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Original Article The evolution of parent–offspring conflict over mate choice

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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. © 2013 Elsevier Inc. All rights reserved.

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).

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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 resourceallocation 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

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