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The Role of Prosocial Behaviors in Mate Choice: A Critical Review of the Literature

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ABSTRACT

Research has focused on the role of prosocial behaviors in mate choice, across both social and evolutionary psychology. Several studies provide strong support for the role of altruism in mate choice, whereby people find prosociality attractive in potential mates. As most research focuses on the role of altruism in mate choice, most research has found that people exhibit altruism towards attractive people, suggesting altruistic behavior is driven by mate choice motivation. Although studies have supported the notion that men's altruism towards women is driven by mate choice, the findings are inconsistent, which may be due to the methodologies adopted by researchers. To our knowledge, this review paper is the first to critically review the literature concerning prosociality and mate choice. We provide an outline of the research thus far, methodological issues, and considerations for future research.

Keywords: Mate Choice, Prosocial Behavior, Sexual Selection, Game Theory

The Role of Prosocial Behaviors in Mate Choice: A Critical Review of the Literature

Definitions

We begin by defining key terms such as *altruism*, *cooperation*, and *fairness* using the guidelines of West, Mouden, Gardner and Mouden (2011), and Debove, Baumard and André (2016). Altruism is defined as behavior which is beneficial to another individual, or a group of individuals, but costly to the altruist (see Fehr & Fischbacher, 2003; Trivers, 1971). *Cooperation* refers to exchange, or interactions between two or more individuals, often being mutually beneficial to all involved. *Fairness* refers to mutualistic behavior that provides equal benefits to two or more people (Chiang, 2010).

Aims of the paper

The aim of this critical review paper is to consolidate and synthesise the findings derived from the empirical literature testing the notion that altruism is an adaptive trait in mate choice, i.e. altruism has evolved as a mating signal. This paper reviews these findings by focusing on the research which has provided support for the role of altruism in mate choice, but equally that which has not. We argue that these inconsistent findings are due to researchers generally relying on behavioral game theory as a theoretical and experimental framework when testing if altruism is a mating signal. Key methodological elements include monetary stakes, differences in experimental design, and parameters set by researchers. Key facets such as methodology, stimuli, and experimental

design are summarised in Table 1 and Table 2. We then offer recommendations for future researchers exploring the role of altruism in mate choice.

Theoretical Explanations for the Evolution of Altruism

According to natural selection, altruism evolved to convey benefits to others, and to increase an organism's fitness, otherwise, due to its costly nature, it should not have evolved (Kurzban, Burton-Chellew & West, 2015). The question is: what are the benefits of being altruistic towards others? To answer this question, we must explore the benefits one receives from behaving altruistically. Kurzban et al. (2015) state 'asking questions why organisms do behavior X really entails asking separate (yet related) questions' (p. 578).

Several theories have been proposed to explain the evolution of altruism, including kin selection (Hamilton, 1963), biological markets (Noe & Hammerstein, 1995), indirect reciprocity (Roberts, 1998), competitive altruism (Roberts, 1998) and reciprocal altruism (Trivers, 1971). Kin selection suggests that altruism is favoured when it benefits those biologically related to us, thus propagating our genes. Biological markets theory refers to social situations as 'markets' whereby we compete with others for the highest quality partners (mates in this context) who provide us with social and reproductive fitness (Barclay, 2013). Markets can refer to mating markets, or any market where people exchange commodities and currencies to achieve desired outcomes (commodities can refer to food, sex, finances etc.). Within a mating market, people compete with one another on traits that increase

their 'market value', and their chances of being selected as a social, or romantic partner. There is ample evidence to suggest men compete with other men in domains such as altruism and cooperation, to appear to be 'good quality' partners, often trading traits that are of the same 'value', adhering to the laws of supply and demand (see Barclay & Willer, 2006), largely because 'altruists attract' (Farrelly, Lazarus, & Roberts, 2007, p. 327). As such, altruism may have evolved because living cooperatively can increase inclusive fitness through reciprocity (Bhogal, 2019; Farrelly, 2019).

Indirect reciprocity suggests that altruistic behavior has evolved because it provides people with reputational benefits, whereby altruistic acts are reciprocated by others at any given time, and via any commodity (Roberts, 1998). Reciprocal altruism however, suggests that altruism has evolved due to immediate benefits between giver and receiver, whereby both parties benefit from a given exchange. Competitive altruism refers to situations whereby people compete in altruistic acts in order to be chosen as partners (Hardy & van Vugt, 2006). As sexual selection theory is the focus of this paper, we now discuss sexual selection in detail, in relation to the literature on the role of sexual selection in the evolution of prosociality.

Sexual Selection Theory (Darwin, 1871)

Sexual selection is operationalised through intra-sexual and inter-sexual competition. Intra-sexual competition relates to members of the same sex competing with one another to attract the opposite sex. These traits can be used to 'fight off' or deter members of the same sex from potential mating partners. Inter-sexual competition relates to characteristics which provide an

individual with an advantage over other members of the same sex, favouring behavioral and/or physical traits that increase one's desirability to the opposite sex, thus increasing reproductive fitness (Miller, 1999; Sefcek et al., 2007). Traits selected through inter-sexual competition can serve as honest signals of one's quality as a partner, assisting in attracting and reproducing with mates, linked to the handicap principle (Zahavi, 1975). The handicap principle suggests that elaborate displays of costly traits are signals which showcase the quality of the individual who holds these traits. As such, this paper explores the literature which aims to suggest that altruism is a costly signal which has evolved through inter-sexual competition, arguing that because women find altruism to be a desirable trait, men engage in acts of altruism towards potential partners, suggesting altruism is a mating signal.

Altruism as a Desirable Trait in Long-Term Romantic Partners

Research suggests that prosocial traits such as altruism and cooperation are sexually selected traits (Miller, 2000; 2007, Tessman, 1995; Zahavi, 1995), increasing one's chances of securing mating opportunities (Gintis, Smith & Bowles, 2001). Farrelly et al. (2007) suggest that investing in altruistic ventures is important to both sexes, as it provides valuable information when engaging with, and evaluating a potential mate. Being willing to share may signal commitment to a relationship, as well as signalling a generous nature, which may be of more importance to women, as women value a man's ability to gain and share resources (Tessman, 1995), thus strengthening the argument that altruism acts as a courtship display and is a reliable indicator of mate quality (Miller, 2007). Furthermore, according to Parental Investment Theory (Trivers, 1972), women invest far more into offspring

than men do, and therefore choose partners who display good partner/parental qualities. In support, altruistic men are expected to be better partners and fathers than non-altruistic men (Miller, 2000; 2007). As a result, altruism contributes to one's mating efforts and reproductive success, which according to Roberts (2015) has been 'overlooked' (p. 425) in the literature.

Much of the research exploring the desirability of altruistic mates began with Barclay (2010), who manipulated altruism and non-altruism in a series of vignettes. He found that men and women (particularly women) found altruistic targets to be more desirable for long-term relationships compared to short-term relationships. Furthermore, using a modified version of Buss's Mate Preferences Questionnaire (Buss, 1989), Bhogal, Galbraith and Manktelow (2019) found that women placed higher importance on altruism when seeking long-term, compared to short-term relationships, signifying the powerful role of relationship length in preferences for altruistic partners. They also found that women placed greater importance on cooperativeness in a mate compared to men, although this preference was not influenced by relationship length.

Research suggests that women prefer altruistic partners (Moore et al., 2013), and this preference is particularly important when seeking long-term relationships (Farrelly, 2013; Farrelly, Clemson, & Gurthrie, 2016). Moore et al. (2013) found that altruistic targets were rated as more attractive than non-altruistic targets. Farrelly (2013) found that both men and women valued altruistic mates when seeking long-term partners compared to short-term partners, a finding which has been recently replicated by Farrelly and King (2019). Farrelly et al. (2016) argue that altruism is a sign of phenotypic quality, as opposed to singularly relying genetic quality. In support, Farrelly (2011) found that women valued cooperative partners when seeking long-term relationships more than

when seeking a short-term relationship. Farrelly (2011) found that preferences did not differ across women's menstrual cycle, thus suggesting altruism is attractive because it signals phenotypic rather than genetic quality.

Furthermore, Farrelly et al. (2016) explored the role of altruism and physical attractiveness when seeking a long-term/short-term relationship. Women rated a series of attractive and unattractive male images, accompanied by scenarios, where they were asked to rate the desirability of men in 12 scenarios including varying levels of altruism. They found that women rated those who were altruistic as more desirable than non-altruistic, seeking long-term mates only. However, non-altruists were more desirable than altruists when women were seeking a short-term mate. Perhaps this is because altruism signals one's positive traits and is indicative of future behavior as a parent and partner rather than genetic quality (Farrelly, 2011; 2013).

However, Farrelly et al. (2016) argue that a limitation of using scenarios and hypothetical situations in research on mate choice, is that these descriptions may relay other qualities, apart from altruism alone, such as heroism or strength. In support, Kelly and Dunbar (2001) found that women rate brave men higher on desirability compared to altruistic men for short and long-term mates. This could be explored in future research, as there is a fine line between acts of heroism that are altruistic, and altruism in the form of generosity in economic games.

To conceptualise the different explanations for the evolution of altruism, it is important to assess why prosocial tendencies appear to be so important in mate choice. Perhaps research should explore the costs related to the altruistic acts being displayed. For example, recent evidence has unpacked prosociality by exploring its varying facets, such as heroism (Margana, Bhogal,

Bartlett, & Farrelly, 2019) and trustworthiness (Ehlebracht, Stravrova, Fetchenhauer, & Farrelly, 2018). Margana et al. (2019) found that women were attracted to attractive, heroic men more so than attractive, altruistic men. This preference was stronger when seeking long-term relationships compared to short-term relationships, providing further support that research must unpack the varying facets of prosocial behavior and mate choice. Thus far, research has largely focused on altruistic and cooperative behavior in mate choice settings, largely ignoring other forms of prosociality (also see Norman & Fleming, 2019).

In addition to unpacking prosociality, research seldom focuses on high vs low cost altruism in relation to mate choice. For example, Fitzgerald, Thompson and Whitaker (2010) argue that differences in self-reported altruism are influenced by whether the altruistic act is of small or of high cost to the altruist. Future research should take this into account, as there also appear to be differences in self-reported altruism and hypothetical scenarios (see Table 1 and 2 for the varying resources and stakes used across the research reviewed here¹).

Although much of the research has found that women express an interest in dating altruistic men, recent findings suggest that in Chinese students, women advertised themselves as altruistic, and men were attracted to altruistic traits in women (Guo, Feng & Wang, 2017). Interestingly, they found the preference for altruistic mates was not influenced by whether they were seeking a short-term or long-term partner, thus suggesting there may be cultural differences in preferences for altruism in mate choice,

¹ Looking at Table 1, we can see that all papers reviewed here which specifically focus on altruism as a desirable trait are fully supported. Six of the studies show that women find altruism desirable compared to men, and two of the studies show that both men and women find altruism equally desirable in a mate. Studies which have an all-female sample are marked as not applicable when referring to whether a sex difference was found or not. Five out of the 12 studies included adopt facial images and scenarios/vignettes to test whether altruism is a desirable trait in mate choice. All studies in Table 1 are experimental.

which to our knowledge have not been fully explored in the literature. Perhaps future research could explore cultural influences on mate preferences for prosocial behaviors in mate choice, as most research exploring these constructs has been conducted in Western cultures. Cultural influences could be prevalent whereby it is against the norm to be non-altruistic, which is more prevalent in Eastern, collectivist cultures compared to Western, individualistic cultures (Yama, 2018).

One final discussion point for this section relates to mutual mate choice (Snowdon, 2013). Farrelly and King (2019) argue that researchers must explore the role of mutual mate choice in the evolution of altruism rather than focusing solely on female mate choice. Although most research discussed (particularly those finding a sex difference in preferences for altruism outlined in Table 1) finds that women prefer altruistic mates to a greater extent compared to men, there is emerging literature which suggests that altruism has not only evolved via female choice, but via mutual mate choice. Mutual mate choice refers to when men and women both exercise similar choice and control over the traits they seek in a romantic partner (Farrelly & King, 2019). The argument here relates to the fact that altruism signals good parental and partner qualities, which can also be important to men, particularly as men and women engage in bi-parental care (Phillips et al. 2008). For example, Farrelly and King (2019) recently found that when asking participants to state how desirable altruistic targets are as potential mates, desirability ratings are very similar. This pattern has also been found in Farrelly (2013) whereby, although women rated altruistic targets as more desirable compared to men, men still rated altruistic women as desirable partners. This signifies the point that although altruism is more important to women in mate choice, this does not necessarily mean men are also not attracted to altruistic tendencies in women.

So far, we have discussed research exploring the desirability of prosocial behaviors in mate choice. We will now discuss the literature aiming to investigate whether men and women display prosocial acts, or public displays of altruism towards potential mates, using a variety of experimental designs, stimuli, and monetary resources.

(insert Table 1 here)

Prosocial Behaviors as Courtship Signals

As altruism has been typically found to be more desirable to women than men, research suggests that altruism is used as a courtship display by men (Griskevicius et al., 2007; Oda, Shibata, Kiyonari, Takeda & Matsumoto-Oda, 2013). For example, men are more helpful towards strangers who are women (Eagly & Crowley, 1986). Men, when alone, give more money to female beggars than male beggars (Goldberg, 1995), and more to street beggars when in the presence of women (Latané, 1970). Men typically show off when hunting in the presence of women (Wood & Marlow, 2013), suggesting public displays of heroism, bravery, and altruism are courtship displays. In support, recent evidence suggests that there are selfish reasons for why men help younger, compared to older women, suggesting altruism is a courtship display (see Kawamura & Kusumi, 2017).

Iredale, van Vugt and Dunbar (2008) explored charitable donations by men and women in the presence of no observer, an observer of the same sex and an observer of the opposite sex. When an attractive woman was present, men donated more of their

earnings to charity compared to when no observer was present; however there was no effect of attractiveness on women's donations. Attempts have been made to replicate the findings of Iredale and colleagues. For example, Jensen (2013) attempted to replicate their findings, with a methodological change. Instead of being observed by a confederate of the same sex, male participants were observed by an unattractive woman instead of a same-sex observer. With this methodological change, Jensen (2013) was unable to fully replicate the findings of Iredale, van Vugt and Dunbar (2008). Jensen (2013) argued that Iredale et al's finding (that altruism decreased when being observed by a member of the same sex), may be due to intra-sexual competition, as opposed to mate choice motivation. Jensen (2013) argues that a reason for why findings in the field are inconsistent, is because researchers are using several methods to identify signalling behavior and prosociality (Table 2 clearly shows the varying methods to use prosociality, including varying stimuli²).

Although the above study shows partial support for the role of altruism in mate choice, several other studies do show further support. For example, McAndrew and Perilloux (2012) found that when taking part in group problem solving tasks, undergraduate men (when paired with women) compete with one another to be more altruistic, thus supporting the theory of competitive altruism, suggesting altruistic behavior is the result of mate choice motivation.

² Of the 14 studies reviewed here, 3 of those studies provide no support that altruism is a mating signal, whereas the majority of those studies do show support. In addition, 3 of those studies adopted designs whereby participants played economic games face to face with live participants, whereas 9 of those studies utilise facial images, hypothetical helping and online simulations as stimuli.

Exploring public displays of altruism, van Vugt and Iredale (2013) used a public goods game³ to test costly signalling and competitive altruism in men, by measuring whether public displays of altruism act as a mating signal. They found that men contribute more of a stake in the presence of women. Similarly, Tognetti, Dubois, Faurie and Willinger (2016) found that single men contributed more in an anonymous, repeated public goods game in groups where there were some men, and one woman, suggesting men are more altruistic when in the presence of a woman. In support, men typically signal handicaps and courtship displays in the form of altruism towards women of a reproductive age (see Tognetti, Berticat, Raymond & Faurie, 2012), suggesting altruism has evolved through inter-sexual competition.

(insert Table 2 here)

Altruism Increases Mating Success

In order to provide clear support as to whether altruism has evolved through mate choice, it is important to know whether altruism translates into mating success, i.e. if altruistic people have better mating success compared to non-altruistic people. For example, Arnocky, Piche, Albert, Oullette and Barclay (2017) conducted two studies exploring whether altruism predicted mating success. In study one they found that, after controlling for personality, men (not women) who scored higher on self-reported

³ A public goods game involves multiple players deciding how much money or tokens to put into a pot, or a 'public good'. This then gets distributed based on players' decisions made during the game.

altruism reported having more sexual partners (lifetime and casual) than those who scored lower on altruism. Furthermore, altruistic men and women considered themselves to be more desirable to the opposite sex than non-altruists. In study two, participants took part in a dictator game, where they could choose to donate a hypothetical win (through a prize draw) to a charity. The authors found that altruism, in the form of donations, predicted the number of sexual partners over a lifetime (for men, not women). Furthermore, men and women who donated reported more casual sexual partners over their lifetime. Donations correlated with the frequency of sexual activity with their current partner, in study one, but not in study two.

Further evidence comes from Stavrova and Ehlebracht (2015) who investigated relationship status and self-reported prosocial tendencies in a large pool of longitudinal data. The authors found that single, prosocial individuals had more successful dating encounters and increased odds of finding a romantic partner than non-altruists, even when controlling for personality and individual differences (the authors identified mating success as a steady partner, thus eliminating one-night stands). These findings provide support that altruism increases mating success in the real world.

Physical Attractiveness

When exploring the link between altruism and mate choice, researchers typically focus on manipulating physical attractiveness, and thus exploring whether there are differences in altruism projected towards attractive compared to unattractive recipients. Previous studies investigating sex differences in altruism have found what Hamermesh and Biddle (1994) call the *beauty*

premium, also known as the *attractiveness halo effect*. For example, physically attractive people are perceived by others to be happier, more successful, and honest than unattractive people (Dion, Berscheid & Walster, 1972). The attractiveness halo effect is present in educational contexts (see Hamermesh & Parker, 2005 who found attractive academic staff were evaluated more positively than unattractive academics) and in the movie industry, with physically attractive people being portrayed in more positive roles compared to unattractive people (Smith, McIntosh & Bazzini, 1999). The beauty premium is also present in recruitment and the business world with employers often seeking and hiring attractive people over unattractive people (Cash & Kilcullen, 1985).

When reviewing the attractiveness halo effect, there appears to be differences in the expectations people have of attractive people, which can differ by sex. For example, attractive females are considered to possess positive personality traits compared to unattractive females (Segal-Caspi, Roccas & Sagiv, 2012). Attractive people are treated more favourably, thought to be more intelligent, kinder, healthier, and socially competent than unattractive people (Langlois et al., 2000). A reason why attractive individuals are seen and expected to be socially competent may be because they are more comfortable in social situations due to the strong halo effect associated with being physically attractive (Colvin, 1993). Attractive people are also treated favourably in romantic relationships (Simpson, Gangestad & Lerna, 1990). These are prime examples of the beauty premium in action, in a multitude of contexts, providing an insight into how powerful a feature physical attractiveness is.

Physical Attractiveness and Altruism

According to Stirrat et al. (2011), sharing during the courting phase may have an impact on gaining a successful mate. For example, men who share and provide food are likely to be favoured by women in the mating market (Bliege, Bird, Bird, Smith & Kushnick, 2002; Gurven, 2004). Furthermore, Stirrat et al. (2011) explored the effects of self-rated attractiveness and the attractiveness of prospective partners on food sharing in men and women, finding women preferred men to pay for a meal. Self-rated physical attractiveness affected the demands made by both men and women, with men agreeing to pay for meals with attractive women, whereas women preferred attractive men to pay for their meals compared to unattractive men. Furthermore, attractive women were more interested in engaging with attractive men who paid for their meal. Stirrat and colleagues provide support for the link between physical attractiveness and altruism in mate choice contexts.

Using facial images, Bhogal, Galbraith and Manktelow (2016a) found that when presented with hypothetical scenarios, men were more altruistic and cooperative towards attractive women compared to unattractive women. They also explored whether sexual and dating intention, i.e. how interested they were in getting close to the person in the image, sexually, and how likely they wanted to go on a date with the person in the image influenced altruism and cooperation. Bhogal et al. (2016a) found that sexual intention and dating intention were drivers of altruistic and cooperative tendencies in men, particularly towards attractive women. This finding has been applied to a real-world task in the digital world, whereby men are more responsive and prosocial towards help requests made by attractive, compared to unattractive women on social networking sites (Schwarz & Basfeld, 2018).

Farrelly et al. (2007) asked participants to take part in a computer simulation task exploring altruistic motivation where participants played four economic games. Those who cooperated were rated as more attractive than those who defected when playing a prisoner's dilemma game. Men were more cooperative with opposite sex targets than women when playing the standard dictator game. Men and women cooperated more with women in the charity dictator game. Both men and women were more cooperative with attractive members of the opposite sex. Furthermore, cooperative players were perceived as more attractive. The authors suggest that 'minor economic costs might bring large reproductive rewards' (p. 326). Farrelly et al. (2007) provided strong support that altruism and cooperation may have been shaped by sexual selection.

Furthermore, Lucas and Koff (2013) tested similar hypotheses using facial images. They found that when asking participants to play ultimatum and dictator games with images (pre-set for attractiveness)⁴, women offered more to attractive men than unattractive men. In addition, women were more selfish when distributing to attractive female images, which may be due to intra-sexual competition. They found that both attractive men and attractive women received more than unattractive people, suggesting that investing in cooperative or altruistic acts may increase one's attractiveness and likelihood of securing a mate.

Van den Bergh and Dewitte (2006) investigated the effect of sexual attraction on whether a responder would accept a proposer's offer before playing an ultimatum game. They found that when male recipients viewed images of attractive women, rates of acceptance were higher compared to the control group where men viewed landscape images. In addition, Zaatari, Palestis and

⁴ The ultimatum game is a two-person game involving a proposer and responder. The proposer is given a sum of resources and must share those with responder. If the responder rejects an offer, neither player receives any of the resource. The dictator game is a simplified version where the dictator can keep the whole stake. The recipient's role in the dictator game is passive.

Trivers (2009) explored whether decisions in the ultimatum game were influenced by facial symmetry and attractiveness of the facial image. They found that participants rated symmetrical faces as more attractive than asymmetrical faces, offering more to images they found to be attractive.

Previous studies investigating physical attractiveness and altruism have largely involved hypothetical scenarios and photographs. For example, using facial images, rated by judges, Solnick and Schweitzer (1999) found that attractiveness influenced the decisions made by participants. Participants were altruistic towards attractive male and female images. In addition, when participants play the prisoner's dilemma, people cooperate more than defect with attractive compared to unattractive people (Mulford, Orbell, Shatto & Stockard, 1998).

A limitation of the research across the field is that researchers seldom take self-rated attractiveness into account when exploring altruism and mate choice. Because men of higher mate value have more mating opportunities, when sharing resources, they may be more conservative, whereas men of lower mate value may provide more resources in order to maximise success in retaining a mate (Hill & Reeve, 2004; Stirrat et al., 2011). For example, when playing the ultimatum game, male responders accept unfair offers from attractive female proposers compared to unattractive female proposers (Ma, Hu, Jiang & Meng, 2015).

Bhogal, Galbraith and Manktelow (2017) argue that much of the literature exploring altruism and sexual selection involves economic games where participants are not engaging with 'live' people, limiting the applicability of research in the area. Much of the literature discussed so far involves hypothetical scenarios, facial images, and hypothetical stakes, which questions the validity of

research tying altruism and mate choice. Saad and Gill (2001) explored sex differences in altruism when playing an ultimatum game, face to face. They also explored the influence of physical attractiveness as a potential moderator of altruism (finding it had no influence, inconsistent with previous literature). They found that men gave more of the stake to women and less to men. Furthermore, Bhogal et al. (2017) asked participants to play a two-round ultimatum game with chocolate coins as the monetary incentive (participants played in opposite-sex dyads). The authors hypothesised that participants would offer more coins and more frequently accept offers from those they considered attractive. Their findings provide no support for the hypothesis that people are altruistic and cooperative towards those they find attractive. In addition, they explored whether self-rated attractiveness predicted altruism, also finding no support. Their study highlights the fact that methodology appears to be an important factor in the field, which will be discussed further.

Furthermore, in Bhogal, Galbraith and Manktelow (2016b), participants took part in two one-shot, anonymous dictator games where dictators were given varied resources to distribute with the recipient. In study one, they found that when distributing chocolate coins, dictators were fair with all recipients, irrespective of how attractive they considered recipients to be. In study two, they included a real-effort task where participants were required to earn their stake through taking part in a quiz. Again, they found that when faced with forced choice (the researchers used 5 £1 coins which participants could take away with them), participants were altruistic towards most recipients, regardless of attractiveness. The authors also found that self-rated attractiveness was not related to offers made.

Evident by the literature, we can see that there is inconsistency in the findings exploring prosocial behavior and mate choice. Although most studies provide support that men display altruistic behavior towards attractive women, we can see from recent evidence that when stakes and procedural changes are made, the findings do not always replicate. Methodology surrounding these studies appears to be inconsistent, which may be driving the inconclusive findings observed. These null effects, which show that not all findings can be replicated in the field, are informative to our understanding of the research and must be discussed, specifically exploring how research was conducted, as opposed to focusing only on significant results (see Earp & Trafimow, 2015; Hyman, 2017; Locascio, 2017), and in this case, research exploring altruism and mate choice. Furthermore, this review paper shows how recent findings in the field are challenging existing research exploring altruism and mate choice, arguing that the findings show that methodology is a crucial factor in the field, particularly when suggesting public displays of altruism are driven by mate choice.

In addition, the resources used to determine altruistic donations also vary across studies, which may be leading to inconsistent findings. For example, Bhogal et al. (2017) used chocolate coins, whereas Bhogal et al. (2016a) included hypothetical scenarios, both yielding varied findings. The research discussed in this section explored studies using economic games, or real effort tasks, whereby participants display altruistic behavior towards potential partners, and those of high attractiveness. Evident from Table 2, we can see how findings differ according to methodology and stakes. Studies adopting correlational designs often yield differing findings compared to experimental designs. Furthermore, studies conducted with 'live' participants do not replicate

significant effects found when studies are conducted using online simulations, facial images and hypothetical mates. Next, we discuss methodology adopted in the field, primarily focusing on the limitations of using game theory to explore the link between altruism and mate choice.

Game Theory

Research exploring prosociality in the laboratory has largely involved economic games based on the paradigms of game theory. Game theory provides us with a useful methodological framework to research the conditions in which cooperation and conflict take place (Camerer, 2003; Tan & Forgas, 2010), allowing us to quantify, describe and model decision making processes in social situations, particularly in relation to interdependent decision making, where outcomes are dependent on the decisions made by multiple persons. Game theory allows us to study the everyday games we play, which can be predicted by models of cost and reward, intended to resemble real life social interactions (Binmore, 2007). The aim of a game-theoretical framework is to investigate the decisions people make, considering the decisions and strategies made by others, and the outcome of those decisions. Typically, the outcomes of the strategies played are influenced by reward and loss, which is further influenced by the strategies adopted by all players involved. Participants' decisions affect the outcomes of both themselves and others (Komorita & Parks, 1999). Game theory provides us with an invaluable set of tools whereby we can predict the strategies we can use, leading us to the best possible outcome.

Game theory relies on studying *rational* behavior, suggesting those involved in exchange are self-serving agents. However, this notion of complete rationality has been challenged, as we do not always have complete information in social situations, thus reducing our ability to make *completely* rational decisions (Simon, 1982). The models within game theory assist researchers to 'break down' real life phenomena, so that behavior can be studied in the laboratory, regarding which predictions can be made, tested and drawn (Williams, 2013).

A Question of Methods: Moving Beyond Game Theory

Research investigating prosocial behavior has observed altruism in virtual environments, which has largely been conducted online, or using online simulations (Wischniewski et al., 2009). According to Eckel and Grossman (1998), the varied findings when using economic games may be due to a lack of control on experimenter effects such as anonymity, monetary stakes, and social distance (Campanhã, Minati, Fregni & Boggio, 2011; Wu, Leliveld & Zhou, 2011a).

Decisions made in economic games are largely driven by strategy and risk (Eckel & Grossman, 1998). There is a cost to not acting prosocially, leading to an increased chance that other players can reject offers made by proposers or dictators, which means we are unable to explicitly state whether prosocial donations are driven by mate choice contexts or reputational influences, particularly when using game-theoretical paradigms to explore altruism and mate choice. Furthermore, there is also a social cost to not cooperating. Rejecting an offer reduces the likelihood of being chosen for future interactions by the proposer/dictator and any of

his or her associates (André & Baumard, 2011). Reputation management and social desirability may be reinforced when participants are playing these economic games. In support, participants have been found to be influenced by the knowledge that they are being observed, not necessarily directly, but even if they are being observed indirectly (Kurzban, DeScioli, & O'Brien, 2007), again suggesting there may be alternate factors at play when using economic games to explore the role of altruism in mate choice. This further emphasizes the need to acknowledge alternative theories explaining the evolution of altruism, which were outlined at the beginning of this paper.

One of the limitations of using economic games is that social desirability and reputation management effects may influence in-game decision making. Participants may be influenced by social desirability as to how much of the stake they should offer to the recipient. In support, increasing anonymity and social distance between the participant and experimenter may influence altruism (see Hoffman, McCabe, Shachat & Smith, 1994).

A further discussion point relates to the validity of economic games, of which there are differing views. On one hand, altruism observed in laboratory dictator games is strongly correlated with dictator games in field studies, thus suggesting the dictator game has ecological validity (Benz & Meier, 2008). Furthermore, natural field data investigating altruistic behavior has found that games such as the dictator game have ecological validity as they can be modified to resemble real-life scenarios (Falk & Fehr, 2003). On the other hand, Winking and Mizer (2013) found that there is no relationship between offers in economic games and real-life cooperation, thus contesting the view that economic games have ecological validity. These varied opinions strengthen the notion

that methodology used to explore whether public displays of altruism are driven by mate choice are driving these inconsistent findings.

Economic games were designed by economists to measure the extent to which behavior diverges from the strict assumptions of rational choice and game theory regarding self-interest and resource maximisation. As a result, there is some contention that economic games do not represent social situations well, thus lacking ecological validity, simply because they do not resemble the way we behave in our day to day lives (Baumard, 2016). As a result, people can see economic games as moral dilemmas, as opposed to economic transactions (see Cronk, 2007). For example, people do not usually receive sums of money without putting any effort in, besides lottery wins or inheritance. As a result, participants view economic games as moral tasks, whereby people behave *moralistically* as opposed to maximising personal profit. People rarely give someone else's money to a beggar or pick random people in the street and decide how to distribute a given stake. These criticisms of economic games further suggest that there may be alternative factors at play when using economic games to explore the link between mate choice and altruism.

As argued previously, one of the major disadvantages of observing prosocial behavior in the lab is related to external validity. Researchers argue that the issue relates to participants behaving as though they are being observed due to methodology adopted in such experiments (Fessler, 2009; Gigerenzer & Gigerenzer, 2005; Hagen & Hammerstein, 2006; Haley & Fessler, 2005), such as the presence of researchers (Winking & Mizer, 2013). A further limitation relates to the fact that human beings have

evolved mechanisms whereby we see social exchanges as potential long-term relationships, particularly as our ancestors lived in close proximate groups, where anonymity was not always possible (Cosmides & Tooby, 2005; Sun, 2013). As a result, humans may have evolved by default, to cooperate (even with those we will not necessarily meet again), rather than defect, as defecting risks the benefits that arise from being cooperative (Delton, Krasnow, Cosmides & Tooby, 2011b; Krasnow & Delton, 2016). These facts suggest how complex prosociality is, and the factors which influence the measurement of prosocial behavior.

Farrelly, Moan, and White (2015), argue and provide strong evidence for the need to adopt alternative measurements and tasks to measure altruistic behavior apart from financial cost/reward. Farrelly and colleagues find that people are willing to incur more costs in order to punish those who violate social norms and contracts, going beyond the typical paradigm of economic games and financial reward/costs. Farrelly et al. (2015) argue that much of the literature exploring the evolution of altruism using economic games can only explain financial altruism. They suggest that future research should adopt experimental methodologies to measure how willing people are to incur non-financial costs to help others. This standpoint provides a further point to consider in research exploring altruism and mate choice, and that is of resources and stakes used in economic games. Much of the research involves either 1) hypothetical financial stakes, or 2) small financial endowments. However, we observe altruism in a variety of ways, which can be non-financial, such as giving up one's seat on public transport or helping someone with directions where there is a time cost. In support, recent evidence suggests that when we replace the dictator game with a simple allocation exercise using a resource which is relevant to the sample, such as research credits for psychology students (research credits are often used by

Psychology students to assist them in collecting data for their own projects), both male and female students show preferential altruism towards attractive, compared to unattractive potential mates (Bhogal, Bartlett & Farrelly, 2018). However, their study found no effect of the participants' gender on altruism, further showing how varied the findings are when methodological changes are implemented.

The findings in relation to sexual selection and altruism have produced mixed results, with contemporary literature using a variety of methods providing mixed support for the sexual selection hypothesis as an explanation for altruistic behavior. Future research should adopt frameworks where the participants' decisions should have no reputational consequences (consistent with Mifune, Hashimoto, & Yamagishi, 2010; Yamagishi & Mifune, 2008 who find that altruism reduces when allocations are made privately). The inconsistent results in research exploring altruism using economic games may be due to what Zizzo (2010) terms as cognitive experimenter demand effects. These are effects related to the experimental instructions associated with economic games. For example, Winking and Mizer (2013) argue that when participants are informed that they *may* offer some of the stake to the recipient, they might be automatically considering the altruistic option. This is because they have been informed that they may choose to give some of the stake to the recipient, compared to if it is explicitly emphasized that they can keep all the stake (Bardsley, 2008; Peterson, Kurzban & McCullough, 2013), suggesting instructions matter when conducting studies using economic games. In support, Hoffman and Spitzer (1985) found that when framing the ultimatum game as a 'sharing game', offers tend to increase compared to when it is framed as a negotiation exercise using the words 'buyer' or 'seller', thus suggesting economic

games are sensitive to framing effects, adding further support that there are limitations to the methodological approaches used by researchers in the field. An issue with rectifying or dealing with this confound is that economic games cannot be played without clear instructions, therefore being completely free from these confounding effects is a difficult challenge to those researching altruistic behavior in the laboratory.

According to previous research (Dana, Weber & Kuang, 2007), increased anonymity has been found to decrease altruistic behavior and increase selfish behavior, although researchers have argued that maintaining anonymity is important in reducing reputation management effects (e.g. Franzen & Pointer, 2012a). Bhogal et al. (2016b) found that increasing anonymity between participants, and between experimenter/dictator had no bearing on altruistic behavior. As Winking and Mizer (2013) state 'despite assurances of anonymity, participants must still somehow record their decision with the knowledge that it will be reviewed and analysed' (p. 289), which is a limitation of using economic games to explore altruism and mate choice, particularly if researchers are arguing that in-game decisions are driven by mate choice motivation. Therefore, the impact of reputation management and social desirability may have been present even when exploring altruism using economic games. Methods should be implemented to allow participants to play economic games free from reputation management, which is a difficult challenge. Due to the benefits of reciprocity evolved through our ancestral past, we intrinsically believe that we may benefit from being prosocial, because we are primed into believing we will meet those we are cooperating with, even though we are told our offers will not be seen by other participants. As a result, game theory, or rational choice theory, fails to consider evolved mechanisms to be fair, cooperative and

reciprocal. This therefore makes us question the use of behavioral game theory when exploring the link between altruism and mate choice.

A further discussion point relates to monetary incentives and how participants acquire them. Traditional economic research involves a stake, which is freely given to participants without any effort made in obtaining it, which is rare in the real world (Wright, 1999). People do not give away resources freely. Participants may see themselves as having more rights over resources they have earned and allocate earned resources differently compared to those which are simply provided to them to distribute (Baumard et al., 2013). Baumard and colleagues argue that when dictators have the chance to earn their resources, they assess whether they or the recipient have a right over the endowment before splitting the stake.

Future considerations

There are limitations to only focusing on physical attractiveness when exploring displays of altruism in economic games. For example, we often assume that a woman's physical attractiveness is the best predictor of her mate value, however, research shows that non-physical traits also contribute to one's mate value and fitness. In support, Kniffin and Wilson (2004) argue that one's attractiveness is a combination of physical and non-physical traits (such as intelligence, sense of humour and whether one is hardworking or not) rather than physical attractiveness alone.

Future research could also incorporate cultural differences as well as attraction when investigating altruistic behavior. For example, nationality and the economic stability of a country have been reported to have an impact on decisions made when playing the ultimatum game (Henrich et al., 2001). Henrich et al. (2005) argue that altruistic behavior may be related to the size of the economies in which the sample resides. The larger the economy, the more altruistic the participant may be. Benenson et al. (2007) argue that those who have been brought up in lower socioeconomic environments may trust less and expect less reciprocation compared to those who have been brought up in higher socioeconomic environments. However, those in developed countries tend to favour fairness in terms of the 50/50 split, regardless of their economic position (Sun, 2013). Therefore, we may find that those from a smaller economy may behave more selfishly compared to those from a larger economy.

In summary, we have reviewed the literature exploring altruism as a courtship display, the desirability of prosocial traits in mate choice, limitations of the methodology adopted in this research and ideas for research to further explore the role of prosocial behaviors in mate choice. We believe that the inconsistencies found in the literature are driven by methodological differences across studies. There are methodological issues in using a behavioral game theoretic approach to exploring the role of altruistic behavior in mate choice, as well as issues surrounding the use of static facial images to assess desirability towards prosocial partners, evident by the variety of methods used across studies, yielding varying findings (see Table 1 and 2).

There are three take-home messages in this review paper; 1) the consistent findings which show that altruism has evolved as a mating signal, 2) the inconsistent findings showing altruism has not evolved as a mating signal, including the fact that

methodology appears to be driving this inconsistency, and finally 3) unresolved issues that future research should attempt to confront.

Compliance with Ethical Standards

On behalf of all authors, the corresponding author states that there is no conflict of interest. No human participants were involved in this study, as this paper is a review paper.

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Table 1: Key features relating to studies exploring the desirability of prosociality in potential mates.

Authors	Methodology and stimuli	Sample Size	Hypothesis supported?	Sex Difference
Barclay (2010)	Vignettes	<i>n</i> =305	Yes	Yes
Bhagal et al. (2019)	Modified Mate Preference Questionnaire (Buss, 1989)	<i>n</i> =102	Yes	Yes
Ehlebracht et al. (2018)	Video clips (Economic game: Dictator Game)	Study 1 <i>n</i> =75	Yes	N/A
Farrelly (2011)	Mate Preferences towards Altruistic Traits scale (Phillips et al. 2008) and vignettes	Experiment 1 <i>n</i> =89, experiment 2 <i>n</i> =289, experiments 3 and 4 <i>n</i> =109	Yes	N/A
Farrelly (2013)	Mate Preferences towards Altruistic Traits scale (Phillips et al. 2008)	<i>n</i> =384	Yes	Yes
Farrelly & King (2019)	Facial images and scenarios	<i>n</i> =189	Yes	No
Farrelly et al. (2016)	Facial images and scenarios	<i>n</i> =202	Yes	N/A
Guo et al. (2017)	Q-sort technique	<i>n</i> =200	No	No
Kelly & Dunbar (2001)	Vignettes/profiles	<i>n</i> =120	Yes	Yes
Margana et al. (2019)	Facial images and scenarios	<i>n</i> =198	Yes	N/A
Moore et al. (2013)	Facial images and vignettes	<i>n</i> =67	Yes	Yes
Phillips et al. (2008)	Creation of the Mate Preferences towards Altruistic Traits scale	Experiment 1 <i>n</i> =380, experiment 2 <i>n</i> =340, and experiment 3 <i>n</i> =398	Yes	Yes

Table 2: Key features relating to studies exploring prosocial behaviours as courtship signals.

Authors	Distribution Task/Economic Game	Design and sample size	Resources	Sex Difference	Hypothesis supported?	Stimuli
Bhogal et al. (2016a)	Hypothetical vignettes/scenarios	Experimental ($n=187$)	Hypothetical stakes	Yes	Yes	Facial images and scenarios
Bhogal et al. (2016b)	Economic game (Dictator Game)	Correlational (Study 1 $n = 212$; Study 2 $n = 188$)	Study 1 = 10 chocolate coins, study 2 = £5.	No	No	Live participants
Bhogal et al. (2017)	Economic game (Ultimatum Game)	Correlational ($n=138$)	Varied	No	No	Live participants
Bhogal et al. (2018)	Economic game (Dictator Game)	Experimental ($n=199$)	Hypothetical non-financial resource	No	Yes	Facial images
Farrelly et al. (2007)	Economic games (Mutualism game, prisoner's dilemma, standard dictator game and the charity dictator game)	Experimental ($n=231$)	Hypothetical stakes	Yes	Yes	Facial images
Griskevicius et al. (2007)	Hypothetical spending	Experimental (Study 1 $n=159$, study 2 $n=168$, study 3 $n=199$ and 4 $n=168$)	Hypothetical spending	Yes	Yes	Facial images
Iredale et al. (2008)	Economic games (charitable donation game)	Experimental ($n=90$)	Earned up to £24	Yes	Yes	Online simulation whilst being observed by a live confederate
Jensen (2013)	Economic games (dictator game, public goods game & trust game)	Experimental ($n=92$)	Hypothetical stakes with a chance to win \$350	N/A	Partial support	Online simulation whilst being observed by a live

						confederate
Kawamura & Kusumi (2017)	Vignettes	Experimental (Study 1 $n=1584$, study 2 $n=1336$)	Hypothetical helping	Yes	Yes	Vignettes
Saad & Gill (2001)	Economic game (Ultimatum Game)	Experimental ($n=238$)	\$10	Yes	No	Live participants
Schwarz & Basfeld (2018)	Email, profiles and help requests	Experimental (Study 1 $n=110$, study 2 $n=132$ and study 3 $n=298$)	Study 1 and 2 (direct helping) and study 3 (hypothetical helping)	N/A	Yes	Help requests via email
Solnick & Schweitzer (1999)	Economic game (Ultimatum Game)	Experimental ($n=70$)	Hypothetical stakes	Yes	Partial support	Facial images
Tognetti et al. (2016)	Economic game (Public Goods Game)	Experimental ($n=320$)	Hypothetical stakes	Yes	Yes	Online simulation
van Vugt & Iredale (2013)	Economic game (Public Goods Game)	Experimental (Study 1 $n=136$, study 2 $n=60$)	£3/£1	Yes (experiment 1)	Yes	Photographs
