of trait or preference expression, mate choice, investment of resources in reproduction and finally reproduction itself. Individuals in the parent generation experience the following sequence of events: exerting influence on their offspring's mate choice, investment of resources in their offspring's reproduction, and finally death. The offspring generation then becomes the parent generation and the newly created generation becomes the offspring generation, before the cycle repeats. For simplicity, we assume that only one of the parents influences the mate choice of their offspring and distributes resources among them. This allows us to explore how the pattern of conflict depends on whether the father or the mother is in control.

All individuals carry diploid loci coding for the following traits: preference for the indicator trait in their own mate p (hereafter referred to as “female preference”; expressed only in females in the offspring generation), preference for the indicator trait in their daughter's mate q (hereafter referred to as “parental preference”; expressed only in the controlling sex in the parent generation), male provisioning ability r_m (expressed only in males in the offspring generation), male indicator trait t (expressed only in males in the offspring generation) and resource-allocation strategy among daughters α (expressed only in the controlling sex in the parent generation). There is independent Mendelian inheritance at all loci and complete additivity within all loci.

2.1. Male provisioning ability and indicator trait

A male's provisioning ability r_m (which ranges between 0 and 1) directly determines the amount of resources he provides to his mate. Males can signal their provisioning ability with an indicator trait. The expressed value of the indicator trait t_e is determined by the male's genetic value t for signaling intensity, but it also depends on his provisioning ability r_m:

$$t_e = t \cdot r_m^2 \tag{1}$$

2.2. Fitness costs of male indicator trait and female preference

In line with standard models of sexual selection (Andersson, 1994), we assume that both male indicator traits and female preferences are costly to express. Following Iwasa and colleagues (Iwasa et al., 1991; Iwasa & Pomiankowski, 1999), the survival probability from birth to reproductive age for males (v_m) is determined by the expressed value of the indicator trait as follows:

$$v_m = \exp\left(-ct_e^2\right) \tag{2}$$

where c is a scaling parameter ($c = 0.1$ for all data shown). The probability that a female mates (v_f) is given by

$$v_f = \exp\left[-b(p+q)^2\right] \tag{3}$$

where p denotes the female's own mate preference, q denotes the parental preference of her father or mother (whichever is the controlling sex), and b is a scaling parameter ($b = 0.01$ for all data shown). In this implementation, the female pays a cost both for her own choosiness and for the choosiness of her parent. This is consistent with the assumption that choosiness, whether exerted by herself or her parent, reduces the probability that a female mates at all. Males that die before reproductive age and females that fail to mate are disregarded in all subsequent stages described below.

2.3. Mate choice

The remaining males and females enter the mating pool. At this stage, each mating female samples a random subset of 10 males from the mating pool and chooses one of them as her mate. The probability w that a given candidate male with expressed indicator trait value t_e is chosen from this subset depends on the female's own preference and the parental preference of her parent, according to

$$w \propto \exp[(p+q)t_e] \tag{4}$$

That is, we assume that the female's own preference and her parent's preference carry equal weight (other weightings are possible, but we do not consider them here).

2.4. Parental investment

The amount of resources r_z a parent allocates to a given daughter depends on the number of daughters they have, the provisioning abilities of the mates of those daughters and their resource-allocation strategy. Each parent has the same total amount of resources, R_z, to invest ($R_z = 1.0$ for all data shown), which must be divided among their daughters. We consider various possible resource-allocation strategies that are determined by the parent's allocation trait α (the specific relation between α and resource-allocation strategy is discussed in the Supplementary Information, available on the journal's Web site at www.ehbonline.org). If $\alpha = 0$, parents use an equal allocation strategy, distributing their resources evenly among their daughters. If $\alpha < 0$, parents use a compensatory allocation strategy, allocating more resources to daughters that have received fewer resources from their mate. If $\alpha > 0$, parents use an augmenting allocation strategy, allocating more resources to daughters that have received more resources from their mate.

2.5. Reproduction

The fecundity of a female depends on the total amount of resources r available to her. This is given by the sum of the amount of resources received from her mate (determined by his provisioning ability r_m) and the amount received from her parent (r_z). We assume diminishing fecundity returns on investment:

$$f(r) = \frac{r}{r+1} \tag{5}$$

(other possible returns-on-investment functions are considered in the Supplementary Information, available on the journal's Web site at www.ehbonline.org). All pairs reproduce and their reproductive output is proportional to the fecundity of the female. An equal number of male and female offspring are produced. For the baseline case of our model (Step 1 in the results below), each pair produced on average 2.0071 offspring. The maximum number of offspring produced per pair averaged 9.51 per generation and 26.8% of pairs had two or more daughters.

During inheritance, the traits t, p, q, α and r_m each mutate with probability μ, with the magnitude of the mutations drawn from a uniform distribution between 0 and s (in all simulations shown here, $\mu = 0.01$ and $s = 0.05$). Upward and downward mutations are equally likely, except in the case of r_m, where the direction of the mutation is affected by a mutation bias. In this case, there is a probability of 0.75 that r_m mutates to a lower value and a probability 0.25 that it mutates to a higher value. This assumption is consistent with the idea that most mutations will decrease provisioning ability (as in Iwasa & Pomiankowski, 1999), and ensures the maintenance of population-level variation in male provisioning ability. If the value of r_m after mutation ($r_{m,\mathrm{mut}}$) is smaller than zero, it is set to zero. If $r_{m,\mathrm{mut}}$ is larger than 1, r_m is replaced by $2 - r_{m,\mathrm{mut}}$ (i.e. the mutation is “reflected” back from the upper limit of 1). In this way, we ensure that the maximal provisioning ability is not reached too easily. After reproduction, the parent generation dies and is replaced by the former offspring generation, which is replaced by the newly created grandoffspring.

We ran 40 replicate simulations for each scenario, using a population of $n = 5000$ individuals and a time span of 500,000 generations. Throughout the paper, we report means and standard errors of the evolvable traits in the last generation across all replicates. We refer to these evolved values as p^* (female preference), q^* (parental preference), t^* (genetic value of the indicator trait) and α^* (resource-allocation strategy).

3. Results

We used a step-by-step approach to investigate how parental influence on mate choice and parental investment change the dynamics of sexual selection. In Step 1, we studied the behavior of the model when q and α are set to zero and not allowed to evolve; R_z is also set to zero. In other words, parents do not influence the mate choice of their daughters, nor do they distribute any resources among them. In Step 2, q is allowed to evolve, but α and R_z still remain at zero. Hence, a parental influence on mate choice can evolve in this situation, but there is no parental resource allocation. In Step 3, q is allowed to evolve, R_z is set equal to 1, and α is fixed at one of three values: $\alpha = -2$ (compensatory allocation), $\alpha = 0$ (equal allocation) or $\alpha = 2$ (augmenting allocation). This means that we allow both parental influence on mate choice and parental resource allocation, but the resource-allocation strategy is fixed and not allowed to evolve. Finally, in Step 4, we allow both q and α to evolve, with R_z again equal to 1.

We investigated two versions of the model: one in which fathers control resource allocation and can influence their daughter's mate choice, and one in which mothers play this role. The only difference between these two versions is whether it is the father's or the mother's values of α and q that are expressed; all other details are identical. The results for maternal and paternal involvement are qualitatively the same. Quantitatively, however, the predicted degree of conflict differs, as summarized in Table 1. In the results below we focus on the case of paternal involvement, to reflect the observation in human cultures that men typically have more say in arranging the marriages of their children than women do (Whyte, 1978); corresponding graphs for the maternal involvement case are shown in the Supplementary Information (available on the journal's Web site at www.ehbonline.org).

3.1. Step 1: No parental involvement

This first step introduces the classic "good parent" sexual selection model where males indicate their provisioning ability with an indicator trait, and females may evolve a preference for that indicator trait. Fig. 1a shows the evolution of trait and preference over 500,000 generations. The male indicator trait t evolves to $t^* = 4.726 \pm 0.016$ (mean ± SE) and the female preference evolves to $p^* = 3.647 \pm 0.060$. These outcomes are in line with the analytical results of Iwasa and Pomiankowski (1999), where stable exaggeration of indicator trait and preference was also found.

While the simulations in Step 1 were initialized at $p = t = 0$, we used $p = q = 2.0$ and $t = 4.5$ as initial values in all subsequent steps; this value of t is close to the evolved value t^* from Step 1, while $p + q$ is close to the evolved value p^*.

3.2. Step 2: Parental influence on mate choice, but no differential resource allocation

In this step, parental preference is introduced as an evolving variable q, but parental investment is not yet introduced. Hence, a female's fecundity is solely dependent on the provisioning ability of her mate. In these simulations, the indicator trait, female preference and parental preference all evolve to stable levels (Fig. 1b). The female and parental preferences are not significantly different in this situation (see Table 1), and their sum is not significantly different from the female preference in Step 1 ($p^* + q^* = 3.803 \pm 0.076$; two-sample t test: $t_{78} = 1.407$, $P = 0.163$). In other words, in the absence of parental investment, we do not predict a conflict over mate choice between parents and their daughters.

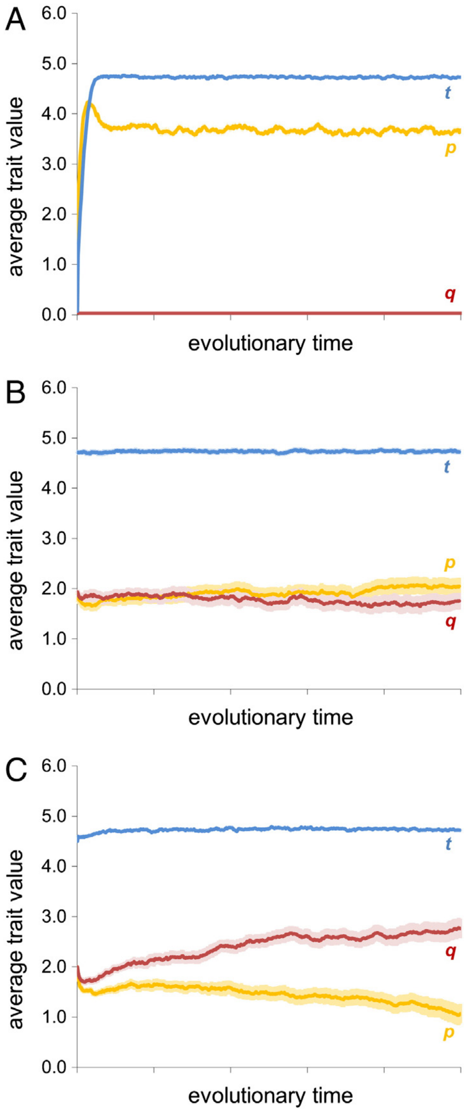

Fig. 1. The coevolution of female preference p, paternal preference q and male indicator trait t in Steps 1–3 of our model. (*a*) In Step 1, there is no paternal involvement in mate choice. (*b*) In Step 2, fathers have an influence on their daughters' mate choice but do not allocate any resources to them. (*c*) In Step 3, fathers both have an influence on their daughters' mate choice and allocate resources among them; specifically, fathers use a compensatory allocation strategy (α was fixed at -2), giving more resources to daughters with low-investing partners. The graphs show mean and standard errors across 40 replicates.

3.3. Step 3: Differential parental resource allocation, fixed allocation strategy

We next investigated the effect of three different fixed parental resource-allocation strategies: (a) equal allocation ($\alpha = 0$), (b) compensatory allocation ($\alpha = -2$), and (c) augmenting allocation ($\alpha = 2$). The summary statistics of these simulations are shown in Table 1 and Fig. 2. When $\alpha = 0$, p^* and q^* are not significantly different. In other words, when parents use an equal allocation strategy, no conflict over mate choice between parents and daughters

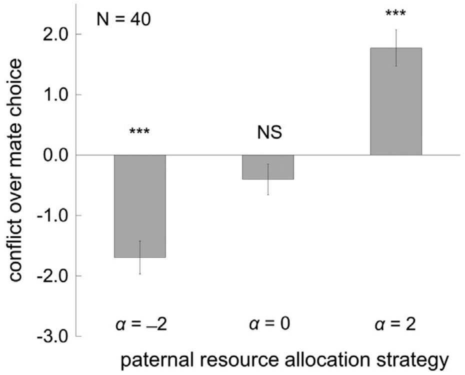

Fig. 2. The evolved difference between female and paternal preferences in Step 3, where fathers distribute resources among their daughters according to a fixed allocation rule. If $\alpha < 0$, fathers allocate more resources to daughters receiving fewer resources from their mate (compensatory allocation); if $\alpha = 0$ fathers distribute resources uniformly across daughters (equal allocation); if $\alpha > 0$, fathers allocate more resources to daughters obtaining more resources from their mate (augmenting allocation). The graph shows the degree of conflict over mate choice, represented as means and standard errors (across 40 replicate simulations) of $p^* - q^*$, the difference between the evolved values of female preference and paternal preference; zero indicates no conflict. Significant differences from zero are indicated with *** ($P < 0.001$); non-significant differences from zero are indicated with NS ($P > 0.05$).

is observed; this fits with our expectations. When $\alpha = -2$, p^* is significantly smaller than q^* (evolutionary trajectories are shown in Fig. 1c). Hence, when parents use a compensatory allocation strategy, the parental preference evolves to higher levels than the female preference. This is in line with our hypothesis that daughters tend to exploit their parents' willingness to compensate them for choosing a mate that provides relatively few resources. In Fig. 1c, it can be seen that female preference and parental preference do not reach a stable level but continue to diverge over evolutionary time, representing increasing degrees of conflict. Finally, when $\alpha = 2$, p^* is significantly greater than q^*. This is also in line with our expectations: females exploit their parents' augmenting resource-allocation strategy by choosing a mate that provides relatively many resources, leading to the evolution of a stronger female preference than parental preference. As in the compensatory case, these preferences continue to diverge over time (results not shown).

3.4. Step 4: Differential parental resource allocation, evolvable allocation strategy

The final step allows the parental resource-allocation strategy to evolve. The evolutionary trajectories are shown in Fig. 3. In this case, α^* is significantly below zero ($\alpha^* = -2.772 \pm 0.157$; one-sample t test: $t_{39} = 17.656$, $P < 0.001$). This is in line with our expectations; if returns on investment are diminishing, parents can maximize the total fecundity of their daughters by using a compensatory allocation strategy. Consequently, the opportunity for daughters to exploit this resource-allocation strategy leads to the evolution of lower levels of female preference, which parents are selected to counteract by increasing their parental preference: thus p^* is significantly smaller than q^* (Fig. 3; Table 1). This represents a conflict over mate choice, with parents having a stronger preference than their daughter for a high-investing son-in-law.

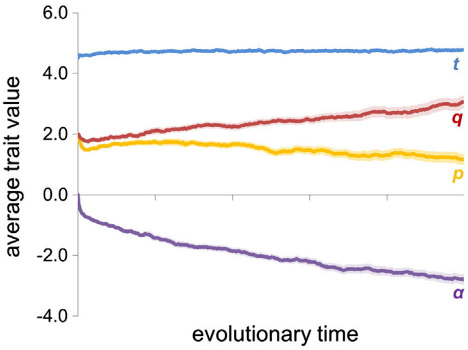

Fig. 3. The coevolution of female preference p, paternal preference q, male indicator trait t and paternal resource-allocation strategy α in Step 4. In this situation, fathers both have an influence on their daughters' mate choice and can control how resources are allocated among them; α represents the father's evolvable resource-allocation strategy (see text for details). The graphs show mean and standard errors across 40 replicates.

3.5. Paternal vs. maternal involvement

Table 1 compares the results of the model for paternal involvement (shown in the figures) with those obtained for maternal involvement (shown in Figs S4 and S5 in Supplementary Information, available on the journal's Web site at www.ehbonline.org). The results are qualitatively the same regardless of which parent is in control. Quantitatively, however, the differences between p^* and q^* are more pronounced under paternal involvement than under maternal involvement, indicating a stronger conflict when fathers, rather than mothers, control resource allocation and influence mate choice. This is the case for every step of the model.

4. Discussion

Our results confirm that parent–offspring conflict over resource distribution can generate conflict between the same parties over the offspring's mate choice. Three conditions are sufficient for this conflict to arise: (i) variability between potential mates in their ability to provide resources, which the opposite sex is able to assess (e.g. via an indicator trait); (ii) additional investment by parents in their offspring's reproduction; and (iii) the ability of parents to exert an influence on their offspring's mate choice. Under these conditions, parental resource-allocation strategies evolve to be dependent on the level of resources provided by their offspring's mates. Subsequently, the offspring evolve to exploit this allocation rule through their mate choice, which is not in the parents' best interests. This results in a conflict over mate choice between parents and offspring, manifested as an on-going divergence of offspring and parental preferences. The widespread occurrence of parent–offspring conflict over mate choice already suggested that it is not contingent on cultural factors alone. The results of this study corroborate the notion that this conflict has an evolutionary basis by providing a possible mechanistic explanation for the observed patterns.

Our evolutionary model suggests that, contrary to some verbal arguments (Apostolou, 2007b, 2008a,b, 2011, 2012), the weaker relatedness of grandparents to their grandoffspring than parents to their offspring is not sufficient to generate conflict over mate choice. This can be seen by comparing the results of Step 2 (Fig. 1b) with the results of Steps 3 (Fig. 1c) and 4 (Fig. 3). The relatedness difference is present in all steps of our model, but in Step 2 there is no opportunity for parental investment in the offspring, and here no conflict emerges (Fig. 1b). Only when parents can allocate resources to their offspring do parental and offspring preferences diverge (Figs. 1c and 3).

The conflict that evolves in our model is a difference in preference strength (i.e. choosiness), not in preference direction. It is important to realize that both a parent and his/her daughter will benefit if the latter happens to pair with a high-investing male; in this respect, their evolutionary interests are overlapping. But a conflict arises because the costs and benefits of being choosy differentially affect the fitness of parents and daughters. If a parent has two or more daughters, they value them equally in fitness terms, whereas each daughter values her own reproduction more than that of her sisters, and should therefore try to ensure that she is the one who profits most from the particular pattern of parental resource allocation (Fawcett et al., 2010). Under a

Table 1
Evolved values of p, q and $p - q$ for all four steps of the model.

Scenario	Paternal influence				Maternal influence			
	p^*	q^*	$p^* - q^*$	*P*-value	p^*	q^*	$p^* - q^*$	*P*-value
Step 1	3.65 ± 0.06	–	–	–	3.64 ± 0.06	–	–	–
Step 2	2.05 ± 0.17	1.75 ± 0.17	0.30 ± 0.24	0.221	1.82 ± 0.16	1.87 ± 0.16	-0.05 ± 0.23	0.825
Step 3, $\alpha = -2$	1.07 ± 0.19	2.76 ± 0.19	-1.69 ± 0.27	<0.001	1.73 ± 0.20	2.63 ± 0.25	-0.90 ± 0.23	<0.001
Step 3, $\alpha = 0$	1.62 ± 0.17	2.02 ± 0.19	-0.40 ± 0.26	0.123	2.01 ± 0.16	2.05 ± 0.17	-0.03 ± 0.24	0.889
Step 3, $\alpha = 2$	2.46 ± 0.21	0.69 ± 0.22	1.77 ± 0.30	<0.001	2.08 ± 0.16	1.52 ± 0.16	0.55 ± 0.22	0.019
Step 4	1.16 ± 0.18	3.05 ± 0.20	-1.88 ± 0.27	<0.001	1.69 ± 0.16	2.58 ± 0.17	-0.89 ± 0.24	<0.001

Mean ± SE across 40 replicates of the evolved values at generation 500,000 are shown. The columns on the left show results for when fathers can exert influence on their daughters' mate choice and allocate resources among them; the columns on the right show results for when mothers play that role. The last column gives the *P*-value of a 2-tailed paired *t* test (D.F. = 39) that tests whether $p^* - q^*$ is significantly different from zero.

strategy of augmenting resource allocation, parents give more resources to daughters who end up with higher-investing mates. Selection therefore favors daughters who have a stronger preference than their sisters, because the extra choosiness costs they pay are balanced by the extra input of resources from their parents. Under compensatory allocation, in contrast, selection favors weaker female preferences, because a daughter can be less choosy than her sisters and yet still end up with abundant resources, thanks to her parent's compensatory input. This is the evolutionary basis of the conflict that emerges in our model.

Our model predicts that parents will have stronger preferences than their daughters for male traits that indicate the ability to provide resources. Empirical evidence on this is mixed. Several previous studies have found that parents and daughters agree on the importance of earning capacity (Apostolou, 2008a; Perilloux et al., 2011) and financial prospects (Apostolou, 2011). A study by Buunk et al. (2008) suggested that poor males are less acceptable to parents than to their daughters, whereas Dubbs and Buunk (2010) found no such difference. A consistent finding across all these studies is that parents value the male's family background more than their daughters (Apostolou, 2008a, 2011; Buunk et al., 2008; Dubbs & Buunk, 2010; Perilloux et al., 2011). Perilloux et al. (2011) also found that parents have a stronger preference than their daughters for males who are “good housekeepers.” In general, though, we are concerned that the interpretation of these empirical results hinges on what particular qualities the characteristics studied are presumed to indicate. Further research is needed to clarify the nature of parental and offspring preferences.

The qualitative pattern of conflict in our model is the same regardless of whether it is fathers or mothers who influence the mate choice of their daughters and decide how to distribute resources among them. Quantitatively, however, the differences between p^* and q^* are more pronounced under paternal control (the more common pattern of control across human societies; Whyte, 1978) than under maternal control. One explanation for this is that daughters subsequently become mothers, and the female preference genes p are exposed to contrasting selection pressures at these two generational stages (see Bossan, Hammerstein, & Koehncke, 2013). Because mothers and daughters are closely related, females who heavily exploit the resource-allocation pattern of their mothers are likely subsequently to have their own resource-allocation pattern similarly exploited by their own daughters. In contrast, females who exploit the resource-allocation patterns of their fathers do not face such consequences; they are not confronted with the negative effects of exploiting parental resource-allocation patterns when in the role of the parent themselves. This may favor the evolution of more exploitative female strategies when fathers influence mate choice and control resource allocation, thereby generating a stronger parent–offspring conflict over mate choice in this case.

The intensity of the conflict is also likely to depend on the degree of parental influence on their offspring's mate choice, which varies widely across cultures (Apostolou, 2010a, b; Buunk et al., 2010). In this study, we assumed that parents and offspring have equal influence on the mate choice of the offspring. An obvious next step would be to study how variation in the degree of parental influence affects the evolution of parent–offspring conflict over mate choice. In our model, one could account for unequal influence by attaching different weightings to the preferences p and q in Eqs. (3) and (4). One could then allow the degree of parental influence to evolve by treating these weightings as two new loci, one for the parents' attempt to influence the mate choice of their offspring, and one for the offspring's effort in resisting the interference of their parents in mate choice. Another interesting extension would be to vary the total amount of resources, R_z, parents can invest. If the ability of parents to accumulate resources is another evolvable trait, we might expect this to influence the coevolution between parental and offspring mate preferences.

One of the most important assumptions in our model is that parents can condition their resource-allocation strategy on the provisioning ability of their offspring's mates. If this is not the case (as in Steps 1 and 2), our model does not predict the emergence of parent–offspring conflict over mate choice. Therefore, to check the plausibility of our model as an evolutionary explanation for parent–offspring conflict over mate choice, we need empirical data on whether parents actually bias their allocation patterns in the way predicted by our model. To the best of our knowledge, such data are lacking. Further studies into parental resource-allocation strategies in humans would be an important next step toward understanding parent–offspring conflict over mate choice.

Buunk et al. (2008) suggest that in choosing a mate, women tend to focus on male traits that may be interpreted as indicators of good genes, whereas their parents place more emphasis on male traits that are indicative of provisioning ability or other direct benefits (see also Apostolou, 2008a,b). Since our model only considers male traits that indicate provisioning ability, it does not make any predictions on such qualitative differences between the preferences of parents and their offspring. One possible extension of our model would be to include variation in both viability genes and provisioning ability, with different indicator traits for these two types of variation. However, even in a simpler scenario without parental influences on mate choice, such multiple-indicator models can have intricate dynamical behavior (Van Doorn & Weissing, 2004, 2006). We therefore leave the analysis of such models in the context of parent–offspring conflict to future work.

In our model, the parents are not directly affected by the resources provided by their children-in-law. In many societies this may be quite different, since in their old age, parents are often supported by one or more children-in-law. It is therefore conceivable that parents prefer specific male traits because they indicate that a potential son-in-law would be inclined to care for them. Indeed, several studies have shown that there is a positive relationship between survival in old age and support from children and/or grandchildren (Okabayashi, Liang, Krause, Akiyama, & Sugisawa, 2004; Esbensen, Osterlind, & Hallberg, 2007). However, a parental preference for sons-in-law that care for their parents-in-law would only be adaptive if it would enhance the parents' inclusive fitness. This will often not be the case, since the parents are typically beyond reproductive age at the stage when they require care. Still, such a preference could persist as a by-product of a more general will to survive that is adaptive in other phases of life. Extending our model with these elements might lead to the evolution of more extreme parental preferences for the caring ability of their sons-in-law, possibly leading to even stronger parent–offspring conflict over mate choice.

In conclusion, our model provides a first proof of principle that parent–offspring conflict over resources can lead to parent–offspring conflict over mate choice. This provides a novel, evolutionary explanation for the robust finding across many human cultures that parents and their offspring frequently disagree over what constitutes a suitable mate for the latter. We hope that our findings will stimulate further empirical and theoretical research aimed at understanding how offspring preferences, parental preferences and patterns of resource allocation interact dynamically in the course of human evolution.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2013.07.004.

Acknowledgments

The authors thank Dr. Justin Park for stimulating discussions, and two anonymous reviewers for valuable comments. P.vdB. is subsidized by a grant of the Graduate Programme of the Dutch Science Foundation (NWO).

References

Andersson, M. (1994). Sexual selection. Princeton, NJ: Princeton Univ Press.

Apostolou, M. (2007a). Sexual selection under parental choice: The role of parents in the evolution of human mating. *Evolution and Human Behavior*, *28*, 403–409.

Apostolou, M. (2007b). Elements of parental choice: The evolution of parental preferences in relation to in-law selection. *Evolutionary Psychology*, *5*, 70–83.

Apostolou, M. (2008a). Parent–offspring conflict over mating: The case of family background. *Evolutionary Psychology*, *6*, 456–468.

Apostolou, M. (2008b). Parent–offspring conflict over mating: The case of beauty. *Evolutionary Psychology*, *6*, 303–315.

Apostolou, M. (2010a). Sexual selection under parental choice in agropastoral societies. *Evolution and Human Behaviour*, *31*, 39–47.

Apostolou, M. (2010b). Parental choice: What parents want in a son-in-law and a daughter-in-law across 67 pre-industrial societies. *British Journal of Psychology*, *101*, 695–704.

Apostolou, M. (2011). Parent–offspring conflict over mating: Testing the tradeoffs hypothesis. *Evolutionary Psychology*, *9*, 470–495.

Apostolou, M. (2012). Sexual selection under parental choice: Evidence from sixteen historical societies. *Evolutionary Psychology*, *10*, 504–518.

Bossan, B., Hammerstein, P., & Koehncke, A. (2013). We were all young once: An intragenomic perspective on parent–offspring conflict. *Proceedings of the Royal Society of London Series B*, *280*, 20122637.

Buunk, A. P., & Castro Solano, A. (2010). Conflicting preferences of parents and offspring over criteria for a mate: A study in Argentina. *Journal of Family Psychology*, *24*, 391–399.

Buunk, A. P., Park, J. H., & Dubbs, S. L. (2008). Parent–offspring conflict in mate preferences. *Review of General Psychology*, *12*, 47–62.

Buunk, A. P., Park, J. H., & Duncan, L. A. (2010). Cultural variation in parental influence on mate choice. *Cross-Cultural Research*, *44*, 23–40.

Coall, D. A., & Hertwig, R. (2010). Toward an integrative framework of grandparental investment. *The Behavioral and Brain Sciences*, *33*, 40–59.

Dubbs, S. L., & Buunk, A. P. (2010). Parents just don't understand: Parent–offspring conflict over mate choice. *Evolutionary Psychology*, *8*, 586–598.

Esbensen, B. A., Osterlind, K., & Hallberg, I. R. (2007). Quality of life of elderly persons with cancer: A 6-month follow-up. *Scandinavian Journal of CaringScience*, *21*, 178–190.

Fawcett, T. W., Van den Berg, P., Weissing, F. J., Park, J. H., & Buunk, A. P. (2010). Intergenerational conflict over grandparental investment. *The Behavioral and Brain Sciences*, *33*, 23–24.

Grafen, A. (1990a). Biological signals as handicaps. *Journal of Theoretical Biology*, *144*, 517–546.

Grafen, A. (1990b). Sexual selection unhandicapped by the Fisher process. *Journal of Theoretical Biology*, *144*, 473–516.

Hawkes, K., O'Connell, J. F., Jones, N. G. B., Alvarez, H., & Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences U S A*, *95*, 1336–1339.

Iwasa, Y., & Pomiankowski, A. (1999). Good parent and good genes models of handicap evolution. *Journal of Theoretical Biology*, *200*, 97–109.

Iwasa, Y., Pomiankowski, A., & Nee, S. (1991). The evolution of costly mate preferences. 2. The handicap principle. *Evolution*, *45*, 1431–1442.

Kokko, H., Jennions, M. D., & Brooks, R. (2006). Unifying and testing models of sexual selection. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 43–66.

Kuijper, B., Pen, I., & Weissing, F. J. (2012). A guide to sexual selection theory. *Annual Review of Ecology, Evolution, and Systematics*, *43*, 287–312.

Lahdenpera, M., Lummaa, V., Helle, S., Tremblay, M., & Russell, A. F. (2004). Fitness benefits of prolonged post-reproductive lifespan in women. *Nature*, *428*, 178–181.

Menon, R. (1989). Arranged marriages among South Asian immigrants. *Sociology and Social Research*, *73*, 180–181.

Minturn, L., Grosse, M., & Haider, S. (1969). Cultural patterning of sexual beliefs and behavior. *Ethnology*, *8*, 301–318.

Okabayashi, H., Liang, J., Krause, N., Akiyama, H., & Sugisawa, H. (2004). Mental health among older adults in Japan: Do sources of social support and negative interaction make a difference? *Social Science & Medicine*, *59*, 2259–2270.

Perilloux, C., Fleischman, D. S., & Buss, D. M. (2011). Meet the parents: Parent–offspring convergence and divergence in mate preferences. *Personality and Individual Differences*, *50*, 253–258.

Sear, R., Mace, R., & McGregor, I. A. (2000). Maternal grandmothers improve nutritional status and survival of children in rural Gambia. *Proceedings of the Royal Society of London Series B*, *267*, 1641–1647.

Trivers, R. L. (1974). Parent–offspring conflict. *American Zoologist*, *14*, 249–264.

Van Doorn, G. S., & Weissing, F. J. (2004). The evolution of female preferences for indicators of male quality. *American Naturalist*, *164*, 173–186.

Van Doorn, G. S., & Weissing, F. J. (2006). Sexual conflict and the evolution of female preferences for indicators of male quality. *American Naturalist*, *168*, 742–757.

Welbergen, J. A., & Quader, S. (2006). Mother guarding: How offspring may influence the extra-pair behaviour of their parents. *Proceedings of the Royal Society of London Series B*, *273*, 2363–2368.

Whyte, M. K. (1978). Cross-cultural codes dealing with the relative status of women. *Ethnology*, *17*, 211–237.

Zahavi, A. (1975). Mate selection—Selection for a handicap. *Journal of Theoretical Biology*, *53*, 205–214.