NONINDEPENDENT MATE CHOICE IN HUMANS

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by

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ABSTRACT

Mate choice copying is the most studied type of nonindependent mate choice, i.e. mate choice that is influenced by the choices of other same-sex conspecifics (usually females). In copying, the probability of a male being chosen by a female ('focal' female) increases if he has previously been chosen by other females ('model' females) and decreases if he has been rejected. I critically review the non-human literature and conclude that from an evolutionary perspective copying is ill-suited to monogamous or relatively monogamous species like humans. I propose instead a related process where females are influenced not by a male's success at securing mates but by the quality of females that choose him. Although sometimes described as copying, this type of nonindependent mate choice is characterized by distinct evolutionary dynamics and ecological requirements, leads to different testable predictions and must therefore be urgently distinguished from mate choice copying. The term mate quality bias is suggested as an appropriate term for this phenomenon. I also report experimental studies that presented female raters with both static and video images of model females and their supposed partners. The two main findings to emerge from these experiments are a) the main - and perhaps the only - relevant cue in the model female is attractiveness and b) experimental studies can suffer from reduced external validity and need to be supplemented with non-experimental approaches. In line with this latter finding, I report one of the first non-experimental studies of nonindependent mate choice in humans. This involved the administration of a novel questionnaire to a large sample (n=401) of male and female undergraduates. The results of this study provide strong

support for nonindependent mate choice in humans a) being an empirical reality and b) influencing female, but not male choice. Finally, I report two experimental studies which examined how a man's partner influences male-male assessment and competition. The first used the dictator and ultimatum games to examine if offers made to male recipients were influenced by the attractiveness of the recipient's partner. The second used the Wason selection task to examine whether male subjects' cheater detection faculties are influenced by the attractiveness of the target male's partner (used here as a proxy for dominance). Although the results were generally in the expected direction, experimental manipulation of female partner attractiveness did not significantly affect male raters' perceptions of, and behaviour towards, the target male. The thesis concludes with a critical evaluation of the results obtained herein and suggestions for future research.

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Chapter 1: Mate choice copying and nonindependent mate choice in non-human animals: a critical review.

While the suggestion that females may be influenced by each other's mate choice has appeared sporadically in the literature since at least the 1970s (e.g. Wiley, 1973; Lill, 1974; Bradbury & Gibson, 1983), the systematic study of mate choice copying did not begin until the early 1990s. It was then that a string of seminal papers (Wade & Pruett-Jones, 1990; Dugatkin, 1992; Pruett-Jones, 1992) formalized our conceptual understanding of this phenomenon and laid the foundations for the large body of research that has since followed. In this chapter I will critically summarize the main findings of the non-human literature, evaluate the progress achieved and suggest avenues for future research.

1.1 Tinkering with the definition.

The standard definition of mate choice copying has been given by Pruett-Jones (1992), and involves two distinct probabilities that a male will be chosen by a female. The absolute probability of choice results from the female's evaluation with her standard (or independent) adaptations for assessment. The conditional probability results when the female has knowledge of other females' choices. According to this definition,

> "Copying occurs when the conditional probability of choice of a given male by a female is either greater or less than the absolute probability of choice depending on whether that male mated previously or was avoided, respectively." (Pruett-Jones, 1992, p.1001).

In other words a female's knowledge of a male having mated with another female increases the probability that she will subsequently also select him as a mate, and knowledge of his having been rejected lowers the probability that she will subsequently select him. Intuitively the idea is straightforward. If a male has been selected or avoided by a female there is probably good reason for it, and a third female would do well to be sensitive to this information as she searches for a mate. Unfortunately, the above definition as it stands can accommodate various phenomena that have nothing to do with mate choice. For example the well-known tendency of animals to move in groups or use conspecifics as cues for habitat selection (Kiester, 1979) can lead to phenomena which outwardly conform to the above definition, but for which the term mate choice copying would be misleading. Such is the case in fallow deer (*Dama dama*), where the tendency of females to stay in groups as a method of avoiding harassment by males while visiting leks can add to the skew in the distribution of male mating success (Clutton-Brock *et al*., 1989). The first female on a male's territory can attract subsequent females, which in turn attract more females and so on (Clutton-Brock *et al.*, 1989). When on the territory, the females are then more likely to mate with the male, if for no other reason than proximity. This, however, could be more constructively viewed as a byproduct of a mechanism that has evolved for reasons other than mating, in particular

protection from harassment, rather than mate choice copying *per se* (Clutton-Brock & McComb, 1993; McComb & Clutton-Brock, 1994; Brooks, 1998).

It was problems like this that led Dugatkin (1996a) to amend Pruett-Jones' definition:

> "Mate choice copying occurs when: The conditional probability of choice of a given male by a female is greater than the absolute probability of choice depending upon whether that male mated previously. Further, the information about a male's mating history (or some part of it) must be obtained by the female via observation" (Dugatkin, 1996a, p.87).

While in the context of this stand-alone definition it is not immediately obvious, the last sentence is meant to mean that observing the mate choices of other females must be the *causal factor* of the difference between the absolute and conditional probabilities (see Dugatkin, 1996a, pp. 86-88).

Some brief remarks before concluding this section. Mate choice copying is a type of *nonindependent mate choice*, meaning female choice that is affected by the actions of other females (Pruett-Jones, 1992; Westneat *et al.*, 2000). The example of female aggregation discussed above is another instance of nonindependent choice, although, unlike copying, the nonindependence is not the direct result but rather the byproduct of

an adaptation, and one that is not even related to mate choice. While the idea of nonindependent mate choice is helpful in highlighting the fact that copying is not the only way females can influence one another, vigorously pursuing this idea to its logical boundaries can lead to an extensive list of generic phenomena, the biological importance of which is debatable to say the least. Westneat *et al*.'s (2000) list includes stimulus enhancement, stimulus reduction, contagion, inhibition, stimulus response, association-to-location, association-to-male, association-to-trait and finally a category they call 'cognition' (for explanation of these terms see Westneat *et al*. (2000)). For example in stimulus enhancement, copulation can attract, due to its conspicuous nature (loud, with violent motions etc.), the attention of a third female, which is thus more likely to accidentally take notice and subsequently copulate with this particular male. The authors conclude by criticizing the literature's narrow focus on mate choice copying (which in their conceptual scheme corresponds roughly to what they term association-to-male) and calling for a more 'balanced' consideration of alternative mechanisms of nonindependent mate choice. It is difficult to see how random non-adaptive processes like stimulus enhancement or other generic phenomena could justify the same degree of scientific scrutiny as an elaborate adaptation that systematically exploits social information for the benefit of its bearers. More importantly, it is difficult to imagine any other outcome to such a research program than an unexciting catalogue of stochastic across-species phenomena. Tellingly perhaps, Westneat *et al*.'s proposal for a more balanced approach has gone largely unheeded, and the research on nonindependent mate choice continues to focus overwhelmingly on mate choice copying.

1.2 The evolution of copying

1.2.1 A cost avoidance adaptation

Two general explanations have been offered to explain the evolution of mate choice copying. The first views it as a cost-avoidance or 'shortcut' strategy (Pomiankowski, 1990), whereby the copying female enjoys the benefits accruing to actively choosing females but avoids the sampling costs associated with active mate choice (Wade & Pruett-Jones, 1990; Gibson & Höglund, 1992; Pruett-Jones, 1992). These costs include the time and energy that must be spent evaluating potential mates, the risks of predation and harassment by rejected males, parasite exposure and sexually transmitted diseases (Pomiankowski, 1987; Reynolds & Gross, 1990; Andersson, 1994; Dugatkin & Höglund, 1995).

Using a simple algebraic argument Pruett-Jones (1992) has shown that a population consisting solely of choosers (x) can be invaded by a single copying mutant. He describes the average fitness E of the choosers as $E(x) = W+f-k$, where W is the mean heritable fitness of males, f the extra fitness benefits choosers gain due to their discrimination, and k the sampling costs (Pruett-Jones, 1992). Given that discrimination has evolved in this population f must be larger than k. A lone copying mutant (y) will gain the fitness advantage that accrues to choosers but without having to pay the sampling costs: $E(y) = W+f > E(x)$. As a result copying will invade the population. On the other hand a population that is made up entirely of copiers will end up making random

choices and revert to $E(y) = W$. A single mutant chooser will invade this population as long as $f > k$.

The preceding analysis illustrates that the ESS will be found somewhere between these two extremes, and will involve a mixed population that contains both choosers and copiers. It is not however necessary for the ESS to be reflected in frequency-dependent allelic frequencies. An alternative would be for all members of the population to be equipped with the cognitive adaptations for using both strategies, and to do so at some evolutionarily determined optimum frequencies. (Pruett-Jones, 1992). These frequencies will depend on a variety of factors. In his paper Pruett-Jones arrives at a chooser frequency of $p = 1 - (k/f)$, but his model includes the assumption that females visit prospective mates in pairs, something which will often not be the case. Nevertheless it can be seen in this simple equation that the lower the costs k relative to the benefits f, the more females will go through the trouble of choosing their mate independently. On the other hand the higher the sampling costs the more frequent copiers will be.

The cost-avoidance framework of mate choice copying provides researchers with a set of broad research avenues which surprisingly have remained almost entirely unexplored. One straightforward deduction is that mate choice copying is most likely to be found in species where females incur great mate choice costs, but to date no direct tests of this prediction have been made. Strong corroboration for this prediction could

be obtained, if, for example, a comparative study of closely related species that differ greatly in the costs of female choice revealed differences in mate choice copying in the expected direction.

Another element of the cost-avoidance framework is the co-existence in a population of the frequency-dependent behavioral polymorphism of choosers and copiers, so that copying is displayed by some but not all females, the rest engaging in active choice. Presumably, as discussed above, this frequency-dependent behavioral polymorphism can manifest within the same female. Alternatively, and this would certainly constitute a more exciting finding, a proportion of females could be genetically disposed to copying and the rest genetically disposed to choosing. We would, in other words, observe some females that always copy and others that never copy. Again, this research avenue has remained unexplored.

The only empirical studies to date that could be construed as bearing directly on the cost-avoidance framework have been conducted in the guppy (*Poecilia reticulata*). In a laboratory setting Briggs *et al*. (1996) sought to manipulate predation risk by placing a predator fish in an aquarium adjacent to female guppies in some but not all trials of a mate choice copying experiment. Their hypothesis was that females should copy more frequently when a predator was present, as a way of minimizing perceived predation costs. The results did not bear out this prediction, and females were no more likely to copy in the presence of a predator than they were in its absence. In another study

(Dugatkin & Godin, 1998), researchers tried to experimentally manipulate the time costs of mate choice by inducing hunger in some females while allowing unlimited access to food for others. The hypothesis was that hungry females should exhibit more copying behavior that satiated ones, in an attempt to minimize the time costs of mate choice and allocate any time thus economized into the search for food. Again, the results did not bear this prediction out. Only the most well-fed females engaged in mate choice copying, while the hungry ones apparently ignored the choices of other females (Dugatkin & Godin, 1998).

Does this mean that the cost avoidance hypothesis has been empirically disconfirmed? The results must be interpreted with caution for a number of reasons. Firstly, these experiments have been conducted on a single species, so it could be premature to generalize. Secondly, the artificiality of the laboratory settings may have affected the females in ways different to what would have been the case in the wild. A predator restrained behind a Plexiglas partition in an adjacent aquarium may represent an entirely different entity in the female's perception to a predator swimming freely down the stream. Thirdly, and perhaps more importantly, the time frame of these studies may differ greatly from that through which mate choice copying mechanisms are 'calibrated' in natural conditions. For example, assume that the general hypothesis is true and that increased predation risk in a natural population raises the frequency of mate choice copying. The most adaptive way in which females could take this increased risk on board would be developmentally, observing predation risks over the long run, not an a day-to-day and largely variable basis. At maturation they would thereby have a more

accurate global estimate of ambient predation risk and could adjust their mate choice tactics accordingly, presumably for life. In those instances where a predator did happen to be present, we should expect females to be more concerned with avoiding the predator rather than selecting sexual partners. An analogous argument could be made for the study that employed experimental manipulation of hunger (Dugatkin & Godin, 1998). Perhaps more important than the negative results of these two studies is the cost-avoidance hypothesis' inability to generate fruitful empirical research, something which is not the case for the second approach to mate choice copying.

1.2.2 Copying as an adaptation to facilitate discrimination

According to this framework, mate choice copying might be better understood by avoiding the classical cost-benefit analysis and focusing instead on the uncertainty or error component in the mate assessment process (Gibson & Höglund, 1992; Nordell & Valone, 1998; Uehara *et al*., 2005). Females try to estimate male quality via various physical, behavioral and social cues, but their estimate is subject to error, and wrong decisions are often made (Ryan *et al*., 2007). Under conditions of increased uncertainty any additional information that can contribute to better assessment should be used. Such is the case when, for instance, the males under consideration are closely matched for the relevant traits (size, coloration, courtship behavior, etc.). Another instance of increased uncertainty concerns young and sexually inexperienced females, which are perhaps not mature enough to evaluate males correctly, even if the males differ considerably in quality. Under such circumstances, copying the choices of others is

preferable to independent choice, even if poor decisions are occasionally copied (Wade & Pruett-Jones, 1990; Gibson & Höglund, 1992; Nordell & Valone, 1998). Without the benefit of copying, a female that cannot decide between two or more males has to make what is essentially a random choice. In the rest of the population, however, at least some of the females will be making successful decisions, so that copying others' choices is necessarily equal to or better than random choice, no matter how small the fraction of females that are choosing successfully. This perspective therefore provides a convincing solution to what was always the most obvious problem with mate choice copying, namely that there is a risk of copying poor decisions (Giraldeau *et al.*, 2002). Note that in this framework there is no generally no tension between choosers and copiers, frequency-dependent or not. All females are selected to rely primarily on their own independent assessment, and resort to copying only under conditions of uncertainty. Copying is therefore viewed as a facultative adaptation, and the relative rarity with which this phenomenon manifests might be due to the rarity with which the necessary conditions obtain in nature.

The predictions of this framework have been confirmed. It has been shown (in guppies and sailfin mollies, *Poecilia latipinna*) that females resort to copying when offered a choice between two closely matched males, but choose independently when the males differ greatly in quality (Dugatkin, 1996b; Witte & Ryan, 1998). This result is now so widely accepted that most studies of mate choice copying use closely matched males so as to maximize the probability of eliciting copying behaviour. Furthermore it has proven possible to manipulate the intensity of mate choice copying in a highly

predictable manner by manipulating not only the difference in quality between two potential mates but also the amount of information provided by other females (Dugatkin, 1998; Witte & Noltemeier, 2002). This second variable can be manipulated in two ways, namely by having more than one female choose a certain male and by having one female spend increasing amounts of time with him. In addition, it has been shown that while younger female guppies copy the choices of older females, the latter do not copy the choices of the former (Dugatkin & Godin, 1993). When given an opportunity to choose between copying an older or a younger female's mate choice, a younger female guppy tends to copy the older female's choice (Amlacher & Dugatkin, 2005). Overall, the choices of younger females are disregarded by older and other young females alike, whereas the choices of older females appear to influence both young and older females (Vukomanovic & Rodd, 2007). It should, however, be noted that Ophir and Galef (2004) found no evidence that virgin Japanese quail (*Coturnix japonica japonica*) females were more likely to copy than sexually experienced females.

In recent years there has been a tendency to place mate choice copying in the much broader context of public information theory (e.g. Nordell & Valone, 1998; Valone & Templeton, 2002; Danchin *et al.*, 2004; Kavaliers *et al.*, 2006; Valone, 2007; Mery *et al.*, 2009). Public information is an instance of inadvertent social information (ISI), or information that is provided inadvertently by animals as they engage in efficient performance of their activities (Danchin *et al.*, 2004). In particular, public information is a type of ISI that pertains to the quality of a resource (other types of ISI pertain to different kinds of information, Danchin *et al.*, 2004). The concept was originally applied to

foraging (Valone, 1989; Templeton & Giraldeau, 1995): an animal which after a brief inspection departs from a poor foraging patch, although merely tending to its own energy needs, inadvertently provides information to nearby animals about the poor quality of the patch. Likewise, animals that experience success in a particular patch persist in its exploitation and inadvertently signal the existence of a high quality patch. The difference between ISI and other kinds of social information (like signals) is that ISI is not produced intentionally. Individuals that generate public information are selected to perform as efficiently as possible, not communicate any information to others (Danchin *et al.*, 2004). The information is therefore highly reliable given that the risk of deception is minimized, but animals are predicted to rely more on public information in conditions of increased uncertainty (Nordell & Valone, 1998; Valone & Templeton, 2002; van Bergen *et al*., 2004).

This general copying strategy, applicable also to contexts outside mating, has been called *copy-when-uncertain* (Laland, 2004). The connection between public information and mate choice copying is straightforward. Females selecting or rejecting a male can be viewed as generating public information about the male's quality, and other females are expected to be sensitive to this highly reliable information when their own private information is insufficient or unreliable (Nordell & Valone, 1998). Apart from foraging and mate choice, the concept of public information has been extended to various other domains like breeding habitat selection and opponent assessment in fighting interactions (Valone & Templeton, 2002; Valone, 2007).

The importance of public information theory as an analogy that places mate choice in the big picture, alongside other domains like foraging and agonistic interactions, is obvious. At the same time, it is important to stress that mate choice is a unique adaptive problem, with special kinds of demands that clearly set it apart from other animal behaviors. As such, there can be no substitute for theory that is targeted specifically to mate choice copying, and, descending to an even lower level of analysis, theory tailored to specific ecologies, mating systems and species. (e.g. Dugatkin & Höglund, 1995; Stöhr, 1998)

1.3 Mate choice copying: social or genetic?

A widespread but inaccurate distinction in the literature pertains to an alleged ontological chasm between mate choice copying on the one hand and the standard or independent mate choice mechanisms on the other. According to this distinction, mate choice copying constitutes a social, and consequently 'non-genetic' influence on mate choice, while independent mate choice preferences constitute 'genetic' and consequently non-social influences on mate choice (e.g. Dugatkin, 1996b; 1998; Applebaum & Cruz, 2000; Witte & Noltemeier, 2002; Witte, 2006). Manifest mate choice is therefore shaped by two distinct forces that act independently of each other, the genetic and the social, and the interesting question concerns the possible outcomes of situations where these two independent forces conflict with one another. If the influence exerted by mate choice copying is strong enough, then its non-genetic/social influence

can ‘override’ the fixed genetic preferences that otherwise generally prevail (Dugatkin, 1996b; 1998; Witte & Noltemeier, 2002; Witte & Ueding, 2003; Witte, 2006).

The following example will help illustrate this line of reasoning. Female guppies have evolved a preference for orange body coloration in males, so that they generally prefer males with larger orange areas over those with smaller ones (Houde, 1987; 1988). Dugatkin (1996b) placed a model female next to the less orange of two males, and allowed a focal female that had observed this simulated choice to subsequently choose between the two males. He found that when the males differed by 12% or 24% on their total body orange area the focal female copied the choice of the model female, but did not copy when the males differed by 40%. Dugatkin couches these results in terms of a conflict between genes and the social environment, suggesting that when the males differed by 12-24%, cultural cues overrode genetic preferences, but when the difference was 40%, genetic preferences masked any cultural effects. He concludes by suggesting that the experimental protocol used in the study could be modified so as to examine ‘the relative strength of genetic and nongenetic factors’ on a variety of traits across species (Dugatkin, 1996b, p. 2773; see also Dugatkin, 1998; Witte, 2006 for similar discussions of these results).

This reasoning is based on the flawed premise that an animal’s environment is somehow independent of its genes. In reality an animal’s genes also determine its environment (Tooby & Cosmides, 1992; Tooby *et al*., 2003). Since the environment

(including the social environment) is infinite, selection, operating necessarily through genes, also must indirectly determine which part of the environment becomes relevant to the central nervous system (CNS) and consequently the behaviour of an animal (Tooby & Cosmides, 1992; Tooby *et al*., 2003). An animal's environment, social or not, is therefore inextricably linked to and determined by its genes, and the suggestion that the two are not only independent, but can even somehow go against each other, is not valid.

The notion of guppies that are caught in a battle between their genes and the environment, each pulling on opposite sides of the same rope, thus presents a misleading picture of Dugatkin's (1996b) fascinating results. To speak of influences and strength of influences, social or genetic, conceals rather than highlights the underlying processes. A more plausible interpretation of Dugatkin's results would be that the genes underlying the mate choice copying adaptations in the guppy have evolved to the point that female guppies are now highly selective as to the conditions under which they are influenced by conspecifics' choices. When two males differ widely in coloration, the guppy CNS does not allow the information about conspecifics' choices to integrate with the information arising from independent assessment, and the guppy does not copy. When the males are closely matched for orangeness, the guppy CNS responds to this similarity by transmitting the information about conspecifics' choices to those regions that underlie independent assessment, and the two streams of information are integrated to produce a final evaluation, which then determines manifest behavior. To achieve this level of sophistication in the guppy CNS more genetic information is

required, not less, regardless of whether on any given trial the guppy copies or not. The fact that this adaptation depends on the social environment for its inputs does not alter the fact that it is as ‘genetic’ in origin as any independent mate choice mechanism or preference.

1.4 The empirical record

I have compiled the available empirical evidence for mate choice copying in different species, along with their predominant mating system and unusual features (Table 1). Individual studies are classified as providing or not providing evidence for mate choice copying, with a separate category reserved for inconclusive studies. In arriving at these classifications I have mainly relied on the respective authors’ evaluations of their results. Earlier studies that were not conducted on the basis of a copying hypothesis but have been subsequently suggested as possible evidence for mate choice copying are not included here (see Pruett-Jones, 1992; Jamieson, 1995, and references therein).

Table 1. Compilation of empirical studies on mate choice copying in non-human animals. Unless noted otherwise, studies listed test for mate choice copying in females; those suggesting mate choice copying in males are indicated with an asterisk (*). Similarly, ** denotes studies that suggest generalized trait copying (i.e. copying of general male traits, not individual males), those marked * suggest mate choice copying via chemical signals, and † denotes field studies.**

Species	Evidence for mate choice copying	Studies providing no support for mate-choice copying	Inconclusive studies	System
Guppy (*Poecilia reticulata*)	Dugatkin 1992, 1996b, 1998, 2007; Dugatkin *et al*. 2002, 2003; Dugatkin & Godin 1992, 1993; 1998; Godin *et al.* 2005**; Vukomanovic & Rodd 2007; Amlacher & Dugatkin 2005 ; Godin & Hair 2009†	Brooks 1996, 1999; Lafleur *et al.* 1997		Promiscuous, no parental care
Sailfin molly (*Poecilia latipinna*)	Schlupp *et al.* 1994; Schlupp & Ryan 1997*; Witte & Ryan 1998, 2002*†; Witte & Noltemeier 2002**; Witte & Massmann 2003; Witte & Ueding 2003; Hill & Ryan 2006; Heubel *et al.* 2008			Promiscuous, no parental care
Japanese medaka (*Oryzias latipes*)	Grant & Green 1996	Howard *et al.* 1998		Promiscuous, no parental care
Deep-snouted pipefish (*Syngnathus typhle*)	Widemo 2006*			Reversed sex roles
Japanese quail (*Coturnix coturnix japonica*), (for reviews see White 2004; Galef, 2008)	Galef & White 1998* White & Galef 2000a**, 2000b*; Ophir & Galef 2003, 2004; Persaud & Galef 2005		White & Galef 1999b	Uncertain, probably mixed (polygamous/monogamous) with some degree of paternal care
Zebra finch (*Taeniopygia guttata*), (for discussion see Brown & Fawcett 2005; see also section 2.6)	Swaddle *et al.* 2005**, Drullion & Dubois 2008**	Doucet *et al*. 2004		Monogamous,life-long pairbonds and biparental investment
Black grouse (*Tetrao tetrix*)	Höglund *et al.* 1995†		Höglund *et al.* 1990†	Lekking

Fallow deer (*Dama dama*)		Clutton-Brock & McComb 1993; McComb & Clutton-Brock 1994		Lekking
Marine isopod (*Paracerceis sculpta*)	Shuster & Wade, 1991			Territorial, polygynous
Whitebelly damselfish (*Amblyglyphidodon leucogaster*)	Goulet & Goulet 2006†			Promiscuous with male territoriality
Sand goby (*Pomatoschistus minutus*)		Forsgren *et al*. 1996		Promiscuous with paternal care
Three-spined stickleback (*Gasterosteus aculeatus*)	Frommen et al. 2008	Patriquin-Meldrum & Godin 1998	Goldschmidt *et al.* 1993†	Promiscuous with paternal care
Perugia's limia (*Limia perugiae*)		Applebaum & Cruz 2000		Promiscuous, no parental care
Humpback limia (*Limia nigrofasciata*)	Munger *et al.* 2004			Promiscuous, no parental care
Ocellated wrasse (*Symphodus ocellatus*)	Alonzo 2008†			Promiscuous, with paternal care and male territoriality
Mouse (*Mus musculus*)	Kavaliers *et al.* 2006***			Polygynous, territorial
Great snipe (*Callinago media*)		Fiske *et al.* 1996†		Lekking
Mexican molly (*Poecilia mexicana*)	Heubel *et al.* 2008			Promiscuous
Amazon molly (*Poecilia formosa*)	Heubel *et al.* 2008			Gynogenetic
Common goby (*Potamoschistus microps*)		Reynolds & Jones 1999		Promiscuous with paternal care
Sage grouse (*Centrocercus urophasianus*)	Gibson *et al.* 1991	Spurrier *et al.* 1994		Lekking
Fruit fly (*Drosophila serrata*)		Auld *et al.* 2009		Promiscuous

Fruit fly (*Drosophila melanogaster*), (for discussion see Leadbeater 2009)	Mery *et al.* 2009**		Promiscuous
Brown-headed cowbird (*Molothrus ater*)	Freed-Brown & White 2009		Brood parasite with no parental care, uncertain mating system
Norway rats (*Rattus norvegicus*)	Galef *et al.* 2008***		Promiscuous, no paternal care
Pied flycatcher (*Ficedula hypoleuca*)		Slagsvold & Viljugrein 1999	Mostly monogamous with biparental care

An examination of the table shows that with the exception of the zebra finch (*Taeniopygia guttata*) all species where results consistent with mate choice copying have been found present with an element of polygyny or promiscuity. By far the best-studied model species are the guppy, sailfin molly and Japanese quail. The volume of operational replications and highly predictable nature of the results (see above, section 1.2.2) leave little doubt that mate-choice copying behaviour in these species is subserved by adaptive cognitive specializations. It should be noted, however, that in the guppy this phenomenon appears to manifest in some, but not all populations (Brooks, 1996; Lafleur *et al.*, 1997; Brooks, 1999). In addition to these species, preliminary evidence for copying exists in the mouse (*Mus musculus*), the Norway rat (*Rattus norvegicus*), deep-snouted pipefish (*Syngnathus typhle*), black grouse (*Tetrao tetrix*), brown-headed cowbird (*Molothrus ater*) whitebelly damselfish (*Amblyglyphidodon leucogaster*), humpback limia (*Limia nigrofasciata*), Mexican molly (*Poecilia mexicana*), Amazon molly (*Poecilia formosa*), a Gulf of California marine isopod (*Paracerceis sculpta*) and the ocellated wrasse (*Symphodus ocellatus*). In contrast to the aforementioned species, the pied flycatcher (*Ficedula hypoleuca*), fallow deer (*Dama dama*), sand goby (*Pomatoschistus minutus*), common goby (*Pomatoschistus microps*), great snipe (*Gallinago media*) and Perugia's limia (*Limia perugiae*) probably don't copy. The Japanese medaka (*Oryzias latipes*), three-spined stickleback (*Gasterosteus aculeatus*) and sage grouse (*Centrocercus urophasianus*) present a mixed picture, and more results are needed before definite conclusions can be drawn. Two very recent studies on different *Drosophila* species (*melanogaster* and *serrata*) have also produced

conflicting results (Auld *et al.*, 2009; Mery *et al.*, 2009; see also Leadbeater, 2009), and it will be interesting to see whether this is due to actual differences in copying behavior or the different methodologies employed in the studies.

Although the idea of mate choice copying first developed through field observations of lekking species[1] (Bradbury & Gibson, 1983; Losey *et al.*, 1986; Höglund *et al*., 1990; Gibson *et al.*, 1991; Marks *et al.*, 1994), the table shows that empirical studies are now overwhelmingly laboratory-based, concentrating mostly on fish (Witte, 2006), and to a lesser extent birds and mammals. This shift in emphasis is due largely to the ease with which certain model fish species can be studied in aquaria, and the increased control over confounding variables these laboratory studies afford (see Amudsen, 2003). Added to this, many fish (like the poeciliids so commonly used in mate choice copying studies) adapt well to captivity and their sexual behaviors are not adversely affected by the artificiality of their aquarium environment (Amudsen, 2003). Studies in leks, on the other hand, are more expensive and logistically demanding, often involve rather limited datasets and are notorious for their difficulty in controlling confounding variables.

The standard experimental design is a binary forced-choice task that takes place in an aquarium or cage (Dugatkin, 1992). A 'focal' female, constrained in a transparent canister in the centre of the apparatus, is typically made to choose between two closely-

[1] More on the historical origins of mate choice copying in section 2.3

matched (for size, coloration etc.) males that are restrained in transparent compartments on opposite ends of the apparatus. One of these males is confined alone in one side, while on the other side the second male courts a 'model' female that is also restrained in an adjacent transparent compartment. From her vantage point in the centre of the apparatus, the focal female can thus observe what appears to be a single, or unsuccessful, male on one side and a successful one on the other. After the focal female has observed this scene for some time (often 10 or 30 minutes) the model female is removed from her compartment, the transparent canister restraining the focal female is lifted, and she is allowed to swim freely around the tank for a predetermined amount of time. The prediction of the mate choice copying hypothesis is that the focal female will spend more time close to the successful male, a proxy measure of her interest and willingness to mate with him (Bischoff *et al*., 1985; Kodric-Brown, 1993; White & Galef, 1999a). Repeated trials of this experiment with different individuals can reveal significant deviations of the number of trials in which subjects prefer successful males from what would be predicted by the null hypothesis that successful and unsuccessful males have an equal probability of being selected (e.g. Dugatkin, 1992; Dugatkin, 1996b; Forsgren *et al*., 1996). The percentage of time or the absolute amount of time spent closer to either male can also serve as the dependent variable (e.g. Dugatkin & Godin, 1993; Dugatkin, 2007).

An alternative and increasingly popular experimental protocol that is used with the above apparatus is the preference reversal task (Dugatkin & Godin, 1992). Here both males are first presented alone, and the focal female expresses her affiliative

preference in the absence of a model female (i.e. on the basis of her independent assessment). Once the focal female's preference has been established, she is restrained in the transparent canister in the center of the apparatus, and a model female is introduced into a compartment adjacent to the male that the focal female did not initially prefer. The experimental design thus simulates a choice by the model female that apparently contradicts the focal female's preference. After the focal female has observed this scene for some time, the model female is removed and the focal female is re-tested to see if her affiliative preference remains the same or has reversed in the face of contradictory information by the model female. The latter case implies mate choice copying. Again, as in the standard protocol described above, a number of measures can be used as the dependent variable. For example, a parallel test-retest series of trials can be run in the absence of any model female to see how consistent focal females' preferences would otherwise tend to be across two consecutive trials. The frequencies of consistent choices in the mate-choice copying and control trials are then compared to test for significant differences (e.g. Dugatkin & Godin, 1992). Measures of absolute and relative time spent with the two males can also be used (e.g. Galef & White, 1998; White & Galef, 2000b; Witte & Massmann, 2003).

So far the discussion has focused solely on females, but the empirical record suggests that, given the appropriate conditions, males can also copy (Schlupp & Ryan, 1997; White & Galef, 2000b; Witte & Ryan, 2002; Widemo, 2006). Widemo (2006) found that male but not female pipefish appear to copy, a result that presents no challenge to mate choice copying theory, since in this species the roles of the sexes are reversed and

males are choosier. Sailfin molly males, like their female conspecifics, also copy each other's choices, which can be understood in light of the short time-window of female sexual activity (Schlupp & Ryan, 1997; Witte & Ryan, 2002). Because of this constraint males are under great pressure to assess a female's sexual receptivity, and mate choice copying could constitute a partial solution to this problem, with courting and mating serving as cues of sexual availability. Male molly copying might therefore contribute to the mating frenzies that are observed in the wild, when several males attempt to copulate with a female at the same time (Schlupp & Ryan, 1997). Also, a study with Japanese quail found that males significantly increased the amount of time they spent near previously non-preferred females after having observed them mating with another male 48 hours ago (White & Galef, 2000b).

An important feature of the empirical record concerns the findings that guppy (Godin et al., 2005), sailfin molly (Witte & Noltemeier, 2002) zebra finch (Swaddle *et al*., 2005; Drullion & Dubois, 2008), Japanese quail (White & Galef, 2000a) and fruit fly *Drosophila melanogaster* (Mery *et al*., 2009) females may copy not only other females' preferences for certain males, but generalize these preferences to other males with similar traits. In other words, a model female's preference for a male with a certain trait predisposes focal females to prefer all males with that trait, a process that if widespread could theoretically lead to cultural inheritance of mating preferences (Brooks, 1998). How generalized trait copying of this sort could evolve is not yet certain, but a simple haploid, two-locus model (one locus coding for copying, the other for the male trait) suggests this could be indirectly, through genetic hitchhiking on high-fitness genotypes (Servedio &

Kirkpatrick, 1996). Studies have often employed artificial, experimentally manipulated male traits, like colored leg bands and glued feathers, but Godin *et al*. (2005) found mate choice copying can even affect female guppies' preferences for male orange coloration, a natural trait that is known to affect mate choice (Houde 1987; 1988). Witte & Noltemeier (2002) also found that mate choice copying can affect female mollies' preferences for male size, a trait known to contribute to female molly choice (Marler & Ryan, 1997). The extent to which generalized trait copying manifests in nature, as well as its actual impact, if any, on cultural evolution, remains unknown. Theoretical studies have shown that female copying of a male trait could have diverse consequences on the evolution of the trait, depending on the set of underlying assumptions (Kirkpatrick & Dugatkin, 1994; Agrawal, 2001).

1.5 Directions for future research

1.5.1 Mate choice copying through non-visual modalities

Recent studies in rodents, animals heavily reliant on olfaction, suggest that mate choice copying in these species is mediated not by visual observation but by olfactory cues (Kavaliers *et al.*, 2006; Galef *et al.*, 2008). This bypasses what is one of the most restrictive prerequisites of mate choice copying, namely that copying females must be in spatio-temporal proximity to third party copulations (see Losey *et al.*, 1986). Kavaliers *et al.* (2006) showed that naïve female mice prefer odors of males that are associated with the odor of an estrous female over those of matched males that are not thus associated. This preference for male odors associated with odors of estrous females can even

negate females' instinctive aversion to odors of parasitized males. Females exposed to odors of parasitized males associated with odors of estrous females preferred them to those of non-parasitized males that were presented alone. These socially-induced responses to male odors appear to be mediated by the oxytocin system, since they are absent in females with deletions of the oxytocin gene (Kavaliers *et al.*, 2006). Evidence of chemically mediated mate choice copying also exists for Norway rats, where it was found that focal females prefer to mate with males that had recently engaged in sexual activity over males that had not, even though they had not witnessed the mating (Galef *et al.*, 2008). This effect was blocked when the focal females were rendered anosmic (Galef *et al*., 2008).

Recently, a study with brown-headed cowbirds provided the first evidence of acoustic mate choice copying (Freed-Brown & White, 2009). Females of this species emit a characteristic chatter sound when being successfully courted by males, and this vocalization makes it easy, in principle, for other females to gauge a male's success. Researchers played back to focal females male courtship songs that were either followed or not followed by female chatter, and found that focal females displayed more copulation solicitation displays (species-typical postures) when the male songs were followed by chatter (Freed-Brown & White, 2009). Results like this and those discussed in rodents above highlight the potential for a fruitful research program that will examine mate choice copying via non-visual modalities in various species, perhaps even in hitherto unimaginable ways.

1.5.2 Copying rejection

It is interesting to note that, with a single exception (Witte & Ueding, 2003), all empirical studies to date have focused on the first part of the definition of mate choice copying, namely the acceptance of a male. There are, however, strong reasons to believe that females should also be sensitive to the rejection of a male (Pruett-Jones, 1992; Witte, 2006). The reason this research avenue has not been pursued probably has to do with the increased difficulty of satisfactorily simulating the rejection of a male in the lab, and the inability of existing protocols to accommodate this scenario. Witte and Ueding (2003) tackled this problem by using video playbacks instead of live males. In a modification of the preference reversal protocol discussed above, focal females first chose between playbacks of males displayed on two opposing video monitors. After affiliative preference was established females were exposed, on one monitor, to pre-recorded video playbacks of a model female escaping the preferred male, while on the other monitor the original playback of the non-preferred male was again displayed. After this, females were retested by exposure to both of the original male playbacks. The results suggested that females modified their preferences on the basis of the information contained in the rejection scene, spending significantly less time near the monitors displaying images of the previously preferred male. More than half of the focal females even reversed their original preferences entirely. Future studies that address this problem with similar or different methodologies will tap into a practically unexplored area of empirical research that could prove at least as equally rewarding as what has been investigated so far.

1.5.3 The genetics of copying

As discussed above, no empirical study to date has examined whether copiers vs. non-copiers constitute two different morphs within the same population, a difference that if found, could perhaps signal the existence of underlying genetic variation.

I am aware of only one empirical study in the literature that has examined the genetics of copying (Dugatkin & Druen, 2007). This did not conceptualize copying versus choosing as discrete behavioral categories, but rather viewed copying as a tendency that varies on a continuum from no copying to extreme copying, and examined whether there is heritable genetic variation in this trait by comparing copying in mother guppies to that of their female offspring. There was very little support for a heritable component in copying behavior (Dugatkin & Druen, 2007).

It is easy however to see the benefit of studies that will examine the genetics of copying by contemplating the questions that would be raised if a future study, perhaps in another species, were to uncover a heritable component in copying behavior. Is the variability indeed maintained by frequency dependent selection or is it the result of correlated variation in the ability of females to discriminate quality? Is there any other, perhaps hitherto unnoticed trait that correlates with this heritability? Will the results generalize predictably to other species? Alternatively, if no heritable component is found, yet discrete behavioral morphs are established, what are the developmental

events which spur development one way or another? Considerations like this suggest that insights into the genetics of copying will undoubtedly feed back into studies of behavior, and enrich our understanding of this phenomenon in ways that may not be forthcoming simply from behavioral studies alone.

1.5.4 Mate choice copying and genetic compatibility

Experimental studies of copying generally make no attempt to identify the precise nature of the benefits that copying confers. Given however that most studies are conducted with non-resource based mating systems, the implicit assumption has probably been that genetic benefits in the form of 'good genes' are the driving force behind the evolution of copying. What happens when mate choice is based not on 'good genes' but on compatible genes, as for example when females seek mates that will lead to heterozygous offspring (Brown, 1997; Trezenga & Wedell, 2000; Roberts & Little, 2008)? In this case the optimal male differs from female to female, and assuming the only benefits are genetic we should never observe copying, unless perhaps the model female is a close relative. In principle, the presence of copying behavior should constitute evidence against a compatible genes hypothesis and in favour of shared mate choice criteria.

1.6 Conclusion

The past two decades have witnessed an explosion of interest in mate choice copying. Theoretical elaboration notwithstanding, mate choice copying is essentially a very simple idea, easily testable in the lab, and research in this area is almost certain to accelerate. Particularly encouraging is the tendency of the field to outgrow itself and expand in previously unforeseen directions (e.g. Nordell & Valone, 1998; Kavaliers *et al.*, 2006; Galef *et al.*, 2008). The concept of copying others' choices has proved so successful in mate choice studies that scientists are slowly beginning to apply it to areas outside mate choice, like habitat selection and even decisions about whom to parasitize (Gonçalves *et al*., 2003; Wagner & Danchin, 2003). Despite of all the progress achieved so far however, I have shown here that researchers have only begun to scratch the surface of this unique phenomenon. The future is therefore certain to greatly improve our knowledge and understanding of why, how and when females copy the choices of others.

Chapter 2: Beyond mate choice copying: adapting nonindependent mate choice to humans and species with similar mating systems.

Having reviewed in Chapter 1 the theory and empirical research pertaining to nonindependent mate choice in non-human animals, I will concentrate in this chapter on humans. I begin with a review of the relevant empirical studies, followed by a brief synopsis of the human mating system. I will argue that mate choice copying is an inappropriate or at best inadequate theoretical tool for exploring nonindependent mate choice in humans and other animals with similar mating systems (ie. relatively monogamous with paternal investment and mutual choice). I will then propose and develop a new theory of nonindependent mate choice which I will argue follows from the biological facts and fits better with the human empirical literature, at the same time suggesting novel and evolutionarily plausible lines of research. In light of what is discussed up to that point, the final section of this chapter is a critique of some studies that have examined mate choice copying in a monogamous bird, the zebra finch.

2.1 Studies of nonindependent mate choice in humans.

2.1.1 'Radiating beauty': nonindependent mate choice in the 1970s.

Although at the time it was not called anything like 'nonindependent mate choice' or 'mate choice copying', the study of this phenomenon in humans originates with the social psychology literature of the 1970s. The first study was published in 1973 by psychologists Harold Sigall and David Landy under the title 'Radiating beauty: effects of having a physically attractive partner on person perception'. Sigall and Landy were interested in explaining some recent studies (notably Walster *et al*., 1966) which indicated that physical attractiveness was a very powerful factor in peoples' choice of romantic partners. They hypothesized that one reason people place so much emphasis on having attractive partners might relate to their expectation that they will subsequently be viewed positively by others and gain prestige. To test whether people actually do view people differently depending on the attractiveness of their partner, Sigall and Landy implemented a 2x2 between-subjects design which used a female confederate who was made – with the use of a wig and makeup - to be either very attractive or very unattractive (attractive vs. unattractive), while being presented as either the girlfriend or simply an unrelated bystander (associated vs. unassociated) of a nearby average-looking young man (also a confederate). The results showed that the attractiveness of the girlfriend interacted with perceived association to determine how the male was rated by the experimental subjects on 'overall impression'. The male received the most favorable ratings on the 'attractive-associated' condition and the lowest in the 'unattractive-associated', while receiving intermediate values in the two 'unassociated' conditions. In other words males received more favorable ratings when presented alone

rather than with an unattractive girlfriend, but received even better ratings when presented with an attractive girlfriend. These results are confounded by the fact that both male and female raters were used in this study and the researchers don't report results separately for male and female raters, although the three-way interaction of attractiveness x association x participants' gender was not significant, indicating that the patterns for male and female raters were roughly similar. Interestingly, Sigall and Landy measured participants' responses on several other dependent variables related to perceptions of the male confederate (apart from 'overall impression'), one of which, 'attractiveness', did not elicit the critical 2-way interaction between attractiveness and association. This latter result would seem to contradict some more recent studies (Waynforth, 2007; Little *et al*., 2008) that used 'attractiveness' as a dependent variable[2]. Of the other dependent variables, 'self-confidence', 'friendliness' and 'likeability' revealed significant interaction effects, while 'intelligence', 'talent' and 'energy' did not (Sigall & Landy, 1973)

Without the benefit of evolutionary theory, Sigall and Landy offered various explanations for their findings which today can be recognized as almost certainly wrong (Tooby & Cosmides, 1992). These included a generalized halo effect and Heider's balance theory (Heider, 1958) which would work as follows: 'Person P (subject) likes Person O (attractive female); Person O likes Person Q (stimulus person); therefore, Person P likes Person Q.' (Sigall & Landy, 1973, p.221). The authors' third explanation, however,

[2] For description see below, section 2.1.2

might contain a kernel of truth: '[…] people who view an individual romantically linked to an attractive person try to make sense of that association. In effect, they may ask themselves "Why is she, desirable as she appears to be, involved with him?" Our observers may answer such a question by attributing favorable qualities to him' (Sigall & Landy, 1973, p. 221). Although this conscious process of rational explanation might sometimes take place, it is likely that evolved nonindependent mate choice in humans is the result of subtle biases in mate evaluations which are not made consciously.

Bar-Tal and Saxe (1976) expanded on Sigall and Landy's study by using a number of slides of males and females that were taken from college yearbooks. These were presented in pairs (supposedly as married couples) to female and male subjects. Four types of supposed couples were used: couples where husband and wife were both of high or low attractiveness, and couples where husband and wife were of dissimilar attractiveness (attractive husband with unattractive wife and vice versa). Unattractive males that were supposedly married to attractive females received the highest ratings on the dependent variables of perceived education level, income level, professional success, intelligence and occupational status, compared to males in the other three conditions. On the other hand unattractive females that were coupled to attractive males received the least favorable evaluations.

Meiners and Sheposh (1977) also employed a design similar to Sigall and Landy's, but presented raters with videotapes instead of live confederates. Again the attractiveness

of a single confederate female was manipulated (through makeup and a wig) so that she appeared as attractive or unattractive, while the same average-looking male was used in all conditions. In addition to manipulating the female's attractiveness, Meiners and Sheposh also tried to examine the effect of her supposed intelligence, by informing half the subjects that she was a medical student and the other half that she was a waitress. All ten of Sigall and Landy's original dependent variables (overall impression, likeability, attractiveness, intelligence etc.) relating to raters' perceptions of the stimulus male were used. The female's attractiveness had a significant positive effect on all ten dependent variables, while her 'intelligence' only had a significant (and relatively weaker) effect on three variables: intelligence, self-confidence and talent. The researchers' manipulation of the female's supposed intelligence is problematic, however, since a medical student and a waitress are likely to differ on a wide range of perceived traits in addition to intelligence. As in the other studies, these results are confounded by the fact that the researchers did not conduct separate analyses for male and female subjects, although they do not report any significant interactions of the aforementioned effects with subjects' gender.

The final study in the 'radiating beauty' series was conducted in Japan in 1990 to examine whether the effect would replicate in a different culture (Onodera & Miura, 1990). Again Sigall and Landy's (1973) 2x2 factorial design was used with static facial images from a yearbook. The distinct advantage of this experiment over previous ones is that only female raters were used. Unfortunately the researchers selected the single most attractive and single least attractive out of a set of 80 female images for use in the

‘attractive’ and ‘unattractive’ conditions; while interesting, this extreme manipulation raises concerns about the generalisability of the results. Eleven dependent variables were measured, of which some had been used by Sigall and Landy but most were new (e.g. tenderness, cheerfulness, sex-appeal). Multivariate analysis of variance revealed a significant main effect of association, but no main effect of female attractiveness and no interaction. The researchers only report univariate analyses for the effects of ‘association’, which was significant for the dependent variables of ‘attractiveness’, ‘intelligence’, ‘sex appeal’ and ‘masculinity’, with men in the ‘associated’ condition receiving higher ratings on all of these variables. The results of this study seem to support a straightforward mate-choice copying effect, but it is unfortunate that the researchers don’t report any univariate analyses for the main effect of female attractiveness or the interaction. It is not apparent why the ‘radiating beauty’ effect found in the other studies did not obtain in this Japanese sample.

In summary, the main findings of these early studies were as follows: a) an attractive woman ‘raises’ her partner in the eyes of both men and women alike, b) this effect is especially pronounced when the male partner is himself unattractive, c) the phenomenon is gender-specific, so that beauty does not radiate from an attractive man to his partner and d) it is premature to generalize from research in the United States to other cultures. These studies were plagued by a number of problems that could scarcely be avoided in a social-psychological approach that ignored the evolutionary origin, function and limits of the phenomenon under consideration (Tinbergen, 1963; Tooby & Cosmides, 1992; Cosmides & Tooby, 1994). Studies were designed intuitively

and employed a large number of disparate dependent variables, most of which were not specific to mating. The results were analyzed with multivariate analysis of variance (MANOVA) in the hopes of detecting some effect, female and male participants were usually lumped together in the analysis, and the explanations offered were in terms of generic social science theories like balance theory (Heider, 1958) or exchange theory (Blau, 1964) rather than specific to mating. As a result it was impossible to make any significant progress after the first few studies and the venture was soon abandoned, a familiar pattern in social psychology (Lykken, 1991).

Onodera and Miura's study was the last of its kind in the social psychological literature, published at the same time that the idea of mate choice copying was beginning to take hold in behavioural ecology (Pomiankowski, 1990; Wade & Pruett-Jones, 1990; Dugatkin, 1992; Pruett-Jones, 1992). Owing to the natural proximity and channels of communication between the animal behavioural ecology and human evolutionary psychology literature, evolutionary psychologists, at least up until the late 2000s, naturally sought recourse to mate choice copying in their exploration of women's nonindependent mate choice (Thornhill & Gangestad, 1999; Dugatkin, 2000; Knight, 2000; Uller & Johansson, 2003; Milonoff *et al*., 2007). The simple insight provided by these earlier social psychological studies, namely that what is of utmost importance is not *if*, but *who* a man is mated to, was initially lost sight of.

2.1.2 ‘Mate choice copying’: nonindependent mate choice in the 2000s.

In his 2000 book ‘The imitation factor: evolution beyond the gene’ biologist Lee Alan Dugatkin reported an experiment he conducted with University of Lousville psychologists Michael Cunningham and Peri Druen on a phenomenon he described as ‘date choice copying’. Seventy-four female undergraduates were presented with written information about a man who had supposedly been interviewed by five women. According to the information given to the female subjects, each of these five women had subsequently rated the man for attractiveness and had indicated if she would be interested in dating him. Manipulating these two fictitious variables, namely the attractiveness ratings and interest in dating, Dugatkin and his colleagues recorded female subjects’ responses to questions like how interested they would be in dating the man or how wealthy, funny and socially skilled they thought he was. The researchers found that the more attractive the 5 women had supposedly found the target male and the more interest they had expressed in dating him, the more interested female subjects subsequently were in dating him, and the more funny, wealthy and socially skilled they thought he was. Dugatkin and colleagues conducted a similar, sex-reversed experiment with male subjects rating fictitious females, and found that a similar pattern of ratings emerged.

I am not convinced Dugatkin’s experiment demonstrates mate choice copying, date choice copying or anything related to nonindependent mate choice. To see this we can

ask whether subjects would have responded differently if instead of potential dating partners they were asked to pass judgment on some other item of interest. Faced with no information about the item of interest except other people's firsthand impressions of it, could we possibly expect participants to have provided a different pattern of ratings? In other words had subjects been provided with no other information except other people's opinions of a same-sex friend, a house, a television set etc., as well as statements of how inclined these people would be to become friends with the same-sex individual or purchase the house or television, would they have any rational option than to follow the judgment of these people who had first-hand experience with the item of interest (as contrasted to their own - i.e. the subjects' - non-existent knowledge of it)? 'Word-of-mouth',[3] rather than 'date choice copying' seems to be the most parsimonious explanation for these results (see also study 2 in Dunn & Doria, 2010 for a somewhat similar design).

A more valid test of the mate choice copying hypothesis was conducted in Sweden, in a study which employed confederate males that were either wearing or not wearing a wedding ring while interacting with female subjects (Uller & Johansson, 2003). This study was inspired by the 'wedding ring effect', i.e. the folk notion that women find married men more attractive (Knight, 2000). One-by-one 97 women met the male confederate in a room and asked him several scripted questions that had been given to them in advance by the experimenters, receiving always the same scripted answers by

[3] A widely studied phenomenon in the marketing literature, with numerous studies resembling Dugatkin's design (e.g. Herr et al, 1991; Buttle, 1998)

the confederate. Female subjects then rated the confederate for physical attractiveness, general attractiveness and perceived socioeconomic status, also indicating how interested they would be in dating him, having a relationship with him or having sex with him. In half the interactions the confederate wore a wedding ring while in the rest he did not. A mate choice copying hypothesis suggests that women should rate men as more attractive when they are wearing a wedding ring, since the ring signals another woman's mate choice. Women however rated the men with the ring as less attractive and indicated less willingness to have any sort of involvement with them (Uller & Johansson, 2003). The authors concluded that their study cast doubts on 'simplified theories of human mate choice copying' (Uller & Johansson, 2003, p.267). Another study in Finland (Milonoff *et al*., 2007) used image processing to manipulate photographs of men taken in a casual setting. Men were presented alone, in the company of women (subjects were told the women had sexual relations with the men) and in the company of men. Again contrary to the mate choice copying hypothesis, the presence of male, not female companions had a positive impact on female subjects' ratings of the target males. Like Uller and Johansson (2003), the authors concluded that 'Copying in humans may well be a more sophisticated process than in other species' (Milonoff *et al*., 2007, p.353), although they did not rule out the possibility that women copy.

A study with a Canadian sample, however, obtained results consistent with mate choice copying (Eva & Wood, 2006). Here a combination of written and photographic stimuli was used, with female subjects being shown a picture of a male and a brief written profile, which for half the women mentioned that the man was single, while for the

others that he was married. Men that were described as married received significantly higher attractiveness ratings (Eva & Wood, 2006). A later British study (Parker & Burkley, 2010) used a very similar design, with half the female subjects viewing a written profile of a target male which informed them that he was single and the rest that he was in a romantic relationship. The target male received higher ratings on various measures of romantic interest when he was presented as being in a relationship. This result was gender-specific: male raters showed no preference between a female target stimulus that was either single or in a relationship (Parker & Burkley, 2010). A similar gender-specificity was found in another British study which used photos of men and women who were pictured either alone or in the company of romantically interested opposite-sex individuals (Dunn & Doria, 2010). While female raters gave higher attractiveness ratings to men who were presented in the company of interested women, male raters showed no such preference when rating images of target females.

In contrast to these studies, another study which used facial photographs (Waynforth, 2007) found that the attractiveness ratings a man receives when presented alone do not differ significantly from the ratings he receives when presented with the image of his supposed girlfriend. It was found, however, that men presented with attractive girlfriends received higher ratings compared to when they were presented alone, while those with unattractive girlfriends received lower ratings. This was a considerably more sophisticated study which examined the interaction of two factors that had not been jointly analysed in the preceding studies, namely the attractiveness of the female

girlfriend and also the attractiveness of the male himself. I will discuss the results of this study below in more detail (section 2.4).

Interestingly, a number of studies that were published subsequently to Waynforth's (2007) paper presented *all* male stimuli as partnered and focused exclusively on the influence of their supposed partners' attractiveness. Employing a within-stimulus design with composite faces Little *et al.* (2008) found that when rating images of prospective long-term partners, women prefer men presented next to feminine rather than masculine girlfriends, and men prefer women presented next to masculine rather than feminine boyfriends. Feminine female faces and masculine male faces are generally also found to be more attractive (Little *et al.* 2008). This effect of partner attractiveness was not found when raters (both female and male) rated the targets' attractiveness as potential short-term partners. Following most researchers before them, Little *et al.* (2008) concluded that 'This is a more sophisticated form of copying than simply being attracted to those who have vs. those who do not have partners' (Little *et al.*, 2008, p.144). Vakirtzis and Roberts (2010) also used a within-stimulus design but with real as opposed to composite facial images and found that a) men presented with attractive ex-girlfriends received higher attractiveness ratings compared to when they were presented with unattractive ones, and b) this phenomenon did not manifest when the roles of the sexes were reversed, ie. when male subjects rated female images presented with attractive and unattractive ex-boyfriends. Similar results were obtained by Yorzinski and Platt (2010) who also used photographic images of men and their supposed ex-partners: they found that female raters expressed more romantic interest

for men when these were presented with attractive partners compared to a baseline of the male image presented on its own (as in Waynforth's (2007) study), and less interest when they were presented with unattractive partners (in comparison to the baseline). In contrast to Vakirtzis and Roberts (2010), however, Yorzinski and Platt found that this preference for opposite-sex targets paired with attractive former partners also manifested with male raters, although here the effect was weaker.

In summary, evolutionarily oriented studies of human nonindependent mate choice began around the turn of the century with the straightforward transplanting of mate choice copying from non-humans to humans (Dugatkin, 2000; Uller & Johansson, 2003, Eva & Wood, 2006; Milonoff *et al*., 2007). The results were not particularly encouraging, and within a few years the emphasis had shifted from simple mate choice copying to experimental designs which presented all men as being in a sexual relationship and focused solely on the attractiveness of the man's partner (Waynforth, 2007; Little *et al*. 2008; Vakirtzis & Roberts, 2010; Yorzinski & Platt, 2010). It would seem that the insights gained by the 'radiating beauty' studies of the 1970s were eventually arrived at anew, and many researchers started to realize that female attractiveness is the single most important cue. Although variously described as a 'copying-like' effect or a 'more sophisticated' form of copying (Uller & Johansson, 2003, Waynforth, 2007; Little *et al*., 2008), I will argue in subsequent sections that the results of these studies considered together with the human mating system lead inevitably to the conclusion that the phenomenon under consideration is qualitatively distinct from mate choice copying.

2.2 The human mating system

For the purposes of the analysis that follows I will now briefly review the human mating system.

Any discussion of this subject must start with the acknowledgment that human mating behaviour is characterized by tremendous variability both between and within sexes (e.g. Buss & Schmitt, 1993; Buss, 1994; Schmitt, 2005; Buss, 2006; Pillsworth & Haselton, 2006; Buss, 2007), situational contexts (e.g. Penton-Voak & Perrett, 2000; Gangestad *et al*., 2005; Starratt *et al*., 2007), individuals (e.g. Roberts & Little, 2008), life-histories (e.g. Belsky *et al*., 1991; MacDonald, 1997) historical periods (e.g. MacDonald, 1995) and socio-cultural milieus (Murdock, 1967). Indeed at the extremes the differences are so striking that they are probably without precedent in biology. For example harem polygyny as practiced in earlier centuries is virtually unknown in modern Western societies: the most reproductively successful man in recorded human history was Moulay Ismail the Bloodthirsty, a 17th century Moroccan emperor who is believed to have sired 888 children with his numerous wives (as cited in Fisher, 1992). Such measures of sexual and reproductive success are unheard of in contemporary Western societies, where men typically average less than 2 children and spend the larger part of their reproductive careers in monogamous bonds (Alexander *et al*., 1979; van de Kaa, 1987).

Having said this, evolutionary principles suggest that when viewed at the appropriate level of analysis universals can be extracted from all this variability (Tooby & Cosmides, 1992). For my purposes I will focus on the following points.

1. Pairbonds are universal. In anthropologist George Peter Murdock's words,

> 'The nuclear family[4] is a universal human social grouping. Either as the sole prevailing form of the family or as the basic unit from which more complex familial forms are compounded, it exists as a distinct and strongly functional group in every known society'. (Murdock, 1949, p.2).

Monogamous pairbonds and paternal investment are rare among primates and more generally mammals (Kleiman, 1977; Clutton-Brock, 1989), and in humans they probably constitute a secondary adaptation in response to the strong pressures for paternal care which followed the evolution of extreme altriciality (Geary, 2000; Marlowe, 2000). Sexual size dimorphism is a good index of the degree to which a species' males are polygynous, and men are taller than women by between 5% and 12%, indicating mild levels of polygyny (Alexander *et al*., 1979). Paleoanthropological evidence suggests that the transition to increased paternal care and monogamous pairbonds is a recent event. *Australopithecus afarensis* specimens reveal a sexual size dimorphism in the range of

[4] The nuclear family consists of a man and a woman with their offspring.

50-100%, a very large difference suggestive of polygyny and minimal paternal care (see Geary, 2000 and citations therein). The steady decline in sexual dimorphism that begins with *Australopithecus* accelerates with the appearance of *Homo erectus*, culminating in early *Homo sapiens* and *Homo neanderthalensis* who display levels of dimorphism typical of modern humans (McHenry, 1996). The positive correlation between paternal care and offspring survival still holds in pre-industrial societies around the world today (Geary, 2000).

2. Social monogamy and serial monogamy are universal. Cross culturally, over 80% of human societies can be classified as polygynous in that they permit a man to have more than one wife at the same time, with the remaining societies being classed as monogamous (Murdock, 1949; Ford & Beach, 1951). Crucially though, even in those societies which are polygamous according to the above criterion most men and women are in monogamous bonds, and polygamous unions are feasible only for a very small minority of men that have reached a mature age and high social status (Murdock, 1949). Murdock concludes that:

> ‘An impartial observer employing the criterion of numerical preponderance, consequently, would be compelled to characterize nearly every known human society as monogamous, despite the preference for and frequency of polygyny in the overwhelming majority’ (Murdock, 1949, pp. 27-28).

Indeed, in a cross-cultural sample of 97 countries for which there is available data, the mean percentage of men who have married by the age of 49 is estimated at nearly 92% (Fisher, 1989; 1994), which assuming a roughly equal tertiary sex ratio means the large majority of all humans mate monogamously. On the basis of this and other evidence Fisher (1989; 1992) reaches the same conclusion as Murdock, characterizing humans as monogamous and polygyny as a secondary opportunistic reproductive strategy, an assessment in line with the data on sexual size dimorphism discussed above (Alexander *et al.*, 1979; Geary, 2000).

Various lines of evidence suggest that these monogamous social bonds are usually, but not always, characterized by sexual exclusivity. Testes size relative to body size offers a highly reliable index of the degree to which males have been under selective pressures arising from sperm competition (Harcourt *et al*., 1981; 1995) and human relative testes size lies between the promiscuous chimpanzee (*Pan troglodytes*) and polygynous gorilla (*Gorilla gorilla*), although considerably closer to the latter than the former (Harcourt *et al*., 1995; Simmons *et al.*, 2004). Genetic paternity data are in line with the anatomical data, with a relatively low median worldwide nonpaternity rate of 1.7% for couples where the man has high paternity confidence (Anderson, 2006).

Another salient characteristic of human pairbonds is that they typically do not last (Lockard & Adams, 1981; Fisher, 1989; 1992; 1994). Fisher argues for the existence of evidence of ‘designed obsolescence’ in the human pairbond (Fisher, 1989; 1992; 1994).

Cross-culturally, the frequency of divorce peaks at around 4 years of marriage,[5] which Fisher suggests would have been the minimum time necessary to ensure offspring survival in ancestral environments. Human divorce and re-marriage follow several predictable, from a sociobiological perspective, patterns. Most divorces occur at a young age, older couples and couples with many children rarely divorce, and after each divorce men typically marry successively younger wives (Fisher, 1989; 1992; see also Lockard & Adams, 1981).

Most cross-cultural data involve formal marital relations, yet far more information can be garnered from a consideration of all types of sexual relations, be they marital or informal. The outbreak of AIDS in the 1980s brought about an unprecedented level of research into the sexual habits and life histories of the United States population, and data from these U.S. studies confirm the general points outlined above[6]. When asked how many sexual partners they have had in the last 12 or 18 months most men (between 60-80%) report that they have had 1 sexual partner, followed in frequency by men who report 2 and then 3 partners, with very small percentages (4-8%) reporting more than 4 or 5 partners (Greeley *et al*., 1990; Seidman & Rieder, 1994; Adimora *et al*., 2007). Across all ages, the mean number of sexual partners reported by men for the preceding 12 months is 1.16, which rises to 1.76 for men aged 18-29 and drops to 1.25 for men aged 30-39 (Smith, 1991). Typically only about 10-20% of men report having

[5] A phenomenon dubbed by Fisher 'the four-year itch'
[6] A general weakness of these studies is that they are based on subjects' self-reports, which are known to be slightly biased (Smith, 1992; Wiederman, 1997)

had no sexual partner in the past year, indicating that at least in modern environments the large majority of men are able to gain sexual access to women (Smith, 1991; Siedman & Rieder, 1994). Similarly low, at 11%, is the percentage of men who report having had concurrent sexual relationships with 2 or more women in the preceding 12 months, indicating mild levels of sexual infidelity and/or polygyny (Adimora *et al*., 2007). Interestingly, when they are asked how many partners they have had in their lifetime, the median number reported by men is around 7 (Billy *et al*., 1993; Adimora *et al*., 2007). About 20% of men report more than 20 lifetime sexual partners, and 3.5% report more than 50 lifetime partners (Billy *et al*., 1993; Adimora *et al*., 2007). Taken together, these figures suggest a predominantly serially monogamous system with relatively low levels of male mating skew and polygyny.

3. *There is mutual choice, with differing mate choice criteria.* Although women are typically choosier and more selective than men (Symons, 1979; Clarke & Hatfield, 1989; Buss & Schmitt, 1993; Buss, 1994; 2000) male choice does operate (especially in the context of long-term relationships, see Kenrick *et al*., 1990; Buss & Schmitt, 1993; Buss, 2000a; Woodward & Richards, 2005) and is mediated by a number of cognitive adaptations (Miller & Todd, 1998). Indeed, the study of male choice and its relation to such female qualities as nubility, ovulation, body shape and facial attractiveness (e.g. Symons, 1995; Thornhill & Gangestad, 1999; Roberts *et al*., 2004; Gangestad & Scheyd, 2005; Rhodes, 2006, Roberts & Little, 2008), forms one of the best-studied fields in evolutionary psychology. One of the most consistent findings in the literature pertains to the marked contrasts in mate choice criteria between the two sexes (Buss,

1989; Townsend, 1989; Buss *et al*., 1990; see also reviews in Buss, 1994; 1999). Although the mate value of women is determined primarily by the aforementioned visual cues of youth and attractiveness, the mate value of men is more heavily dependent on relatively complex cues like social status, resource holding potential and willingness to invest in a relationship, gender differences which are predicted from the different selection pressures ancestral males and females faced (Buss, 1999).

Predictably, these gender differences in mate choice criteria result in assortative mating with respect to mate value, as it is well documented that more attractive women tend to mate with more desirable (i.e. of higher socioeconomic, financial and educational status) men (Elder, 1969; Taylor & Glenn, 1976; Udry, 1977; Udry & Eckland, 1984; reviewed in Townsend, 1998). It is worth noting that the relevant studies are conducted in modern large, socioeconomically stratified nation-states like the United States, so it is likely that the sometimes small effects these studies detect would have been considerably larger in smaller, more homogeneous and less stratified ancestral societies.

After this brief overview of the predominantly monogamous human mating system, in the next section I will ask whether mate choice copying should be expected to evolve in monogamy. This will be a general discussion that focuses on the general characteristics of monogamy, with implications for numerous species outside our own. Subsequently I will return to humans and tie these two discussions together.

2.3 Mate choice copying and monogamy: do they go together?

As discussed in the previous chapter, the idea of mate choice copying originally arose from the study of lekking species. In particular scientists were trying to explain the extreme skew in male mating success that is often seen on leks, where a small proportion of males enjoy substantial mating success, and a far greater number remain unmated (Bradbury & Gibson, 1983; Wiley, 1991). The idea was that the first few females on the lek choose males independently and the rest copy these initial choices, which only amplifies the top males' mating success (Bradbury & Gibson, 1983; Losey *et al*., 1986; Pomiankowski, 1990; Wade & Pruett-Jones, 1990; Gibson et al, 1991). It is easy to see why mate choice copying can evolve in these kinds of systems, as the successful research program that has since followed demonstrates. Male choice is minimal, and males simply compete with each other to maximize their number of sexual partners. The relation between the number of sexual partners a male secures and his quality is therefore presumably monotonically increasing and unambiguous. At the top of the male distribution a few conspicuous males will mate with most females, with the alpha male mating with the most. At the low end of the spectrum there will be a surplus of celibate males which can be more or less dismissed by focal females, substantially narrowing down the pool of potential mates. In addition, since there is no paternal care and females can gain nothing but sperm from males, a female has nothing to lose if her chosen male has mated or will mate with other females (assuming an ample supply of sperm to achieve fertilization). Similar promiscuous mating systems (i.e. no pair bond, no paternal investment and no male choice) occur in the large majority of non-human

species where mate choice copying has been studied (with the sole exception of the zebra finch, which is discussed extensively in a later section).

In contrast to these promiscuous species, a careful examination of the core characteristics of monogamous or socially monogamous species and how these would, theoretically, relate to mate choice copying, illustrates with a high degree of certainty that mate choice copying cannot evolve in these systems. I discuss five major problems that any suggestion to the contrary must solve before even constituting a viable hypothesis in principle (summarized in Table 2).

	Lekking/promiscuous species →	Why mate choice copying can evolve	Monogamous/socially monogamous species →	Why mate choice copying cannot evolve
1.	No paternal care	No risk of diminished paternal care.	Paternal care	Copying females will suffer diminished paternal care for their offspring.
2.	No female competition	No costs from female competition.	Female competition	Copying females will suffer costs of female competition from male's current mate.
3.	High male mating skew	The top males will easily stand out from the rest.	Low male mating skew	Since all males will tend to have one mate at a time, this cue will not be a useful aid in discrimination.
4.	No male choice	Copying females can treat a male's mates as homogeneous units, summing them up to obtain a gauge of his overall success.	Substantial male choice	Simply tracking the number of a male's mates will not suffice due to substantial differences in female mate value. From the vantage point of a male, one high-quality female might even be preferable to two low-quality females.
5.	Unambiguous, monotonically increasing relation between a male's quality and the number of his mates	Copying females can be confident that the more mates a male has the higher his quality.	No clear relation between number of mates and quality of male	1. Various males might allocate differential effort to parenting vs. mating, and which allocation is preferable will depend on a female's needs. 2. Although it can generally be expected that males of higher genetic quality will engage in more extra-pair copulations (EPCs), these will be covert matings of which copying females will probably have no knowledge. 3. Males in successful breeding pairs will have no reason to dissolve them, whereas the opposite will be true for males that find themselves in unsuccessful relationships, perhaps even leading to a negative correlation between male quality and lifetime number of mates.

Table 2. Five reasons why the concept of mate choice copying has proven so successful in the lekking/promiscuous species where it has mostly been studied (left half of the table), with the corresponding reasons why it is almost certain to fail in monogamy (right half). References are provided in the text.

1. The problem of paternal care. A substantial part of monogamous males' reproductive effort will be allocated to parenting (Trivers, 1972), and monogamous females that copy other females' choices will likely suffer reduced reproductive success due to the fact that they will have to share the male's parental care and resources with his other mates (Orians, 1969). The only way this problem can be overcome is if the copying female is successful in terminating the male's involvement with his other mate(s) (Schmitt & Buss, 2001; Buss, 2006), but this is a precarious strategy that is likely to be resisted by the male. Even if the female is successful in this however, she inevitably incurs the cost of female competition (see below). These problems are absent in the promiscuous, non-economic systems where the study of copying has primarily been confined: here there is no post-copulatory paternal care, so females who are attracted to the most successful male will suffer no reduced paternal care for their offspring relative to non-copying females.

2. The problem of female competition. In species with no paternal investment and minimal male choice, female competition is reduced, at most, to a prospective female mate having to wait a few seconds while the male services the female that arrived before her. As paternal investment increases, however, so does female competition, although even in monogamous species it typically doesn't reach the intensity of male competition (Trivers, 1972; Burley, 1977; Campbell, 2004). In our species, for example, competition among younger females over mates is typically confined to verbal derogation, social exclusion and other similar non-violent methods, although it can sometimes escalate to physical violence (Campbell, 1995; 2004). This competition

constitutes another source of costs for monogamous copying females which is absent in other systems.

3. The problem of low male mating skew. As discussed above, it is no accident that the study of mate choice copying has focused mostly on promiscuous and lekking species, where the male's primary concern lies in securing as many mates as possible (e.g. Dugatkin, 1992; Clutton-Brock & McComb, 1993; Höglund *et al*., 1995; Grant & Green, 1996; Witte & Ryan, 2002). The marked skews in male mating success, as well as the significant proportion of males that fail to secure any matings at all, provide ample relevant information for selection to work on. To see why this so, consider that in order for a male trait to adaptively guide female choice there needs to be meaningful variation in that trait, so that females can reliably discriminate between males on the basis of that trait. The traits with the widest meaningful variation should be most favored; on the other hand, traits that manifest uniformly across all males would be useless. In mate choice copying the 'trait' is quantitative sexual success in the form of frequency of sexual partners or copulations. Because this trait varies most among males in promiscuous and polygynous species, these will usually be the types of mating systems most conducive to copying. In these systems there are, in other words, a sufficient proportion of unmated males to repay a female's interest in the mated ones (Figure 1). Pursuing the idea of mate choice copying in monogamous systems that lack significant variance in male mating success will probably turn out to be a largely futile enterprise.

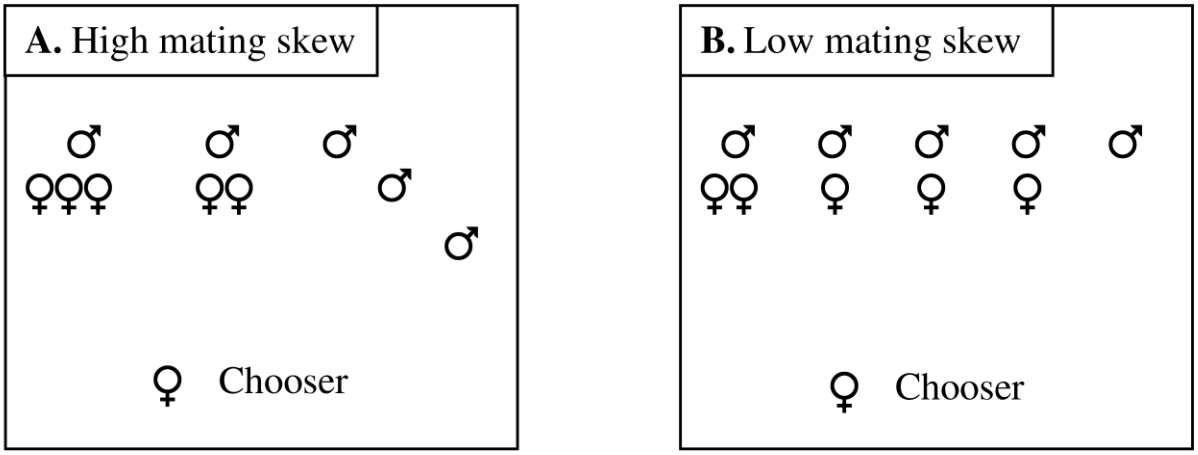


Figure 1. Mating skew and potential for mate choice copying. In A, the mating status (mated vs. unmated) of males is a cue that reveals the high quality males. This is not the case in B, where the great majority of males are mated. Mate choice copying is less likely to occur in B.

4. The problem of male choice and unequal female mate value. In species with no paternal investment male choice will be minimal and males will generally mate indiscriminately with any conspecific female (Trivers, 1972; Burley, 1977), meaning that from the vantage point of male competition all females will be of more or less equivalent mate value. Simply tracking the total number of mates a male has secured over the time period the focal female has been observing the mating ground suffices, therefore, as an index of his mating success and, consequently his mate value. For example in a species like the sage grouse (Gibson *et al*., 1991) or guppy (Dugatkin, 1992; 1998) a focal female can be confident that a male that has mated with 7 females has probably outcompeted - and is of higher quality to - one that has mated with 3 females. In monogamous species with significant male choice, on the other hand, various females will be of widely differing mate value, so that simply trying to determine which male

obtains the most mates will often obscure rather than reveal the top male. For example a highly desirable monogamous male may prefer to forego other mating opportunities so that he can direct all his investment to a high-quality female. To take an intuitive case in point from our own species, it is not too hard to imagine that given a choice between one supermodel and two or even three unattractive women, almost all men would prefer the former. Copying females that don't start making more fine discriminations with regard to the quality of the model females (as opposed to only their number) are certain to miss out on a precious source of biological information and consequently make poor choices.

5. The problem of an unclear relationship between a male's quality and the frequency of his mates. Although partially related to the previous point this constitutes a problem on its own, and stems not only from unequal female mate value but from the diversity of - condition-dependent, context-dependent, environment-dependent etc. - reproductive strategies monogamous males employ in search of an optimal balance between mating and parenting effort (Gangestad & Simpson, 2000). This diversity of reproductive strategies stands in sharp contrast to the straightforward maximization of sexual partners all promiscuous males monolithically pursue, a reproductive strategy which follows naturally from the absence of paternal care. Since these promiscuous males all pursue the same goal and compete on the basis of the same goal, and since females select mates on the basis of one criterion (presumably genetic quality, Bradbury & Gibson, 1983), it follows that there must exist in these species an unambiguous, monotonically increasing relation between the number of mates a male secures and his

quality. A copying female can be confident that the more mates a male has secured the higher his quality, and she should therefore always prefer the male with the highest number of partners. Things are quite different in monogamy. For example a monogamous male that is successfully paired to a high-quality female will have little reason to dissolve the bond (resulting in one lifetime partner), while the opposite would be true for a male that finds himself in successive unsuccessful bonds with low-quality or incompatible mates (large number of lifetime partners) across breeding seasons (e.g. Diamond, 1987; Johnston & Ryder, 1987; Linden, 1991; Dubois & Cézilly, 2002). To take another example from humans, there exists a large literature on men's reproductive strategies that documents the dichotomy between those who channel the greater part of their reproductive effort to mating and those that invest more in paternal care. There exists therefore a substantial trade-off for women, involving the choice between sexually successful males that are more likely to provide heritable fitness benefits but little or no paternal care and less successful males that are more likely to provide paternal care (Penton-Voak *et al*., 1999; Penton-Voak & Perrett, 2000; Gangestad *et al*., 2005). Which of the two is more desirable will depend on the woman's particular condition and reproductive strategy, i.e. short or long-term mating (reviewed in Gangestad & Simpson, 2000). Females in non-resource-based systems face no tradeoffs of this sort. Finally, although it may be expected that socially monogamous males of high genetic quality will engage in more EPCs compared to their low-quality peers (Kempenaers *et al*., 1992; Kempenaers & Dhondt, 1993; Penton-Voak *et al*., 1999), these EPC's will by their very nature tend to be covert events, which third females will probably not be privy to.

Although these problems all follow from a relatively straightforward analysis of the relevant differences in mating systems (Trivers, 1972; Burley, 1977), they have not been systematically discussed in the literature. On the contrary a handful of researchers in recent years have made the transition to 'monogamous copying' without questioning its suitability for the problem at hand. Earlier I discussed Dugatkin's and his colleagues' (see Dugatkin, 2000) experimental study in humans, where the scientists were satisfied that the only theoretical modification necessary to study nonindependent mate choice in humans was merely to rename 'mate choice copying' to 'date choice copying', while ignoring the night-and-day differences between the human system and the other species where copying had been studied (like the guppy on which Dugatkin has conducted his research). In her discussion of this matter Dubois (2007) acknowledges that monogamous copying females might face a problem with diminished paternal care, but suggests that other than this cost '[…] mate choice copying provides the same benefits to females from monogamous species' (p.1785). Brown & Fawcett (2005) and Drullion & Dubois (2008) also identify diminished paternal care as a problem with monogamous copying, but seem willing to accept that if this problem is overcome, the adaptation can evolve. Other researchers who conducted copying experiments with monogamous birds simply avoid discussion of theoretical problems altogether (Doucet *et al*., 2004; Swaddle *et al*., 2005).

2.4 Mate quality bias

In seeking plausible alternatives to mate choice copying for monogamy, one must begin with the logically necessary condition that there must be a turnover of mates for any kind of nonindependent mate choice to operate. This will permit the evolution of nonindependent mate choice by allowing a male's prospective partner to act on the information furnished by the previous partner. In lifelong monogamy, where once bonded a male is rarely released unto the mating market again, unmated females simply cannot act on this information, even if it is readily available. This immediately disqualifies all monogamous species that bond for life. On the other hand the higher the turnover of mates, the easier nonindependent mate choice can evolve, meaning that species like humans (see discussion above, section 2.2) or birds with high divorce rates (Ens *et al*., 1996) would, at least in principle, constitute plausible candidates for some kind of nonindependent mate choice.

Having clarified this point, it must also be stressed that it does not seem promising to seek recourse to EPCs as the building blocks upon which monogamous nonindependent mate choice will have evolved. As discussed above, EPCs are by their nature secretive and fleeting events, and it is unlikely that information about them would be readily available to other females. Even if the odd female happened to be privy to an EPC, this would constitute too fragmentary and unreliable a source of information to allow for the evolution of adaptations. Later (section 2.5) I will criticize a theoretical

model (Dubois, 2007) that seeks to do precisely this, namely describe the evolution of mate choice copying via focal females' observations of EPCs. For now, however, I reiterate that nonindependent mate choice must offer some sort of evolutionary advantage over classical independent choice; if this is not the case females will simply evaluate males independently, as they probably do in the large majority of species. Once again, it is easy to see why the idea of mate choice copying originated with lekking species: here the majority of what are anyway conspicuous copulations take place in a few concentrated central locations of the mating arena (Bradbury & Gibson, 1983), in plain sight of all visiting females. The advantage to copying females lies precisely in that they have costless and reliable access to this information about other females' mating activities. When contrasted to these conspicuous lek matings, monogamous EPCs seem perhaps the most inappropriate type of mating activity for nonindependent choice to evolve. The male's primary partner, on the other hand, will constitute a salient and readily available cue for focal females of gregarious species, so it this primary partner that I will focus on here.

The theory that I develop here is based on the relevant characteristics of the typical monogamous species, namely minimal to non-existent male mating skew, mutual choice and assortative mating in terms of quality. Males have one mate at a time, so the frequency of males' partners does not enter the model, but only the quality of this single mate. Focal females vary their evaluation of males in accordance to the quality of the males' partners, so that males with high-quality partners increase their probability of choice, whereas males with low-quality partners decrease their probability of choice.

The relevant contrast is therefore now not between mated and unmated males (or between the number of mates each male has secured), but between the quality of a male's mate and the quality of other males' mates. Although the former involves necessarily discrete and often binary variables, the latter involves variables that can potentially manifest in fine continuous gradations, and the concept of 'copying' something does not apply. I propose the term *mate quality bias* to describe this process.

So as to simplify the discussion that follows, I will confine it to the most common scenario, where the female furnishes most parental investment and is the choosier of the sexes. Obviously, where these prevailing conditions are reversed, the roles of the sexes in relation to mate quality bias might also be reversed (Trivers, 1972; Widemo, 2006). In order for mate quality bias to evolve, at a minimum the following conditions must be satisfied:

1. An evolutionarily exploitable positive correlation between a random female's quality and her partner's quality. The most common way through which this might come about is probably an element of male choice coupled to the stronger female choice.

2. A difference in the ease, speed or accuracy with which the quality of male or female individuals can be assessed, with the assessment of females being preferable (i.e. easier, faster or more accurate) to that of males. This difference is indispensable as motivation for focal females to move beyond independent mate choice. Given the general pattern of dullness and averageness in the female compared with the variation in elaborate secondary sex characters and condition-dependent badges of males

(Darwin, 1871; Andersson, 1994) we should not be surprised if mate quality bias turns out to be a less common biological phenomenon than mate choice copying.

3. The advantage arising from the exploitation of condition 2) must be sufficiently large to overcome the drawback arising from the imperfect correlation in condition 1).

The first two conditions should generally be easy to evaluate across species, whereas the third will pose a more serious challenge to the researcher. At any rate, the empirical finding of mate quality bias in a species that satisfies the first two conditions should provide indirect evidence for the satisfaction of the third.

Due to the open-endedness of condition 2) above, the evolutionary mechanics of mate quality bias might be explored in a variety of ways. For example, assume that what is selected for is maximal accuracy in assessing the male's quality, that is, minimization of error. It is a reasonable assumption that the length of time that can be spent assessing mates is often variable across females and at different times of the breeding period. If, within the constraints of a particularly brief assessment time, a female's quality can be more accurately evaluated in relation to that of her mate's, it would pay a choosing female to be sensitive to the female's quality, assuming that the expected error component due to the imperfect correlation of male and female quality in the population is relatively small. Mate quality bias could therefore be an auxiliary or facultative strategy, complementary to the independent assessment machinery of a species' females (as in mate choice copying, Nordell & Valone, 1998). Furthermore, such a

process would be well suited to situations where females aggregate, spending the majority of the season in close proximity, a context that would allow ample opportunity for one to evaluate the other. If the time spent with males occupies a relatively small part of the entire season, we can, assuming certain basic cognitive faculties of individual identification and memorization, see that it could be beneficial for females to pay attention to one another's quality during the remainder of the season when they are aggregated. This could be done at virtually no cost, as the females go about their daily business, but the additional information might improve the accuracy of females' assessments of males.

Predictably, given the absence of significant male skew, mate quality bias allows for the presence of a relatively low-quality female mate to reduce a male's probability of choice. To see this we revisit Pruett-Jones' (1992) definitions of a male's conditional and absolute probability of being chosen by a focal female[7], the former being that which arises when the focal female has knowledge of the male being chosen by the model female, and the latter when she does not and simply evaluates the male on his own merits. Let a male enjoy an absolute probability of choice by a given female equal to $p_{b,}$ a constant between 0 and 1. In mate quality bias we move from independent choice to a limited set of contexts in which the female, instead of assessing the quality of the male, evaluates instead the more easily assessable quality of his mate. This results in a conditional probability that is, theoretically, a continuous and monotonically increasing

[7] See section 1.1 for discussion.

function h of female quality that ranges from 0 to 1, with $h'(x) > 0$ for all x. The function must be monotonically increasing, for otherwise we are confronted with the *non sequitur* of males enhancing their attractiveness by mating with less attractive model females. By the intermediate value theorem there must be a value x_0 of female quality for which $h(x_0) = p_b$. Moreover, since the function is monotonically increasing, x_0 must be unique. All values of female quality larger than x_0 will therefore satisfy $h(x) > p_b$, whereas $h(x) < p_b$ for every $x < x_0$. There exists therefore in mate quality bias the potential for a male's mating success (with a certain range of females) to actually lower his probability of choice, a possibility that is entirely absent from mate choice copying. Recall that in copying the only way a male can lower his probability of choice is if he is rejected by a female (Pruett-Jones 1992; Witte & Ueding 2003); in mate quality bias this necessarily happens when a male is accepted by a female. The two processes are therefore very different from one another, not only in the background assumptions from which they begin, but in the predictions to which they logically lead, although there will be cases where they produce superficially similar results. In addition to highlighting the differences between the two processes, this analysis leads to the following prediction:

In mate quality bias, the larger the male's absolute probability of choice, the larger the proportion of the entire female population that, when mated to the male, decrease his probability of choice. (Equivalently, the smaller the male's absolute probability of choice, the larger the proportion of the entire female population that, when mated to the male, increases his probability of choice.)

Put another way, the higher the quality of the male, the higher the corresponding “parity value” of female quality over which the male starts to increase his probability of choice and under which he starts to lower it. Symbolically, for every $p_h > p_b$ there must exist an $x_1 > x_0$ for which $h(x_1) = p_h$, and letting F represent the cumulative distribution function of female quality in the population, it follows that $F(x_0) < F(x_1)$ (see Figure 2).

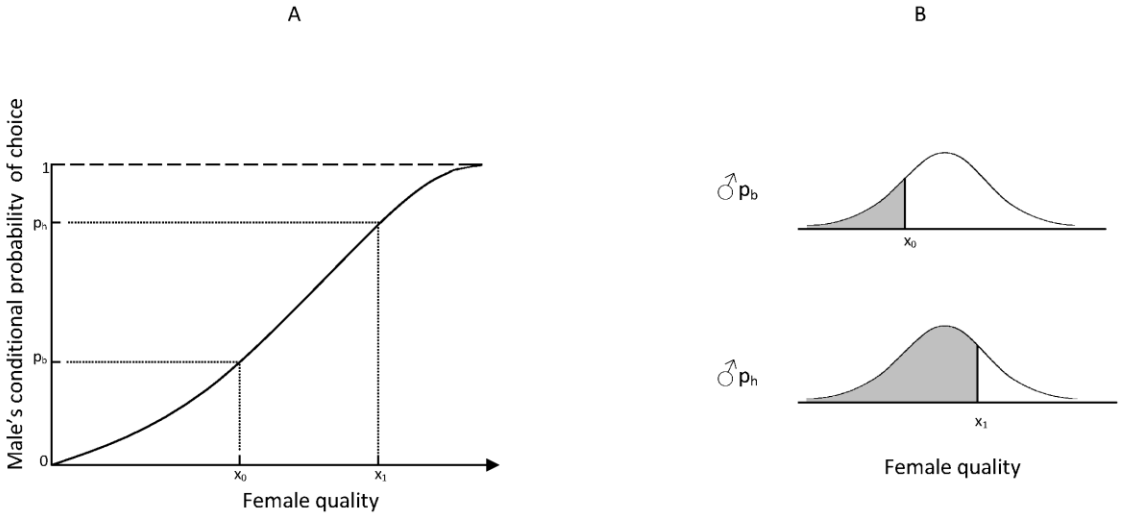


Figure 2. (A) The conditional probability of a male being chosen as a function of his past mate's quality. Two values of conditional probability ($p_h > p_b$) are plotted with their corresponding values of female quality ($x_1 > x_0$). (B) The effects of mate quality bias on 2 males of differing quality, the first having an absolute probability of choice equal to p_b (top) and the second a higher absolute probability of choice equal to p_h (bottom). The shaded area of the female quality distribution (assumed here to be normal) corresponds to those females in the population that, if mated to the males, would lower their attractiveness as mates for an observing female. The higher quality male suffers a reduced probability of choice in most cases, whereas the opposite is true for the low quality male. This analysis leads to obvious predictions about when these males should 'flaunt' their mates and when they should not (Wachtmeister, 2001).

Is there empirical support for this prediction? Yes. Waynforth (2007) had a sample of men's facial photographs rated for attractiveness by female subjects (a measure of absolute probability). Two weeks later, the female subjects re-rated the male images, but this time they also were simultaneously shown a facial image of each man's supposed girlfriend (conditional probability). The female stimuli that were used as girlfriends had been randomly assigned to each male stimulus and covered a wide attractiveness range from very attractive to very unattractive. Waynforth initially tested whether the attractiveness ratings of men presented with a girlfriend increased compared to when they had been presented alone, as a mate choice copying hypothesis would predict. He could find no change, a negative result which corroborated earlier studies that had used different methodologies (Uller & Johansson 2003; Milonoff *et al*. 2007). A meaningful pattern in the data only emerged when Waynforth examined the effect of the supposed girlfriends' attractiveness, and found that the difference in individual men's attractiveness rating between the two conditions was primarily attributable to their girlfriend's attractiveness. Men presented with attractive girlfriends tended to increase their baseline attractiveness ratings, while men who were presented with unattractive girlfriends lowered their attractiveness ratings (see also Little *et al*. 2008; Vakirtzis & Roberts, 2010; Yorzinski & Platt, 2010). Interestingly, and in support of the predictions I derive above, Waynforth (2007, p. 268) gives a graphical summary of his results which breaks down the change in ratings for the male stimuli (between test and retest) by the attractiveness of the men (low, medium, and high attractiveness). The results show that the large majority of girlfriends caused a decrease in the

attractiveness ratings of highly attractive men, and that these men could only retain, but not increase, their initial attractiveness when they were paired to attractive partners. Unattractive men, on the other hand, gained in attractiveness regardless of who they were paired with, although when paired with unattractive girlfriends the positive change in attractiveness is so small that it is probably statistically insignificant. The pattern for men of intermediate attractiveness falls between the two extremes, and these men unmistakably lost in attractiveness by being paired with unattractive girlfriends, but gained by being paired with attractive ones. Results like this don't fit with the notion of women 'copying' mate choice; indeed Waynforth concluded that "the results did not suggest a simple mate choice copying effect" (p.269). Mate quality bias can also easily accommodate the results of the 1970's 'radiating beauty' literature reviewed above in section 2.1[8]. Recall that Sigall and Landy (1973) found that average looking men received most favorable ratings when they were presented with an attractive girlfriend, intermediate ratings when they were presented without a girlfriend, and least favorable ratings when they were presented with an unattractive girlfriend. Bar-Tal and Saxe (1976) similarly found that unattractive men presented with attractive wives received the most favorable ratings.

The qualitative predictions derived above are not altered if we loosen the assumption that the male's conditional probability of choice will be a function exclusively of his mate's quality, and allow the male's own fixed quality into the model. It is not even

[8] Although as discussed there these early results should be interpreted with caution due to the lumping together of male and female raters.

necessary to assume that his conditional probability of choice will span the entire range from 0 to 1; assuming it is constrained to span a narrower range around his absolute probability of choice leads to the same predictions.

The simple model I have described here is merely a description of how a process like mate quality bias should be expected to regulate males' probabilities of choice. The goal of future theoretical work could be, on the basis of the bivariate normal distribution which theoretically describes assortative mating in terms of quality, to determine the boundaries of the parameter space in which mate quality bias could evolve, with emphasis on ρ, the correlation coefficient between male and female quality, and its relation to the putative 'advantage parameter', symbolizing the advantage gained by females that engage in mate quality bias (condition 2 above, p.70). There almost certainly exists a state of tension between ρ and the advantage parameter, with lower values of the former necessitating higher values of the latter and vice versa, and the goal of future theoretical work could be to more precisely describe this relation.

In humans, the advantage lies in the much greater contribution physical attractiveness makes to female as compared to male mate value (the latter being more heavily dependent on non-physical characteristics like social status and resource holding potential), which renders the mate value of a man's mate much easier to visually assess than his own (discussed in section 2.2, see also Buss, 1994; Uller & Johansson, 2003; Waynforth, 2008). Given that there is some cross-cultural variation in the relative

importance women assign to men's physical attractiveness versus non-physical characteristics (due, perhaps, to pathogen prevalence or other hitherto unidentified factors, see Gangestand & Buss 1993; Eagly & Wood 1999; Gangestad & Simpson 2000), it is straightforward to assume that the significance of mate quality bias should correlate negatively with this relative importance. In other words the greater the importance of men's physical attractiveness in a particular society the lesser the advantage offered by mate quality bias and the weaker its effect should be. Conversely, the more significance women assign to non-physical characteristics, the greater the advantage offered by mate quality bias, and, therefore, the more powerful its influence on women's assessments should be.

It is my view that as a first approximation the model developed here is a far more powerful theory than mate choice copying, both in the extent to which it fits with the human mating system and the results already obtained as well as the extent to which it suggests realistic avenues for future research. As discussed in section 2.2 however, the human mating system is not strictly monogamous, so in the future this simple model will need to be modified to take account of these deviations from monogamy. Already some of the results in the literature (Eva & Wood, 2006; Dunn & Doria, 2010; Parker & Burkley, 2010) would seem to suggest that it is inadequate as a comprehensive framework, and this is a point I will return to in later sections. The extent to which the model will require modification probably depends on the degree to which the relevant adaptations constitute open or closed developmental programmes (Mayr, 1964; 1974; Tooby & Cosmides, 1992). Closed developmental programmes are more or less

impervious to environmental inputs during development and develop in a predetermined (or 'fixed') form in accordance to information acquired over evolutionary time. Open developmental programmes are more flexible and allow information acquired during development to impact their final form. In this particular instance, if the relevant adaptations come about as the result of more open developmental programmes, information about the almost complete absence of polygyny in modern Western societies would probably channel women's' relevant adaptations towards a more 'pure' form of mate quality bias. If the relevant developmental programmes are closed, and women in Western societies are unable to track the modern shift towards monogamy (Alexander *et al*., 1979; MacDonald, 1995), then the pure mate quality bias model outlined here will have to be substantially modified.

As a final caveat, studies of mate quality bias, either in humans or other species, should always be conducted bearing in mind that male choice might prevent females' experimentally manipulated desires from resulting in actual matings because high-quality males might reject the advances of low-quality females.

2.5 Mate choice copying in the zebra finch? A re-evaluation.

In light of what has been said above I revisit the studies that have examined mate choice copying in zebra finches.

The zebra finch is a socially monogamous finch of the estrildine group, found in mainland Australia and some islands of eastern Indonesia[9]. These birds form life-long pair bonds, which are only dissolved when one of the partners dies (Zann, 1996). The pairs are inseparable in both breeding and non-breeding seasons, except for when the animals are incubating. There is biparental care, with the male contributing to nest-building, incubation and the feeding of the young. Zann (1996) writes that when their partner dies, zebra finches of both sexes are generally more willing to pair with a non-preferred individual than to not pair at all, which means that even less desirable males will have mates. Zann's evaluation, the result of years of field studies in Australia, is supported by experimental studies with captive zebra finches. For example Immelmann *et al.* (1978) placed a total of 64 unpaired birds (32 male and female) in a large aviary, and found that all but two of them formed pairs. Thus even relatively undesirable males were able to obtain mates. Similar results were obtained by Clayton (1990). Given these conditions, the only way there could have been a useful surplus of unmated males for mate choice copying to have evolved would be a male-biased sex ratio throughout this species' evolution. Zann (1996) reports a slight male-biased adult sex ratio in 6 Australian populations, with the deviation from parity becoming significant only when data from all populations were pooled (52% males). Results for the secondary sex ratio (i.e. the ratio for young that have just finished receiving parental care) were mixed across 2 populations. These data are too fragmentary and limited to allow for safe generalizations, but suggest that even if a male-biased ratio exists, it is too small to be

[9] There are two subspecies. The Australian Zebra Finch (*Taeniopygia guttata castanotis*) is found on mainland Australia and the Lesser Sundas Zebra Finch (*Taeniopygia guttata guttata)* on the islands of the Lesser Sundas archipelago (Zann, 1996). Research is usually conducted with the Australian subspecies.

of significance. A reasonable assumption is that the high dispersal and mortality rates that are so characteristic of this species could ordinarily swing local sex ratios either way.

A priori, from these considerations alone it seems highly unlikely that copying could evolve in this species. There is substantial paternal care, minimal male mating skew and lifelong pair-bonds. Indeed, the notion of copying in the zebra finch stands what is generally accepted about mate choice in birds on its head. It is usually thought that females will maximize their fitness by avoiding mated males and seeking unpaired males that will provide their full support in rearing the young (Alatalo *et al*., 1981). Males, in turn, should have evolved behavioral strategies that deceive females into believing they are single (Alatalo *et al*., 1981; 1990). The notion that zebra finches copy suggests the exact opposite, and with no good theoretical reason. I turn now to the relevant empirical studies, as well as a theoretical treatment of this subject, and examine them in turn.

The first study to investigate mate choice copying in captive zebra finches used the preference reversal paradigm (see section 1.4) and found no evidence for copying (Doucet *et al.*, 2004). The focal females in the experimental group observed the model female court the focal female's previously non-preferred male for 30 minutes, while a separate control group of focal females witnessed no model female. Upon being retested however, both the experimental and control groups of focal females spent

significantly more time near the previously non-preferred male, a result with no obvious explanation but at any rate inconsistent with mate choice copying.

Swaddle *et al.* (2005) used the standard binary choice paradigm, randomly pairing the model female with one of two males while the other male was placed in a cage with a second male. They also greatly increased the length of the observation period, from the 30 minutes in Doucet *et al.*'s study to two weeks. When tested after two weeks of observation, the focal females spent significantly more time with the previously paired male, avoiding the male that had been caged with another male. Interestingly, Swaddle *et al.* conducted a second experiment with a similar design which investigated whether zebra finches exhibit generalized trait copying. The trait in question was the colour of the plastic leg band[10] worn by the males, and the results suggested that the focal females preferred novel males that were wearing the same color band as the apparently mated males over novel males that were wearing the same color band as the males that had previously been caged with another male.

A problem with this study is that Swaddle *et al.* paired the supposedly unsuccessful male with another male. Usually in these experiments the unsuccessful male is either left on its own or has a female placed next to in a compartment that is out of the focal

[10] For reasons that have not been fully determined, these leg bands alter the attractiveness of the bird that wears them, be it male or female (reviewed in Zann, 1996). For example females prefer males that wear red colour bands and avoid males that wear light-blue or light-green bands (Burley *et al.*, 1982).

female's line of sight, so as to control for differences in courting behaviour or 'priming' between the two males (e.g. Schlupp *et al.*, 1994). In this instance, however, the researchers chose 'to use a same-sex pair of males, rather than a lone male as the alternative stimulus to the mixed-sex male-female pair, to control for the number of birds associated with each treatment' (Swaddle *et al*., 2005, p. 1054). Swaddle *et al.*'s design did not control for a number of other potential confounds (differences in courting behavior between the two males during the observation period, quality of the males, the fact that the supposedly successful male could have been 'primed' from just having spent two weeks with another female and subsequently courted the focal female more vigorously during the choice period), so their emphasis on controlling for number of birds appears to me unjustified. This experimental setup, however, resulted in the supposedly unsuccessful male spending two weeks enclosed in a small cage (30x20x40 cm) with another male. That there were problems of aggression between the two confined males is implicitly acknowledged by Swaddle *et al.* when they concede that 'It may be that behavioural differences between males associated with a female versus males housed in single sex groups could influence the shift in mate preferences' (p.1056). They then state that 'none of the birds in our study exhibited the consequences of overt aggressive or dominance encounters (e.g. feather plucking)' (p. 1056). These problems, then did not reach the point where the supposedly unsuccessful males started to pluck their feathers, but this is hardly any defense regarding the soundness of the experimental design or the validity of the results.

As for why or how mate choice copying could have evolved in this species, Swaddle *et al.* devote only a handful of lines in their paper (*p*. 1056), but provide essentially no explanation. They first note that zebra finches can switch partners from one breeding season to the next[11], and then state that it may be advantageous for a previously unpaired female to attempt to pair with a previously successful male in a subsequent breeding attempt. It is not clear what they mean by 'successful' male: if they are referring to success with regard to breeding (i.e. number of successfully reared young, frequency of clutches etc), then this is not mate choice copying, nor does their experiment have any bearing on such a process. If, on the other hand, 'successful' refers to a previously mated male, the fact that normally all male zebra finches find partners means that it is not clear why it would be advantageous for a female to prefer a previously mated male (see section 2.3).

The final experimental study (Drullion & Dubois, 2008) focused solely on generalized trait copying, using, as in Swaddle *et al.*'s study, plastic leg bands as the focal trait, and producing a marginally significant result (*p*=.048). An elaborate version of the preference reversal paradigm was employed that used no live males or model females but only video-recorded stimuli on TFT monitors. At the first stage of the experiment, where focal females' initial preferences were determined, the monitor simultaneously displayed two videos of males (wearing different colour leg bands), one on either side of

[11] They cite Zann (1996) as a reference to this fact, but as I discussed above Zann states clearly that in the wild zebra finches only switch to a new partner when their old one has died (Zann, 1996; *p*.83).

the screen, both played without sound[12]. The researchers presumed that they could accurately gauge the focal females' preference for one versus the other type of male by the amount of time the females spent on two perches that were placed in front of the screen, one perch on either side. The authors provide no evidence that the females were responsive to the TFT monitors and perceived what was displayed on them as a human would. There was, in other words, no evidence of correspondence between the two-dimensional images of the males displayed on the screen and their three-dimensional counterparts in the real world (for a discussion of this problem and critique of similar studies see Weisman & Spetch, 2010). Indeed, by the authors' own admission, there was very strong, if not conclusive, evidence to the contrary: 'During all the duration of the observation period and the choice test, the females could hear but not see conspecific males that were placed behind the TFT screen. Their presence was necessary because otherwise, the females in the apparatus remained mostly inactive' (Drullion & Dubois, 2008; p.271). In other words the researchers had to hide live males behind the monitor in order to elicit any response from the focal females. The authors provide no details as to how many males were placed behind the screen and at which side. At a later stage, the experiment involved the image on the TFT monitors being split into four quadrants, with different videos of males being played simultaneously in each one. Two of the males were with females, two alone. Again, the authors provide no evidence that the zebra finches could properly perceive the image on the screen or assimilate this highly artificial 4-way information stream being presented to them. Like

[12] Although song rate is one of the most crucial cues in female mate choice (Houtman, 1992; Zann, 1996; Collins *et al.*, 1994).

Swaddle *et al*., Drullion & Dubois (2008) provide no explanation as to how or why generalized trait copying might have evolved.

Interestingly, a year before Drullion and Dubois published their experimental results, Dubois (2007) published a theoretical paper which examined whether copying might have evolved in monogamous species to aid females in their pursuit of high-quality extrapair mates. This novel idea was something that was not addressed in any of the experimental studies, including the one that Dubois herself co-authored the following year (Doucet *et al*, 2004; Swaddle *et al*., 2005; Drullion & Dubois, 2008). Accordingly, Dubois (2007) concedes that no direct evidence supports her theory. Her model is a linear algebraic game involving approximately 20 independent parameters. To understand how she arrives at her conclusions, it is necessary to briefly describe the model's assumptions. Dubois envisages a female population where some females choose males randomly at the start of the breeding season ('random females'), while the rest ('selective females') assess males (with an error parameter) and only select a male they perceive to be of high quality. These selective females tend to select higher quality males but suffer the costs of mate assessment. There is no variation in female quality, and no male choice. Once all females have found mates, they can then engage in EPC's (which besides the benefits also involves a cost of the cuckolded partner reducing his parental investment), but only with males that have been chosen by selective females. Predictably, given these assumptions, the model finds that selective females should never engage in EPC's, while it may sometimes be profitable for

random females to engage in EPCs with selective females' mates, depending on the values of the various parameters.

Clearly, although Dubois advances this as a model for monogamous species, its assumptions do not describe a monogamous species[13]. These are the species where male choice should be most intense and males most sensitive to the variations in quality of prospective mates (Trivers, 1972; Burley, 1977). Given the costly consequences of a wrong choice, these are also the species where is it least likely that any females will be randomly selecting their mates (Trivers, 1972), so the notion of random versus selective females, while an interesting theoretical device in promiscuous and lekking species, cannot be applied here. The typical monogamous model, in contrast, should involve strong mate choice for all females, slightly weaker male choice, and assortative mating in terms of quality, with high quality individuals of both sexes selecting each other first, leaving the less desirable individuals to pair amongst themselves (Burley, 1983; Johnstone, 1997). This is a completely different distribution of pairbonds to the one Dubois' model envisages.

In conclusion, these studies began without a careful examination of the zebra finch's mating system in relation to copying (the 'lock-and-key' approach to the study of adaptation, see Tooby & Cosmides, 1992), and this initial omission has resulted in what

[13] In all, the only substantial assumption I could find in Dubois' model that resembles a monogamous species is the fact that every male is paired with one female.

appears to me to be a very unpromising line of research. The suggestion that these females copy, while certainly counterintuitive and therefore impressive, is not justified by the evidence. What I have discussed in this chapter suggests that a more realistic alternative to monogamous copying is to view nonindependent mate choice in monogamy as a very unusual occurrence, and seek those rare species with some unusual feature which would permit the evolution of nonindependent mate choice. Mate quality bias or a process akin to that should then be the tested hypothesis, not mate choice copying.

Chapter 3: Experimental approaches

3.1 Introduction

As discussed above (section 2.1) every study that has examined nonindependent mate choice in humans, both in the 1970's and in recent years, has used experimental techniques. While some studies have employed live confederates (Sigall & Landy, 1973; Uller & Johansson, 2003), or video-recorded stimuli (Meiners & Sheposh, 1977), or have relied primarily on written stimuli (Dugatkin, 2000; Eva & Wood, 2006), most studies have used photographic stimuli (Bar Tal & Saxe, 1976; Onodera & Miura, 1990; Milonoff *et al*., 2007; Waynforth, 2007; Little *et al*., 2008; Vakirtzis & Roberts, 2010). Each approach has its own strengths and weaknesses. The use of confederates makes for more ecologically valid experiments but introduces potential confounding variables which are difficult to quantify or control for. For example it is reasonable to assume that a naturally attractive confederate that is made up to appear unattractive (Sigall & Landy, 1973) may unconsciously alter her behaviour in ways which neither she nor the experimenter realizes. Nor is it easy to satisfactorily manipulate independent variables like attractiveness when working with only one or two confederates. The use of photographs, on the other hand, allows the experimenter to retain a high degree of control over confounding variables but suffers from reduced ecological validity and involves artificially impoverished stimuli. Studies that employ video-recordings as stimuli could be classified as falling in between the other two categories with respect to these strengths and weaknesses. Designs that rely on written narratives are a potentially very

useful research avenue in that they allow the manipulation of variables that are difficult to assess through photographs or videos, like, for example, whether or not the stimulus men are married (Eva & Wood, 2006), their relationship history, personality descriptions etc.

In this chapter I describe two experimental studies, the first based on photographs and the second on video-recordings of a sample of women that were recruited to serve as 'model females'. The first is an extension of earlier studies (Waynforth, 2007; Little *et al.*, 2008; Vakirtzis & Roberts, 2010) that sought to replicate and possibly go beyond previous findings. The second study employed a novel design that aimed to utilize the dynamic, non-structural information contained in motion pictures so as to determine the possible relevance of model female factors other than attractiveness (and possibly age), such as personality factors and behavioural tendencies.

3.2 Study I

3.2.1 Introduction

Perhaps the most basic method of experimentally examining human nonindependent mate choice using photographic stimuli is to present images of men next to images of their supposed female partners, and vary the attractiveness of these partners across or within raters (Little *et al*., 2008; Vakirtzis & Roberts, 2010; Yorzinski & Platt, 2010). This is a within-stimulus design, where the prediction is that the male will receive higher

attractiveness ratings when presented with the more attractive of the two partners. The problem with this method is that it doesn't provide a baseline attractiveness rating of the male, i.e. it doesn't provide information on how attractive a male would be if he were simply presented alone. To answer this a third group of raters would be needed which would assess the attractiveness of the male image by itself, without any partner present. Although Waynforth (2007) employed this 'no partner' condition, he subsequently only presented males with one partner, and compared the 'no partner' condition solely against this single 'with partner' condition (see section 2.4 for discussion). Although such a comparison is the only way to compare absolute with conditional probabilities of choice, it inevitably suffers from a slight degradation of the within-stimulus condition. Fortunately there is nothing in the structure of these two designs that doesn't allow them to be combined in a single study, and this is what I did here.

The aims of this study were manifold:

a) To replicate Waynforth's (2007) findings regarding the predictable - from the vantage point of mate quality bias - relationships between male attractiveness, female attractiveness, absolute and conditional probabilities of choice[14].

b) To better operationalise 'attractiveness' as an independent variable in the domain under consideration, and in particular to examine whether male or female judgments of the model female's attractiveness are a better predictor of mate quality bias. At first the

[14] See section 2.4 for discussion.

answer to this might seem obvious: since it is focal females' brains inside which this process takes place, it should be female judgments of the model female's attractiveness that best predict the outcomes of this process. This ostensibly straightforward answer seems less certain, however, when one considers that in the actual mating market the model female's mate value is determined solely by the attractiveness evaluations of men, since it is only for them that the model female can serve as mate. In other words, and to couch this idea in more practical terms, if there is disagreement between a set of male and a set of female judges as to the relative attractiveness of a woman's photograph, it is the male judges' ratings that are a more valid indicator of her 'true' attractiveness. This objection would still seem to run into the obstacle that focal females can have no way of knowing how males would evaluate the model females other than to rely on their own (i.e. the focal females') evaluations as a proxy for the 'real thing'. Although this is true, the distinction must be drawn between females' explicit evaluations of other females' attractiveness and possible parallel unconscious processes (e.g. Todd *et al*., 2007). Keeping in mind that the process of nonindependent mate choice is probably largely subconscious (and depending on the degree of sophistication of the relevant adaptations), it is not implausible to assume that dedicated cognitive mechanisms have evolved to simulate the male evaluative mechanisms and feed this input into the focal female's nonindependent mate choice machinery in a non-conscious manner. There might therefore be a divergence between the focal females' explicit evaluation of model females' attractiveness and the way they evaluate this attractiveness unconsciously for the purposes of nonindependent mate choice. If this is

indeed the case, then male ratings of the model females' attractiveness should best predict the outcomes of mate quality bias.

c) To examine the relevance of model female age, and assess its relative contribution vis-a-vis model female attractiveness. As discussed in Chapter 2, there exists substantial evidence from non-human animals that older females are preferred as model females over younger females (e.g. Dugatkin & Godin, 1993; Amlacher & Dugatkin, 2005; Vukomanovic & Rodd, 2008), due presumably to their greater experience in mate choice (Nordell & Valone, 1998). In line with these findings, Vakirtzis & Roberts (2010) found that aside from the primary effect of partner attractiveness women raters viewing static male and female facial images - supposedly partners - also seemed to be influenced by the age of the target men's supposed partner. In particular men that were paired with older partners tended to receive higher desirability ratings compared to those who were paired with younger partners. All the female partners used in that study were very young (below 25 years), and it is almost certain that there is a ceiling effect to this phenomenon, since after a certain age the mate value of women declines (Symons, 1979; 1995). Here I sought to replicate this finding and determine, via multiple regression, the contribution of model female age (if any) relative to model female attractiveness.

d) To examine sources of variance arising from the 'focal female' raters. This line of inquiry was inspired by Waynforth's (2007) finding that there are between-subject differences in the degree to which women are influenced by the men's partner, with some women less prone than others to complementing their independent assessment of males with information from their partners. Waynforth found that women with higher

numbers of lifetime sexual partners, and women with more unrestricted sociosexuality (Simpson & Gangestad, 1991) were less influenced by the attractiveness of the target males' supposed partner, and tended to evaluate the target males independently (see also Dugatkin & Godin, 1993; Nordell & Valone, 1998; Vukomanovic & Rodd, 2008).

3.2.2 Materials and methods

3.2.2.1 Collection and preparation of stimuli

Fifty four women (mean age ± SD = 22.7 ± 2.9 yrs, range 18-29), of which 52 were staff and students at the University of Liverpool and two were drawn from my personal contacts, were recruited to serve as stimuli in the study. Towards the end of the study one subject withdrew consent, reducing the sample size to 53[15]. No pay was given. Subjects were photographed in a studio with artificial ceiling lighting. They were instructed to adopt a neutral expression and had their facial photograph taken with a digital Fuji Finepix S6500 at 6 megapixels resolution. In order to avoid glare I did not use flash, and compensated with the use of a tripod, slow shutter speed (1/20th of a second) and ISO 200. For best results I typically took several photographs of each subject. After having their picture taken, subjects were filmed (in video mode) for 1 minute with the same camera and filled out a battery of psychometric tests for the purposes of study 2 (reported in detail below, see section 3.3.2.1).

[15] Due to this late withdrawal and the way the study was set up, I describe the design of the study with all 54 subjects, but report results for 53 of these (see below).

I subsequently selected one facial photograph for each subject on the basis of such criteria as correct focus, exposure and neutrality of expression. Some of the images were slightly edited where necessary (cropped, rotated etc.) using Microsoft Office Picture Manager and finally all 54 images were resized to a standard size of 800×600 pixels. The images were then rated for attractiveness on a scale from 1 (least attractive) to 10 (most attractive) and perceived age by 20 male (21.1 ± 2.7 years) and 20 female (21.3 ± 1.7 years) students, recruited by convenience at the University of Liverpool Sydney Jones library. The images were presented in randomized order on a computer screen using a Visual Basic 6.0 application, and raters gave their ratings by pressing the appropriate key on the keyboard. Half the raters (half the men and half the women) rated the facial photographs for attractiveness before rating them for perceived age, whereas the other half rated them for age first and then attractiveness.

The mean attractiveness ratings given by male and female raters correlated very highly (r=.902, n=53, p<.001) although female raters gave higher average ratings (mean ± SE = 4.63 ± 0.13) than men (4.03 ± 0.13), and significantly so (paired t-test, t=10.36, df=52, p<.001). As was the case with ratings of attractiveness, mean perceived age attributions by male and female raters also correlated very highly (r=.912, n=53, p<.001). Female raters were marginally better at estimating the real age of the female images (r=.642, n=53, p<.001) compared to male raters (r=.619, N=53, p<.001).

For the target male stimuli I randomly selected 54 male facial images (mean age 21.8 ± 2.3, range 18-28) from a larger set of male photographs (staff and students at the University of Newcastle) that had been used in previous mate choice experiments (e.g. Roberts *et al*., 2005a; b; Vakirtzis & Roberts, 2010). To every male image I then randomly assigned two female images by using each female image twice in the following manner (see Figure 3): two female images were randomly assigned to the first male, then two more to the second male and so on, until all 54 female images had been used up for the first 27 male images. I then repeated this process for the next 27 male images until a total of 54 stimuli had been created, each stimulus consisting of one male image and two different male images.

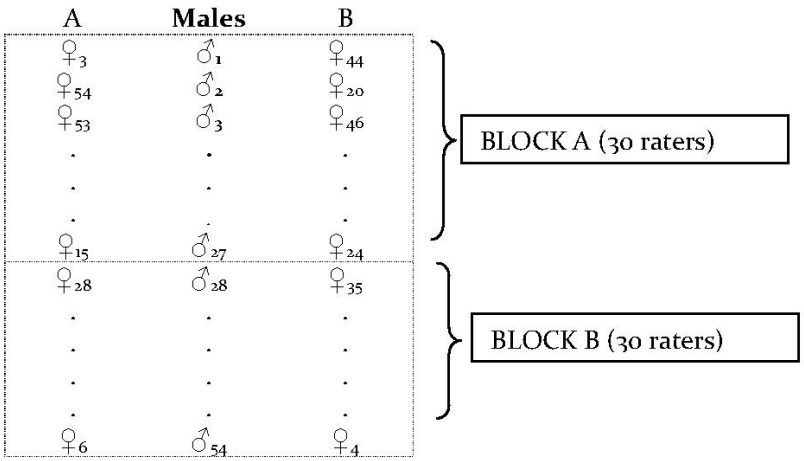


Figure 3. Schematic illustration of experimental design. Fifty-four male stimuli were randomly ordered from first to last (centre column). Two female stimuli, randomly selected from an ordered set of 54, were assigned to the first male stimulus (one placed randomly in column A and the other in column B), then two more to the next male stimulus etc, till all 54 had been used. This process was then repeated for the next 27 males (#28-54), for a total of 2 replicates (blocks). Each block was then rated by 30 female subjects altogether, of which 15 rated the males presented with the females in column A, and 15 rated the males presented with the females in column B. The 27 males of each block were always presented to the raters in random order.

3.2.2.2 Procedure

Sixty female subjects were recruited by convenience at the University of Liverpool Sydney Jones library. To conceal the purpose of the experiment, participants were told they would be participating in a study examining 'social aspects of person perception' and that the experiment was aimed at comparing the social judgments made by undergraduate females with those made by females of various other socio-economic groups (following Bar-Tal & Saxe, 1976). Participants were then informed that they would be shown images of men and their ex-girlfriends from various universities in the Northwest region, and that in all instances the relationship between the man and his girlfriend had lasted a minimum of 4 months. Participants were then instructed to indicate how 'interested they would be in going out on a romantic date' with each male (following Vakirtzis & Roberts, 2010) on a scale from 1 (least) to 10 (most). The computerized rating procedure took place through a VB6 application, with pairs of male and female images (each 540x405 pixels) presented sequentially, the male image on the left part of the screen and the female on the right part of the screen. Thirty participants (15 for each 'ex-girlfriend') rated the 27 males from block A and the other 30 participants rated the remaining 27 males from block B (see Figure 3). After participants had finished with the rating procedure, they were asked to fill out a brief questionnaire with information about their age, relationship status (single or in relationship), self-perceived experience in romantic relationships (on a scale from 1-10) and self-perceived physical attractiveness (on a scale from 1-10). The questionnaire also included 4 items from the Sociosexuality orientation inventory (SOI; Simpson & Gangestad, 1991) that related to sexual strategy and which Waynforth (2007) found

were useful in predicting the degree to which females are prone to nonindependent mate choice. Three of these four items were statements with which participants had to agree or disagree (on a 9 point scale): “Sex without love is OK”; “I can imagine myself being comfortable and enjoying casual sex with different partners”; “I have to be closely attached to someone before I could feel comfortable and fully enjoy having sex with him”. The fourth item asked participants how many different partners they realistically envisioned themselves having sex with over the next 5 years. Lastly, subjects were asked to answer “yes” or “no” to the following question: “Do you think that viewing thee images of these men’s ex-girlfriends influenced the ratings you gave the men?”

In order to provide a set of baseline attractiveness ratings for the 54 male images, a separate set of 10 female participants (mean age 21.0 ± 1.7, range 19-25 yrs) rated the male images presented on their own, without any female image on the screen. These participants were simply told that they were participating in a dating preferences study, and were asked to rate all 54 males (presented in random order) for the same question (i.e. how interested they would be in going out on a date with them) on the same 10 point scale. These 10 female participants only gave me their age, and did not fill out the questionnaire that the other 60 participants had filled out. At the end all participants were told the exact purpose and aims of the study and gave final informed consent.

3.2.3 Results

3.2.3.1 Descriptive statistics

Descriptive statistics for the 60 female subjects that participated in the main part of the study are given in Table 3. Thirty eight (63%) subjects were single and the rest in a relationship. A large majority (78%) of subjects (*n*=47) indicated that they were *not* influenced in their ratings by the images of the men's supposed partners.

Table 3. Descriptive statistics of female subjects

Variable	Min	Max	Mean	SD
Age	18	29	21.3	1.9
Self-rated attractiveness	3	8	5.66	1.3
Self-rated relationship experience	1	9	5.6	1.9
Sexual strategy score (from SOI)	4	35	16.6	7.7

3.2.3.2 Model female attractiveness and age

The first part of the analysis examined the importance of model female attractiveness and age. I averaged the rating given to each target male when he was viewed with the female in condition A and then averaged the rating given to him when he was viewed with the female in condition B. The dependent variable was the signed difference in average rating each male received between being viewed in the two conditions [(with

female A)-(with female B)]. This signed value was then regressed against the signed difference between the two females in attractiveness and age[16]. Initially I included as predictors the difference in attractiveness ratings between the model females based on attractiveness estimates of male raters and the difference in model females' actual (as opposed to perceived) age. The overall model was not significant ($F_{2, 49}$=2.105, p=.133), and neither model female attractiveness (*beta*=.092, t=0.668, p=.508) nor age (*beta*=-.274, t=-1.993, p=.052) made significant contributions to the model. I ran subsequent regressions using all possible combinations of model female attractiveness (male and female estimates) and age (actual and perceived[17]), but all models were not significant (all p>.1).

The reason for these null results becomes evident through an inspection of the correlation matrix (Table 4) summarizing the relationships between the ratings the target males received when they were presented in the three conditions (alone, with females in condition A and with females in condition B). The correlations are all so high that there can be little doubt female raters were simply ignoring the images of the model females and giving their ratings solely on the basis of target male attractiveness.

[16] For example, assume one male received a rating of 3.1 when he was viewed with female A and 3.5 when viewed with female B. The value of the dependent variable for this particular male would be -0.4. Now assume that female A had an attractiveness rating of 3.4 and was 22.5 years old, while female B had an attractiveness rating of 4.1 and was 19.3 years old. The values of the predictor variables for this particular male would be -0.7 for attractiveness and 3.2 for age.

[17] I averaged the perceived age ratings across both male and female raters, since the correlation between the two sets was already very high, and there was no reason to expect any gender differences in rating patterns.

Table 4. Correlation matrix of desirability ratings given to target males in various conditions.

	Female A	Female B
Baseline	.732***	.785***
Female A		.848***

***p<.001

3.2.3.3 Comparisons between absolute and conditional probabilities

Following Waynforth (2007), I conducted a one-way repeated-measures ANOVA with three levels (baseline, female A, female B) to examine whether target males received higher desirability ratings when presented with a model female compared to when they were presented alone. The differences between conditions were highly significant ($F_{2, 102}$ =104.5, p<.001, partial η^2=.672). Planned orthogonal contrasts showed a significant difference when baseline (mean ± S.E. 2.00 ± .095) was compared to A (2.87 ± .118) and B (2.8 ± .105) ($F_{1, 51}$ =175.9, p<.001, partial η^2=.775), but no difference when A was compared to B ($F_{1, 51}$ =0.372, p=.545, partial η^2=.008). These results are depicted graphically in Figure 4, and would seem to suggest a simple mate choice copying effect.

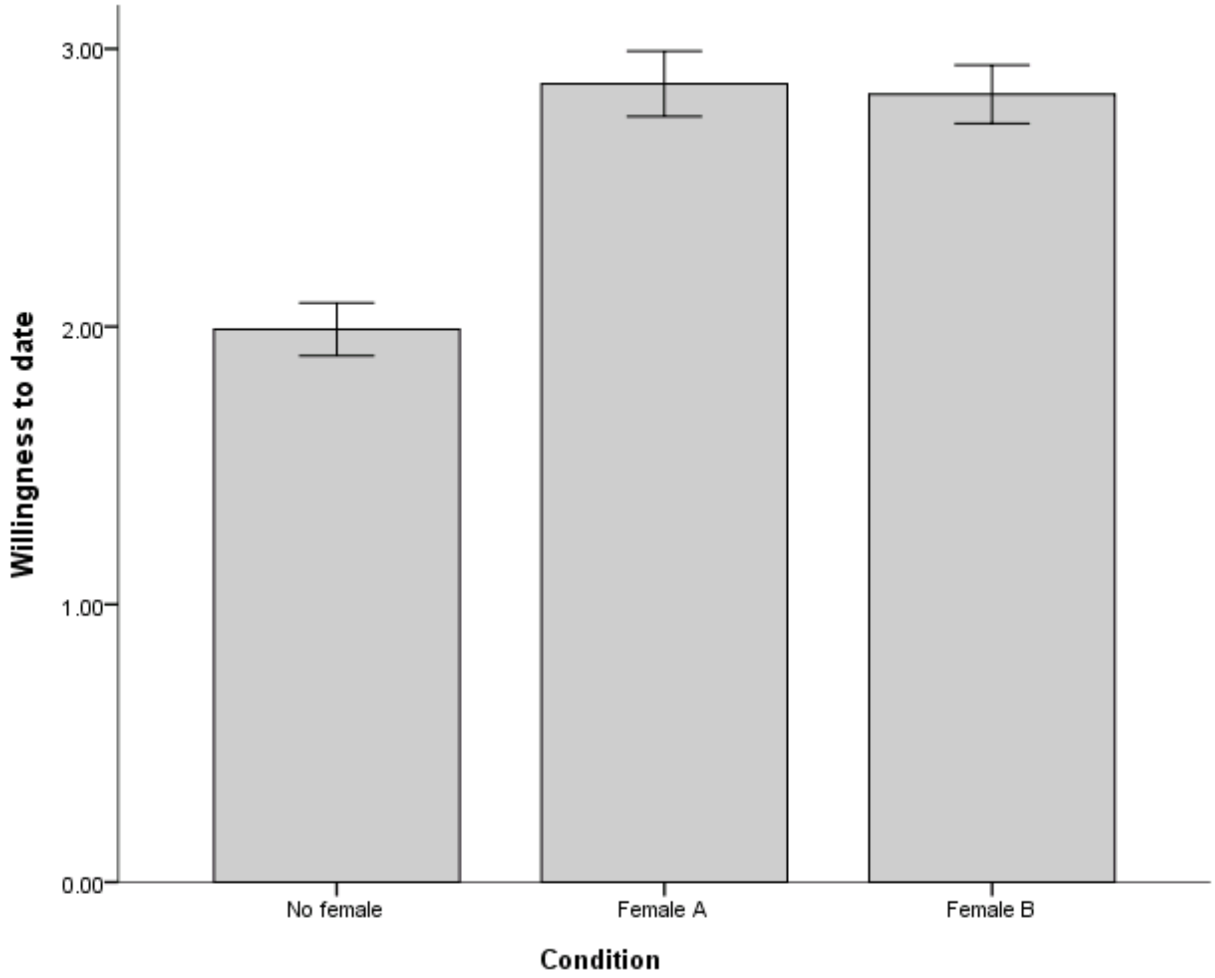


Figure 4. Comparison of average ratings target males receive when presented alone and with a supposed partner. Error bars are standard errors.

To test for mate quality bias I followed Waynforth's analysis (*p*. 268) and divided the target male stimuli into three attractiveness groups (attractive, average and unattractive) based on their ratings in the baseline condition. The males in the attractive set ranged from the most attractive one to the one in the 67th percentile, the ones in the average from the 66th to the 33rd percentile, and the unattractive set contained the remaining males. I also divided the model females into the same three attractiveness groups, and

plotted the data with the mean change in attractiveness ratings (from baseline to condition A) as the dependent variable (Figure 5).

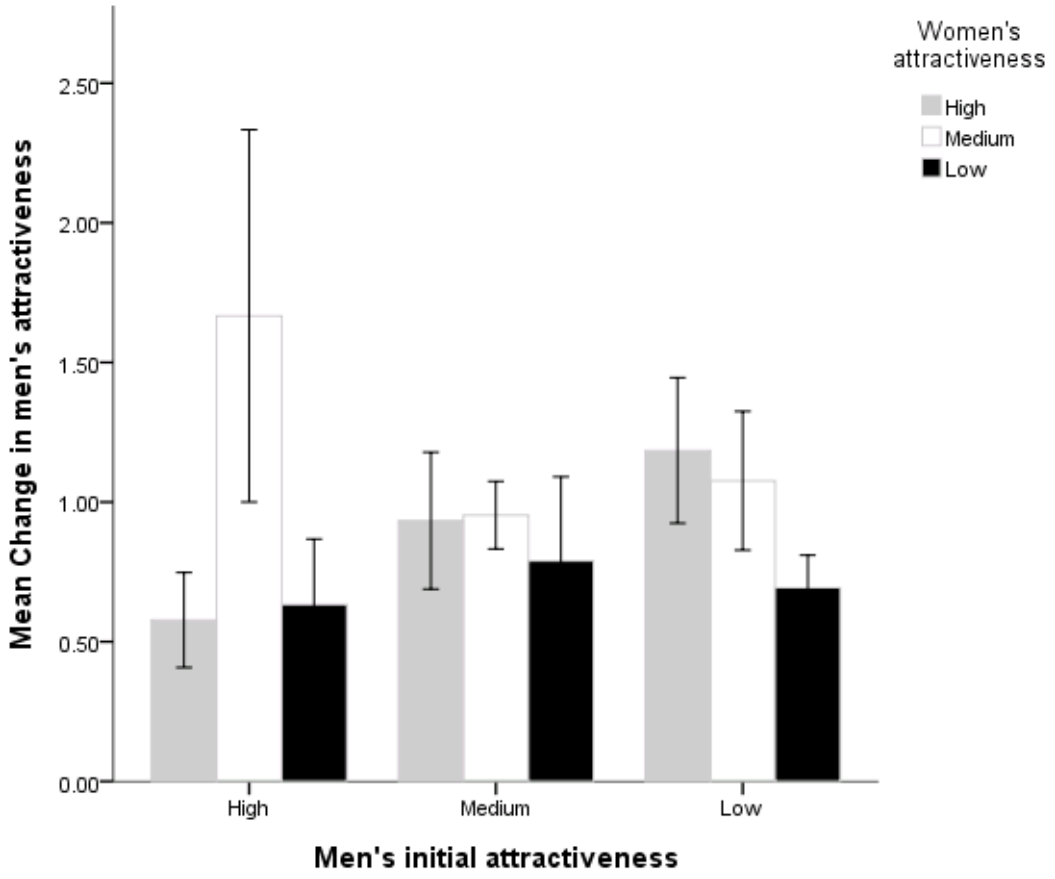


Figure 5. Change in desirability ratings from baseline to condition A. Positive values on the y axis indicate that men gained in their desirability rating when they were presented with a woman compared to when they were presented alone, while negative values would indicate that they lost (no negative values recorded here). Error bars are standard errors.

Figure 5 does not resemble Waynforth's orderly results, nor does it bear out the predictions of mate quality bias[18]. To more formally examine the role of male and model female attractiveness I conducted a 3x3 ANOVA with male and model female attractiveness as factors and the attractiveness levels specified above. A mate quality bias hypothesis would predict both main effects to be significant, but concerning the interaction between the two variables it would make no specific predictions; an interaction effect would depend on whether or not the phenomenon was linear across all levels of male and female attractiveness, and also on the precise partitioning of the groups. At any rate, the results presented by Waynforth (2007, p. 268) seem to suggest no interaction effect. The results of the factorial ANOVA are shown in Table 5. As can be seen the overall model was not significant, as were both main effects and the interaction.

Table 5. Two-way ANOVA of change in male attractiveness ratings, with male and female attractiveness as factors.

	SS	DF	Ms	F	p
Model	3.33	8	.417	1.34	.249
Male attractiveness	.070	2	.035	.113	.893
Female attractiveness	1.81	2	.906	2.92	.065
Male*female attract.	1.69	4	.422	1.36	.264
Error	13.3	43	.310		
Total	16.7	51			

R^2=.200 (adjusted R^2=.051)

[18] See section 2.4 for discussion and predictions.

I ran a very similar analysis comparing baseline to condition B (essentially baseline vs. condition A and baseline vs. condition B could be considered two replications of the same experimental design, made possible due to the setup of the study). This is shown in Figure 6. The results of the ANOVA (table 6) confirm the visual estimates, with no significant main effects or interactions (see Table 6).

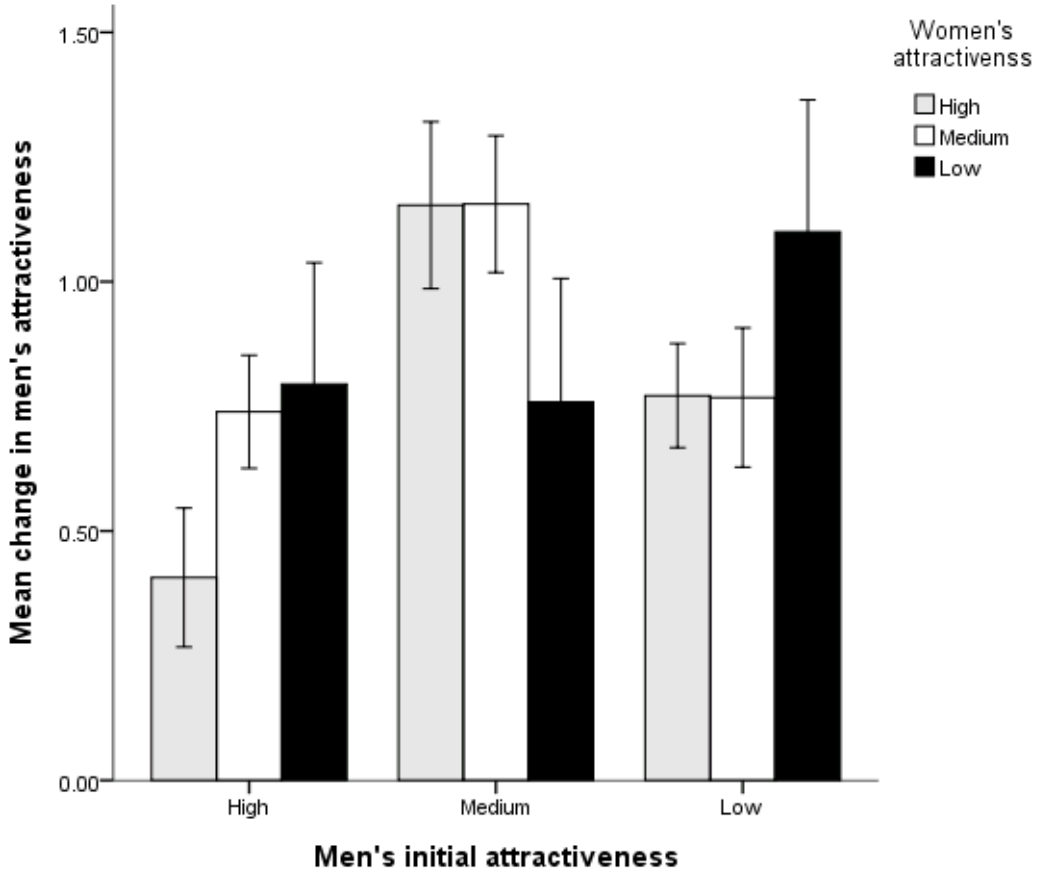


Figure 6. Change in desirability ratings from baseline to condition B. Positive values on the y axis indicate that men gained in their desirability rating when they were presented with a woman compared to when they were presented alone, while negative values would indicate that they lost. Error bars are standard errors.

Table 6. Two-way ANOVA of change in male attractiveness ratings, with male and female attractiveness as factors.

	SS	DF	Ms	F	p
Model	2.54	8	.318	1.608	.151
Male attractiveness	1.24	2	.619	3.13	.054
Female attractiveness	.132	2	.066	.335	.717
Male*female attract.	1.39	4	.347	1.75	.156
Error	8.50	43	.198		
Total	11.0	51			

R^2=.230 (adjusted R^2=.087)

3.2.3.4 Variance arising from raters

The last part of the analysis focused on variance arising from the side of the females raters. Recall that after they had given their ratings subjects were explicitly asked whether or not their ratings had been influenced by viewing the images of the men's former partners, and that 47 out of 60 raters (78%) had answered negatively. Unfortunately the subset of women that had answered positively was far too small to allow a separate examination of their (presumably more interesting) ratings. Instead I examined if any of the other self-reported variables predicted whether or not raters had (according to their own statement) been influenced by the model female images or not. I conducted a binary logistic regression with 'yes/no' as the dependent variable and rater age, self-rated romantic attractiveness, self-rated romantic experience, relationship status (single vs. in a relationship), and SOI score as predictors. The model was not

significant (χ^2=3.7, *df*=5, *p*=.59), as were all predictors (all *p*>.17).Simple univariate comparisons similarly showed no differences between the two groups of women.

3.2.4 Discussion

I employed a within-stimulus design that compared the desirability ratings female raters gave to target males when these were presented alone and with women of varying attractiveness and age. The results obtained here, unlike those of previous studies (Waynforth, 2007; Little *et al*., 2008; Vakirtzis & Roberts, 2010; Yorzinski & Platt, 2010), did not show an influence of model female characteristics on female raters' pattern of ratings. If anything, the results suggest a simple mate choice copying effect, with men presented with their partners receiving higher attractiveness ratings compared to the baseline condition of being presented alone.

But what can explain this failure of model female attractiveness to influence ratings of male attractiveness? An analysis of the ratings suggests that female raters were largely ignoring the images of the model females and focusing almost exclusively on the images of the target males. Given earlier results, it is clear that this behaviour is not indicative of a natural indifference on the part of raters to the model female[19], but is

[19] If this were the case, of course, it would perhaps be a valid indicator of real-life processes, and in particular the absence of nonindependent mate choice.

specific to the way the stimuli were presented in this study. It is worth discussing the probable reasons for this in some detail.

In my previous study (Vakirtzis & Roberts, 2010) I used a more basic but quite similar within-stimulus between-subjects design, with each target male being presented to different female raters with two supposed partners of differing attractiveness. Instead of a correlational design I had opted for a comparison-of-means approach: from a larger set of female photographs I had selected two sets of 20 female images of similar attractiveness, one set for the attractive model female condition and one for the unattractive. I then compared the ratings given to males when they were presented in the two conditions, and predictably found that when they were presented with the attractive females, the males received higher desirability ratings. It is unlikely however that this statistical manipulation (i.e. comparison of means vs. correlational design) is responsible for the difference in results. Rather it would seem that the cause lies with the way the stimuli were presented to raters on the screen. In the previous study (Vakirtzis & Roberts, 2010) I presented to female raters a large, centrally-placed image of the target male, with a much smaller image of the model female (a supposed ex-girlfriend) at the lower-left corner of the screen. A speech bubble emanated from the smaller picture of the model female, containing a fictitious description of the target male in the form of a couple of bullet points like ‘I just found our relationship unexciting’ or ‘Sometimes he would get upset for no apparent reason’. A target male image (*n*=20) carried the same speech bubble contents across both conditions, and the only thing that changed was the image of the girlfriend supposedly giving the description. Even though

the image of the model female was inconspicuously placed in the lower corner of the screen and was substantially smaller in size to that of the target male, the fact that the speech bubble contained an interesting real-life description of the target male presumably prompted female raters to devote a few seconds to examine the image of the model female who was supplying this information (see Dunbar, 2004). In contrast to that earlier study, here I adopted the more straightforward presentation format of other studies (Waynforth, 2007; Little *et al*., 2008; Yorzinski & Platt, 2010) and simply presented raters with two large images of equal size and salience, the target male on the left half and the model female on the right, asking raters to rate the desirability of the male. I did this in order to eliminate the additional sources of variance the contents of the speech bubble likely generated[20] and make the image of the model female more conspicuous, so as to elicit a stronger effect. Contrary to my expectations the exact opposite happened. Faced with a tedious sequence of unknown pairs of faces the female raters apparently just ignored the image of the model female and completed the given task in the quickest way possible, i.e. assessing only the male image.

We are still left with the puzzle of how other investigators (Waynforth, 2007; Little *et al*., 2008; Yorzinski & Platt, 2010) obtained results different to the ones I obtained even though they used a similar presentation format. As concerns the study of Waynforth (2007), the answer probably lies in the fact that although subjects in the baseline

[20] Although these contents were held constant across the two conditions, it is conceivable they interacted with the image of the target male or model female in various obscure ways, thus introducing additional variance in the final results.

condition (no model female) viewed a series of male faces, subjects in the model female condition viewed only a single male with his partner. A reasonable assumption would be that faced with the task of rating only one male, female subjects took their time and carefully evaluated the images of both the target male and his model female. Such an explanation, however, cannot account for the results obtained by Little *et al.* (2008) or Yorzinski & Platt (2010), since they presented to female raters a series of paired faces. Especially intriguing with regard to Little *et al*.'s study is the fact that the researchers used masculinized and feminized faces of composite images for both the target males and model females. Although these are quite similar in appearance, the large effect sizes obtained in that study indicate that subjects nonetheless remained highly motivated and attuned to differences in model female attractiveness throughout the experiment.

The preceding discussion highlights a more general point with regard to the experimental study of this phenomenon. Nonindependent mate choice in humans is a higher-level social psychological process which does not lend itself to experimental manipulations in the laboratory without problems. As this study has shown, and as the often contradictory or non-replicable results obtained to date also suggest (see section 4.1 for discussion), slight variations in factors like the preparation of the stimuli, the presentation of the stimuli, the number of stimuli, the instructions given to subjects, the wording of the dependent variable ('short-term attractiveness', 'long-term attractiveness', 'willingness to date', 'overall impression' etc.), could have a major impact on the results obtained, and what is obtained might not always be meaningfully

interpretable. In social psychological parlance, experimental studies of this phenomenon may often suffer from *reduced ecological validity* (Bracht & Glass, 1968). Two static facial images are substituted for a real-life romantic couple, and the rater is asked, in essence, to imagine that the two faces staring back at her are a real couple, that she is familiar with the couple, and that her scalar rating captures the complex ways in which she would react towards the target male in a real-life setting (mate-poach, ignore, flirt, show interest, be jealous, excited and so on). These are the minimum requirements for these experiments to have external validity. The difficulty of this task becomes apparent when one compares the ease with which other domains of evolutionary psychological research lend themselves to experimental research. Take for instance the experimental study of female preferences for masculinity in male faces (e.g. Penton-Voak *et al*., 1999; Rhodes, 2006; Feinberg et al, 2008). Here the domain of enquiry pertains to a lower-level set of sensory adaptations, and there is not much for the female rater to mentally simulate or imagine. She is presented with a photographic image that almost perfectly matches the real-life stimulus (the male face) and is asked to quantify her subjective attraction in a way which experience has shown is straightforward and undemanding. Considerations like these lead the student of human nonindependent mate choice to the realization of the urgent need to make the transition from the laboratory to the real world, all complexity and confounding variables notwithstanding[21].

[21] This is done in chapter 4.

3.3 Study II

3.3.1 Introduction

As discussed previously, research on human nonindependent mate choice to date has relied mostly on static (usually facial) images of model females and their supposed partners. While these static images suffice to convey structural information relating to model female attractiveness (Waynforth, 2007; Little *et al*., 2008; Vakirtzis & Roberts, 2010; Yorzinski & Platt, 2010), age (Vakirtzis & Roberts, 2010) or masculinity (Little et al, 2008) etc, they are probably inadequate for more dynamic information that pertains to personality and behavioral traits of the model females (Rubenstein 2005; but see Roberts *et al*., 2009). Here I expand on previous studies by using muted video recordings of women (model females) who were supposedly describing an ex-boyfriend. These video recordings were presented to a set of female raters who were asked to indicate how interested they would be in dating the men being described by the model females. The model females also filled out a battery of psychometric instruments that allowed me to examine the possible relevance of dynamic personality or behavioral traits. In addition to the broad-brush 'Big Five' factors of personality (openness to experience, conscientiousness, extraversion, agreeableness, and neuroticism; Goldberg, 1993) I examined specific personality traits like self-esteem and assertiveness that seemed plausible, a priori, as relevant cues (see Discussion for elaboration). Extending principles derived in part from animal studies, I also examine the importance of condition-dependent nonindependent mate choice arising from the side of the raters. Specifically, I tested whether their pattern of ratings was contingent

upon differences in their own attractiveness (e.g. Penke *et al*., 2007), sexual experience (Nordell & Valone 1998; Vukomanovic & Rodd, 2007) and relationship status.

3.3.2 Materials and methods

3.3.2.1 Collection of stimuli

As discussed in section 3.2.2.1, 53 women (mostly undergraduate and postgraduate students, mean age 22.7 ± 2.9, range 18-29 years) were recruited by convenience from the School of Biological Sciences, the School of Veterinary Sciences and from personal contacts. The subjects had their faces filmed in high-quality 640x480 AVI format for approximately 40-60 seconds while they were describing, towards the camera, their ideal romantic partner. I asked subjects to describe their ideal (as opposed to a real) romantic partner so as to obtain relatively constant expressions while retaining the relevant romantic content. Subjects were informed at the outset that the video clips would be shown to raters but that they would be muted and participants would therefore not be able to hear what was said. Each video clip was subsequently edited to a shorter 20-sec continuous clip using Windows Movie Maker and converted to 640x480, 25 fps WMV format. In selecting the 20-seconds of continuous video I tried to avoid instances where subjects made extreme or erratic expressions or gestures, or where they spoke in a manner which would make lip-reading easy.

After they had been filmed subjects completed an array of psychometric instruments (see Appendix A): a) The TIPI (Gosling *et al*., 2003), a brief, ten-item inventory of the Big Five with satisfactory psychometric properties that converges adequately with larger measures of the Big Five (Gosling *et al*., 2003). b) The 7-item Social Skills subscale of the Tromso Social Intelligence Scale (Silvera *et al*., 2001) which includes items like 'I fit easily in social situations' and 'I have a hard time getting along with other people. c) The Rosenberg self-esteem scale (Rosenberg, 1965), a 10-item instrument with statements like 'At times I think that I am no good at all' and 'On the whole I am satisfied with myself'. d) The Rathus Assertiveness Schedule (Rathus, 1973), a 30-item scale of assertiveness. e) The Shyness and Sociability Scale (Cheek & Buss, 1981), which is composed of two parts, a 9-item shyness and 5-item sociability subscale[22]. In addition to these standardized questionnaires subjects answered the following two questions (on a 10-point scale, 10 being most) that were designed to serve as self-report measures of sexual experience and self-perceived mate value, respectively: f) 'Overall, how experienced would you say you are in romantic relationships with men?' g) Overall, how interested and attracted are men generally in you?

The 53 20-sec muted videos were subsequently rated for attractiveness by eight male students from other departments (mean age 24.4 yrs) on a 7-point scale, and the scores averaged to produce a single attractiveness rating for each female video (*alpha*=.868). As demonstrated in meta-analysis (Langlois et al., 2000), inter-rater agreement on

[22] Internal reliabilities were high for all scales: Social skills (alpha=.802), shyness (alpha=.855), sociability (alpha=.836), self-esteem (alpha=.889) and assertiveness (alpha=.889).

attractiveness judgements is very high (both within and across cultures), and for this reason it is common practice in attractiveness studies to use small samples (unless one is interested in the remaining inter-individual variation). The high inter-rater reliability already achieved with 8 judges here suggested any additional judges would be of only marginal utility. Furthermore, the correlation between the attractiveness ratings given here by the 8 male judges to the videos of the model females correlated very highly (r=.78, df=51, p<.0001) with the attractiveness ratings given by a larger sample of 20 male judges to the photos of the same model females, reported above in Study 1. This suggested that the small sample of 8 male judges used here was not unrepresentative of the larger male population.

Although the women had all described their ideal romantic partner, it was evident by viewing the muted videos that there were emotional differences in manner in which they gave their description, some displaying more positive affect than others. To account for these differences I told seven female undergraduate students (mean age 20.3 yrs) that they would be shown muted videos of women describing an ex-boyfriend and asked them to rate each video on a 4-point scale (from '0-not positive' to '3-extremely positive') for the degree to which the woman's description of the man seemed to be positive. The seven raters' scores were then summed to produce a single 'positive expression' score for each female video that could range from 0 to 21.

3.3.2.2 Ratings

Ratings were carried out by 52 female students (20.9 ± 2.5 yrs old). These were recruited by convenience at a university library and were from other faculties than the model females (mostly Arts and Social Sciences) in order to minimize the chance that raters would know models. I gave subjects a very general explanation as to the purpose of the study, telling them only they would be participating in 'a study of how women are influenced in their romantic choices by the choices of other women'. Prior to viewing the videos the subjects gave information regarding their age, sexual orientation (all were heterosexual), self-perceived physical attractiveness (on a 10-point scale, 10 being most attractive) and self-perceived sexual experience (also a 10-point scale), although for these last two questions subjects had the option of refusing to supply the information. The instructions for the experiment were viewed on screen prior to presentation of the videos, and informed the subjects that the experimenters had asked some women to think back and bring to mind an ex-boyfriend of whom they had 'the most fond memories'. The experimenters had then recorded these women while they were describing this ex-boyfriend, and the subjects would now be shown these video recordings, though they would be played mute. Their task was to indicate how willing they would be to go out on a blind date with each man being described, on a 7-point scale from '1-least' to '7-most' (subjects were assured there were no right or wrong answers).

The 53 muted videos were presented in random order with a custom-made application designed in C-Sharp programming language (the same application as had been used with the eight male and seven female raters in the preliminary part of the study).

Subjects could give their rating and move on the next video before they had viewed an entire 20-sec clip (I observed that it was relatively uncommon for subjects to watch a 20-sec clip in its entirety). After they had completed the task subjects were debriefed and asked if they had recognized any of the women in the videos, in which case their ratings for those particular stimuli were excluded from the analysis. I also excluded from the analysis altogether the ratings of 3 women who stated they had understood the videos were descriptions of imaginary, not real men (two of them by lip-reading one particular model female with whom they were acquainted and who made characteristic mouth movements, the third due to a technical error on my part which resulted in her viewing the videos with sound), thus reducing the sample of raters to 49 women (20.9 ± 2.5 yrs old).

3.3.3 Results

I averaged the 49 ratings given to each video and used hierarchical multiple regression (assumptions satisfied) with each video as a data-point (*n*=53). Based on existing theoretical and empirical evidence I forced model female attractiveness (Waynforth, 2007; Little *et al*., 2008; Vakirtzis & Roberts, 2010; see also section 2.4) b), age (Nordell & Valone, 1998; Vakirtzis & Roberts, 2010) and 'positive expression' (Dugatkin, 2000; Jones *et al*., 2007; Place *et al*., 2010) into the first block of the regression. This first step was highly significant ($F_{3,49}$=43.3, R^2= .726, p < .0001) with the three variables accounting for nearly three fourths of the variance in ratings. Surprisingly, while attractiveness (*beta*=.543, *t*=7.04, *p*<.001) and positive expression (*beta*= .538, *t*= 6.98,

p<.001) made significant contributions to the model, age did not (*beta*= .023, *t*= 0.303, *p* = .76). This means that while female raters were more interested in dating the ex-boyfriends of model females who were more attractive and seemingly more positive in their descriptions of the man, they were not more interested in dating the ex-boyfriends of older model females. The second step of the model was a stepwise regression with all the measured personality and behavioral variables (the Big Five, social skills, self-esteem, assertiveness, shyness and sociability), self-rated mate value and self-rated sexual experience as predictors. Of all these previously excluded predictors, only emotional stability entered the model at the .05 level of significance, but the resulting increment in R^2 was a marginal .022, raising the overall explained variance to 74.8%. The final model is presented in Table 7. As can be seen, the relationship between the dependent variable and emotional stability was a negative one, i.e. the opposite of what one would probably expect given *any* relationship between these two variables. None of the other excluded variables approached significance (all *p* > .19).[23]

Table 7. Multiple regression predicting female raters' romantic interest in a man from characteristics in the model female describing him.

Independent	*beta*	*t*	*p*
Attractiveness	.557	7.42	<.001

[23] An examination of residuals revealed a generally tight fit of predicted to actual values, with the exception of a single case. This was a 20-year old undergraduate student who, although unexceptional in terms of both attractiveness and positive expression (37th and 11th percentile, respectively) had a very large positive standardized residual (2.8) and studentized deleted residual (3.1). In other words this was a case of low leverage but high influence. Deletion of this influential case substantially improved the predictive power of the model (R^2=.775), although now no independent variables entered the model in the second step of the regression (all *p*>.08).

Positive expression	.531	7.10	<.001
Age	.047	.632	.530
Emotional stability	-.150	-2.03	.048

$F_{4,48}$=35.57, p<.0001, R^2=.748

I ran the regression anew with all variables entered stepwise at α =.05. Model female attractiveness was the first variable to enter the model, accounting for 45.2% of the variance in ratings, and positive expression explained another 27.3% of variance, raising the total to 72.6%. Emotional stability marginally failed to enter the model (p=.054), and all other variables were clearly not significant (all p >.15). It could be argued that 'positive expression' is itself causally linked to underlying personality differences of the model females, and that its inclusion in the model obscures the significance of otherwise relevant personality predictors. To ensure this was not the case I reran the stepwise regression with all predictors *except* positive expression, but after attractiveness no other predictor entered the model, and the only excluded variable that neared significance (agreeableness) was in the opposite direction to what one would expect (*beta*= -.200, t= -1.98, p = .053). Finally, to better examine the effects of attractiveness on its own (and given that attractiveness was slightly correlated with positive expression, although not significantly (r=.240, n=53, p=.084)) I regressed attractiveness against positive expression, and plotted the residuals against the dependent variable (Figure 7). The scatter plot reveals a strongly linear relation (r=.528, p<.001), with a relatively constant effect of attractiveness at all levels.

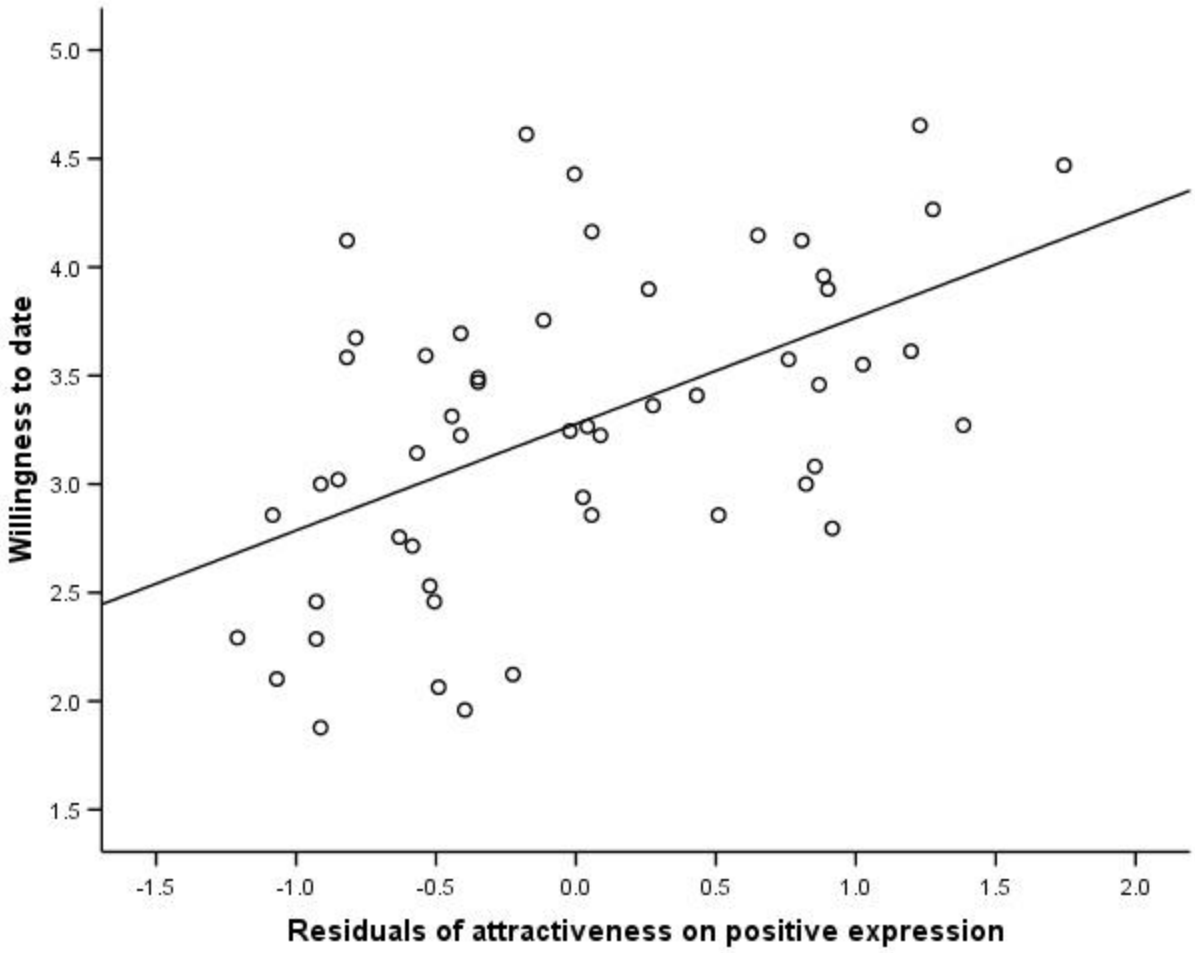


Figure 7. Scatterplot depicting the effect of model female attractiveness after positive expression has been controlled.

The second part of the analysis focused on variance arising from the side of the raters. Recall that prior to giving their ratings the raters had given self-ratings (on 10-point scales) of attractiveness (*n*=46, ranging from 3 to 8, mean 5.84, median 6) and romantic experience (*n*=48, ranging from 1 to 9, mean 5.67, median 6). I wanted to examine more closely the ratings of the raters in the top and bottom quartiles for both of these variables, but due to the limited scale used no cut-off values gave the exactly desired

subsets of raters, and faced with a choice between more extreme subsets but less ratings on the one hand and less extreme subsets but more ratings on the other, I chose the latter. First I ran the stepwise regression using only the ratings of the lesser attractive raters (attractiveness self-rating of 5 or less, *n*=14). Attractiveness again emerged as the most important predictor, accounting for 47% of the variance, with positive expression accounting for an additional 14.4% (final R^2 = .614, all excluded variables $p > .2$). Thus even the less attractive raters preferred attractive model females, and did so at a level comparable to that of the overall sample. I then ran the stepwise regression using only the ratings of the more attractive raters (attractiveness rating of 7 or more, *n*=15). Positive expression emerged as the most important predictor (R^2 = .569), followed by attractiveness which explained an additional 13.5% of variance and finally self-rated romantic experience which explained another 2.8% (final R^2 = .732, all excluded variables $p > .13$). As with emotional stability in previous analyses, the relationship between the dependent variable and the self-rated romantic experience of the model females was in the opposite to expected direction (*beta*= -.172, *t*= -2.277, p = .027). These results show that the preference for attractive model females holds for both attractive and unattractive sets of raters; if anything, the more attractive raters depended less on model female attractiveness. I also reran the regressions to compare the ratings of more against less romantically experienced raters, and single raters against those in relationships, but no interesting differences emerged (see all comparisons in Table 8). Finally, to systematically and more formally examine the influence of all three variables (attractiveness, romantic experience and relationship status) simultaneously I a) calculated the predicted value for each model female from

regression of the dependent variable on attractiveness and positive expression and then b) for each rater, summed the absolute differences between her own rating of each model female[24] and the predicted value across all 53 model females (i.e. $\sum=|k_i-p_i|$, i=1,2…53, where *k* is the rating given by a rater to a model female and *p* is the predicted value for the model female). This produced, for each rater, a measure of her propensity to be predictably influenced by model female attractiveness and positive expression, with smaller values indicating a stronger influence. I then regressed this sum (n=49) against rater attractiveness, romantic experience and relationship status simultaneously, but the resulting model was clearly not significant (p>.5, all predictors p>.2), indicating no condition-dependent nonindependent mate choice.

[24] Where there were missing values we used the average value given by a rater to all model females.

Table 8. Stepwise multiple regressions by female rater subgroup. Attractiveness and romantic experience categorizations are based on self-ratings given by the raters on a 10-point scale.

Group of raters	Predictor	R^2	ΔR^2	*beta*[a]	*F*
Attractive (≥7, *n*=15)	Positive expression	.569	.569	.681	
	Attractiveness	.704	.135	.407	
	Romantic experience	.732	.028	-.172	44.6***
Unattractive (≤5, *n*=14)	Attractiveness	.470	.470	.592	
	Positive expression	.614	.143	.390	39.7***
Romantically experienced (≥7, *n*=23)	Positive expression	.544	.544	.626	
	Attractiveness	.721	.177	.452	
	Emotional stability	.753	.032	-.180	49.8***
Romantically inexperienced (≤5, *n*=21)	Attractiveness	.482	.482	.582	
	Positive expression	.691	.208	.470	
Single (*n*=30)	Attractiveness	.450	.450	.561	
	Positive expression	.705	.255	.514	
	Emotional stability	.728	.023	-.154	43.7***
In relationship (*n*=19)	Positive expression	.445	.445	.543	
	Attractiveness	.695	.250	.515	56.9***

[a] standardized coefficients appearing in the final regression equation

***p<.001

3.3.4 Discussion

The preceding has been an attempt to answer the following question: from the viewpoint of a prospecting female, what information in the face of a potential mate's ex-girlfriend can she use to improve her assessment of the male's mate value? I used video recordings of model females to allow the examination, for the first time, of dynamic cues like personality and behavioural factors, while at the same time withholding any stimuli that related to the actual target male (like a video, a photograph, a written description etc.). This design forced the female raters to rely solely on the model female for their assessments and allowed me to avoid additional sources of variance that would arise from the target males. The results presented here suggest that in regard to the question I posed, namely what cues can be found in a girlfriend's face from the vantage point of a focal female rater, the one-word answer is 'looks', and that this preference for more attractive model females is universal among raters, be they attractive or unattractive, experienced or inexperienced (but see Waynforth, 2007), single or in a relationship. Model female attractiveness alone accounted for 45% of the total variance in ratings, and when coupled to 'positive expression', i.e. a measure of how positive a model female's descriptions of her supposed ex-boyfriend appeared to be, the two variables explained over 70% of the variance in ratings. The importance of positive expression is a straightforward and rather intuitive finding that has already been documented in various studies (e.g. Jones *et al*., 2007; Place *et al*., 2010), and here, after realizing it would probably confound the results, I was primarily interested in controlling for it with the aim of revealing the relevance of other variables.

Surprisingly, I found no evidence that female raters are more interested in the partners of slightly older model females (up until their late 20s), a finding that contradicts a recently reported *post-hoc* result (Vakirtzis & Roberts, 2010). The importance of model female age has been well-documented in the non-human literature (Dugatkin & Godin, 1993; Amlacher & Dugatkin, 2005; Vukomanovic & Rodd, 2007), and is typically attributed to the greater experience of more mature females and their superior mate-choice skills (Nordell & Valone, 1998). The fact that here I used a design specifically designed to uncover this effect (among others) and that I employed a substantially larger sample size (n=53 vs. 20) suggests that the earlier finding (Vakirtzis & Roberts, 2010) was perhaps a chance result.

The suggestion that focal women might be sensitive to cues in the model female other than attractiveness (like age) led me naturally to examine whether some of these cues, if they indeed exist, might be found in the personality/behavioral domain. I included here those traits that should have been associated, throughout our evolutionary history, with women securing more desirable males. The first and most obvious candidate was self-esteem, whose adaptive function based on input received from the 'mate-value sociometer' has now been studied extensively (reviewed in Penke *et al*., 2007). Briefly, cues of acceptance or rejection from members of the opposite sex lead to adaptive shifts in self-esteem which cause women to raise or lower their ambitions with regard to a mate, and, presumably, adjust their romantic pursuits accordingly (Zeigler-Hill *et al*., 2009). In support of this hypothesis I found a correlation of .483 between self-esteem and a one-item self-report measure of mate value (see e.g., Brase & Guy, 2004; Penke

& Denissen, 2008, for similar results). The hypothesis suggests that throughout our species' evolution women with higher self-esteem would have probably secured more desirable mates. Analogous arguments can be made for female assertiveness, sociability and social intelligence, namely that these traits would have correlated positively with male partner mate value, whereas a negative correlation would perhaps hold between shyness and male partner mate value, with more shy women shunning social contact and missing out on potential mates. In addition to these more specific traits I included a measure of the Big Five (Gosling *et al*., 2003) in our analysis. This was done with the expectation that due to their salience (Buss, 1991; 1996) and generality the Big Five factors of personality (Extraversion, Agreeableness, Conscientiousness, Emotional Stability, Openness to Experience) would perhaps be able to capture, even if very coarsely, relevant traits that could then be more accurately dissected in future studies. Of all the traits examined only emotional stability achieved statistical significance (p=.048), but the sign of the correlation (negative) and the marginal increment in explained variance suggest that this relationship is probably a type I error, owing to the large number of predictors in the regression. Having said this, the possibility that there are indeed other relevant cues in the model female which this study failed to detect cannot be excluded. For example, the fact that the videos were played mute and that they only showed the faces of the model females constitutes an impoverishment of the real-life stimulus that future studies could amend.

Finally, a number of interesting variations on the current design suggest themselves. For instance, model females could be asked to describe an *actual* ex boyfriend (for

example the most recent one) and the video recordings could be played with sound, so that a wide array of positive and negative real-life descriptions would be available to focal females. Of particular interest in such a scenario would be those instances where highly attractive women gave very negative descriptions of their former partner (or where very unattractive women gave positive descriptions). Would model female attractiveness still have an effect in these extreme conditions? I predict that it would: in the end there is no more concrete proof of a man's mate value than the fact that through a (typically) protracted period of courtship (Trivers, 1972) and sequential evaluation stages (Miller & Todd, 1998) an attractive female formed a relationship with him. What this female subsequently says can never cancel out what she actually did, and given that words are cheap whereas eggs are expensive, her actions should always carry more weight. This design would more accurately simulate real-life social situations where women discuss their romantic lives and gossip about potential mates.

3.4 General discussion

Using one sample of women that served as model females, this chapter has presented two separate experimental studies that used different methodologies. The first study employed a rather elaborate design and presented static facial images of the target males in various conditions, with and without model females, in order to replicate and expand on earlier results from similar studies (Waynforth, 2007; Little *et al*., 2008; Vakirtzis & Roberts, 2010). The study was designed in such a way so as to allow a detailed examination of the interplay between target male and model female

attractiveness, absolute and conditional probabilities of choice. The second study used video recordings of model females in a design whose aim was to not only validate results obtained previously with static images but also to uncover hitherto unrecognized cues in model females, apart from attractiveness, that influence focal females in their assessment of potential males. In line with the aims of this experiment no target males were presented to the males, so it was not possible to examine any possible interactions between features of the target male and model female.

Two main findings emerge from these studies. Firstly, when it comes to human nonindependent mate choice the only relevant cue of the model female is probably her attractiveness[25]. As a qualification, it should be added that even if other cues exist, their importance is dwarfed in comparison to the effect of model female attractiveness. Secondly, experimental studies in this domain produce results that are highly sensitive to even slight variations in the setup of the study and the presentation of the stimuli, something which is probably not the case in other 'lower-level' domains of evolutionary psychological research. As a case in point, whereas model female attractiveness was a non-significant predictor in the first experiment, it accounted for over 45% of the variance in female ratings in the second study. Contrasts like this naturally lead to the realization of the urgent need for non-experimental studies of this phenomenon using real-life data, in order to establish the extent to which the rather mixed experimental

[25] I am referring here to cues relating to the model female *per se* (like attractiveness, age and personality traits), not to the more contingent and fickle cues that relate to the model female's interpersonal relation with her mate (as in the 'positive expression' variable of the previous study; see chapter 6 for further discussion.

results correspond with real-life conditions. Chapter 4 is devoted to the description of exactly such a study, to my knowledge the first direct non-experimental investigation of this phenomenon.

Finally, two general methodological improvements for future studies should be discussed here. Firstly, future experimental studies should recruit from a more representative sample of the general population, and not just from undergraduates. Recently considerable attention has been paid to the overreliance of academic psychology on undergraduate samples from industrialized Western societies, which in many aspects are not representative of the broader populations, both in industrialised, and of course traditional societies (Henrich et al, 2010; Jones, 2010). As I have argued in chapter 2, cross-cultural variation in nonindependent mate choice is to be expected on the basis of the strength of women's preference for physical versus non-physical traits in men, so cross-cultural research will clearly provide valuable insights. Even before venturing to non-Western societies, however, studies in the West should recruit from the general population, so as to ensure that a) results are representative of the general population and that b) the widest possible variance in predictor and outcome variables is attained. Which leads to the next point, namely that in the future attention should be paid to the distribution of the various independent variables in the samples, and particularly attractiveness. It is entirely possible that the differences between the results in Study 1 above and those of Waynforth are due to differences in the distribution of female attractiveness. Naturally, recruiting a sample (to create a stimulus set) by convenience, as I have done here, will lead to a more or less normal distribution

for attractiveness and most other variables. But though presumably representative of the general population, this distribution could turn out to be less desirable than, say, a uniform distribution, where the attractiveness differences between stimuli female are amplified. Future studies could therefore aspire to alternative distributions to the normal one.

Chapter 4: Non-experimental approaches: A questionnaire study.

4.1 Introduction

As I described in previous chapters, the study of human nonindependent mate choice to date has been almost exclusively experimental. With the exception of one earlier questionnaire study which indirectly touched on nonindependent mate choice (Platek et al., 2001; see Discussion) there has been no examination of whether results obtained experimentally have their counterparts in natural social environments. This is troubling given that, some broad findings notwithstanding[26], the results obtained via the experimental approach have often been conflicting. In particular scientists have not been able to agree on a 'standard' experimental procedure or set of procedures and construct a cumulative, progressive research program. A wide variety of dependent variables are used and often, even when similar ones are used, results do not replicate. A case in point is two recent studies which used different experimental methods and produced almost entirely different results. Whereas Little *et al.* (2008) found that both male and female raters are influenced by model attractiveness with regard to long-term but not short-term relationship attractiveness, Place *et al*. (2010) found that only male raters are influenced by model attractiveness, and are thus influenced for both types of relationship (short and long-term). Table 9 summarizes the relevant evolutionary psychological studies, revealing the extent of the empirical disagreement.

[26] See section 2.1

Study	Methodology	Manipulated: presence vs. absence of female partner	Manipulated: attractiveness of female partner	Is there an effect with male raters?	Dependent variable(s)
Uller & Johansson, 2003	Confederate	×			Array
Eva & Wood, 2006	Written profile	✓			Attractiveness
Waynforth, 2007	Photos	×	✓		Attractiveness
Milonoff et al, 2007	Photos	×			Attractiveness, willingness to date
Little et al. 2008	Photos		✓	✓	Attractiveness for long-term relationship (but no effect for short-term)
Vakirtzis & Roberts, 2010	Photos		✓	×	Willingness to date
Parker & Burkley, 2010	Written profile	✓		×	Composite score of interest in romantic pursuit
Yorzinski & Platt, 2010	Photos		✓	✓	Willingness to have long-term relationship
Place et al, 2010	Video	✓	x	✓	Interest in short and long-term relationship

Table 9. Compilation of published empirical studies on women. Studies are listed as manipulating either presence or absence of partner (mate choice copying) or quality of female partner (mate quality bias), although note that some manipulated both. Some studies also performed the sex-reversed experiment of male raters rating target females (5th column). The dimension on which female raters evaluated the target male is given on the far right column. Positive results are denoted by ✓ and null ones by ×. Older social psychological studies that were not conducted through an evolutionary framework are not listed (see section 2.1.1 for summary), nor are recent studies which merely presented women smiling at the target male, without explicit clues to sexual/romantic involvement (Jones *et al*., 2007; Hill & Buss, 2008; Dunn & Doria, 2010).

Although this empirical confusion is often glossed over or simply ignored, Table 9 leaves little doubt that non-experimental approaches are urgently needed, for two reasons. Firstly, to weigh in favor of some experimental results and against others, since at present there is no satisfactory external criterion for doing this apart from purely theoretical considerations. Secondly, to guide the experimentalist into formulating more focused and promising hypotheses. But how does one proceed from the straightforward, minimalistic experimental protocol to the real social world with all of its myriad complexities, confounds and subtleties? A number of possibilities suggest themselves, none of which is without problems. I list them in no particular order.

a) The qualitative, semi-structured interview (Weiss, 1994). Since, as I have suggested earlier, women are probably not consciously aware of the influence a man's mate can have on their assessment faculties, the person to interview is the man himself. The selection of the sample would be critical to the success of this approach: males that rank low on sociosexual orientation, introverts, or men with limited sexual histories would probably not make the most suitable subjects.
b) The qualitative study of nonindependent mate choice in popular culture, the media, films, marketing, the mass novel etc. (for examples of what such an evolutionarily oriented study might look like see Barkow, 1992; Salmon & Symons, 2003; 2004).
c) Non-invasive observation in a naturalistic setting. As a recent study (Hendrie *et al.*, 2009) and common sense would suggest, the nightclub or bar is probably the place to begin. The problem here would be one of controlling for confounds, for

example making sure the attention a male receives is due to his escort and not characteristics of the male himself. Another problem would be the actual recording of the dependent variables, i.e. the recording by a third observer of discreet and subtle signals of interest under the far from ideal conditions that prevail in a nightclub or bar (although this is feasible, see e.g. Perper, 1985).

d) The structured mass questionnaire. Precisely because it is structured, this approach should logically constitute the first step in a transition from the lab to the real social world.

A comparison of all alternatives listed above suggests that the structured mass questionnaire is probably the best place to start. Here I report a questionnaire study which constitutes, to the best of my knowledge, the first ever non-experimental undertaking in this field. I recruited both male and female subjects (*n*=401) and asked them to indicate their agreement with certain statements that were intended to gauge romantic interest from opposite-sex individuals. I recruited both participants who were in a relationship and single participants, and analyzed each group separately by a)comparing male to female responses and b)correlating participants' responses with various variables like reported partner attractiveness, self-attractiveness, length of the relationship (or length of time being single) and patterns of social activities. Following from the discussion in chapter 2, I predicted that paired men would report more opposite-sex interest than paired women (in comparison to when they were single), and single men less opposite-sex interest than single women (in comparison to when they were in a relationship). I also predicted, for paired participants, that partner

attractiveness would correlate positively with opposite-sex interest reported by male participants, but this would not be the case (or be less pronounced) for female participants.

4.2 Method

4.2.1 Recruitment of subjects

Four hundred and one subjects were recruited by convenience, mostly at various libraries of the University of Liverpool and Liverpool John Moores University. A limited number of these (approx. 10-20) were also recruited through social networking websites like Facebook. An effort was made to recruit British subjects so as to reduce variance in the results due to cultural differences. I approached candidate subjects, identified myself and explained the general research area of my PhD and the aims of the study. Subjects were then given a small piece of paper with the link to the website which hosted the online questionnaire (*www.qualtrics.com*) and asked to fill it out at their own time. Qualtrics.com offers state-of-the-art online questionnaire technology, including a wide variety of question types (forced choice, Likert scale, free text box, image selection etc.) and advanced features such as skip logic, randomization, and elaborate customization options. Skip logic means that participants' answers to an earlier question can determine which answers will be shown to them later on, so that for example men and women (or single and married people etc.) answer different questions. This technology affords a kind of interactive flexibility that traditional paper-based questionnaires cannot match.

4.2.2 Overview of questionnaire

The questionnaire consisted of an information sheet, a brief introductory fact-gathering section and three major sections. The introductory section asked for basic information such as sex, age, ethnicity, lifetime number of sexual partners, sexual orientation, self-rated attractiveness (on a 10-point scale, 10 being most attractive) and relationship status, i.e. single or in relationship. Subjects in a relationship were asked to clarify the type of relationship (dating, dating and living together, engaged, engaged and living together or married). The answers given to the fields in this introductory section determined which parts of the questionnaire the subjects would subsequently view. The three main sections of the questionnaire were as follows. The first section was viewed by those subjects (male and female) who were in a relationship. This part of the questionnaire asked subjects various kinds of factual information regarding their relationship, such as the duration of the relationship and how frequently the couple visited places like clubs, bars, eateries and so on. Subjects were also asked to rate their partners for attractiveness on a 10 point-scale, 10 being most attractive. Finally, and, most importantly, this section contained a number of statements about how respondents felt they were viewed by members of the opposite sex in the context of their relationship. Subjects indicated their agreement or disagreement with each of these statements on a 7-point scale from ‘strongly disagree’ (1) to ‘strongly agree’ (7). These statements along with subjects’ answers are given in the Results section below. The second major section of the questionnaire was targeted to male and female subjects who were single. This part of the questionnaire asked respondents to indicate how long

they had been single for and how attractive their last partner had been, on the same 10-point scale as above. As with the first section, this section also contained a number of statements with which participants were asked to agree or disagree. These statements related to how subjects felt they were viewed by the opposite sex outside the context of a relationship. The third and final section of the questionnaire was viewed by all subjects, both male and female, regardless of whether they were in a relationship or not. This section presented a number of more general statements that related to various aspects of nonindependent mate choice. Finally, all subjects filled out the Rosenberg self-esteem scale (Rosenberg, 1965) and the Social Information Processing subscale of the Tromso Social Intelligence Scale (Silvera et al, 2001).

In order to test for the predicted gender differences in nonindependent mate choice male and female responses to the same items were juxtaposed throughout all sections of the questionnaire. In particular I expected that men would express higher levels of agreement with statements that indicated the opposite sex was influenced by their (i.e.the respondents') partner. Due to the somewhat subjective nature of many of these statements, the self-esteem and social intelligence scores were used as covariates in Analysis of Covariance (ANCOVA) to ensure any gender differences were not spurious. Within each sex, variables like participants' self-rated attractiveness, the attractiveness of their partner (whether current or past), the type of relationship, the social activities of the couple, participants' age and sexual experience were used as predictors for the variance in responses. All tests were two-tailed.

4.3 Results

4.3.1 Descriptive statistics

A total of 401 subjects participated in the study. Of these 13 reported being homosexual (although the information sheet at the beginning of the questionnaire informed subjects the study was aimed at heterosexual people) and were excluded from the analysis. An additional 7 participants didn't answer past the questions on the first page of the questionnaire (relating to age, sex etc.) and were also excluded. A small number of the remaining 381 questionnaires were not completed in their entirety, which, in addition to the fact that some questions were not 'forced', i.e. the participant was not required to fill them out in order for the questionnaire to continue, accounts for the fact that the results given below for various answers sometimes have slightly differing sample sizes. Three hundred and fifty eight of respondents were students, the non-students probably originating mostly from participants who were recruited via social networking websites. All but 54 of the participants were British. Of these 54 non-British subjects, 20 were Irish and only 10 were non-European (Mexican, Brazilian etc.), meaning that culturally this was a relatively homogeneous sample. Two hundred and six subjects were male (mean age ± SD 21.6 ± 2.2 yrs) and 175 female (21.2 ± 2.2 yrs). Men reported a median number of lifetime sexual partners of 5 (mean 9.7, range 0-89), whereas the corresponding median for women was 4 (mean 6.3, range 0-50). The slightly higher number of lifetime sexual partners reported by men is a result well-known from previous studies (Smith, 1992; Wiederman, 1997). Interestingly, although the self-reported

attractiveness of both males and females was approximately normally distributed, men on average gave themselves higher attractiveness ratings (mean±SE: 6.6 ± 0.1 vs. 6.1 ± 0.1 for females, t=3.5, p=.0005).

4.3.2 People in relationship

The first analysis focused on the responses of 200 people who reported being in some type of romantic relationship. Of these 104 were men (21.8±2.5 yrs, range 18-32) and 96 were women (20.0±2.2 yrs, range 18-32). Of these 200 people 70% (73 men and 67 women) described their relationship as 'dating only', 22% (22 men and 22 women) as 'dating and living together' and the remaining 8% as 'engaged', 'engaged and living together' or 'married'. Although in the following I report the results for all categories of relationships combined, I ran separate analyses for the 'dating only' category and the results were similar to those obtained for the overall sample. The remaining relationship categories were too small to allow for separate analysis.

I compared these men and women's responses (from 1 to 7, or 'strongly disagree' to 'strongly agree', respectively) to the 6 statements that served as dependent variables for this section. These were always presented in random order. Table 10 presents these statements together with the results of the sex comparisons.

Table 10. Comparison of responses by men and women (words in brackets) who were in a romantic relationship. Persons who were married saw identical questions with 'wife' instead of 'girlfriend' for men and 'husband' instead of 'boyfriend' for women.

Statement	Male mean±SE	Female mean±SE	*t*	*p*	Cohen's *d*
S1. In general, I feel that I have become more attractive to other women (men) since I started dating my girlfriend (boyfriend).	4.38±0.15	3.68±0.15	3.28	.001	0.46
S2. When I go to a bar or club with my girlfriend (boyfriend) other women (men) seem to take notice of me.	4.26±0.14	4.28±0.14	-.076	.940	0.01
S3. Women (men) seem to look at me more when I'm with my girlfriend (boyfriend) that when I'm alone.	4.09±0.15	3.24±0.15	3.95	<.0001	0.56
S4. Some women (men) who previously showed little or no interest in me seem to flirt with me since I started dating my girlfriend (boyfriend).	4.16±0.16	3.45±0.16	3.11	.002	0.44
S5. The last time me and my girlfriend (boyfriend) went out together to a bar or club, I noticed that other women (men) were paying attention to me.	4.17±0.15	4.29±0.15	-.587	.558	0.08
S6. In general, women (men) flirt more with me since I started dating my girlfriend (boyfriend).	4.01±0.15	3.44±0.15	2.70	.008	0.38

The table reveals two very different classes of statements. Statements 1, 3, 4 and 6 all showed highly significant gender differences with substantial effect sizes. As predicted men agreed more than women with all of these statements. On the other hand statements 2 and 5 unexpectedly showed no gender differences at all. Why this difference? A closer examination of the way the statements are structured suggests a

very likely explanation. Statements 1, 3, 4 and 6 all explicitly ask participants to make a comparison between their experiences before and during their current relationship (1, 4 and 6), or between when they are alone in public and when they are with their partner (3). They are, in other words, statements of the difference between some measures of absolute and conditional probability of choice. Assuming that nonindependent mate choice is more important in female mate choice, then this difference should be larger for the male population, and indeed this is what the results suggest. Statements 2 and 5, on the other hand, do not ask participants to make a comparison of this kind. They probably measure some aspects of conditional probability of choice, and at an aggregate population level there is no reason to expect any *average* difference between the female and male conditional probabilities of choice. In hindsight, therefore, it appears that statements 2 and 5 could have been better constructed or avoided altogether, although I think that their inclusion here can be very informative for future studies of this kind.

Given the somewhat subjective nature of some of these statements, it could be argued that the sex differences reported here are not genuine but stem from differences in third variables like social intelligence or self esteem. In particular more socially intelligent people could be more attuned to subtle signals of interest from opposite-sex members, and people with higher self-esteem could be more inclined to perceive friendly interactions as flirtation. To rule out this possibility I repeated the previous comparisons

but used participants' scores on the social intelligence and self-esteem scales as covariates in ANCOVA[27]. Table 11 shows the results. As can be seen the inclusion of the two covariates did not alter the previously obtained sex differences, which remained highly significant for statements 1, 3, 4 and 6 but did not obtain for statements 2 and 5. Each covariate was significant for some but not other statements.

To see if a clearer pattern could be discerned via an aggregation of items, I created a composite score by averaging participants' responses to statements 1,3,4,6 (*alphas*: men .780, women .778). Due to the principle of aggregation (Rushton *et al*., 1983), this composite score is almost certainly a more accurate measure of the dependent variable than any single statement in isolation. An ANCOVA (with the same factors and covariates as above) on this composite score revealed a highly significant gender difference (estimated means±SE: men 4.15±.12, women 3.46±.12, $F_{1,191}$=15.7, p=.0001) with social intelligence ($F_{1,191}$=7.04, p=.009) but not self-esteem ($F_{1,191}$=0.26, p=.636) emerging as a significant covariate. This more informative aggregate score would thus seem to indicate that the more relevant covariate is social intelligence rather than self-esteem.

[27] There were no significant group differences in either of these variables between men and women, so their use as covariates in this instance is warranted.

Table 11. Comparison of responses by men and women in a relationship with social intelligence and self-esteem as covariates (see Table 10 for description of statements).

Statement	Estimated male mean	Estimated female mean	$F_{1,191}$	p	Social intelligence $F_{1,191}$ (p)	Self-esteem $F_{1,191}$ (p)
S1.	4.32	3.75	6.76	.010	5.49 (.020)	5.017(.026)
S2.	4.20	4.34	0.56	.455	5.01 (.026)	6.36(.013)
S3.	4.11	3.21	15.5	.0001	1.78 (.183)	0.33(.565)
S4.	4.17	3.43	12.1	.002	.5.31 (.022)	.041(.839)
S5.	4.06	4.41	2.76	.098	3.19 (.076)	14.1 (.001)
S6.	4.01	3.43	6.76	.010	4.88 (.028)	0.01 (.920)

I then examined the relation of participants' responses with the following variables: the reported attractiveness of their partner, their self-rated (i.e. the participants') attractiveness, the length of their relationship (in months), and the length of time for which they had been single prior to entering their current relationship (on an ordinal scale from 1-'I was never single, went straight from my previous relationship to this one' to 7-'single for more than a year'). I included relationship length as a variable of interest in the questionnaire due to the simple fact that the longer a relationship lasts the more opportunities its members have to observe the reactions of the opposite-sex. Similarly, the length of time for which participants had been single prior to entering their current relationship should be related to the accuracy of one's estimate of his/her baseline attractiveness. For men the composite score (S1, S3, S4 & S6) correlated only with

partner attractiveness (*rho*=.208, *n*=103, *p*=.035) but not with self-rated attractiveness, relationship length, or length of being single prior to the current relationship (all *p*>.28). For women the composite did not correlate with partner attractiveness (*rho*=.050, *n*=92, *p*=.639), or with any of the other three variables (all *p*>.26). Examining each statement separately yielded similar, although less clear-cut results: in particular partner attractiveness correlated significantly with S2 (*rho*=.254, *n*=103, *p*=.010) and S6 (*rho*=.199, *n*=103, *p*=.043) for male participants, but did not correlate with any statement for female participants (all p>.27). Self-reported attractiveness correlated with S1 (*rho*=.194, *n*=103, *p*=.049) and S2 (*rho*=.292, *n*=103, *p*=.003) for male participants but S5 for females (*rho*=.209, *n*=92, *p*=.046). The correlation of self-reported attractiveness with statements 2 and 5 is further indication that these items were not particularly suited to capture aspects of nonindependent mate choice but simply measured general aspects of mate value or desirability.

I then examined the relationship between participants' answers on the dependent variables and the couples' patterns of social activities, i.e. how frequently they visited the following public places: bars/clubs, cafes, cinemas, restaurants/fast food eateries, and house parties. Frequency of visits was ordinally recorded on a 7-point scale as follows: 'almost never', 'less than once a month', 'once a month','2-3 times a month', 'once a week', '2-3 times a week', and 'almost daily'. The relationship between a couple's frequency of social outings and nonindependent mate choice is a logical necessity; a couple that stay at home all the time and never venture together in public afford third individuals no possibilities to observe them together and adjust their

evaluations accordingly. With regard to nonindependent mate choice, however, we should expect to find differences between the opportunities afforded, for instance, in a bar or club compared to, say, a restaurant (Hendrie *et al*., 2009). For male participants the composite score (S1, S3, S4 and S6) correlated significantly only with reported frequency of visits to house parties (*rho*=.292, *n*=103, *p*=.003), but, somewhat surprisingly, nonsignificantly with frequency of visits to bars/clubs (*rho*=.-.070, *n*=103, *p*=.480). For female participants there was no relation between the composite score and frequency of visits to any of these social places (all *p*>.19)

Examining each of the six statements separately corroborated the impression afforded by examination of the composite score alone. For men, frequency of visits to house parties correlated with S2 (*rho*=.248, *n*=103, *p*=.012), S3 (*rho*=.246 *n*=103, *p*=.012) and S5 (*rho*=.282, *n*=103, *p*=.004), while frequency of visits to restaurants/fast food correlated only with S2 (*rho*=.235, *n*=103, *p*=.017). For women, on the other hand, there was no relationship between frequency of visits to any of the five social places and any of the six statements (30 correlations: all *p*>.056). I aggregated the frequency of visits to all five types of social places to produce a single composite score of ‘overall frequency of social outings’ but this did not correlate with the composite dependent variable for either men or women (both *p*>.3). It would thus seem that in relation to frequency of social outings every category of venue represents a qualitatively distinct class, and aggregation should be avoided.

The last analysis for this section involved participants' answers to the question 'To what degree do you and your partner share the same social network (friends, acquaintances, colleagues etc)?' Participants could select one of four options: 'entirely/almost entirely separate', 'mostly separate', 'mostly shared', 'entirely/almost entirely shared'. This 'social circle overlap' item was intended to gauge another aspect of couples' social life, namely the extent to which the two partners' shared social circle could afford opportunities for nonindependent mate choice to take place. There was no correlation between participants' responses to this item and the composite score, or any of the 6 statements separately for either men (all $p>.13$) or women (all $p>.27$).

4.3.3 Singles

This part of the analysis examined responses given by singles. In total 178 subjects were single, and of these 102 were men (21.5±1.9 yrs, range 18-29) and 76 (21.3±2.2 yrs, range 18-28) were women. All of these single subjects were asked to indicate the length of time since their last relationship ('how long have you been single for?'). Their responses are given in Table 12, broken down by gender. As can be seen the single largest category of respondents reported having been single for over a year. The subjects that reported never having been in a relationship were redirected to a later section of the questionnaire (see 'General questions' below) and thus excluded from this part of the analysis, since the items of interest in this section asked subjects to compare their experience of being single with their experience of being in a relationship, and those subjects that had never been in a relationship could not, by definition, make

such a comparison. Twenty-two subjects reported never having been in a relationship, thereby reducing the sample size for this section of the questionnaire to *n*=156 (88 men and 68 women).

Table 12. Length of time since last relationship for single participants.

	<1 month	1-3 months	3-6 months	6-12 months	>12 months	Never been in a relationship
Men	9	13	8	10	48	14
Women	4	12	6	16	30	8
Total	13	25	14	26	78	22

Table 13 presents the four statements that subjects were asked to evaluate in this section (presented in random order), breaking down participants' responses by sex. Statement 10 is reverse-keyed (a correlation matrix confirmed that S7, S8 and S9 were all highly positively correlated and were, in turn, all negatively correlated to S10, and that this pattern held for both men and women). As predicted men on average gave higher scores for the first three statements, but women scored higher on statement 10, although this last difference was not significant. It is interesting to note that, qualitatively, the gender difference in statement 9 seems to fall into a category of its own as witnessed by the large effect size. In contrast to the other questions which are more general and refer to overall perceptions of self-attractiveness, this item is more circumscribed, directing the participant's attention to a very specific autobiographical domain.

Table 13. Comparison of responses by men and women (words in brackets) who were single. Persons who were married saw identical questions with 'wife' instead of 'girlfriend' for men and 'husband' instead of 'boyfriend' for women.

Statement	Male (*n*=86) mean±SE	Female (*n*=68) mean±SE	*t*	*p*	*d*
S7. In general, I feel that I have become less attractive to women (men) since I became single.	3.33±0.19	2.79±0.20	2.0	.052	0.32
S8. Women (men) seem to pay less attention to me since I broke up with my ex-girlfriend (ex-boyfriend).	3.16±0.15	2.71±0.16	2.1	.039	0.34
S9. When I used to go to a bar or club with my ex-girlfriend (ex-boyfriend) other women (men) took notice of me; now they don't.	3.86±0.14	2.82±0.16	4.8	.001	0.78
S10. Women (men) flirt more with me since I broke up with my ex-girlfriend (boyfriend).	3.95±0.15	4.29±0.18	-1.4	.153	0.23

Do these sex differences stand out in sharper relief when individual differences in social intelligence and self-esteem have been controlled? To answer this I conducted a series of ANCOVAs with sex as the factor and social intelligence and self-esteem as covariates. The results are shown in Table 14. The inclusion of the two covariates generally make the sex differences stand out in sharper relief. Self-esteem was a more useful covariate, contributing significantly to the model in three out of four statements, while social intelligence did not contribute to any statement. After the inclusion of these two covariates the only statement that still failed to reach significance, albeit only

marginally, was S10, the reverse-keyed one. Even here, however, the predicted order of means (women higher than men) obtained.

Table 14. Comparison of responses by single men and women with social intelligence and self-esteem as covariates (see Table 13 for statements).

Statement	Estimated male mean	Estimated female mean	$F_{1,148}$	p	Social intelligence $F_{1,150}$ (p)	Self-esteem $F_{1,150}$ (p)
S7.	3.34	2.74	5.58	.030	2.19 (.141)	6.68(.011)
S8.	3.19	2.62	6.32	.013	.925 (.338)	5.86(.017)
S9.	3.89	2.79	22.9	<.001	1.04 (.309)	3.06(.082)
S10.	3.90	4.37	3.68	.057	.035 (.851)	4.31(.039)

I reverse-scored statement 10 and subsequently combined all four statements into one composite score for every participant (alphas: male= .722, female=.822). An ANCOVA (with the same factors and covariates as above) on this composite score confirmed the impression afforded by the examination of each statement separately: there was a highly significant effect of sex ($F_{1,148}$=13.5, p<.001) with a significant contribution of self-esteem (b=-.054, p=.004), while social intelligence was an non-significant covariate (b=-.128, p=.277). These results are in contrast to those obtained for people in a relationship (section 4.3.2) where social intelligence rather than self-esteem was the relevant covariate.

Finally, I examined the relation between the composite of the four statements in this section and a number of independent variable, namely self-rated attractiveness, attractiveness of previous partner and length of time since last relationship. For both men and women, attractiveness of previous partner and time since last relationship were unrelated to this composite measure; self-rated attractiveness, however, correlated negatively with the composite for both male (*rho*= -.265, *n*=86, *p*=.014) and female participants (*rho*= -.357, *n*=67, *p*=.003). An examination of each statement separately confirmed that while previous partner attractiveness and length of time since last relationship were unrelated to every statement for both male and female participants, self-rated attractiveness, on the other hand, showed a significant correlation with S7 for men (*rho*= -.394, *n*=86, *p*<.001) and S7 (*rho*= -.410, *n*=67, *p*=.001), S8 (*rho*= -.346, *n*=67, *p*=.004) and S9 (*rho*= -.294, *n*=67, *p*=.016) for women.

4.3.4 General questions

This last section comprised a number of more general statements that were presented in random order and were evaluated by all participants, regardless of relationship status[28]. By 'general' I mean that they did not ask participants to reflect on their experiences during their current relationship or since their last relationship, but asked them to look at the more global picture of their sexual/romantic career. Two of the

[28] This included the 200 subjects who were in a relationship, the 178 who were single, and 3 who had selected 'not sure/rather not say' in the relationship status question.

statements (S11 and S12) related to participants' perceptions of their attractiveness when single as compared to being in a relationship (i.e. in their capacity as a 'target male/female'). These two statements essentially asked the same thing, and were only phrased differently to establish the importance of phrasing. The next two (S13, S14) pertained to participants own perceptions of how they would assess a current or potential mate in their capacity as 'focal' males or females. The final two statements (S15, S16) pertained to the 'flaunting' of an attractive partner. As with the first two statements, these two statements asked very similar things, although it is worth noting that in contrast to the first two statements which are logically equivalent, these are not equivalent. Table 15 presents the statements and breaks down the answers by sex.

Table 15. Comparison of responses by men and women (words in brackets).

Statement	Male mean±SE	Female mean±SE	*t*	*p*	Cohen's *d*
S11. When I'm in a relationship women (men) seem more interested in me.	4.28±0.09	3.53±0.11	5.2	<.001	0.54
S12. When I'm single women (men) seem to show less interest in me.	3.89±0.01	3.25±0.11	4.3	<.001	0.45
S13. I would be turned off if I found out that my partner's ex-boyfriend (girlfriend) was very ugly.	2.97±0.11	2.4±0.11	3.6	.001	0.38
S14. I would lose some of my interest in a prospective dating partner if I found out she (he) had an unattractive ex.	2.71±0.11	2.25±0.10	3.1	.002	0.32
S15. I would be less inclined to introduce my partner to other women (men) if she (he) was unattractive.	3.96±0.12	3.54±0.14	2.2	.025	0.23
S16. I would be more inclined to 'show off' my partner to other women (men) if she (he) was attractive.	4.94±0.12	4.34±0.15	3.2	.001	0.33

As can be seen there were significant sex differences across all statements, although in contrast to earlier sections these were not always in the expected direction. Men score higher on every statement compared to women, whereas I had predicted that this would have been the case only for S11, S12, S15 & S16. Statements S13 and S14 asked participants to adopt the viewpoint of a focal male/female, and if nonindependent mate choice is indeed more influential in female compared to male choice then women should indicate more agreement with these statements.

The next part of the analysis focused on accounting for the variance in participants' responses to these questions on the basis of their age, lifetime number of sexual partners (used as a proxy for sociosexual orientation) and self-rated attractiveness. While self-rated attractiveness was normally distributed, lifetime number of sexual partners and age were skewed, so I tried various transformations to normalize them. Logarithmic transformation was successful for lifetime number of sexual partners, but age resisted all attempts to normalization and it was used untransformed in all subsequent analyses (which calls for a degree of caution in generalizing the results). It should be noted that in this analysis lifetime number of sexual partners was used as a proxy for sociosexual orientation. Table 16 presents the results of this regression, separately for men and women.

Table 16. Regression of responses by age, lifetime number of sexual partners and self-rated attractiveness, separately for male and female participants.

	Men					Women				
Statement	Age b *(p)*	Lifetime number of sexual partners *b(p)*	Self-rated attractiveness *b (p)*	Model *p*	Model Adjusted R^2	Age b (p)	Lifetime number of sexual partners *b (p)*	Self-rated attractiveness *b (p)*	Model *p*	Model Adjusted R^2
S11.	-.111 (.161)	.126 (.126)	.075 (.352)	.153	.014	.030 (.726)	.056 (.509)	-.007 (.932)	.879	<0
S12.	-.130 (.102)	-.044 (.592)	-.040 (.620)	.244	.007	.038 (.653)	-.010 (.903)	-.233 (.005)	.048	.033
S13.	-.138 (.081)	.124 (.131)	.113 (.158)	.057	.027	.075 (.378)	-.204 (.015)	.024 (.771)	.103	.022
S14.	-.083 (.290)	.123 (.132)	.132(.099)	.067	.025	.010 (.909)	-.120 (.155)	.074 (.383)	.454	<0
S15.	-.200 (.011)	.183 (.026)	-.034 (.666)	.024	.038	-.083 (.334)	-.002 (.981)	.133 (.116)	.406	0
S16.	-.240 (.002)	.308 (<.001)	.031 (.689)	<.001	.108	.024 (.784)	-.033 (.697)	.046 (.588)	.912	<0

As can be seen from the table, the three predictors generally failed to produce a significant model, and even when they did, the proportion of explained variance was generally low. The most interesting results were obtained for the questions which referred to partner 'flaunting', where the models obtained for males were highly significant whereas those for females were not. It is interesting to note that, the logically necessary positive correlation between age and lifetime number of sexual partners notwithstanding, the relation of these two variables with the dependent variable was of a different direction: age was (unexpectedly) negatively related to males' tendency to flaunt an attractive partner, whereas lifetime number of sexual partners was positively related.

4.4 Discussion

Prior to this study there had been only one indirect non-experimental study of human nonindependent mate choice. Platek et al. (2001) asked an undergraduate sample whether they had ever experienced an increase in dating opportunities upon entering a new relationship. The large majority of both males and females indicated that they had this experience; moreover, the frequency of this effect correlated with the frequency of participants' heterosexual intercourse. Platek et al.'s study was primarily interested in the relationship between sexual activity and hormonal levels, which could, presumably, render sexually active individuals more attractive to members of the other sex. Here I administered a more detailed questionnaire to a large sample of men and women which

focused directly on nonindependent mate choice. Summarizing the results briefly, the predicted sex difference of men reporting more interest from opposite-sex individuals when in a relationship vs. when single *in comparison* to what women report was confirmed both for participants who were in a relationship and those who were single at the time of the study. For example, men who were in a relationship expressed more agreement with statements like 'In general, I feel that I have become more attractive to other women (men) since I started dating my girlfriend (boyfriend)' (p=.001), or 'Some women (men) who previously showed little or no interest in me seem to flirt with me since I started dating my girlfriend (boyfriend)' (p=.002) than women who were in a relationship. The responses of single participants followed a similar pattern. Single men were more likely to agree with statements like 'In general, I feel that I have become less attractive to women (men) since I became single' (p=.030) compared to single women. Aside from the differences arising from these direct comparisons between the two sexes, there were other differences which suggested nonindependent mate choice influences primarily female but not male choice. Most importantly, while the reported attractiveness of male participants' partners correlated positively with reported opposite-sex interest, there was no such correlation for female participants. The responses of male participants also correlated with aspects of the couple's social life, whereas those of female participants did not. These results cast doubt on some recent experimental results which not only suggest men employ nonindependent mate choice heuristics, but that that their influence is comparable to or even greater than it is for women (Little et al, 2008; Place et al, 2010). As detailed in chapter 2, given the peculiarities of the human mating system there are strong theoretical reasons to expect that in our species only

women resort to nonindependent mate choice, and the results of this study lend support to these theoretical predictions (see also Parker & Burkley, 2010; Vakirtzis & Roberts, 2010).

Although statistically significant, the correlation between the reported attractiveness of men's partners and sexual/romantic interest from other women was rather low at *rho*=.208. This figure is not in line with the central role that the attractiveness of a man's partner is presumed to play in the process[29], and should be treated as a lower bound estimate of the real relationship, produced here due to the measurement error arising from participants' self reporting of partner attractiveness. A more satisfactory but at the same time more logistically demanding alternative would be the elimination of self-reports of attractiveness (both for partner and self) and their substitution with more objective measures. Ideally researchers could obtain actual photographs of the couple and have these photographs rated for attractiveness by a panel of impartial third raters. In addition to providing a very accurate gauge of overall female attractiveness, such a procedure would also allow the more reliable recording of the various subcomponents of attractiveness like BMI (Tovée & Cornelissen, 2001**),** WHR (Singh, 1993; Singh & Young, 1995) or height and even non-attractiveness related cues like perceived personality traits (Penton-Voak *et al*., 2006, see also chapter 3).

[29] See chapter 2, section 4.1

The diversity of items on this questionnaire brings into sharp relief the contrast between the simplicity of experimental manipulations and the complexity of the real social world. Does the couple go out a lot together? Where do they go? Do they have many friends, or colleagues, or acquaintances in common? How long has the relationship lasted? For example here I found that, consistent with predictions, there was a positive correlation between the frequency with which a couple went to house parties and the attention the man reported receiving from women in the context of his current relationship (see Hendrie *et al*., 2009). This positive correlation did not obtain for frequency of outings to less 'sexy' places like cinemas or eateries. Other independent variables like the length of the relationship or the extent to which the two partners' social circle overlaps did not predict men's responses. But the list of variables that must be included does not end here, since personality differences between respondents must also be controlled. How adept or motivated is the man in picking out subtle indicators of interest from other women while with his partner? Does his inflated self-esteem (from having an attractive partner) get in the way of how he interprets these signals? These are all questions that the social psychologist must take into account if he is to succeed in shedding light on real-life processes. Furthermore, as the number of variables increases, so does the sample size necessary to achieve satisfactory statistical power, which is another drawback of the non-experimental approach.

In the end, no matter how well one controls for confounds, a statement like 'In general, I feel that I have become more attractive to other women since I started dating my girlfriend' is bound to involve substantial error variance. It is for this reason that the

items in the questionnaire must be aggregated to produce a single composite score for each participant. The principle of aggregation in psychological research states that the sum of a set of measurements provides a more stable and accurate estimate than any given measurement in isolation (Rushton *et al*., 1983). This is due to the fact that in aggregation the measurement errors associated with any particular measure tend to cancel each other out (Rushton *et al*., 1983). The results reported here support the notion that a composite score from the items administered to subjects in a romantic relation is a more meaningful measure than any single item on its own. Future studies with couples could use some of the items presented here as the basis for the creation of a validated scale. Also, future questionnaire studies of a slightly different format to the present one could perhaps employ more objective measures such as number of EPCs obtained over the course of various relationships, number of dates, telephone numbers secured and mate poaching attempts (Schmitt 2004; Schmitt & Buss 2001; Parker & Burley 2010).

Chapter 5: Do men take stock? Impact of model females on male-male perception and behavior.

5.1. Introduction

So far this thesis has examined the ways in which human and non-human females are influenced by males' sexual partners. Naturally, since males' primary biological use to third females is in their capacity as potential mates, this influence takes place with regard to female mate choice (Pruett-Jones, 1992). A related and potentially very promising area of research, which to my knowledge has never been systematically undertaken in any species, involves the ways in which third males are influenced by a given male's partner(s). Given that males compete amongst themselves for access to resources (which include females), it is to be expected that this influence will take place primarily in relation to male-male competition (for discussion see Andersson, 1994).

When it comes to humans the logic of this prediction is straightforward. Given that many determinants of a man's mate value relate to social status, rank and dominance (Sadalla *et al*., 1987; Buss, 1999), a male that is paired to an attractive woman will tend to be a) a high mate value mate *and* b) a formidable competitor for other males in the group. The opposite would be true for a male that is paired to an unattractive woman, so that in addition to being a relatively undesirable mate he should also tend to be a weak competitor for other group males. Given this it would be adaptive for men in conditions of uncertainty to modify their evaluations of - and behavior towards - another man as a

function of his mate's attractiveness. As discussed in chapter 2, already in the 1970s social psychologists found that both male and female raters modify their explicit evaluations of a target male depending on the attractiveness of his partner (Sigall & Landy, 1973; Bar-Tal & Saxe, 1976; Meiners & Sheposh, 1977). Unfortunately the lack of an evolutionary framework led to experimental designs in which male and female raters rated the target males on the same generic dimensions (e.g. 'overall impression', Sigall & Landy, 1973) rather than more relevant sex-specific dimensions related to mating for females and male-male competition for males (see section 2.1.1).

This chapter presents two studies that were designed to address this issue, namely the manner in which third males are influenced in their assessments of a target male as a function of the attractiveness of the latter's' partner. Both studies relied primarily on implicit (and presumably more revealing) measures, although for completeness explicit measures of target evaluation are included as well. The first study was based on two widely used experimental economic games and examined whether the female's attractiveness impacts resource allocation decisions. The second one employed the Wason selection task to examine whether the female's attractiveness impacts subjects' ability to detect violations of social norms.

5.2 Study I: Economic games

5.2.1 Introduction

The ultimatum and dictator games are experimental tools that are widely used by economists, psychologists, biologists and anthropologists to examine various aspects of human cooperation (Sigmund, 2007). The ultimatum game was developed in the early 1980s and is structured as follows (Thaler, 1998). An economist gives the first player (the proposer) an amount of money *c* (the stake), typically $10 or a similar amount, and instructs him to transfer a portion *x* of the money to the second player (the recipient), thus keeping *c-x* for himself. The recipient then has two options: he can either accept the allocation, in which case both players walk away with the agreed upon amount, or he can reject the allocation, in which case the experimenter takes back the money, leaving both players with nothing. Assuming that both players are rational income maximizers, the recipient should accept any offer made by the proposer - no matter how low - since rejection automatically means he gets nothing, and something is always better than nothing. Knowing this, the proposer should offer the minimum allowable sum, i.e. 1 cent. In reality, however, experimental subjects usually don't conform to this prediction. Proposers rarely offer the minimal allowable sum, and about two thirds of offers are between 40-50% (Sigmund, 2007). In many traditional societies 'hyperfairness' is also observed, with the proposer offering the recipient more than 50% of the stake, sometimes even 100% (Henrich *et al*., 2006). Recipients' behaviour also deviates markedly from the income maximization prediction, and recipients frequently reject offers as high as 30% of the stake or even higher.

A problem with the ultimatum game involves disentangling two different possible motivations of the proposer, namely his sense of 'fairness' (Fehr & Gächter, 2000) on

the one hand and strategic considerations that the recipient will reject his offer on the other. This problem is eliminated in the dictator game, which is simply the ultimatum game but with the twist that the recipient cannot reject the proposer's offer, and must accept whatever offer is made (Engel, 2010). The dictator game is therefore presumably free of strategic considerations and proposer uncertainty. The offer predicted by income maximization is zero, but again experimental results deviate markedly from this prediction. A meta-analysis of over 100 studies (Engel, 2010) finds that the mean offer in the dictator game is 28.3% of the stake, while only 36.1% of proposers give nothing. 16.7% of proposers give the recipient half the stake, while 5.4% give him everything.

Why do players behave in this altruistic manner? A group of researchers (primarily economists) have tried to exclude a number of standard explanations for this behavior (Bowles & Gintis, 2002; Fehr *et al*., 2002; Fehr & Gächter, 2002; Gintis *et al*., 2008). In these experiments participants are non-kin (excludes kin-selection, Hamilton, 1964; Dawkins, 1976), interactions are one-off, (excludes reciprocal altruism, Trivers, 1971; Axelrod and Hamilton, 1981) and the identity of players remains anonymous (excludes costly signaling and reputation building Zahavi, 1975). Yet despite all these manipulations proposers still make substantial offers (even in the dictator game) and recipients reject non-zero offers, even relatively large ones, if they consider them unfair. The aforementioned scientists have proposed the term *strong reciprocity* to describe this behavior (Fehr *et al*., 2002; Gintis *et al*., 2008). Strong reciprocity manifests as both a) positive strong reciprocity, which involves altruistically rewarding kindness, and b) negative strong reciprocity, which involves altruistically punishing unkindness (Fehr *et*

al., 2002). Given negative strong reciprocity's powerful effects in maintaining in-group cooperation in the face of defectors (Fehr & Gächter, 2002; Fehr *et al*., 2002), these researchers have proposed that some type of group selection could have been responsible for the evolution of strong reciprocity and cultural norms of fairness (Bowles & Gintis, 2002; Boyd *et al*., 2003; Gintis *et al*., 2008).

This interpretation of the evidence has been heavily criticized (Johnson *et al*., 2003; Burnham & Johnson, 2005; Price, 2008). According to the *mismatch hypothesis*, players' tendency to share and punish more than is warranted by selfish profit maximization is not an adaptive tendency that evolved via group selection but merely the result of a mismatch between ancestral environments and the modern conditions under which these economic experiments are held (Burnham & Johnson, 2005; Price, 2008; see also Crawford, 1998). For example it would have been highly unlikely or unusual for ancestral humans to routinely encounter anonymous strangers in one-off interactions and be certain of no future interaction. Even if they did meet a total stranger, how could ancestral humans be sure that the anonymous stranger would not eventually discover their identity, or would not unilaterally extend an unfair 'one-off' interaction with, say, immediate retributive violence? (Price, 2008). In Burnham & Johnson's words,

> 'Behavioral mechanisms are not perfect, always-optimal, goal seeking devices, but rather context-specific physiological systems that respond to

> environmental cues in order to engage what was, on average over the course of evolutionary history, the appropriate action. When those cues convey information out of context, then proximate mechanisms will often, unsurprisingly, produce maladaptive and costly behavior. Consequently, we see no need for the misnomer “strong reciprocity” to describe cooperative dispositions that are not repaid. To accept it would be to invite a host of similarly misleading labels for other ancestral mechanisms gone awry in modern settings, such as “obesity drive”, “strong sperm bank cuckoldry”, and “death instinct via adaptive heroin addiction”’. (Burnham & Johnson, 2005, p.129).

An alternative approach to invoking strong reciprocity and group selection, therefore, and the one that I will utilise here, views behavior in these games as simply reflecting ‘tendencies selected in a world of frequent interactions’ (Zaatari *et al*., 2009, p.631). Rather than striving to exclude standard theories of human cooperation, this approach utilizes these games in order to enrich our understanding of contextual and individual variables that are known or believed to affect human behavior. Social and evolutionary psychologists working within this approach have examined how factors like gender (Eckel & Grossman, 1998; Solnick & Schweitzer, 1999; Saad & Gill, 2001a; 2001b; Solnick, 2001), attractiveness (Solnick & Schweitzer, 1999; Hancock & DeBruine, 2003; Rosenblat, 2008), fluctuating asymmetry (Zaatari & Trivers, 2007; Zaatari *et al*., 2009), testosterone (Burnham, 2007; Eisenegger *et al*., 2010), or 2D:4D (Van den Bergh & Dewitte, 2006) can affect players’ behavior. For example Saad & Gill (2001a) used the

four possible proposer-recipient sex combinations in the ultimatum game, and viewing it as a convenient measure of evolved resource-allocation predispositions made the following predictions. When paired with a female recipient male proposers should behave altruistically in order to exploit this potential mating opportunity by displaying generosity, a trait highly valued by females (Buss & Schmitt, 1993). More selfish behavior should be observed in the male proposer/male recipient condition, reflecting male-male competition for resources. Given that ancestral women had no access to resources, and that modern women do not use resources as a strategy for mate attraction, the authors predicted that female proposers would not be affected by recipient gender. Moreover their offers should be less than those made by male proposers to female recipients, but higher than those by male proposers to male recipients. The results confirmed this prediction. Note that rather than excluding evolved mating mechanisms as motivating factors in male proposers' behavior – the ultimatum game is after all ostensibly related to economics, not sex - the authors used the game to demonstrate their powerful effects in seemingly unrelated contexts.

Here I use the ultimatum and dictator games to examine how male proposers are influenced in resource-allocation interactions by the attractiveness of a male's sexual partner. Using a simple one-way between-groups design, I presented male proposers with a fictitious profile of a male recipient (description and photograph) and an image of his supposed girlfriend. One group viewed the recipient with an image of an attractive girlfriend, the other with an image of an unattractive one, and one group without any image of the girlfriend. Apart from the girlfriend's image all other aspects of the male

stimulus were held constant across the three groups. My prediction was that the manipulation of female partner attractiveness would influence male proposers' sense of 'fairness', their eagerness to appease the recipient, and their expectations of recipients' demands (in the ultimatum game), and that this influence would be evident in the actual offers proposers made. I predicted that proposers would offer most in the 'attractive girlfriend' condition, least in the 'unattractive girlfriend' condition and make intermediate offers in the 'no image' condition.

5.2.2 Materials and methods

5.2.2.1 Materials

The images used in this study were part of a set of male and female facial images of staff and students at the University of Newcastle which have been used in previous mate choice studies (e.g. Roberts *et al*., 2005a; 2005b; 2008; Vakirtzis & Roberts, 2010). The entire set is made of two subsets of 185 female and 141 male images. These images had previously been rated for attractiveness by seven male and seven female raters, respectively (Vakirtzis & Roberts, 2010), and an average attractiveness rating had been assigned to each stimulus. The two sets of images were subsequently ranked from most to least attractive, rank 1 assigned to the most attractive image of each set. From the male set I chose the image of one moderately attractive man (rank 62, or 57th percentile of attractiveness). This was the only male image used in this study, and was of a 20 year-old male with no piercings, scars or any unusual facial characteristics. For the female stimuli I selected four highly attractive images (between

ranks 7-12, 96th to 93rd percentiles; mean age 19.8 years) and four unattractive (between ranks 169-178, i.e. 8th to 4th percentiles; mean age 20.1) images. As with the male image, these images had no conspicuous ornamentation or unusual facial features.

Using this material I created a profile of the male stimulus which consisted of two slides. The first slide contained an image of the male (placed roughly in the centre of the slide), his name ('Steven') and a textbox with a deliberately unexceptional profile describing him as 21 years old, 6 ft tall, 189 pounds, heterosexual, and in a stable relationship with his girlfriend of a few months. The textbox also informed subjects that with Steven's permission researchers had contacted his girlfriend to learn some more things about him. All male participants viewed this first slide, and the only thing that differed between groups was the second slide. This second slide depicted the images of both the male (centrally placed as before) and his supposed girlfriend. The image of the girlfriend was considerably smaller and placed in the bottom left part of the slide so as to implicitly emphasize that the object of interest was the male and not the female (see Vakirtzis & Roberts, 2010 for description). From the image of the female a speech bubble emanated, containing the text of the female's description of her boyfriend[30]. Again, this was an unexceptional description whose only purpose was to justify the inclusion of the female image in the stimulus slides.

[30] "Steven in a nutshell: he's a real fun guy, laid back and easygoing. His hobbies are basically football, playing pool, listening to music and watching DVDs. Oh, and spending time with his mates! He's not the kind of man that is afraid to show his feelings. We get along very well, rarely argue".

Using this two-slide template and the 8 female images I had selected, and varying only the image of the supposed girlfriend in the second slide, I created three different groups of stimuli: four ‘attractive’ slides, four ‘unattractive’ slides and finally one slide with no female image. For this last slide instead of a real facial image I used a stylized sketch (downloaded from the internet, royalty-free) of a female which contained no cues to attractiveness, but merely the outline of a female face. Other than the image of the girlfriend (attractive, unattractive or sketch) the two slides were identical across all three groups.

5.2.2.2 Procedure

One hundred and fifteen male participants (mean age±SD 22.1±2.2) were recruited by convenience at various libraries of the University of Liverpool and Liverpool John Moores University. The study was conducted online; subjects were given the relevant URL and asked to follow the online instructions. Forty males saw an attractive image of the male’s girlfriend, another 40 an unattractive image and lastly a ‘control’ group of 35 males saw the stylized sketch (‘no-image’ treatment). In order to minimize variance arising from any unique (non-attractiveness related) features of a particular female image, four females ($4\times10n=40n$ per treatment) were used in each of the ‘attractive’ and ‘unattractive’ conditions. In all other aspects the procedure was identical across the three groups.

The instructions informed subjects they would be asked to imagine playing some standard economic two-player games, and that prior to playing the games they would be given some information about their fictional playing partner. The use of images of supposed players instead of live players is common in the literature (e.g. Hancock & DeBruine, 2003; Zaatari *et al*., 2009), and meta-analysis has shown that the use of hypothetical questions (i.e. asking subjects how much they would be willing to give) instead of real money has no effect on proposers' decisions in the dictator game (Engel, 2010). All subjects played first the dictator and then the ultimatum game (given the aims of the study there was no need to counterbalance the order of presentation). The narratives for the two games are given in Appendix B. Subjects made their offer by dragging a slider on the screen. The stake for both games was £10, and offers could be made in increments of £0.1.

Following each game subjects were asked to indicate the motives behind their offer (after Zaatari *et al*., 2009; see results section for details). After they had played both games subjects were also asked to indicate the degree to which various adjectives described their co-player. These adjectives were *dominant, submissive*, *adventurous*, *bold*, *interesting* and *talented*, with ratings on a 7 point-scale from 'very poorly' (1) to 'very well' (7). Finally, as a manipulation check, subjects rated the attractiveness of their playing partner and his supposed girlfriend on a 10-point scale.

5.2.3 Results

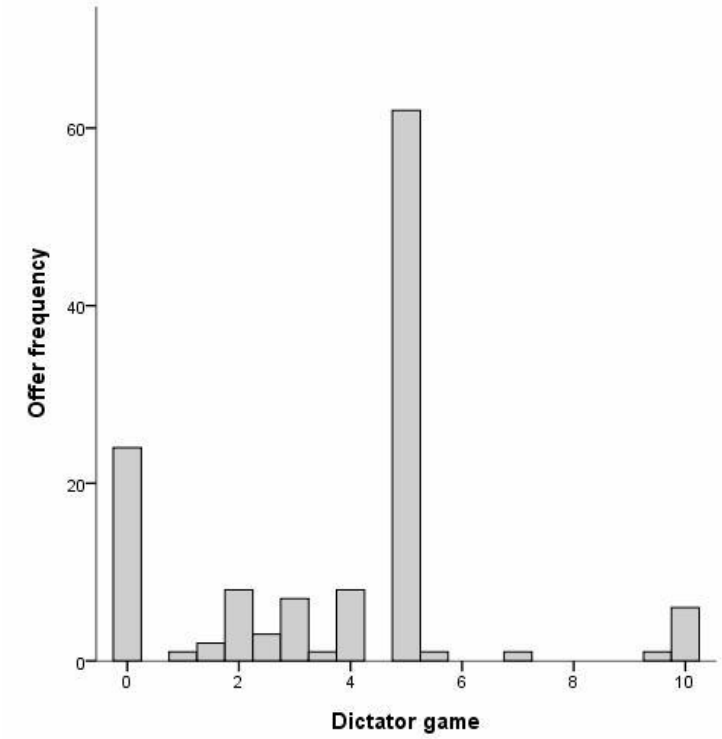
Ninety-five percent of the subjects were British or Irish, the remaining 5% being mostly from European countries. The sample was thus relatively culturally homogenous. Due to the non-normal distribution of the monetary offers, non-parametric tests were used for analysis of the offers; otherwise I used parametric tests. All tests were two-tailed.

5.2.3.1 Did the subjects understand the instructions? Did their offers follow the expected patterns?

Yes. As expected, the 115 subjects offered on average more in the ultimatum game (mean offer ± S.D. 4.82±1.44) than in the dictator game (3.80±2.50), and this difference was highly significant (Wilcoxon signed ranks test, Z=-4.69, p<.0001). While 59 subjects offered the same amount across both games, 48 of the remaining 56 subjects offered more in the ultimatum game (sign test, p<.001). A graphical comparison of subjects' offers (Figure 8) reveals the by now well-known (Thaler, 1988; Engel, 2010) divergent patterns of offers. Whereas a sizeable fraction of subjects (n=20 or 17.4%) made zero offers in the dictator game these zero offers were almost absent in the ultimatum game (n=2 or 1.7%; Fisher's exact test, two-tailed, p<.0001). Fully 31.3% of subjects (n=36) gave less than £3 in the dictator game compared to only 3.48% (n=4) in the ultimatum game. An examination of subjects who gave something but less than half in the two games (i.e. between £0.1-4.9), showed a striking difference in the distribution of these 'less than fair' offers: for the dictator game the mean of these offers (n=54) was £1.79 whereas for the ultimatum game (n=30) it was £3.45. The modal offer was £5 in both games (n=53 or 46% or offers in the dictator game and n=71 or 61.7% in the

ultimatum). Hyperfair offers (i.e. more than 50% of the stake) were rare, made in only 6.9% (*n*=8) of instances in the dictator game and 10.4% (*n*=12) in the ultimatum game.

It should be noted that the frequency of 50:50 offers for the dictator game found here (46%) is relatively high (see Engel, 2010). The fact that subjects knew they would be playing a second game, the within-group status of the recipient (fellow student), as well as the fact that the money had not been earned (the 'manna from heaven' scenario, Engel, 2010) and was not real, as well as the fact that each subject had played the game seconds or minutes after being approached by the recruiter (possible perception of reduced anonymity) may account for this large percentage of 50:50 offers in the dictator game.



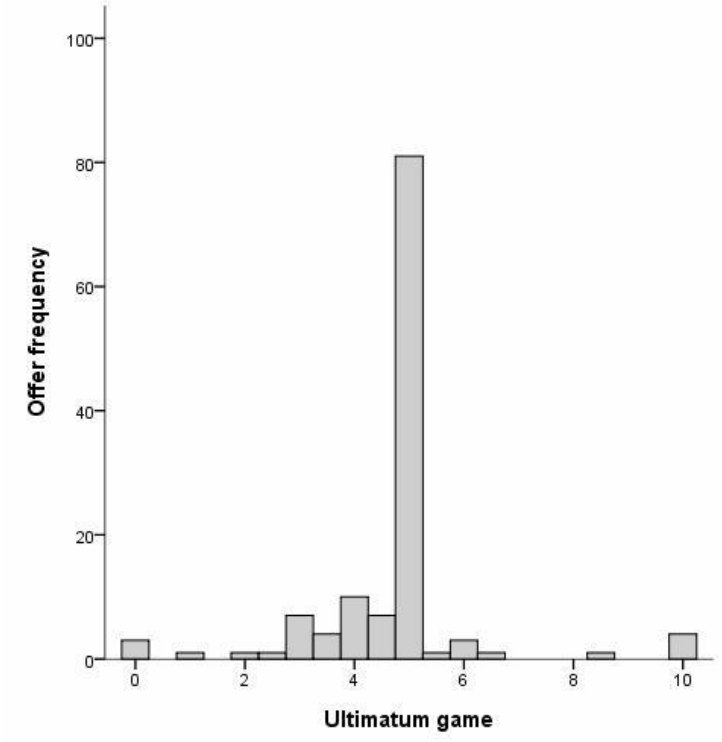


Figure 8. Frequencies with which offers were made in the two games.

5.2.3.2 Was the experimental manipulation successful? Was there a halo effect?

Recall that as a manipulation check at the end of the online procedure subjects rated the attractiveness of the recipient male and his supposed partner on a 10-point scale, 10 being most attractive. These ratings showed that the manipulation of female partner attractiveness had been successful: subjects rated the four attractive partners as significantly more attractive than the four unattractive ones (mean ± SE 5.75±0.25 vs. 3.58±0.27; t=5.91, df=78, p<.0001, *Cohen's d*= 1.35). There was no halo effect: the recipient male received the exact same average attractiveness rating (4.18) regardless of his partner's attractiveness (t=0, df=78, p=1). Interestingly, the 35 subjects who saw no image of the female partner (but only a sketch) rated the recipient male as somewhat less attractive (3.54) in comparison to the other two groups, although not significantly so (one-way ANOVA, $F_{2,112}$=2.47, p=0.89).

5.2.3.3 Were subjects' offers influenced by the attractiveness of the recipient's partner?

a) The Dictator game.

As predicted, proposers in the Dictator game made the largest offers in the 'attractive partner' condition (mean±SD 4.20±2.4), the lowest in the 'unattractive partner' condition (3.39±2.4), and made intermediate offers in the 'no-image' condition (3.82±2.7). However, these differences were not statistically significant (Kruskal-Wallis one-way

ANOVA, x^2=1.264, *df*=2, *p*=.531), nor was the pairwise comparison between 'attractive' and 'unattractive' significant (Mann-Whitney U test, *Z*=-1.58, *p*=.114), While 25% (10/40) of offers made in 'unattractive' were zero, the corresponding percentage for 'attractive' was 12.5% (5/40), but again this difference was not significant (Fisher's exact test, two-tailed, *p*>.2). There was no difference in the percentage of 50/50 offers made across 'attractive' and 'unattractive', these being made in 50% of the games (20/40) in both conditions. Hyperfair offers were observed 3 times in 'attractive' and once in unattractive (Fisher's exact test, two-tailed, *p*>.6). Table 17 summarizes these results.

Table 17. Summary of offers made across the 3 treatment conditions in the Dictator game.

	Mean offer	£0	50/50	Hyperfair
Attractive	4.20	5/40	20/40	3/40
Unattractive	3.39	10/40	20/40	1/40
No-image	3.82	5/35	13/35	4/35

b) The Ultimatum game.

As with the Dictator game discussed above, proposers in the Ultimatum game offered more in 'attractive' (mean±SD 4.88±1.5) compared to 'unattractive' (4.51±1.2); the offers for the 'no-image' condition (5.10±1.6), however, were slightly higher even than the attractive condition. As in the dictator game, these differences did not achieve significance (Kruskal-Wallis x^2= 1.971, *df*=2, *p*>.3). There was no difference in the frequency of 'fair' 50/50 offers made in attractive and unattractive (26 vs. 27) nor in the

frequency of hyperfair offers (2 for both conditions). A comparison of unfair but non-zero offers (i.e. between £0.1-4.9) made in 'attractive (mean±SD 4.12±0.57); and 'unattractive' (3.36±1.0) revealed a nonsignificant difference with the non-parametric test (Mann-Whitney U test, Z=-1.70, p=.089), but a significant one with its parametric equivalent (t=2.14, df=19, p=.046). Note that for this truncated range of offers the data do not deviate markedly from normality due to the exclusion of the modal offer of 5, so the use of a parametric test is justified. Table 18 summarizes the results for the ultimatum game.

Table 18. Summary of offers made across the 3 treatment conditions in the Ultimatum game.

	Mean offer	Mean 'unfair' offer (£0.1-4.9)	50/50	Hyperfair
Attractive	4.88	4.12	26/40	2/40
Unattractive	4.51	3.36	27/40	2/40
No-image	5.10	3.51	18/40	8/35

5.2.3.4 Did partner attractiveness influence proposer motivations?

Following each game subjects were asked to select, from five statements, the one that best described their motivation for offering the recipient the amount that they had. For the dictator game the 5 statements were a) 'I thought that was a fair offer', b) 'I took advantage of the fact that I was calling the shots', c) 'He seemed like he needed the money', d) 'I don't know/I'm not really sure', and e) 'Other (please specify)'. The first 4 options were presented in random order, and option e) was always presented last.

Subjects who selected this last option could provide additional explanations in their own words in a text box. For the ultimatum game the same five statements were given but with a single modification: option b) was changed to 'If I gave him any less he probably would have rejected the offer'. The patterns of participants' choices were quite similar across both games: more than half the participants justified their offer by appealing to fairness (i.e. choice a); dictator: 55.2%, ultimatum: 58.6%), with the second largest group selecting the option which derived from the possibility or impossibility of rejection (i.e. choice b); dictator 22.4%, ultimatum, 23.3%). Furthermore upon analysis of the supplementary explanations given by subjects who chose e) it was apparent that some responses could be unambiguously reclassified into category a). Table 19 summarizes these results, further breaking down participants' responses by treatment. Owing to their small frequencies options *c*, *d* and *e* were grouped together.

Table 19. Summary of professed motivations behind players' offers across both games, broken down by treatment. See text for description of options a, b, c, d and e.

	Dictator game			Ultimatum game		
Options	*a*	*b*	*c, d, or e*	*a*	*b*	*c, d or e*
Attractive	28	7	5	28	8	4
Unattractive	24	9	7	24	9	7
No-image	16	10	9	19	10	6

Chi-square analyses confirmed what is evident from the table, namely that the choices subjects made were independent of treatment (dictator: χ^2=4.68, *df*=4, *p*=.32; ultimatum χ^2=2.33, *df*=4, *p*=.67).

The classification of offers by underlying motivation allows for more focused tests and meaningful comparisons (Zaatari *et al*., 2009). Instead of lumping all offers together researchers can compare only those offers that stem from similar motivations. First I compared the choices of subjects who had identified fairness as their motive, but there were no differences among treatment groups in the dictator (Kruskal-Wallis χ^2=.487, *df*=2, *p*>.7) or ultimatum game (Kruskal-Wallis χ^2=.876, *df*=2, *p*>.6). This comparison was similarly not significant for subjects who had identified the impossibility (in the dictator game: Kruskal-Wallis χ^2=.1.29, *df*=2, *p*>.5) or possibility of rejection (in the ultimatum game: Kruskal-Wallis χ^2=1.61, *df*=2, *p*>.4) as the motivating factor behind their offers.

5.2.3.5 Did partner attractiveness influence subjects' evaluations of the target male?

The last part of the analysis involved the evaluations subjects had made of the stimulus male. Recall that after playing both games each subject had been asked to rate how well each of 6 adjectives described the stimulus male on a 7-point scale (7 being most). Two of these adjectives, namely *dominant* and *submissive* were the primary adjectives of interest, whereas the remaining four adjectives were secondary attributes that could plausibly characterize dominant, successful or high-status males: *bold*, *talented*,

adventurous, and *interesting*. Of the six adjectives, only *submissive* showed significant between-group differences ($F_{2,112}$=6.67, p=.035), but note that due to the multiple (six) ANOVAs carried out in this section a smaller p value would be needed to be confident of this result. At any rate, the differences in *submissive* were in the expected order so far as the male was rated as less submissive in 'attractive' (3.65) compared to 'unattractive (4.10)', although he was rated even less submissive in the 'no-image' condition (3.26). Tukey's post-hoc comparisons showed that the significant difference was between 'unattractive' and 'no-image' (p=.026), the other contrasts being nonsignificant.

In contrast to the analyses of game offers discussed previously, the failure to detect statistically significant differences among groups in this part of the study was most likely not due to low power. The difference in means between the 'attractive' and 'unattractive' groups was in the predicted direction for 3 adjectives (*submissive*, *talented*, *interesting*) and in the opposite direction for the remaining 3 (*dominant*, *bold*, *adventurous*), a pattern strongly supportive of the null hypothesis.

5.2.4 Discussion

The results of this study generally didn't confirm the predicted effects of partner attractiveness on proposers' offers in the dictator and ultimatum game. Although participants who viewed the recipient male with an attractive partner made higher mean offers in both the dictator and ultimatum game compared to those who viewed him with an unattractive partner, these differences were not statistically significant. Extrapolating from the trends in the current data, a sample size of two-and-a-half to three times the present size would have been necessary to achieve statistical significance for most tests. In hindsight, a future replication of this study with a larger sample should perhaps drop the 'no-image' treatment and allocate as many participants as possible to the two attractiveness conditions alone.

More surprising than the aforementioned is the fact that partner attractiveness did not influence subjects' perceptions of the stimulus male on a variety of dominance and status related evaluations, given that earlier studies had obtained results of this nature (Sigall & Landy, 1973; Bar-Tal & Saxe, 1976; Meiners & Sheposh, 1977). The random pattern of results suggested that the null results were not merely an artifact of small sample size but rather that the attractiveness of the male's partner was not influencing participants' evaluations. The reasons for this are not clear, but there are several possible explanations. Firstly, the effect may be sensitive to subtle contextual factors, similar to what is the case with experimental studies of nonindependent mate choice in women (discussed in earlier chapters). Secondly, the fact that subjects gave their

evaluations after they had made the stimulus male offers in the two games means that their evaluations may have been affected by these offers and not been independent thereof as was originally assumed in the analysis. In other words it may be the case that what I give to someone in the dictator or ultimatum game may affect how I subsequently regard him, and given that the differences in offer size were small at best this process might have resulted in the masking of perceived differences that might have otherwise manifested. Finally, these null results could be taken at face value, suggesting that (earlier studies notwithstanding) there is no effect, although the evolutionary rationale which inspired this study (see Sadalla *et al*., 1987; Buss, 1999) strongly suggests otherwise.

5.3 Study II: A study with the selection task

5.3.1. Introduction

The Wason selection task (Wason, 1968) is a logical reasoning test that requires subjects to indicate which of four cards need to be turned over to test whether there has been a violation of the conditional rule *if p, then q.* Subjects are told that one side of the cards shows the antecedent of the conditional (*p*) or its denial (*not-p*), while the other side shows the consequent (*q*) or its denial (*not-q*), and are presented with four cards reading *p*, *not-p*, *q*, and *not-q*. The task can be presented in a variety of contexts. For example subjects can be given the rule 'If you go to Phoenix, you travel by train', and presented with the following four cards: *Phoenix* (p), *Tucson* (not-p), *train* (q), *car* (not-q) (Cummins, 1996). Logically, the conditional rule can only be falsified by turning over the cards *p* and *not-q*, which in this example would be *Phoenix* and *car*. The *p card* must be turned over to see whether the other side is indeed *q*, whereas the *not-q* card must be turned over to make sure the other side is not *p* (in this example participants should turn over *Phoenix* to see whether there is *train* on the other side, and they should also turn over *car*, to make sure that the other side is not *Phoenix*). The other two cards (*q* and *not-p*) cannot disconfirm the rule and need not be turned over.

Even though the underlying logical relations always remain the same, subjects' performance on the selection task varies widely depending on the content of the conditional rules that are used (Cosmides, 1989, Cosmides & Tooby, 1992, Dominowski, 1995; Cummins, 1996). One of the most robust content effects pertains to

the so-called indicative-deontic distinction (Cummins, 1996). Indicative reasoning involves descriptive rules that simply describe a purported state of affairs. Deontic reasoning is about rules, prohibitions or obligations. For example the rule 'If a card has a D on one side then it has 5 on the other side' is related to indicative reasoning, whereas the rule 'If a person is drinking beer, then the person must be over 19' involves deontic reasoning. Decades of research with the selection task have shown that experimental subjects are consistently more successful in selecting the correct cards (*p* and *not-q*) when the conditional rule involves deontic reasoning (reviewed in Cosmides & Tooby, 1992; Cummins, 1996). This happens even though the logical structure of indicative and deontic conditionals is identical. When presented with indicative content subjects tend to adopt a rule-confirming perspective and typically select the *p* card alone or the *p* and *q* cards. Confronted with deontic content, on the other hand, subjects adopt a more appropriate violation-detection perspective and usually select the correct cards. Table 20 brings this so-called 'deontic effect' (Cummins, 1996; 1999) into sharp relief. The table shows a sample of indicative and deontic rules that have been used in various studies, together with the percentage of subjects in the respective studies who made the correct choice of cards.

Table 20. A compilation of some conditional rules that have been used in the Wason selection task (adapted from Cummins, 1996). The first column contains the percentage of subjects in the respective studies who chose *p* and *not-q*. Typically less than a quarter of subjects choose correctly in indicative versions of the task, whereas a clear majority is successful in deontic versions (see Cummins, 1996, for original extended version of table).

% *p* & *not-q*	**Indicative Conditionals**
9%	Everytime I go to Miami, I travel by car (Griggs & Cox, 1982).
4%	If I eat haddock, then I drink gin (Reich & Ruth, 1982).
17%	If a bird on the island has a purple spot under its wing, then it makes its nest on the ground (Cheng & Holyoak, 1985).
12%	When I go to work, I hurry (Reich & Ruth, 1982).
% *p* & *not-q*	**Deontic conditionals**
72-96%	If a person is drinking beer, the person must be over 19 (Cox & Griggs, 1982).
63%	If you tidy your room, then I will let you go out to play (Manktelow & Over, 1991).
85%	If a purchase exceeds $30, then the receipt must have the signature of the department store manager on the back (Griggs & Cox, 1983).

What are the underlying cognitive mechanisms responsible for the deontic effect? According to Denise Cummins' *Dominance Theory* (Cummins, 1999; 2002; 2003), the deontic effect reveals the operation of evolved psychological mechanisms that are involved in navigating and negotiating social dominance hierarchies. Social dominance hierarchies are defined as 'a set of implicit social norms that reflect which behaviors are permitted, prohibited or obligated given one's rank (Cummins, 1999, p.231). Dominant individuals have priority of access to resources, and promote their fitness by enforcing the group's social norms. Subordinate individuals, on the other hand, attempt to improve

their access to resources through cheating and deception (Cummins, 1999; 2000). While high-ranking individuals should thus actively monitor and enforce lower-ranking individuals' violations of social norms, the reverse should not be the case. Because historically low-ranking individuals have been unable to enforce social norms on higher-ranking individuals, the theory predicts that the former should not be sensitive to the latter's' violations. These low-ranking group members should be prone, rather, to 'rational ignorance'[31] with regard to higher-ranking individuals' transgressions.

To summarize, Dominance Theory explains the deontic effect in terms of domain-specific cognitive adaptations about social norms. These adaptations evolved due to the intense selection pressures of living in highly hierarchical social groups (Cummins, 2006). Furthermore, Dominance Theory makes the specific prediction that performance in deontic tasks will be a function of subjects' dominance rank. Specifically, it predicts that when adopting the perspective of a dominant individual that is investigating possible transgressions of subordinates, experimental subjects should adopt the appropriate violation-detection strategy and select the correct cards on the selection task. When adopting the perspective of a low-ranking individual who is asked to investigate possible transgressions of dominants, however, subjects should fail the task. This rank-dependent differential performance of subjects should only be observed for deontic content; performance in indicative versions of the task should not vary as a function of rank, but should remain poor throughout.

[31] To borrow an expression from public choice theory.

To test these predictions Cummins (1999) gave two groups of male undergraduates different versions of the selection task. In the deontic version subjects were told of a rule in their college dormitory which specified that '*if someone is assigned to tutor a study session, that person is required to tape record the session*'. Subjects were also told that students were allowed to tape record study sessions even if they were not assigned to tutor it, and were presented with the 4 cards '*Assigned to tutor the session*' (*p*), '*not assigned to tutor the session*' (*not-p*), '*Taped the session*' (*q*), and '*Did not tape the session*' (*not-q*). The study was a 2 (rank of subject) $\times$2 (rank of fictional character whose compliance with the rule was being investigated) factorial design, where high-ranking persons were Resident Assistants (students chosen by the administration to run the dormitory) and low-ranking persons were simple students. As predicted by Dominance Theory, performance in the higher-ranking perspective, where subjects adopted the role of Resident Assistant checking on students, was considerably better (65% chose correctly) in comparison to the other 3 cells (15-20%). In the indicative version of the task, subjects were asked to imagine they had overheard someone say '*If I'm assigned to tutor a session, I always tape record the session*' and no mention of a rule was made; all other aspects of the narrative remained the same. As predicted, there was no differential performance in this version of the task, with the percentage of correct choices ranging between 15-20% in all 4 cells.

Here I examined whether the dominance rank effects predicted by Dominance Theory in the deontic versions of the selection task (Cummins, 1999) could be replicated by a method other than explicitly telling subjects about a fictional male character's rank. In particular I examined whether manipulating the attractiveness of the fictional character's supposed partner would induce male subjects to display similar differential performance, i.e. if partner attractiveness could be used as a proxy for dominance. The study repeated Cummins' (1999) 2×2 factorial design, with half the subjects viewing the fictional character (whose possible transgressions were being investigated) paired to a highly attractive girlfriend (presumably a high rank male) and the other half to a highly unattractive girlfriend (presumably a low rank male). Within each group half the subjects were asked to imagine that they themselves (i.e. the subjects) were high-ranking and the other half low-ranking.

5.3.2. Materials and methods

5.3.2.1 Materials

All participants were given the same deontic selection task, which is reproduced *verbatim* in Appendix C. Although I developed an original story, I followed the structure and presentation format of Cummins' (1999, see pp.244-245) original experiment as closely as possible. Briefly, the problem asked each participant to imagine that he was either a senior member (high rank) or a new member (low rank) of his university hiking club. Every week a different club member was assigned to organise the club's weekly trip. Among other duties, the member assigned to organize the trip was also responsible

for bringing along a first aid kit. If other club members (i.e. those not assigned to organize that particular trip) desired, they could also bring along a first aid kit, although this was not required of them. On every hiking trip records were kept for every member in the form of a card: the front side of the card indicated whether or not that particular member was assigned to organize the trip, and the back indicated whether or not that member brought along a first aid kit. Participants were asked to check if another club member, Steven, had been following the rule: "*If a member is assigned to organize the trip, he must bring a first aid kit"*. The faces of the four cards showed the following: "*Steven was assigned to organise the trip*", "*Steven was NOT assigned to organise the trip*", "*Steven brought a first aid kit*", "*Steven did NOT bring a first aid kit*". With regard to the given deontic rule these cards represent *p*, *not-p*, *q*, and *not-q*, respectively.

From the same set of female facial images used in the previous study[32] I selected one highly attractive (rank 4 out 185, 23yrs) and one highly unattractive (tied for least attractive with 3 other images, 21 yrs) female facial image. Both images had no distinct piercings, scars or any unusual facial characteristics of any sort. No male images were used in this study.

5.3.2.2 Procedure

[32] See section 5.2.2.1 for details.

Eighty one male participants (mean age ± SD 22.7±2.7) were recruited by convenience from various libraries of the University of Liverpool and Liverpool John Moores University. The study was conducted online; subjects were given the relevant URL and asked to follow the online instructions. Half of the subjects were given the high ranking version of the task and the other half the low ranking version. Within each of these two conditions, further, the fictional subject whose compliance with the rule was being examined was presented with either the attractive or unattractive partner (see below for details). The four resulting cells were a) high rank/attractive partner, b) high rank/unattractive partner, c) low rank/attractive partner, d) low rank/unattractive partner. With the exception of one cell (low rank/attractive partner) which had 21 participants, all other cells had 20 participants.

The instructions informed subjects they would be presented with a fictional story that involved a logical reasoning task, and that prior to that they would be given some background information about the fictional character in the story ('Steven'). This information was in the form of two slides (very similar to the ones described in section 5.2.2.1, with the difference that no male image was used). The first slide was a simple text-box with a generic description of the male, who was described as a 21-year old undergraduate with a keen interest in hiking (but no image was given). The second slide contained an image of the male's supposed partner (placed in the lower left corner of the screen) from which a speech bubble emanated with a description of her boyfriend.

The description was intentionally unexceptional, intended only to justify the inclusion of the female image[33]. Only the image of the female changed across groups, while in all other aspects the male profile was identical across both groups. Subjects were then presented with the Wason task, and made their selection by placing a tick beneath the card(s) of their choice.

After they had completed the Wason task subjects were asked to indicate the degree to which various adjectives described the target male, with ratings on a 7 point-scale from 'very poorly' (1) to 'very well' (7). Four of the adjectives (*dominant*, *submissive*, *interesting*, *talented*) had been used in the previous study, while *confident* and *assertive* were used for the first time (instead of *adventurous* and *bold* which had not produced promising results earlier). Finally, as a manipulation check, subjects rated the attractiveness of the target male's partner on a 10-point scale.

5.3.3 Results

5.3.3.1 Manipulation check

A comparison of male subjects' ratings confirmed that subjects perceived the 'attractive' female image as significantly more attractive than the 'unattractive' image, and that this

[33] "Steven in a nutshell: he's a real fun guy, laid back and easygoing. His hobbies are basically hiking, hiking and more hiking! Oh, and spending time with his mates! He's not the kind of man that is afraid to show his feelings. We get along very well, rarely argue".

difference was very large (mean±SE 5.9±0.3 vs.2.5±0.3, respectively; t=8.55, df=79, p<.0001; Cohen's d=1.92).

5.3.3.2 Selection task

The percentage of subjects who adopted a violation detection strategy and chose the correct cards was between 23.8-35% across all four cells. As predicted, the high rank/unattractive partner cell had the highest rate of violation detection responses at 35%, while the low rank/attractive partner had the lowest rate at 23.8%. These differences across the 4 cells, however, were not significant (χ^2=0.81, df=3, p=.85). A pairwise comparison between these two most extreme categories of high rank/unattractive partner vs. low rank/attractive partner[34] was similarly not significant (*Fisher's exact test, p*=.505). Figure 9 summarizes these results graphically.

[34] Corresponding, presumably, to Cummins' 'higher rank' and 'lower rank' categories, respectively. The other two cells were intended to correspond to Cummins' categories of 'equally high rank' and 'equally low rank'.

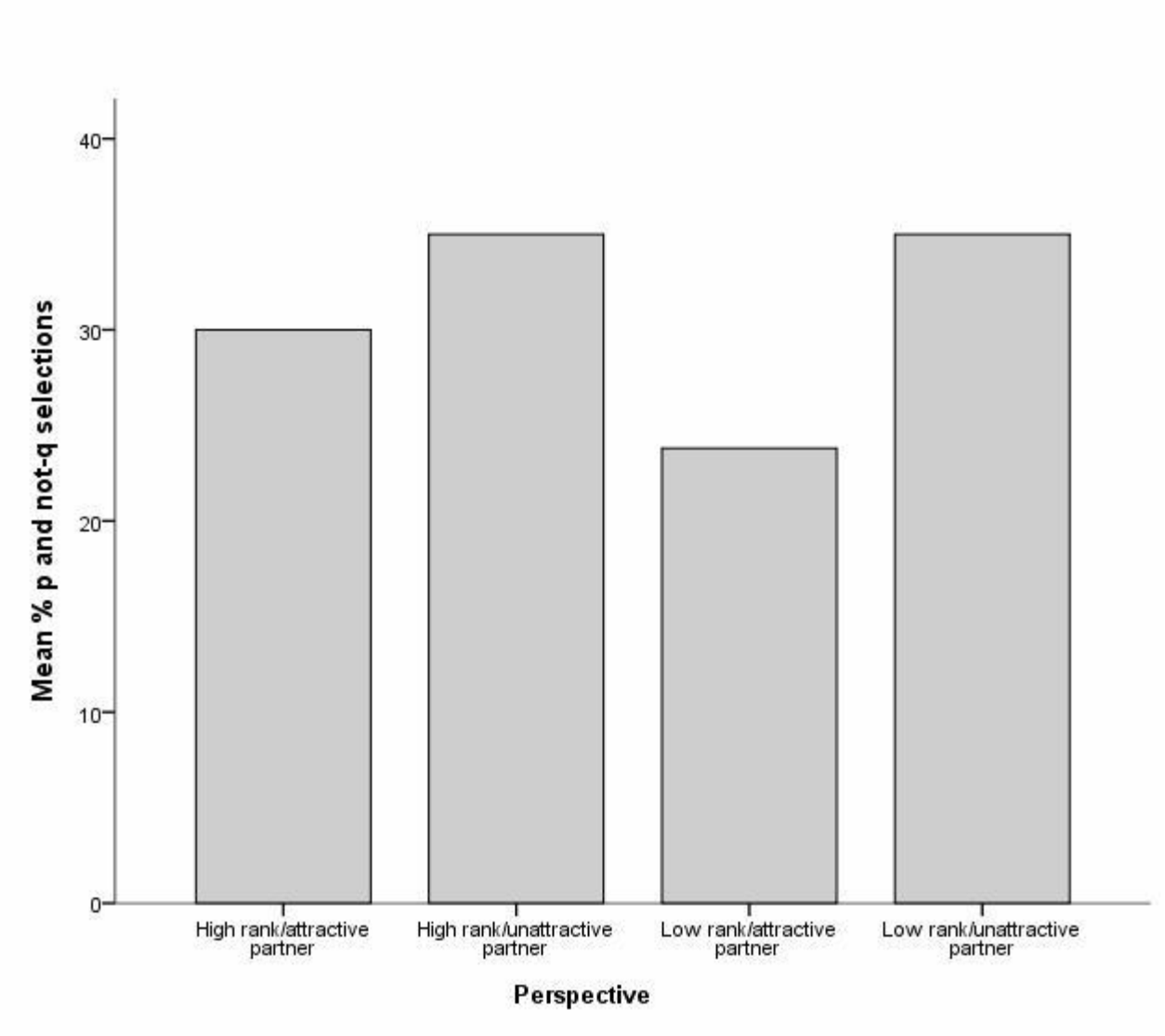


Figure 9. Percentage of violation detection responses when subjects were asked to test compliance with a social rule from four different perspectives.

5.3.3.3 Target male evaluations

The last part of the analysis involved the evaluations subjects had made of the stimulus male as a function of his supposed partner's attractiveness. Recall that after they had made their choices on the Wason task subjects were asked to rate how well each of six adjectives described the stimulus male on a 7-point scale. Interestingly, of the six adjectives, only the primary adjective of interest, namely *dominant*, showed a significant between-group difference, with men in the 'attractive' partner condition evaluating the target male as significantly more dominant (3.85±.0.18 vs. 3.20±.0.19, t=2.54, df=79, p=.013). The other five comparisons were not significant (all p>.36). The inclusion of subjects' rank as a factor in a 2x2 factorial ANOVA did not alter these results: rank did not have a significant main effect on any of the six models, while partner attractiveness was only significant for *dominant* ($F_{1,77}$=8.71, p=.013) and not significant for the other dependent variables.

5.3.4 Discussion

Can a *prima facie* unrelated aesthetic cue like attractiveness impact performance on a logical reasoning task? Although most evolutionary social scientists would expect a variety of seemingly 'illogical' influences on the Wason selection task (Cosmides, 1989; Cosmides & Tooby, 1992; Cummins, 1996; Fiddick *et al*., 2000), the idea that performance can be manipulated by an aesthetic cue has, to my knowledge, never been explored.

Here I relied on Denise Cummins' Dominance Theory (Cummins, 1999; 2002; 2003) to examine whether subjects' violation detection faculties would be biased towards detecting violations of men paired to very unattractive partners and ignoring violations of men paired to highly attractive partners. Dominance Theory predicts that higher ranking individuals should be sensitive to violations of their subordinates, whereas lower ranking individuals should not be sensitive to violations of higher ranking group members. In her original paper Cummins (1999) manipulated these rank relationships by giving subjects a selection task narrative which explicitly told them whether they were higher ranking, lower ranking, equally high ranking, or equally low ranking in relation to the fictional character in the task. As predicted by Dominance Theory subjects in the higher ranking cell detected violations of the fictional character significantly more often compared to the other three cells. In the present study I used a narrative which explicitly informed subjects about their own rank, but I tried to manipulate the fictional character's rank by manipulating the attractiveness of his partner. The results showed that this manipulation was not successful, since subjects did not treat the attractiveness of the partner as a proxy for the male's rank (accepting of course, that Dominance Theory is valid[35]).

[35] Given that, in Cummins' words, 'No competing theory predicts differential reasoning performance as a function of perceived social rank', (Cummins, 1999, p.233).

5.4 General discussion

In general, high-ranking male primates enjoy greater mating and reproductive success (Cowlishaw and Dunbar, 1991; de Ruiter & van Hoof, 1993). This relationship between rank and social status on the one hand, and mating/reproductive success on the other, also holds for humans, and particularly those in pre-industrial societies (Betzig, 1982; Turke & Betzig, 1985; Barrett *et al*., 2002). Curiously, in contemporary Western societies the relationship between rank and reproductive success does not generally hold, although it is very likely that this lack of association is due to contraception and socially enforced monogamy, and does not reflect a lack of association between male rank and mating success (Pérusse, 1993; Mazur *et al*., 1994; Barrett *et al*., 2002).

In line with primate studies, evolutionary social scientists have generally focused on the relationship between male rank and quantitative indices of mating or reproductive success (e.g. lifetime number of sexual partners, children sired) rather than qualitative parameters like female attractiveness. There is, however, every reason to expect that there is a relationship between female attractiveness and male rank for both preindustrial and western societies. Older sociological studies suggest that in the United States men of higher socioeconomic status marry more attractive women (Elder, 1969; Taylor & Glenn, 1976; Udry, 1977; Udry & Eckland, 1984; reviewed in Townsend, 1998), while psychological studies find that dominant males are perceived as more sexy (Sadalla *et al*., 1987) and that status is highly valued by women in a prospective partner (reviewed in Buss, 1999). Given this empirical evidence and the dynamics of assortative

mating (Burley, 1983; Johnstone, 1997), it is a near certainty that throughout our evolutionary history men of higher rank tended to mate with more attractive females, and that this relationship still holds today in most if not all societies.

In this chapter I relied primarily on indirect methods (the dictator and ultimatum games and the selection task) to examine whether men are influenced by the attractiveness of a man's partner and adjust their behavior towards him accordingly. Although the results did not allow the rejection of the null hypothesis, I find it unlikely that men are impervious to such a conspicuous and potentially revealing cue. The same informational dynamics which render female partner attractiveness a very revealing cue with regard to mate choice for women should render it useful in the context of male-male contests and assessment (sections 2.4, 5.1). It is possible that, as with nonindependent mate choice, the experimental study of these influences is prone to problems of external validity and alternative experimental protocols need to be used (it was for this reason that I altered various aspects of the procedure in the second study[36]). It should, however, be noted that for both studies reported here the results were generally in the expected direction, suggesting that larger samples could, perhaps, yield significant results. Alternatively, non-experimental techniques can be used, in the form of questionnaire studies, observational studies etc.

[36] Like not presenting an image of the target male and using new dependent variables.

Chapter 6: Conclusion

In this final chapter I will first summarize the most important conclusions to emerge from this thesis. I have not devoted a separate section on directions for future research, since these are implicit in the points listed below[37]. I will then address an earlier published critique of some of the ideas that have been presented in this thesis.

6.1 Summary of important points

1. Mate choice copying is not a useful mating heuristic for monogamous or relatively monogamous species.

The existence of low male mating skew, female competition, paternal investment, unequal female mate value and an unclear relationship between male quality and number of mates, all suggest that monogamous species are unlikely to evolve mate choice copying. These problems were illustrated with reference to the zebra finch, the only monogamous non-human species for which some results consistent with copying have been obtained. I argued that these experimental studies have been conducted in a theoretical void, and are unlikely to lead to a successful research program.

[37] See also sections 1.5, 2.4 and 'Discussion' sections of chapters 3, 4, and 5.

2. Mate quality bias is a more probable form of nonindependent mate choice for monogamous or relatively monogamous species.

The transition from high to low male mating skew systems inevitably suggests a different kind of nonindependent mate choice. In mate quality bias, females adjust their evaluation of a given male in accordance to the quality of his mate. In the simplest, most unambiguous scenario each male is mated to a single female, and there is frequent turnover of mates. This process can be easily described algebraically and leads to testable predictions. Unlike copying, the acquisition of a mate is no longer necessarily an asset for a male; whether his probability of being chosen by focal females will increase or decrease is a function of variables like the quality of the male and the quality of his mate. Mate quality bias is considerably more difficult to evolve in comparison to copying, and a strong *a priori* case for its evolution should be made in advance of empirical tests. In species with more mixed mating systems (combining elements of monogamy and promiscuity/polygyny, like humans), elements of both processes might be found.

3. *In humans, the phenomenon is more difficult to study experimentally compared to other domains of evolutionary psychology, and is sensitive to subtle variations in the experimental procedure.*

A review of the human literature presents a very mixed picture, and I have had to impose order *ex-post* on an array of studies that were conducted with differing theoretical outlooks, methodologies and dependent variables, and with often

contradictory results. This is a fact that is often glossed over in the literature, but the lack of replication and inability to achieve consensus might be indicative of problems with external validity. As the results obtained here indicate, experimental subjects are indeed very sensitive to variations in methodology, and even slight modifications can lead to large changes in results. For example as described in chapter 3, using an experimental methodology with static facial images I found no influence of model female attractiveness on women's' ratings of target males, but using a methodology with videos I found a very large effect size of model female attractiveness, with R^2 >.4.

4. *For this, among other reasons, experimental approaches need to be supplemented with other methods. Questionnaire studies are a logical first step, and this thesis has shown that they are both feasible and promising.*

Given the problem outlined above in (3), non-experimental approaches are necessary in order to corroborate experimental results and open avenues for experimental studies. The most obvious way to go about this is to simply ask people questions. In other domains of mating research the questionnaire is the default first step (e.g. Buss, 1989, Buss *et al*., 1990; Haselton & Buss, 2001); for some reason researchers of human nonindependent mate choice have shown no interest in this approach. In chapter 4 I presented such a questionnaire study. The results provided clear evidence in support of a) nonindependent mate choice in humans being an empirical reality and b) women being more sensitive than men. This particular questionnaire developed here can be used as the basis for the construction of a validated scale. Future studies can also build on this first attempt by using more accurate measures of partner and self attractiveness

than participants' self-reports, like photographing the couple and having the photographs rated by a panel of impartial judges. Other that strengthening the correlation between partner attractiveness and the dependent variable(s), such a procedure would allow for the highlighting of more subtle real-life relationships between variables that weren't apparent here. Apart from, or in addition to, Likert-type items, it is also possible to include more objective data like prospective recording of matings, EPCs and other indicators of opposite-sex interest.

5. When it comes to the model female, it is necessary to distinguish between two types of cues. These are what can be called a) structural cues*, i.e. cues relating to relatively constant properties of the model female like attractiveness, age, height and stable personality dimensions and b)* interactive cues*, i.e. context-specific cues that arise from the interaction of the model female and her mate, and in particular from her behavior towards him.*

This is a distinction that is often not appreciated (see Dugatkin, 2000; Jones *et al*., 2007). The problem with interactive cues, as discussed in chapter 2, is that it can often be difficult to know whether focal females are utilizing them in the context of a dedicated mate choice mechanism or a more generic social-psychological process. For example if a woman is smiling at a man (Jones *et al*., 2007) or giving glowing public testimonies to third females about him (Dugatkin, 2000) and female raters consequently rate this target male as more desirable, is it necessary to invoke cognitive specializations dedicated to mate choice to account for this? Can more general social psychological explanations

like peer-pressure or social conformity (Asch, 1956) word-of-mouth (Buttle, 1998), social proof (Cialdini, 2001), or even common sense not account for these effects? This is not the case with structural cues like, say, model female attractiveness or assertiveness, which make a much stronger case for the operation of evolved mechanisms dedicated to mate choice.

That interactive cues can be very powerful was evident in the second study reported in chapter 3. There, using video recordings of model females I found that their attractiveness had an only slight larger impact on female raters than their - positive or not so positive - disposition towards the target male (see also Jones *et al*., 2007). The smaller impact of disposition in comparison to attractiveness was surely due to the fact that (owing to the study's design) all model females were more or less positively disposed toward the target male; allowing their attitudes to span the entire positive-negative spectrum would no doubt have led to disposition emerging as the most important predictor (at least in the context of that particular experimental design). That more advanced research will also reveal interaction effects between structural and interactive cues seems very likely. For example I find it unlikely that the disposition of highly attractive or highly unattractive model females would be as important a factor in influencing focal females as the disposition of moderately attractive or moderately unattractive model females.

6. The all-important structural cue, and quite possibly the only one, is model female attractiveness.

An earlier report (Vakirtzis & Roberts, 2010) had suggested that model female age might be a relevant cue, but this finding was *post-hoc* and the research presented here failed to replicate it. Indeed the results of the second study reported in chapter 3, whose primary aim was to uncover additional structural cues, not only failed to highlight a possible role for model female age (or any other structural cue), but suggested that attractiveness and interactive cues alone can account for most of the variance in female subjects' ratings.

7. Model females are relevant not only in nonindependent mate choice, but perhaps also in male-male competition.

The same informational dynamics which render a model female a revealing cue as to a target male's mate value render her revealing with regard to his rank in the male dominance hierarchy. I devoted a chapter of this thesis to this largely neglected area, conducting what are, to my knowledge, the first evolutionarily oriented studies of this kind. The results did not support the evolutionary hypothesis, and although the results were generally in the predicted directions, male participants did not significantly alter their perceptions of and behavior towards a target male as a function of the attractiveness of the target's partners. Studies similar to those conducted here but with larger sample sizes, or, alternatively, studies with differing methodologies (perhaps

even non-experimental) can be utilised. Future research in this area is certain to accelerate.

6.2 Reply to a critique

The theory of mate quality that I developed in this thesis was first communicated to the scientific community through a brief paper in the journal Behavioral Ecology in the summer of 2009 (Vakirtzis & Roberts, 2009). Shortly thereafter Klaudia Witte and Jean-Guy J. Godin published a critical two-page reply in the same journal (Witte & Godin, 2009), where they concluded that:

> "The notion of 'mate quality bias' […] adds nothing new to our understanding of nonindependent mate choice that is not already incorporated in the concept of mate choice copying. To the contrary, this proposed new term could potentially lead to more confusion than clarity in the research area of mate choice copying". (Witte & Godin, 2009, p.194)

To reach this conclusion Witte & Godin rely heavily on an older paper by Westneat et al. (2000), whose main message they summarize as '[…] the general view that mate choice copying best corresponds to an associative learning mechanism, wherein a focal (observer) female associates a cue from the model female with the accepted or rejected male involved. *Such an association to a male could occur regardless of the type of cue*

received by the observer female' (cited in Witte & Godin, 2009, p.193; my emphasis). Witte & Godin then go on to suggest that situations I would describe as mate quality bias can simply be described as the association between a male and the quality of the females that choose him. Now there are several problems with the statement quoted above, not least of which is that it is so general that it doesn't even constitute a working scientific hypothesis, as witnessed by the fact that not a single researcher, prior to Witte & Godin's commentary, had claimed to have used it as a research heuristic. Nor could anyone have possibly used it, since, just as it 'consistent' with mate quality bias, it is consistent with every other theory and empirical result imaginable (since anything can be associated with everything else there is nothing that can falsify this theory). Indeed, the notion that naturally occurring, complex functional behaviors could be reduced to a handful of behaviorist mechanisms of association is an old idea that has long been abandoned in mainstream psychology (see, e.g. Chomsky, 1959; Breland & Breland, 1961; Laurence & Margolis, 2001; Miller, 2003) even though Witte & Godin baselessly assert that, in the case of nonindependent mate choice at least, it is a 'generally accepted' fact (see White & Galef, 2000; Galef, 2008 for descriptions of copying as an adaptive specialization, i.e. the exact opposite of a generic association mechanism). Setting these broader problems aside, the associationist mechanism Witte & Godin propose makes staggering computational demands on the observing female and cannot possibly have evolved, not even as a remote theoretical possibility. The problem is that quality is not a readily perceptible cue, like, say, body size and courtship behavior. The observing female would have to divine, through repeated trial and error, which specific stimuli out of an infinite array of possibilities (size, wing colour, beak colour, fluctuating

asymmetry, song frequency, melody, dominance status, frequency of courting ritual, previous clutch size, egg mass, parasite load; the list is endless) contribute to female quality and how they weigh against each other in determining it. Because the possible association pairs are infinite, this cannot be done through association, and it certainly cannot be done in an animal's lifetime. Every association 'trial' would necessarily consist of the focal female observing a female, selecting the male that mated with her, and mating with that male, but, since there is no human experimenter nearby to provide immediate reinforcement, this reinforcement would have to come many years later, after the clutch has hatched, the offspring themselves have bore descendants and the female can get an even rough first estimate of fitness, assuming she has not died long before the first trial was even completed. She would then need to somehow go cognitively back in time and associate her recently calculated fitness with the specific female that her partner had mated with all that time ago, but she would still have no way of knowing which aspect of the female's phenotype or life history to associate fitness with. The only way mate quality bias (or mate choice copying for that matter) could ever evolve is if selection ran its own trials through geological time, in the process arbitrarily (i.e. in a manner not logically warranted by a generic process of association) biasing females' sensory and cognitive systems towards the adaptive outcome, so that they did not have to undergo this protracted and impossible process of generic associations or 'social learning' (see Tooby & Cosmides, 1992). In my original paper (Vakirtzis & Roberts, 2009) I described a circumscribed set of biological contexts which could, in principle, lead to such selection for mate quality bias. There is, therefore, nothing that involves

associative learning in mate quality bias, nor can a process of association lead to anything resembling the empirical predictions I derive.

In support of their assertion that mate quality bias is nothing new, Witte and Godin then discuss three older studies in guppies (Dugatkin & Godin, 1993; Amlacher & Dugatkin, 2005; Vukomanovic & Rodd, 2007; discussed in section 1.2.2 above). Dugatkin and Godin (1993) found that while smaller female guppies copied the choices of larger females, the latter did not copy the choices of the former. The experimenters here used size as a proxy for females' age and sexual experience (Dugatkin & Godin, 1993, pp. 290-291). In Witte's own words, 'In [Dugatkin & Godin's] study, only small and possibly young females, which might be inexperienced in mate choice, copied the choice of large model females, which were older and presumably more experienced in mate choice. This shows that copying is an optional mate-choice strategy which females use only in specific situations' (Witte & Ryan, 1998, p.538). In other words this is facultative, or context-dependent mate choice copying, equivalent to the cognitive algorithm 'copy older females when you are young, but do not copy younger females when you are old' (and indeed, this is how this result has been universally interpreted, see Dugatkin, 1996; Nordell & Valone, 1998; Ophir & Galef, 2004; White, 2004). The two subsequent studies only improved our understanding of how this facultative adaptation functions. Amlacher and Dugatkin (2005) found that small females only copy large, not small females, while Vukomanovic & Rodd's (2007) study used various combinations of possible copying pairs that largely replicated the results of the previous two studies, so that we now know that the algorithm can be described as 'copy the choices of large, not small females' or

even more simply ‘always reject small females as model females’ (see Vukomanovic & Rodd, 2007). This sort of facultative mate choice copying is unrelated to mate quality bias as I have described it in this thesis. The only reason I can find for Witte and Godin citing these studies is the view that simply because some older studies had paid attention to female quality (or size), mate quality bias is nothing new.

I will end by answering the two questions posed by Witte and Godin in their critique:

> We question whether the proposed new term ‘‘mate quality bias’’ actually describes a new mechanism of nonindependent mate choice that is fundamentally different from that of mate choice copying. In other words, does this new term offer a new understanding of the mechanism(s) of nonindependent mate choice in females in general? (Witte & Godin, 2009, p.193).

The first question asks if mate quality bias is fundamentally different to mate choice copying. The answer to this depends on how one interprets ‘fundamentally’. Is ‘nonindependent mate choice’ *fundamentally* different to ‘mate choice’? Is ‘mate choice copying’ *fundamentally* different to ‘nonindependent mate choice’? This could be anyone’s personal opinion. That there are similarities between mate choice copying and mate quality bias is undeniable; they are, after all, both instances of nonindependent

mate choice, and as I have made clear above there will exist in nature many cases where they overlap within a single species. That Witte and Godin are hesitant to admit a new term to the field is understandable, but parsimony in terminology should only be valued to the extent that it promotes empirical progress.

Which leads to the next question posed by Witte and Godin, namely whether mate quality bias offers a new understanding of nonindependent mate choice in females in general. To this I can answer affirmatively. As I have discussed at length in chapter 2, mate choice copying is unsuitable or at best inadequate to describe nonindependent mate choice processes in monogamous species, and the dearth of relevant empirical studies on these species highlights how urgently a new theoretical framework is needed. The theory presented here offers just that, together with the prospects for a potentially fruitful research program in monogamous species. And it is precisely this, namely the extent to which it can afford empirical successes, that will eventually determine the fate of mate quality bias (semantic arguments over whether or not a new term is justified interest few researchers). In the place of mate quality bias and the research program it suggests Witte and Godin offer only unfalsifiable generalities and ex-post reappraisal of some older studies.

In conclusion, I have proposed a falsifiable theory that makes a number of testable predictions. The theory a) is different from mate choice copying, both in its definition as well as its biological context and the predictions is derives b) follows from basic

biological reasoning (Trivers, 1972) which has proved remarkably successful in other lines of mating research, c) is not only consistent with human studies in a way in which copying is not, but illuminates previously unnoticed patterns in the already existing data, d) provides an empirical heuristic which can guide research among a wide range of monogamous species while e) avoiding the pitfalls that the application of copying in these species is bound to hold. Far from leading to 'confusion', as Witte & Godin suggest, the theory has the potential to unlock research into nonindependent mate choice in a wide range of species, research which is currently being deadened by the monolithic application of mate choice copying.

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Appendix A. Questionnaires and scales

Ten-Item Personality Inventory (Gosling et al, 2003).

I see myself as:

1. Extraverted, enthusiastic

2. Critical, quarrelsome

3. Dependable, self-disciplined

4. Anxious, easily upset

5. Open to new experiences, complex

6. Reserved, quiet

7. Sympathetic, warm

8. Disorganized, careless

9. Calm, emotionally stable

10. Conventional, uncreative

Scoring ("R" denotes reverse-scored items): Extraversion: 1,6R; Agreeableness:2R, 7; Conscientiousness:3,8R; Emotional Stability:4R, 9; Openness to Experience: 5, 10R.

Rosenberg Self-Esteem Scale (Rosenberg, 1965).

1. On the whole, I am satisfied with myself.

2.* At times, I think I am no good at all.

3. I feel that I have a number of good qualities.

4. I am able to do things as well as most other people.

5.* I feel I don not have much to be proud of.

6.* I certainly feel useless at time.

7. I feel that I'm a person of worth, at least on an equal plane with others.

8.* I wish I could have more respect for myself.

9.* All in all, I am inclined to feel that I am a failure.

10. I take a positive attitude toward myself.

**Reverse scored.*

Shyness and Sociability Scale (Cheek & Buss, 1981).

Shyness:

-I am socially somewhat awkward.

-I don't find it hard to talk to strangers (*reverse-scored item*).

-I feel tense when I'm with people I don't know well.

-When conversing I worry about saying something dumb.

-I feel nervous when speaking to someone in authority.

-I am often uncomfortable at parties and other social functions.

-I feel inhibited in social situations.

-I have trouble looking someone right in the eye.

-I am more shy with members of the opposite sex.

Sociability:

-I like to be with people.

-I welcome the opportunity to mix socially with people.

-I prefer working with others rather than alone.

-I find people more stimulating than anything else.

-I'd be unhappy if I were prevented from making many social contacts.

-***Rathus Assertiveness Schedule***

1. Most people seem to be more aggressive and assertive than I am.*

2. I have hesitated to make or accept dates because of shyness.*

3. When the food served at a restaurant is not done to my satisfaction, I complain about it to the waiter or waitress.

4. I am careful to avoid hurting other people's feelings, even when I feel that I have been injured.*

5. If a salesperson has gone to considerable trouble to show me merchandise that is not quite suitable, I have a difficult time saying "No".*

6. When I am asked to do something, I insist upon knowing why.

7. There are times when I look for a good, vigorous argument.

8. I strive to get ahead as well as most people in my position.

9. To be honest, people often take advantage of me.*

10. I enjoy starting conversations with new acquaintances and strangers.

11. I often don't know what to say to people I find attractive.*

12. I will hesitate to make phone calls to business establishments and institutions.*

13. I would rather apply for a job or for admission to a college by writing letters than by going through with personal interviews.*

14. I find it embarrassing to return merchandise.*

15. If a close and respected relative were annoying me, I would smother my feelings rather than express my annoyance. *

16. I have avoided asking questions for fear of sounding stupid. *

17. During an argument, I am sometimes afraid that I will get so upset that I will shake all over.*

18. If a famed and respected lecturer makes a comment which I think is incorrect, I will have the audience hear my point of view as well.

19. I avoid arguing over prices with clerks and sales-people.*

20. When I have done something important or worthwhile, I manage to let others know about it.

21. I am open and frank about my feelings.

22. If someone has been spreading false and bad stories about me, I see him or her as soon as possible and "have a talk" about it.

23. I often have a hard time saying "No".*

24. I tend to bottle up my emotions rather than make a scene.*

25. I complain about poor service in a restaurant and elsewhere.

26. When I am given a compliment, I sometimes just don't know what to say.*

27. If a couple near me in a theater or at a lecture were conversing rather loudly, I would ask them to be quiet or to take their conversation elsewhere.

28. Anyone attempting to push ahead of me in a line is in for a good battle.

29. I am quick to express an opinion.

30. There are times when I just can't say anything.*

**Reverse scored.*

Social Intelligence Scale (Silvera et al., 2001).

Social Information Processing subscale

1. I can predict other peoples' behavior.

2. I know how my actions will make others feel.

3.I understand other peoples' feelings.

4. I understand others' wishes.

5. I can often understand what others are trying to accomplish without the need for them to say anything.

6.I can predict how others will react to my behavior.

7. I can often understand what others really mean through their expression, body language etc.

Social Skills subscale

1. I often feel uncertain around new people who I don't know.*

2. I fit in easily in social situations.

3. I am good at entering new situations and meeting people for the first time.

4. I have a hard time getting along with other people.*

5. It takes a long time for me to get to know others well.*

6. I am good at getting on good terms with new people.

7. I frequently have problems finding good conversation topics.*

**Reverse-scored*

Appendix B. Narratives used for dictator and ultimatum games.

Dictator game.

Suppose that there is an economist in your university who is interested in studying the economic behaviour of students. He randomly selects you and Steven as participants in an economic game. The game is as follows: initially the economist gives you £10, and gives Steven nothing. The economist then tells you that you can give Steven a portion of the £10. You can give Steven any amount you want or nothing at all. For example, if you give Steven £6 then you will be left with £4 for yourself. Or, to take another example, if you give him £1.5 you will be left with £8.5 for yourself. Or then again if you give him nothing, you will be left with £10 for yourself. Steven has no say in this game, and must accept whatever amount you give him. Once you have given him the money the game is over and the economist dismisses you and Steven. How much money would you give Steven? Using the mouse cursor, drag the slider below to choose the amount. Remember that you can choose absolutely any amount you want.

Ultimatum game.

Now imagine that the same economist randomly recruits you and Steven as participants for a different kind of game. As in the previous game, the economist initially gives you £10, and gives Steven nothing. You must now offer Steven a portion of the £10, and you can offer him any amount you want, keeping the rest for yourself. Unlike the previous game, however, Steven now has the power to reject your offer

if he doesn’t like it. If Steven rejects your offer, the economist will take back the £10, leaving both you and Steven with nothing. If, on the other hand, Steven accepts your offer, you will give Steven the money you offered him and keep the rest for yourself. How much money would you offer Steven? Use the slider below to choose the amount.

Appendix C. Material for the Wason selection task

Underlined text: High-rank treatment; Italicized text: Low-rank treatment

Imagine you are a senior [*new*] member of your university hiking club, where Steven is also a member. The club organises weekend hiking trips to various locations around the country such as the Lake District, Snowdonia, the Yorkshire Dales, and the Peak District. You are one of the most popular members of the club, your opinion is greatly respected among everyone and members turn to you for advice [*Since you have just joined the club you don't know any people, and no one seems to pay attention to you*].

For every trip a different member is assigned to organise the trip. This member must set up transportation arrangements, collect registration fees etc. The hiking club also takes health and safety very seriously. One of the most important rules in the club has to do with the person who is responsible for bringing a first aid kit to the hike. The rule is that **IF A MEMBER IS ASSIGNED TO ORGANISE THE TRIP, HE MUST BRING A FIRST AID KIT. (**Sometimes members will bring first aid kits even though they have not been assigned to organize that particular trip. Though this is not compulsory it is perfectly acceptable, and can result in more than one first aid kit being brought to a trip).

To make sure everything is in order, records are kept of each week's trip. This is done by writing information on cards every time a trip is made. **The front side of the cards indicates whether or not a particular member was assigned to organise the trip, and the back side indicates whether or not the member brought a first aid kit.**

Below are four records for Steven, each one from a different hiking trip. Two of the cards are shown front-side up and the other two are shown back-side up. **Your job is to make sure Steven has been following the rule. Look at each card and decide which one(s) needs to be turned over to make sure Steven is following the rule. Place a tick below your choice(s).**

Remember the rule: **IF A MEMBER IS ASSIGNED TO ORGANISE THE TRIP, HE MUST BRING A FIRST AID KIT**

Steven was assigned to organise the trip	Steven was NOT assigned to organise the trip	Steven brought a first aid kit	Steven did NOT bring a first aid kit