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#### **Mate Value**

# **Synonyms**

potential mate or partner fitness value; partner reproductive value; mate worth; expected additions to reproductive success.

## **Definition**

The "mate value" of a mating partner is the inclusive fitness gain another individual that is assessing potential mates could make from them; also, in humans, it is the value of partners on the "mating market".

# Introduction

Mate value is the total potential fitness value to be gained from a prospective mate or partner. It includes all aspects of fitness, incorporating a mate's phenotypic condition, genetic quality and resource holding. These factors need to be evaluated as to how they affect the fitness of the chooser, for example, given variation in the chooser's resource holding or where genetic compatibility is important. It is expected that individuals will be selected to maximize the mate value of their partners, leading to the evolution of the criteria used in mate choice. As it is unlikely that mate value can be directly assessed, it must be inferred from morphological and behavioral traits, which evolve under the pressure of the choosers. This leads to the evolution of traits that reveal mate value, as well as to counter-selection for the ability to amplify apparent mate value. In animals, plants and even unicellular organisms, assessment of mate values involves a variety of sensory abilities that lead to the discrimination between mates. In "higher" animals, it has been suggested that the evolutionary assessment-advert feedback was critical to the evolution of cognitive capacities, complex social behaviors, and even human language.

Here is presented, an outline of the component aspects of mate value, how they can vary over time, and how the relative value of each component can depend on specific attributes of potential partner pairs. After this, a wider view is taken, explaining the different sex roles in mate value, and looking at mate value in social species, in human interactions, in sexual selection and social evolution, and in the evolution of human psychology, cognition and language.

## Aspects of Mate Value and its Variation

Mate value includes all aspects of fitness that can be imparted, and is thus similar to the broad-sense attractiveness of an individual as a potential mate (Buss & Shackelford 1997, Gangestad & Simpson 2000, Edlund & Sagarin 2014). In humans, mate value is sometimes considered in narrower terms as, "the extent to which mating with ... and retaining ... a partner would have increased a ... person's ancestral reproductive success" (Sugiyama 2005). In fact most work on "mate value" conducted in humans has used this narrow sense, while that in animals has used the wider "reproductive value". Yet, the areas are not disparate, and a more serious effort to unify them would be useful. A list of mate value fitness attributes would include: the condition of an individual in relation to its environment (e.g. its fat reserves, disease status), the quality of the individual in terms of its genes (e.g. "good genes", level of heterozygosity), the quality of the individual's current resources (e.g. territory size, nest site) and their capacity to hold them over the reproductive period and contribute to the fitness of the chooser (e.g. the individual's "resource holding potential", age, capacity to provide parental care) (Gangestad & Simpson 2000). These attributes of mate value are valued by a chooser in as far as they will increase its current or future fitness. In a human specific sense, mate value can also incorporate more subtle traits, including the "Big Five" personality traits: openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism; as well as complex attributes such as trustworthiness, social status or aspects of wealth, in relation to the trait-state of the perceiver (Goldberg 1993, Edlund & Sagarin 2014). This list could be extended ad nauseum to cover the particular life history details of a species or the intricacies that surround human social and cultural values.

What matters from a biological viewpoint is how the survival and reproductive output of the chooser (and that of their offspring) is improved by the mate choice value they ascribe to potential partners when choosing a mate.

In addition to these traits, which are mate value indicators of signaler quality, it has been widely recognized that attractiveness per se can be a feature of mate value. This came out of one of the first attempts to model the evolution of animal and human aesthetic appreciation, by the statistician and geneticist Ronald Aylmer Fisher in the 1930s (Andersson 1994). Fisher saw that arbitrary sexual preferences could be evolutionarily self-reinforcing, because the trait preferred would be inherited by offspring along with the preference itself, coupling the evolution of ornament size and preference intensity. This force - the so called self-reinforcing Fisherian runaway - may explain the bewildering diversity of sexual signals used in nature - which are often the only obvious traits that differ between closely related species. What remains unclear is why some mate value traits are stable whereas others turn-over. For example, species of peafowl related to the renowned peacock all have exaggerated tail feathers, but differ in coloration. There are parallels here to the diversity of cultural ornamentation and display found in human populations. It has been suggested, for instance, that courtship traits that have high mate value persist whereas those just serving as attractants are subject to rapid change. This explanation both fits for evolutionary time in animal species, and cultural change in human courtship traits, where it could be the case that being fashionable is the true mate value.

Each of these aspects will be discussed in various contexts below. But it is first important to make the general points that: 1] the rating of different parts of an individual's mate value may vary over their lifetime (for example, a female may become more or less fertile with age), 2] that what is, or is not important in mate value varies among species, the mating system and across the sexes (for instance, a male may value different partner attributes to a female), and 3] the mate value of an individual can be relative, to that of the set of competitors or potential partners (a "large" male in one context may be "small" in another; the value of two individuals as a partners can depend on their compatibilities).

# Mate Value in Mate Choice – Perception & Reflection

A female or male will benefit their inclusive fitness if they mate, or partner, with an individual of the opposite sex with a high mate value: either from direct benefits (for instance, nuptial gifts, or parental input) or indirect benefits to their offspring (such as "good genes", heterozygosity, or "sexy genes") (Andersson 1994, Roberts & Little 2008). Given this, it is in the interest of high value individuals to signal their quality, for instance through high cost, condition-dependent sexual ornaments, or handicaps (Andersson 1994). This increases the chances that they will be chosen as partners. It allows them to be distinguished from lower value individuals who can't signal in the same way without incurring punitive costs to their survival chances (Pomiankowski 1988). With handicap signals, individuals signal their quality "honestly" allowing the chooser to discriminate and obtain the highest value mates, albeit

within the constraint that errors occur as choosers are always to some degree limited in their abilities to make assessments and to detect cheats (Andersson 1994). A consequence is selection for traits associated with discrimination and perception, such as visual and auditory senses, or even more complex neurocognitive traits, for instance when "ornament traits" involve aspects of intelligence.

Another consequence of the desirability of high value mates is selection for self-reflexive perception and discrimination. All individuals "want" to maximize their own fitness and seek to mate, or partner, with high mate value individuals (Andersson 1994). But, the quality of partner an individual can obtain will be relative and dependent on others with whom they have to compete. It is a waste of resources – both in energy and time, and sometimes in risk – to seek partners with unobtainable mate values; for instance, for a low value male to seek access to a high value female, if she has the opportunity to be choosy; or vice versa (Andersson 1994). A high quality individual might therefore "want" to behave differently to one of lower value, becoming choosier, or more promiscuous (dependent on its sex and species mate system) (Andersson 1994). Likewise, if compatibility is important, then, in prospecting for potential mates, an individual will "want" to account for aspects of itself (Mays and Hill 2004, Buss et al. 2017). In both cases, the tools used for discrimination and assessment, which are used to make an external choice of partners, may be turned inward and provide a basis, consciously or not, for the assessment of self. While the evolving traits will depend on species, sex, and mate system, the search for high mate value partners will feed back on itself and so play a role in driving the evolution of complex behaviors and cognitive capabilities.

# **Sex Differences: What Males and Females Want**

The two sexes are fundamentally distinct due to differential selection either for numerous, small, motile gametes (sperm), or for few, large, static gametes (eggs) (Beukeboom & Perrin 2014). This gamete dimorphism is absent from unicellular species, but almost universal amongst multicellular forms. It is widely believed that sex differences flow from this number-nutrient distinction, and lead on to differences in what constitutes mate value in the two sexes (Andersson 1994). A demonstration of this can be found in an iconic experiment carried out by Bateman (1948), on the fruit fly Drosophila melanogaster. He allowed males and females to mate multiply and showed males had much higher variance in reproduce success than females. Male reproductive success increases with each mating as this results in more fertilization, whereas female output is limited by the resources available to invest in eggs, rather than the number of times they mate. The implication is that, because male sperm are cheap relative to female eggs, males seek to maximize their mate and offspring numbers, while females choose amongst potential partners in order to maximize the quality of each of their offspring. Although there are notable exceptions - such as sex-role-reversed sea horses (where males carry out the work of parental care) - this number versus quality rule holds out over a wide range of species including insects, fishes, amphibians, reptiles, birds and mammals (Beukeboom & Perrin 2014).

The translation of this rule into mate value is complex, including many species-specific factors, but is dominated by the mating system of the species in question. For example, in a promiscuous mating system, in which males do not contribute parental care or any resources, a female only gains sperm from a male. Hence, male mate value relates primarily to aspects of a male's genetic quality or attractiveness, as exemplified by the peacock's train or stalk-eyed fly eyestalks, and by material or mental constructions, such as the bower bird's decorated maypole and avenue structures (Andersson 1994) or even human conversational ability (Fitch 2010). In these cases, the male is largely indiscriminate and simply values all females with similar mate value (Andersson 1994). In male-dominant systems, typified by the elephant seal or red deer, females largely let male fighting determine which males are potential mating partners, which presumably pre-sorts male genetic quality. Females avoid consorting with sub-dominant males in order to avoid dangerous conflicts, in order to minimize the costs of mating (Andersson 1994). However, male discrimination has been demonstrated within these systems, as males can attract or herd several females and can't necessarily mate with all of them in the same time period. For instance, in stalk-eyed flies, males show a burst of sexual activity at dawn, and evaluate female mate value associated with size and so fecundity, mating first with large females when they have a choice.

Alternatively, the mating system can be more sex-balanced leading to much less difference in male and female reproductive success. In the extreme, there is pair bonding, and both parents contribute equally to parental care.

Here, the distinction between male dominance and female choice is far less apparent. Females value males in relation to their condition, and how this predicts his parental care (Andersson 1994, Trivers 1972). Males now value female condition for the same reasons, as their investment will be far larger than in low contribution scenarios. Indeed, many examples are known where male and female indulge in mutual mate choice, using ornaments and behavior equally in their courtship displays, as in the albatross (Andersson 1994, Trivers 1972). However, extra-pair copulation can result in greater fertility for males and trade-up genetic quality in females, or other more subtle fitness gains (e.g. outbreeding, avoidance of neighbor aggression), so even within monogamy, subtle differences may persist in male and female mate value.

### **Sex Differences: What Men and Women Want**

Human mating systems are complex, and highly variable, but can be characterized, roughly, as serially monogamous, with individuals paired in one or more semi-exclusive long-term relationships across a lifetime, with extrapair copulation more or less present, phases of polyandry and polygyny common in some cultures (Buss & Schmitt 1993, Gangestad & Simpson 2000). The recent emergence of easier birth control may have permitted greater levels of promiscuity by both sexes (Gangestad & Simpson 2000). Females are often the choosier sex, although males also exert notable choice. Because human mating systems vary across cultures and over time it is difficult to make unifying claims about mate value and mating system (Gangestad & Simpson 2000). However, there are several reasons to believe

that the sort of systems outlined above held true across much of human evolution (Simmons *et al.* 2004). Human men tend to be larger than human women, that is, humans are sexually dimorphic, which implies sexual selection, with potential roles for female and male choice. Further, men have large testes, and produce large ejaculates relative to many primates, indicating that sperm competition was historically common (Simmons *et al.* 2004). Finally, cross-cultural records and observations show that variants on serial monogamy with extra-pair copulation are and were common (Buss & Schmitt 1993, Marlowe 2003), with extreme exceptions, like the "reproductive factories" of the ancient Chinese Imperial Harem or the Ottoman Grand Seraglio (Pinker 2011).

Humans also fit with Bateman's observations. Men produce large numbers of sperm, and can father 10s, 100s or even 1000s of children, for example in the famous cases of Gengis Khan and Ismail ibn Sharif (Zerjal *et al.* 2003, Oberzaucher & Grammer 2014). In contrast, lifetime reproduction by women is at most in the 10s of children; the current record is held by the Russian Mrs. Feodor Vassilyev, with 69 (Urban 1783). In fact, the averages for total and inter-sex variation in reproductive output are far lower than these maxima (with means nearer 1-3 children and variance around 1-5 in most modern cultures studied, van Daalen & Caswell 2017, and with modest differences between men and women, being slightly higher in males, Brown *et al.* 2009), but this information can still be informative about mate value.

At a broad stroke then, the traits *expected* to count in women's assessments of men, when looking for long-term partners, include those associated with a man's ability to provide parental care, such as his condition, wealth, rank and mental disposition, with traits associated with his resources, genetic quality, and physical attractiveness (Trivers 1972, Buss & Schmitt 1993). In contrast, attributes counted in women's assessments of men as short-term or extra-pair partners should relate more directly to a prospective male partner's genetic quality and attractiveness, or to additional advantages presented through gifts, wealth, or social connections, with little concern given to direct parental input (Buss & Schmitt 1993, Gangestad & Simpson 2000). Likewise, mate value assessments made by men looking for long-term female partners should relate primarily to traits associated with a woman's ability to produce and rear healthy children, such as her condition, age and overall genetic quality (Buss & Schmitt 1993), or related to her attractiveness, though traits such as "curviness", which may be associated with fecundity. In contrast to assessments made of men by women, however, men's assessments of women as short-term or extra-pair partners should still be based on estimates of the women's capacity to produce offspring and provide maternal care (Trivers 1972, Buss & Schmitt 1993). The reason for this sex difference is that additional reproduction is more costly for women. In most cultures, the woman contributes more to raising children than do men and, if she is in a long-term relationship, likely has a partner to act as a father already. If a woman is to have a short-term or extra-pair partner, genes or gifts are required; a man requires only a partner, and can then leave (Andersson 1994, Trivers 1972, Buss & Schmitt 1993, Gangestad & Simpson 2000).

In line with this, recent large-scale cross-cultural studies have found that single women do indeed prefer men exhibiting traits such as wealth, generosity, intellect, dominance, cultivation, sociability, reliability, similarity, kindness, understanding, humorousness and pleasantness as potential long-term or marriage partners, while single men prefer women who are attractive, creative and domestic (Schwarz & Hassebrauck 2012). Further, while women will consider long-term male partners 5 years younger to 8 years older, men will consider female partners 10 years younger but only 4.5 years older (Schwarz & Hassebrauck 2012). Finally, women are also less likely to consider an opposite sex partner for marriage if the individual earns less, is less educated or is irregularly employed, but are more likely than men to consider a less attractive opposite sex partner for marriage (Schwarz & Hassebrauck 2012). However, these observations have only been made in a limited set of cultures and environments, and may not be as general as is usually assumed.

Additional studies have shown that predicted patterns also follow within relationships. Partnered women are more likely to prefer extra-pair partners with more "masculine" faces, symmetry associated scent, deeper voices and other behavioral displays associated with intra-sexual competitiveness (Gildersleeve *et al.* 2013), while partnered men focus more on traits like attractiveness and youth, associated with fertility and fecundity (Roberts & Little 2008). An important point though is that in each case, the traits preferred by men and women vary with self-assessment, such as that reflected in self-

esteem, self-assessed quality or complementary mentalities (Roberts & Little 2008, Reeve et al. 2017). An important demonstration of this relative-to-self mate value, is that female mate preferences have been shown to vary with the menstrual cycle. This cycle causes a fluctuation in female mate value, which increases near ovulation, but is very much reduced post-menses. Complementing this, there is temporal variation in female mate preference as a female approaches ovulation, with increased interest in "masculine" traits (Roberts & Little 2008, Gildersleeve et al. 2012). Mate-value feedback plays a role too (Roberts & Little 2008, Reeve et al. 2017). Another example of relative-to-self mate value is the finding that women become less choosy after rejection (Reeve et al. 2017), with an accompanying drop in their levels of self-esteem (Schwarz & Hassebrauck 2012). Likewise, men's assessment of their own mate value is linked to their partners mate value and influences their self-esteem and retention behaviors (Starratt & Shackelford 2012, Holden et al. 2014). Men with higher self-esteem do more provisioning behaviors and give fewer negative comments or violence, but can be more likely to cheat as too can women with higher self-esteem and components ofmate value (Starratt et al. 2017). All of these behaviors arise though selection for selfperception, and the constant assessment of relative mate value, shaping the human psychology, and playing a crucial role in influencing phenomena such as mate switching, and predicting partner fidelity (Buss et al. 2017, Starratt et al. 2017).

In short, as is theoretically expected, women appear to be interested in, and to value men in relation to their intelligence, mentality, wealth and resources, while men value women as mates more in relation to attractiveness, youth, creativity and domesticity, with variations in the targets of preference arising in line with partnership status.

### Mate Value in Social Evolution

An important class of mate value traits, for animals and humans, are the context-dependent mental traits associated with society and socialization. Forms of society are exhibited by animal classes as diverse as ants, bees and wasps (the eusocial insects; discussed elsewhere in this volume), crows and parrots, dolphins and elephants, monkeys, apes and humans (Whiten & van Schaik 2007). In each case, the social environment influences mate value. A simple near-universal instance, touched upon above, arises from rank or social status. Rank is a social construct, but its consequences are very real. High rank can be inherited by birth, or emerge from physical strength, or from aspects of intelligence such as the capacity to make alliances or manipulate other members of the social group to obtain "political" power (Chapais 2015). When rank differences are pronounced, they confer advantages to those with higher rank, including but not limited to, better access to resources, reduced stress, reduced effort in food searches, and increased access to sex and reproduction (Rodriguez-Llanes 2009). So rank itself tends to increase an individual's mate value.

This observation applies to all animals, including humans. In the case of monkeys and apes such as macaques and chimpanzees, rank can be comprised of strength, alliances, and birth, as signified by behavior (Rodriguez-Llanes 2009). In humans, rank is a less concrete trait (Chapais 2015). It comprises traits such as "political" power, wealth and positional power (e.g. in a work place) (Chapais 2015). All traits associate with this rank-power will be selected via mate choice; and all traits that assist in obtaining rank-power will also be selected. This is one example of socially context-dependent mate value contributor: but others include the ability to make friends, form alliances or manipulate individuals/groups (Brent 2015).

# Mate Value & Mental Evolution: Cognition, Language & Deception

As can be seen, the need to assess mate value between prospective human mate partners has the potential to enhance discrimination, both through physiological and neurological mechanisms. Moreover, as mate value will be in part determined and assessed in a social context in human societies, it has been suggested that it contributed to the evolution of mental capacities, including the ability to make accurate self-assessment and to detect inaccurate and deceptive displays of mate value (Shettleworth 2000, Whiten & van Schaik 2007). For instance, as soon as language or proto-language evolves, musical, voiced, or signed, it is plausible that linguistic ability becomes a mate value focus, with similar to how bird and whale song are included in mate value assessments, as well as in pure communication (Fitch 2010). While linguistic ability, like vocabulary, originality or construct complexity, could be a condition-dependent trait used to assess mate value, language could then be used to exaggerate claims about the self, or used to "trick" high value partners to mate with oneself (Fitch 2010). The consequence should be selection for better abilities to detect such deception and to direct mate value assessment towards honest expressions of quality, possibly leading to various selective feedback loops leading to better abilities in both language and intelligence (Fitch *et al.* 2010). In this way, mate value may have played and to play a role on the evolution of human language, cognition, and psychology, but this remains to be fully tested.

### Conclusion

Mate value is the total value of a potential mate to the current, future or inclusive fitness of an individual that is assessing prospective mating partners. Which traits contribute to mate value will depend on species, mating system, and sex. Further, mate value will vary over an individual's life, and in relation to the current state, situation, or context that an individual is in. Mate value can influence mate choice, social interactions and behaviors. It must play a crucial role in sexual selection and social evolution. Moreover, selective feedback between choosers and chosen, mean that mate value assessment will have important consequences for the evolution of intelligence, psychology, cognition, and at last, human language. Looking to the future, it would be useful to more fully integrate across narrow human mate value studies and the wider reproductive value ideas used in animals. This will bring new insight.

## **Cross-References** [.]

Body Attractiveness; Costly Signalling; Cultural Differences in Mate Preference; Dominance Predicts Sexual Access; Evolutionary Standards of Female Attractiveness; Facial Attractiveness; Fecundity; Female Mate

Choice; Female Sneak Copulation; Fisher's Reproductive Value; Fisherian Runaway Selection; Game Theory; Good Genes and Sexy Son's Hypothesis; Husband's Status and Wife's Attractiveness; Indicators and Correlates of Status and Dominance; Long-Term Mating; Male Perception of Cycle-Related Fluctuations in Women's Attractiveness; [Male Protection]; Male Mate Choice; Marrying Up; Mate Preferences; Mate Value Inflation; Mating Systems (Behavioral Ecology); MHC Compatibility; [Musical Protolanguage]; Parental Investment Attractiveness; Hypothesis; Physical [Political **Alliances** and Dominance]; Resource Access and Benefit to Women of Short-Term Mating; Reproductive Potential; Reproductive Value; Reproductive Value Curve of Women; Self-Esteem Tracks Mate Value; Self-Evaluations Track Perceived Mate Value; [Sex Differences in Human Mate Preferences (Buss, 1989)]; Sex Differences in Reproductive Variance; Sexual Selection; Sexual Signalling; Short-Term Mating; Status and Dominance Hierarchies; The Evolution of Intelligence; [The Phenotype Linked Fertility Hypothesis]; The Handicap Principle; Vocal Women's Attractiveness; Mate Value; Youth and Fertility.

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