It Takes Two:

Sexual Strategies and Game Theory

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Abstract

David Buss's Sexual Strategies Theory is one of the major evolutionary psychological research programmes, but, as I try to show in this paper, its theoretical and empirical foundations cannot yet be seen to be fully compelling. This lack of cogency comes about due to Buss's failure to attend to the interactive nature of his subject matter, which leads him to overlook two classic and well-known issues of game theoretic and evolutionary biological analysis. Firstly, Buss pays insufficient attention to the fact that, since mate choice is a cooperative decision, what is adaptive for the two sexes individually is irrelevant to the evolutionary explanation of our sexual strategies; instead, all that matters is what is adaptive given the choices made by the other sex. Secondly, Buss does not pay enough attention to the difference between polymorphic and monomorphic evolutionarily stable states in his attempt to empirically confirm his theory. Because of this, the data he presents and analyses are unable to show that natural selection is the most important element in the explanation of the origins of our sexual strategies. In this way, I try to make clear that, at least as things stand now, Buss has failed to provide compelling grounds for thinking that Sexual Strategies Theory can make a major contribution to human psychology.

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I. Introduction

David Buss's Sexual Strategies Theory (SST) is one of the major evolutionary psychological research programmes and has been very influential in the study of the human mind (see e.g. Buss, 1989, 1998, 2003, 2007b; Buss and Schmitt, 1993). This success, however, has not prevented it from also being very controversial: in particular, critics have questioned the interpretation and robustness of Buss's empirical studies, and the theoretical and ideological presuppositions behind them (see e.g. Buller, 2005; Dupre, 2001; for some replies, see e.g. Buss and Haselton, 2005; Machery and Barrett, 2006; Delton et al., 2006; Carruthers, 2002).

Interestingly, though, there are two aspects of the theory that have received only very little attention to date, and that despite the fact that they relate to issues that, in their general form, have long been known about. These aspects are, firstly, the sex-specific methodology of the theory, and secondly, its conflation of the distinction between monomorphic and polymorphic evolutionarily stable states. However, as I seek to show in this paper, the lack of attention to these two issues is problematic, since there are good reasons for thinking that they make SST – at least as it is currently articulated – theoretically and empirically flawed.

More concretely, I argue that, firstly, without analysing mate choice as a *game*, no insights about what sexual strategies are likely to have evolved can be obtained. *Only* by taking the strategies of both sexes into account *at the same time* can evolutionary considerations be brought to bear on mate choice. While often acknowledged in passing, this point is still not sufficiently assimilated into the theory – and that despite the fact that a version of it had already been articulated by Dawkins (1976). Secondly, I try to show that, even if Buss did provide the relevant game theoretic analysis, SST would not yet be shown to have explained the origins of our sexual strategies. The reason for this is that the data Buss presents and analyses fail to clearly distinguish between evolutionarily stable states involving a monomorphism of complex strategies and those involving a polymorphism – a distinction that, as has been made clear by Orzack and Sober (1994), Thomas (1984), and Bergstrom and Godfrey-Smith (1998), needs to be respected for a trait to be corroborated as an adaptation.

Before laying out this criticism in more detail, though, it is useful to be more explicit about what, exactly, its scope is. As it turns out, this scope is at the same time quite restricted and quite wide-ranging. It is *restricted*, in that the focus of the criticism presented here is strictly on *Buss's version of SST*. This is important, as his is not the only evolutionary approach to the study of how we make mating decisions (for alternatives, see e.g. Gangstead & Simpson, 2000; Li & Kendrick, 2006). Since these other theories are quite different in structure from that of Buss, one must not assume that the worries raised here *automatically* affect them also. On the other hand, the scope of the present discussion is also quite *wide-ranging*, in that the issues raised here apply, at least in principle, to *any* evolutionary psychological theory that is concerned with matters of social interaction. This is important, as it may entail that other parts of evolutionary psychology, too, would profit from closer attention to their game theoretic presuppositions. While spelling this out in more detail calls for a paper of its own, it is enough for present purposes to note that the discussion here has at least great *potential* relevance for many other parts of evolutionary psychology as well.

This paper is structured as follows. In section II, I set out the key aspects of Buss's theory. In section III, I show why introducing game theory explicitly into the framework of the theory is necessary to make it theoretically compelling. In section IV, I show why a closer attention to the monomorphism / polymorphism distinction is necessary to make it empirically compelling. I summarise the argument in section V.

II. Sexual Strategies Theory

Mate choice is a hugely important event for all sexually reproducing organisms: as one of the key factors determining their reproductive success, it contributes directly to their biological fitness (see e.g. Sober, 1993). According to evolutionary psychologists, events of this kind – i.e. types of behaviours having a major adaptive importance – tend to lead to the evolution of psychological mechanisms that help the organism to shape them to its advantage (see also Cosmides and Tooby, 1992).

In the present case, therefore, evolutionary psychologists contend that human beings (who are sexually reproducing) have evolved psychological mechanisms that aid in making successful mating decisions (see e.g. Buss, 1992, 2007a). Further, they argue that, since human beings spent most of the period that is evolutionarily significant for them – the Pleistocene – as hunter-gatherers, we should expect these mechanisms to be adapted to the conditions prevalent during that time (which thus becomes their 'environment of evolutionary adaptedness' or EEA: see e.g. Cosmides and Tooby, 1992).

On this basis, David Buss develops his theory of the evolution of sexual strategies.[1] Specifically, he reasons that, since the adaptive problems of males and females in the EEA were importantly different, we should expect that the two sexes have evolved *different* strategies for finding a mate (see e.g. Buss, 1989, 1992). Moreover, and again because of differences in the adaptive problems to be solved, he argues that we should expect them to have evolved different strategies for *long-term mating* (marriage, joint child rearing) and *short-term mating* (brief sexual encounters) (see Buss and Schmitt, 1993). This last distinction is quite important, but I shall postpone discussion of it until the second part of section III; for now, I concentrate just on *short-term* strategies.[2]

To explain why the adaptive problems of mate choice were different for males and females, Buss falls back onto Trivers's theory of 'minimal parental investment' (see e.g. Trivers, 1972; see also Buss and Schmitt, 1993, pp. 206-207; Buss, 1992, pp. 249-252). This theory estimates the amount of parental expenditure of resources (time, energy, food, etc.) that is just sufficient to raise viable offspring and derives from it predictions about evolved behavioural dispositions. Importantly, these predictions tend to differ for the different sexes. For example, Trivers predicts that the sex for which minimal parental investment is higher will be more circumspect in picking a mate, since it has more to lose when making a sub-optimal choice. This prediction has been empirically confirmed for many species (see also Trivers, 1985; Buss, 1992, p. 251; but see also Kitcher, 1985, pp. 168-172).

Buss applies this theory to human mate choice as follows. Firstly, he argues that, for short-term mating, males should be expected not to be very "choosy" in deciding on a partner to mate with (see e.g. Buss and Schmitt, 1993, pp. 210-214). In terms of minimal parental investment, reproduction for them is "cheap": they can increase their expected reproductive success by increasing the number of copulations, since that in turn increases their probability of having more viable offspring. Thus, Buss concludes that, when it comes to short-term sexual strategies, males should favour a largely *promiscuous* lifestyle (see e.g. Buss and Schmitt, 1993; Buss, 1989).[3] It is useful to note that this contrasts with their approach to long-term mating, which is based on *commitment* to their mate (see Buss and Schmitt, 1993, pp. 214-215).

Secondly, he argues that females – due to their facing much higher costs of reproduction (e.g. from metabolic changes and lost reproductive opportunities during pregnancy and lactation) – should in the short term be mostly interested in assessing the potential of their mates to turn into long-term partners (see Buss and Schmitt, 1993, pp. 218-219).[4] In particular, Buss predicts that females evaluate this potential by determining their mate's *ability* and *willingness* to spend resources on them and their offspring (see Buss, 1992; Ellis, 1992). Here, only the latter is of interest; for more on the former, see Ellis (1992).

Further, Buss argues that female assessments of a male's *willingness* to spend resources on his mate are likely to be based fundamentally on signs of *promiscuity* of the male in question (see e.g. Buss and Schmitt, 1993, pp. 221-222; Buss, 1992, p. 252). This is the case, as male promiscuity functions as an (involuntary) signal of a disposition to avoid committing to – and thereby spending resources on – any *one* female. Thus, Buss predicts that, as far as short-term mating is concerned, females seek to establish whether the male is promiscuous: their goal is to *estimate* the "mate-value" of their current partner in a way that requires no commitment on their part.

Using various studies – including large-scale, cross-cultural ones – Buss claims to have corroborated the existence of these strategies in present-day males and females (see especially Buss, 1989; Buss and Schmitt, 1993): in the short term, males, on average, seem to prefer a more promiscuous lifestyle than females, and females, on average, seem to be more concerned about the promiscuity of their short-term partners than males are. Importantly, Buss also takes these studies to support the above argument about the origins of these sexual strategies (see e.g. Buss and Schmitt, 1993; Buss, 1998) – a point to which I return below.

Most of the criticism of SST has been directed at this last, empirical step. Doubts have been raised about the interpretation of Buss's findings: in particular, it has been questioned to what extent they *in fact* corroborate his hypotheses about what our sexual strategies are (see e.g. Buller, 2005; for responses, see e.g. Buss and Haselton, 2005; Machery and Barrett, 2006; Delton et al., 2006). Here, though, I want to sidestep this kind of debate to concentrate on two prior issues: firstly, whether we should agree with Buss that his theory makes the predictions he claims it makes, and secondly, whether the data he provides could even *in principle* confirm these predictions. As the next two sections aim to make clear, there are reasons to doubt both of these claims.

III. Game Theory and Sexual Strategies Theory

When Buss's theory is discussed (both by defenders and detractors of it), it is frequently remarked that deriving sex-specific sexual strategies from claims about minimal parental investment alone is overly hasty. Since mating is a cooperative venture, both sexes need to be taken into account *simultaneously* when reasoning about the evolution of their sexual strategies (see for example Buss and Schmitt, 1993, pp. 227-228; Buss, 1992, pp. 256, 262-263; Fernald, 1992, p. 396; Buller, 2005, p. 212). In fact, a version of this point had already been made in the context of discussions of Trivers' theory of minimal parental investment, long before SST was conceived (see e.g. Dawkins, 1976, chap. 9; Maynard-Smith, 1982; Kitcher, 1985, pp. 168-172).[5]

However, despite this surface-level attention to the interactive nature of the subject matter, this fact has not been sufficiently incorporated into the theory as yet. The above remarks concerning SST all remain completely undeveloped, and the vast majority of research surrounding Buss's theory still considers the two sexes independently from one another (see e.g. Buss, 1998, 2007b).[6]

This lack of attention to the interactive nature of SST's subject matter, though, is very detrimental to the theory's plausibility: as this section aims to show, on their own, differences in minimal parental investment (or in any other sex-specific costs and benefits) cannot tell one *anything* about what sexual strategies the sexes have evolved. Only by developing in detail the implications of the entire game the two sexes were involved in can one even begin to derive and test hypotheses about the evolution of these strategies.

I develop this criticism in two parts. In the first half of this section, I lay out the main issues without paying attention to the distinction between long- and short-term strategies; in the second half, I re-introduce this distinction to see if it alters any of the conclusions reached in the previous part.

1. Interactive Sexual Strategies: The Need for Game Theoretic Analysis

Begin by noting that, since it takes two to mate, what turns out to be evolutionarily advantageous depends not just on the strategies of one individual, but also on those of his or her partner. In general, in situations of (strategic) interaction, what is of importance – from an evolutionary point of view – is which strategy is most advantageous, *given* the strategy chosen by the partner, not what strategy is *individually* most advantageous. To make this more vivid, it is useful to briefly consider the basic logic of a specific evolutionary game.[7]

Assume there are two types of individuals, each of which has two strategies available to her: player 1 can play *up* or *down*, player 2 *left* or *right*. Assume further that the payout matrix is as follows (the numbers refer to the fitness of the different players, given the strategy-combination in question):

[Figure 1: Payout Matrix for an Evolutionary Game]

Given this setup, it would clearly be fallacious to conclude that it is strategy *up* that *must* be being selected for on the part of player 1: it is true that those individuals of the player 1-type who play *up* whenever those of player 2-type play *left* are evolutionarily more successful than those who play *down*, so that in this case, playing *up* would be the strategy that is being selected. However, what matters on the whole is whether it will in fact be the case that player 2 plays *left*. If this is not the case, then playing *up* might *not* be the most advantageous strategy for player 1: in the present case, it would result in player 1 having a payoff of 0 (not 3). This shows that, in order to determine which strategy on the part of player 1 gets selected, one needs to determine which strategy on the part of player 2 gets selected – and vice versa.

In turn, in order to do this, one could appeal either to the game's *Nash Equilibria* (see e.g. von Neumann & Morgenstern, 1944) or to its *Evolutionarily Stable Strategies* (or ESS – see e.g. Maynard-Smith and Price, 1973; Maynard-Smith, 1982).[8] These two differ, in that an ESS is either a member of a *strict Nash Equilibrium* (a set of strategies, unilateral deviations of which would result in strictly *worse* outcomes for the players), or a member of a *weak Nash Equilibrium* (a set of strategies, unilateral deviations of which would result in *worse or equally good* outcomes for the players) and such that it does better against all non-equilibrium strategies than the alternatives do (see also Taylor, 1979).[9]

Now, for present purposes, it seems clear that it is appealing to the game's Nash Equilibria that is most appropriate. This is so for two reasons. Firstly, it has been shown that, in most cases, the set of ESS is coextensive with the set of Nash Equilibrium strategies (see e.g. van Damme, 1987; Weibull, 1995). Accordingly, the results of the analysis to follow are unlikely to fundamentally differ if ESS are used instead of Nash Equilibria.[10] Secondly, from conceptual point of view, appealing to Nash Equilibria is more in line with the goals of the present inquiry: we are interested in evaluating interactions among rational individuals (i.e. human males and females), who choose their strategies by explicitly taking into account the fact that they are playing a game, and who are aware of the fact that the opposing player is equally engaged in choosing the appropriate action.[11] This is exactly what Nash Equilibria are meant to capture. By contrast, ESS solutions concern *population games* – situations where two populations of organisms interact with each other, but whose members are not necessarily aware of the fact that they are playing game at all. For this reason, appealing to the latter seems less conducive to the circumstances at hand than appealing to Nash Equilibria (see also Weibull, 1995).

Given this, one can solve the game in figure 1 by noticing that that it has two (strict) Nash equilibria in pure strategies: *up* / *left* and *down / right*. Now, for present purposes, what is most important about this is that it makes obvious the fact that, even though player 1 can only achieve the highest logically possible payoff by playing *up*, it might in fact be *down* that gets selected (as this strategy, too, is part of a Nash Equilibrium). In other words, what is fitness maximising in absolute terms might not be what is in fact selected: the outcome of the game and the strategies that yield the highest logically possible amount of fitness need not coincide.

Noting this point is crucial here, as it illustrates a set of issues that directly impact the theoretical plausibility of SST. To see this, consider the evolution of a *promiscuity* strategy.

Assume (following Buss) that males do best – in absolute terms – by pursuing such a strategy. Assume also (again following Buss) that females do best by *caring* about (i.e. determining) whether males are pursuing such a strategy. Even if all this is the case, it is still possible that the game that the two sexes are playing is exactly the game laid out above:

[Figure 2: Payout Matrix for an Evolutionary Game Consistent with Buss's Reasoning]

This possibility increases in likelihood when it is noticed that the logic of the payoffs can be cogently justified within Buss's theory. One way of doing so is as follows (moving counter-clockwise from the top left hand corner of the matrix).

Firstly, in the world where females do not care about what males do, males do very well by following a promiscuous strategy: this lets them maximise the number of copulations without incurring many costs. This seems to follow directly from Buss's argument that reproduction for males is cheap, and that they therefore do best by having a large number of children. However, females do quite badly in this case, as they get no help in bringing up their children and have to pay the cost of the pregnancy. On the other hand, if males are *committed* (and females remain indifferent), their fitness is only mediocre, since they then waste reproductive resources on one set of offspring, instead of fathering many further children. Females do slightly better in this case than they did before, though, as they get help in bringing up their children; however, since they do not expect this help, they cannot derive great profit from this.

Secondly, when switching to the world where females *care* about the promiscuity of their partners, if males remain *committed*, there is a Pareto improvement relative to *Commitment* / *Don't Care*. As Buss makes clear, the combination of *commitment* and *care* allows for beneficial 'mutual cooperation' among the sexes: by *consciously* engaging in joint child-rearing, the partners can divide the necessary labour, and thus accomplish it more efficiently (see e.g. Buss and Schmitt, 1993, p. 215). Finally, the case in which females *care* and males are *promiscuous* is the worst one for both males and females, since their chances of successfully reproducing are extremely slim: most females will be unwilling to mate with any male at all. In many ways, therefore, this can be seen to be the baseline level of fitness – the state in which no reproduction happens.

What makes this game crucial is that it points to the possibility that Buss is correct in his Trivers-inspired reasoning that males do best by being promiscuous *and* that he is correct in his reasoning that females do best by desiring partners who are *not* promiscuous. However, if the game the two sexes were playing in the EEA is like the one just described, Buss might still be wrong about the fact that male promiscuity is an adaptation: it is entirely possible that the strategies that were selected are *commitment* and *care* (since they, too, are a Nash Equilibrium). This means that, on the whole, even when accepting the basic tenets of SST, we should not necessarily expect males to have evolved a desire for mating with many different females after all. Crucially, this is a consequence not of any flaw in Buss's reasoning about the *individual* strategies, but of the fact that he did not consider the *entire game*.[12]

Of course, in cases like this, where there are multiple Nash Equilibria, even considering the game in its entirety cannot determine which of its equilibria will, in fact, come about. However, what matters for present purposes is just that it is only via game theoretic analysis that we can see that there is even an issue to be addressed here. In particular, it is only by noting that something like figure 2 is an accurate representation of the reasoning underlying SST that it becomes clear that this theory, by itself, cannot say anything about whether male promiscuity is an adaptation. That is, it is only through considering the situation from a game theoretic viewpoint that we come to realise that we can just as reasonably expect males to be *committed* than to be *promiscuous* – and that SST on its own does not make any predictions about this.[13]

Given this, Buss has two options in order to place his theory on a solid theoretical foundation. On the one hand, he could show that the game that was played in the EEA had only one Nash Equilibrium, and that this equilibrium involved male *promiscuity* – in other words, he could provide grounds for thinking that figure 2 is (contrary to appearances) *not* a good representation of the situation in the EEA. On the other hand, he could accept that the game that was played in the EEA had multiple Nash Equilibria (as in figure 2), but also claim that there are reasons to think that the equilibrium involving male promiscuity is the one that actually came about.[14] The trouble with either of these options is that, so far at least, Buss has done nothing to support them – in fact, as noted above, it is not even clear that he is aware of this being something that needs to be done. Hence, it must be concluded that SST, as it has been developed up to now, is theoretically flawed.

At this point, Buss might object that this is too simplistic a picture of scientific enquiry: one should not think that there is a neat and tidy division between theory construction and data collection. In fact, he might suggest, it is more realistic to see science as involving a complex interplay of theory construction, empirical investigation, and theoretical revision. Given this, he might point to the data he has collected to corroborate SST and claim that he is endorsing *whatever game and whatever equilibrium* is consistent with these data. That is, Buss might argue that his *data* can be used to make clear which game was played in the EEA and which equilibrium came about, and that this is all the game theoretic analysis that is needed.[15]

However, this response to the above argument is inadequate. While it is true that there is no *precise* division between theory and data, this does not mean that there is no such division at all. In fact, if Buss were to follow this idea of using the data meant for *confirming* his theory to *theoretically ground* it as well, he would be begging the question: he would build the evidence for SST into the theory itself, and thus would make it impossible for the theory to be false (for more on this issue, see also Sober, 2008, chap. 2). What is needed instead is an *independent* justification for the assumptions that go into the game theoretic analysis at the base of SST. That is, Buss needs to provide evidence *other than* the currently obtaining state of affairs for it being the case that the best game theoretic model of the EEA involves male promiscuity in one of its equilibria, and that it is this equilibrium that actually came about. Short of that, SST can be said to be the correct account of our mating psychology merely by *fiat*, and not by means of its explanatory power.

Two further remarks are worth making concerning this criticism. Firstly, the above analysis does not depend on the fact that I have assumed that it is *common knowledge* which strategy males and females are playing. Allowing for uncertainty greatly increases the complexity of the model, but does not entail that this model must come out in Buss's favour. In particular, explicit modelling of the two sexes' beliefs, as well as the ways they signal them, does nothing to address the fact that, for all that Buss has said, it may still be the case that male *commitment* is an adaptive strategy (in the appendix, I show this more formally).

Secondly, it needs to be noted that this issue is separate from that of whether the payoffs of different strategies for males depend on what other *males* are playing (see e.g. the well-discussed case of 'cad / dad' conditional strategies: Gangstead and Simpson, 2000). The last is probably true, but does not impinge on the present analysis; the issue here is just that in order to determine which sexual strategy is most successful, it is necessary to not only consider *one* sex's perspective, but that of *both*. In situations of strategic interaction, *only strategy pairs* evolve.

In a nutshell: what is needed to improve Buss's theory is the explicit construction of payoff-matrices that are consistent with his reasoning about the situation in the EEA, and which are then analysed game-theoretically and evaluated for their fit to known empirical facts about our evolutionary history. *Only* in this way can the evolution of sexual strategies of both sexes be systematically and convincingly studied. Moreover, it is only in this way that important questions in the background of the theory can even be *asked* – for example: how many stable states are there of the game in the EEA? Which of these stable states represent Pareto-optimal outcomes? What further features of the game are noteworthy – are there dominant strategies, mixed-strategy equilibria, etc.? Providing an analysis that answers these questions might not be easy, but it cannot simply be ignored.

2. Long-Term and Short-Term Strategies: No Substitute for Game Theory

It is now useful to consider a rejoinder that Buss could – and seemingly does – put forward to mitigate the impact of this criticism. While this rejoinder fails to be convincing, considering it is still useful, as it, on the one hand, shows that the above criticism hits the heart of Buss's theory, and on the other, brings out clearly the implications of that criticism for the further development of SST.

This rejoinder returns to Buss's distinction between long- and short-term strategies; it claims that one of the most important reasons for the existence of this distinction – i.e. for why males adopt a long-term perspective in the first place – is that females do not *let* males pursue only short-term strategies (see e.g. Buss and Schmitt, 1993, pp. 214-215; Buss, 2007a, 2007b). That is, males adopt *both* long-term (i.e. commitment) and short-term (i.e. promiscuity) strategies since playing just the latter is incompatible with the strategies of the females. In this way, Buss can claim that he *has* taken both sexes into account at the same time, and that the above game theoretic criticism misses its target.

Now, quite obviously, in order for this to be at all plausible as a rejoinder to the above criticism, it must be expressible as a claim about the structure of some game. On the face of it, three possible suggestions about how this could be done come to mind. Consider them in turn.

The first and most obvious suggestion is to construe it as involving *two* games – one for the short-term, and one for the long-term – with various game-exogenous factors (e.g. intra-sexual competition) determining *which* game is being played. This suggestion fits very well to the way Buss discusses this situation, and also makes some intuitive sense: the situations in which males and females interact with a view to short-term and with a view to long-term matings might be quite different and fairly independent from each other.

However, this suggestion is a complete non-starter in the present context: the appeal to long-term games simply *cannot* mitigate the criticism raised above. The reason for this is that the *existence* of a second game cannot be used to explain the *outcome* of a first game: the above worry concerned the fact that Buss's assumptions about the payoff structure of the short-term game are consistent with the relevant Nash Equilibrium being *commitment* and *care*. This worry is not addressed *at all* by an appeal to a long-term game – in fact, this appeal seems to make matters *worse*, since the same concerns now arise for this second game as well (i.e.: why should we expect that the relevant equilibrium there involves male *commitment*?). For this reason, this does not seem to be a compelling way of spelling out Buss's reply.

A more promising route seems to lie in appealing to *mixed strategies*. On this reading, Buss's distinction between the long- and the short-term should be seen to be equivalent to the statement that the sexes' game in the EEA has had a stable state in mixed strategies. An example of such a game is the following:

[Figure 3: Payout Matrix for an Evolutionary Game concerning Sexual Strategies with a Stable State in Mixed Strategies]

Here, the game's only Nash Equilibrium consists in males pursuing a promiscuous strategy with probability 1/2 and a committed (i.e. long-term) strategy with probability 1/2, and females caring about male promiscuity with probability 1/2 and not caring with probability 1/2.[16] However, before considering this suggestion about how to spell out the long-term / short-term distinction in more detail, it is best to first introduce the last such suggestion, which is in many ways a variant of the present one.

This last suggestion consists in increasing the number of strategies available to the two players.[17] In particular, it claims that, in appealing to the short-term / long-term distinction, Buss points to the fact that people really choose among complex *bundles* of sexual strategies involving both short-term and long-term components. For this reason, it may be thought that we ought to expand figure 2 as follows:

[Figure 4: Payout Matrix for an Evolutionary Game Involving Complex Strategies with both Short-Term and Long-Term Components]

Given this expanded matrix, it may then turn out that the resulting Nash Equilibrium (represented by the shaded cell in figure 4) contains, as part of the male strategy, *large amounts of* promiscuity, but *not only* promiscuity.

When considering these last two suggestions (the one based on mixed strategies, and the one based on an expanded strategy-set) further, however, it becomes clear that, despite their sophistication, neither of them on its own vindicates Buss's theory. This is so for two reasons. On the one hand, this is because if this is what Buss *intends* to say, it is at variance with what he actually *does* say. As made clear in section II, in laying out his theory, he discusses long- and short-term strategies *separately*, and (with the help of Trivers's theory) derives behavioural predictions from the outcomes of these separate discussions (see e.g. Buss and Schmitt, 1993; Buss, 1989, 1998). This, though, is (at least) seriously misleading, as the separate discussion of long- and short-term strategies makes it seem like he is deriving predictions about the outcome of the game from the fitness values of just *one* of the sexes. However, from the fitness values of only one of the sexes, *nothing* follows for the game as a whole. To make predictions about which strategies have evolved, the fitness values of *both sexes* have to be taken into account *simultaneously*.[18]

On the other hand (leaving aside these issues of presentation), it is simply not true that in order to overcome the problems raised above, it is sufficient to *wave* at the fact that the relevant stable state of the game in the EEA ought to comprise much male promiscuity – any genuinely game theoretic methodology needs to take into account the *details* of the case at hand. To adequately handle the interactive nature of the evolution of the sexes' mating strategies, it is not enough to merely *state* that the game that was played in the EEA had some equilibrium involving much male promiscuity (either in the sense of the second suggestion, based on mixed strategies, or in the sense of the third suggestion, based on an expanded strategy set) – instead, an *explicit* game theoretic model needs to be constructed, whose specific stables states are then *shown* to involve much male promiscuity (at least to the extent that they can be expected to have evolved).

Put differently, to address the above criticism, it is not enough to *say* that the relevant game has the appropriate stable state (as Buss seems to want to do with the long-term / short-term distinction): it is just not *obvious* that the outcome of a proper game theoretic model of this situation really is in line with the conclusions that Buss wants to draw. For example, it is not clear that the game in figure 3 will do the trick: the probability of male promiscuity there seems too low, and that of female indifference too high; moreover, it is not clear that the payoff matrix can be justified using Buss's assumptions. On top of this, many of the games that have equilibria in mixed strategies *also* have equilibria in pure strategies (for example, this is true for the game in figure 2); in these cases, all of the issues raised in the previous sub-section (concerning the need to justify which equilibrium we ought to think actually emerged) are re-introduced without alteration. Without further argument, therefore, we are still lacking a scientifically compelling evolutionary analysis of our mating strategies.

In short: the distinction between short- and long-term strategies is no substitute for a full-scale game theoretic analysis of the evolution of sexual strategies. As it stands, this distinction is neither consistent with Buss's actual methodology, nor is it precise enough to do justice to the issues that need to be addressed.

In all, this shows that the deeply interactive nature of the subject-matter of Buss's theory cannot be handled successfully with a combination of sexual strategies of different time-frames and a set of empirical data. However, apart from these theoretic difficulties at the base of SST, there are also some empirical worries that are closely related to them. The next section is dedicated to bringing them out.

IV. States, Strategies, and Sexual Strategies

In order for SST to be a convincing and interesting contribution to psychology, it needs to be empirically substantiated. To be clearer about what exactly this requires, it is useful to begin by noting that, at bottom, SST has two major aims: firstly, it seeks to provide an account of *which* sexual strategies we pursue, and secondly, it seeks to provide an account of *why* we pursue these strategies. Therefore, for SST to be empirically corroborated, Buss must show, on the one hand, that we *in fact* pursue these sexual strategies, and on the other, that we do so *because* they were selected for.

As noted earlier, I here focus only on this latter claim. Specifically, in what follows, I try to show that there is no reason to think that Buss has made a compelling empirical case for the conclusion that our sexual strategies have evolved solely or primarily by natural selection. In the main, this is due to the fact that the data he presents to support his theory do not have the right kind of structure to do this – they do not provide the information needed to show that our sexual strategies are *adaptations*. Note that the claim is *not* that Buss's data do not match the predictions of SST (as has been argued by Buller, 2005 – but see also Buss and Haselton, 2005; Machery and Barrett, 2006; Delton et al., 2006); this may be true, but is irrelevant for present purposes. Instead, the claim is that, *whatever* the fit of the data to the predictions, this fit *could not* corroborate the theory – the data are simply of the wrong kind to do this.[19]

To see this most easily, assume (for the sake of the argument) that (a) an independently grounded game theoretic model can be found that fits to Buss's reasoning; (b) the game has a

Nash Equilibrium involving males being very, but not exclusively promiscuous (either due to them playing mixed strategies as in figure 3, or due to them playing a pure strategy involving much promiscuity as in figure 4); and (c) there is reason to think the latter equilibrium actually evolved. Given this, what Buss needs to show is that the *sexual strategies of individual males and females* match what is predicted by this model. That is, he needs to show not only that the stable state that males and females have actually evolved towards fits the relevant equilibrium of his model; he also needs to show that this stable state is *monomorphic*, and *not* one involving a *polymorphism* (i.e. one that merely concerns the 'average male' or the 'average female').

The reason for this is that, if it were to turn out that only the behaviour of the two sexes *as a whole* (i.e. that of the 'average male' and 'average female') agrees with the stable state of the model, then factors *other than* natural selection must be appealed to in order to explain the origin of the sexual strategies of individual males and females. For example, it might be the case that various *cultural norms* determine whether a male is promiscuous or committed; if so, then it will be necessary to make appeal to these norms when trying to make sense of the origins of the sexual strategies played by any particular male or female.

This is a point that has been made, in a more general setting, by Orzack and Sober (1994), Thomas (1984), and Bergstrom and Godfrey-Smith (1998). As these authors make clear, in order to test for the presence of an adaptation, it is not enough to consider whether the population *on average* fits to the stable state of the relevant model. Instead, it is necessary to determine whether the phenotypes of *individual organisms* fit to the relevant stable state. A fortiori, therefore, providing data solely on population averages cannot be sufficient to corroborate that some trait is an adaptation – instead, data on the phenotypes of individual organisms is needed (see e.g. Orzack and Sober, 1994, pp. 366-367).

However, as noted earlier, Buss's data fail exactly this test. All that he has provided is evidence of the sexual strategies of the 'average male' or the 'average female' (see e.g. Buss, 1989; Buss and Schmitt, 1993). As just noted, though, this is not sufficient to confirm SST: without presenting and analysing data on *individual males and females*, the importance of natural selection for our sexual strategies is left open. In slightly more detail, this worry can be expressed as follows.

What Buss has shown is that, at least in the short term, males *on average* desire to be fairly promiscuous (and that they desire to be more promiscuous than females do). However, this average could come about *either* because most males cluster around it – i.e. because the distribution of male sexual strategies is bell-shaped as in figure 5 – *or* because males are polymorphic in this respect, with some desiring to be very promiscuous, and some desiring not to be very promiscuous at all – i.e. because the distribution of male sexual strategies is multi-peaked, as in figure 6.[20]

[Figure 5: Single-Peaked Distribution of Short Term Male Promiscuity]

[Figure 6: Multi-Peaked Distribution of Short Term Male Promiscuity]

Now, for SST to be corroborated, it must be the case that figure 5 is the correct description of reality, not figure 6. This is because, as noted earlier, one of key aims of SST is to show that the sexual strategies we follow are *adaptations*. However, if it is figure 6 that is correct, then this aim will not have been attained: in that case, no *actual person* behaves according to how SST predicts they do – males then are either *more* or *less* promiscuous than what would be adaptive according to it. Alas, Buss's data do not allow one to rule out this possibility (i.e. they cannot distinguish between figures 5 and 6): all he shows is that the *sex-averages* fit his predictions, not the strategies of individual people.

Note that the point of this criticism is not that it is *immensely difficult* to test for the possibility of the presence of a polymorphism, or that the lack of this test is some sort of *fatal flaw* in SST. In fact, the data in Buss's possession might allow him to rule out this possibility quite easily. The point is just that this test needs to be *done* – for only then could the theory be corroborated. As it stands, Buss's analysis of the empirical data underlying SST is simply incomplete: without making clear that this is indeed a case of monomorphism, the data he presents *cannot* show that SST explains our sexual strategies.

That said, it also needs to be noted that conducting this kind of test it is not a trivial matter, either. In particular, just *eyeballing* the appropriate data is not enough: instead, a thorough *statistical analysis* of them is needed, so as to ensure that their fit to Buss's model is not merely apparent. How exactly this is to be done raises some complex issues (see also Orzack and Sober, 1994, p. 367); for present purposes, though, it is sufficient to note that this requires more than a quick glance at how close the overlap seems to be between the distribution found in the data and figures 5 or 6. In short: as matters stand, more work is needed for Buss to present data that even have the *ability* to provide compelling empirical support for SST.

Overall, therefore, it becomes clear that there are worries not just about the theoretical foundations of SST, but also about its empirical testability. Without providing data that show that the stable state we have evolved towards involves a monomorphism, Buss cannot claim to have presented a plausible argument for the origins of our sexual strategies. For this reason, it may well be the case that the surface-level fit between Buss's predictions (however they are derived) and his data belies the empirical support his theory really has.

V. Conclusion

I have tried to argue that Buss's theory rests on weak theoretical and empirical foundations, unless it takes into account the fact that the two sexes were engaged in a strategic interaction. This need not mean that its conclusions are wrong, but it does point to the fact that, as it stands, it is intellectually unconvincing. Firstly, this is because the selection of cooperative strategies cannot plausibly be analysed without taking into account both partners of the exchange – only by doing that can it be made clear what sexual strategies we ought to expect to evolve. Secondly, this is because Buss obfuscates the distinction between an equilibrium state involving a stable polymorphism and that involving a complex monomorphism – only by respecting this distinction can an evolutionary explanation of our sexual strategies convincingly be tested. In short: game theoretic analysis must not be seen as merely an *extension* to sexual strategies theory – it must be seen as being part of its *core*.

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Notes

[1] It is worthwhile to note that Buss's views about these matters have changed somewhat over the years (see e.g. Buss, 2003). However, in the relevant respects, the following presentation still makes for an accurate description of his theory.

[2] I also concentrate on *male* strategies, as the issues to be raised are somewhat more clear-cut there.

[3] Buss also argues that, to further increase their chances of having viable offspring, males should prefer partners that are *fertile* and high in *reproductive value* – i.e. having a high expected number of offspring (see e.g. Buss, 1992, pp. 249-250). Since these two features are not directly observable, Buss predicts males to therefore also have evolved preferences for observable features that are correlated with these, like signs of good health and a young age (clear skin, full lips, bodily symmetry – Buss, 1992, p. 250). However, these further predictions are not relevant in the present context.

[4] It is often argued that they should also be concerned with increasing the probability that their offspring has 'good genes' (see e.g. Buss and Schmitt, 1993, p. 219; Gangstead and Simpson, 2000). However, since this is still controversial and anyway merely complicates the analysis without adding anything of substance, I disregard it here. Note also that Buss identifies two further goals of females using short-terms strategies: extracting resources from the mate for immediate use, and using him as a protector from abuse (see Buss and Schmitt, 1993, pp. 220-221). Neither of these is important here, however.

[5] A word about Trivers's theory (as well as that of Clutton-Brock, 1991) is useful here. These theories do have quite a lot of empirical support – which may be puzzling, given that the criticisms raised below also seem to apply to them (as noted in the text). To understand what is

going on here, two points need to be noted. Firstly, the game theoretic models are different in the case of Triver's and Clutton-Brock's theories on the one hand, and that of Buss's theory on the other: the former are best seen as involving Evolutionary Stable Strategies, and the latter as involving Nash Equilibria (I return to this point below). Secondly, note that at stake in the present context is merely the plausibility of Buss's theory as an *explanation* of the nature of our sexual strategies. Exactly the same applies to the (more general) theories of Trivers and Clutton-Brock: these authors may be *right* in thinking that the sex with the lower level of minimal parental investment is more promiscuous than the one with the higher; however, they may still be wrong about what the *explanation* for this is. To provide the latter, a game theoretic approach is needed – without it, too many options about the origins of an animal's sexual strategies are left open.

[6] Gangstead and Simpson (2000, pp. 577, 586, 588) and some of their respondents (e.g. Berry and Kuczaj; Kendrick et al.; Mealey) do raise issues in the vicinity of the present paper; however they either do not develop them to a sufficient degree, or consider them *extensions* to the theory. By contrast, the point of the present paper is that game theory is *integral* to sexual strategies theory: the latter cannot even get off the ground without it. Similar remarks apply to Hill and Reese (2004) and Woodward and Richards (2005). In a different context, D'Arms et al. (1998) also see much of evolutionary psychology as not being sufficiently game-theoretic.

[7] Note that what follows is not meant as an in-depth introduction to (evolutionary) game theory. The aim is just to provide enough details to be able to spell out the worry that Buss's theory overlooks the importance of interaction between the two sexes.

[8] This restricts the solution concepts to *static* ones. However, since modelling of the dynamics of this type of situation introduces some complex issues (for examples of this kind of analysis, see

e.g. Taylor and Jonker, 1978; Skyrms, 1996; Binmore and Samuelson, 1999; Samuelson, 2002; Alexander, 2007), and since, for present purposes, these complex issues are not relevant, this restriction is justified.

[9] This characterisation deviates slightly from the most common definition of an ESS ('a strategy doing well against itself' – see e.g. Dawkins, 1982) due to the fact that the game here is asymmetric in both strategies and payoffs. In these kinds of asymmetric games, the usual definition of an ESS does not apply, as a strategy cannot meet itself. However, the above is the most straightforward extension to this case. See also Maynard-Smith (1982); Swinkels (1992); Mailath (1998).

[10] In fact, since all games have Nash Equilibria, but not all games have ESS solutions, concentrating on the former makes it *easier* for Buss's account, not *harder*.

[11] This is made even more plausible by the fact that the kind of deliberations that are relevant here are consistent with the players being only *boundedly rational*, and using various simple heuristics to determine what strategy to choose (see e.g. Gigerenzer & Selten, 2001)

[12] In some ways, this is an instance of the more general fact that evaluating what maximises the reproductive success of an organism in abstraction from the constraints that it faces yields theoretically empty claims (see also Sober, 1994; Maynard-Smith, 1984). In the present context, this means that looking at what maximises male reproductive success in abstraction from the sexual strategies of females leaves out of consideration an important constraint on male strategies.

[13] Of course, Buss could be content with using figure 2 to show that it is at least *possible* that male promiscuity is an adaptation. However, doing this would not be very interesting, as *this much* is granted by virtually everyone in this debate.

[14] One way of doing this is to use models of group selection (see e.g. Sober and Wilson, 1998, p. 152); another is to consider a dynamical analysis and model the situation with multiple different starting assumptions (see e.g. Skyrms, 1996).

[15] As will made clearer in section IV, this would still leave a number of important questions open; however, this point can be left aside here.

[16] These values are the solutions to the set of equations: $p(4)+(1-p)(1)=p(2)+(1-p)(3)$ and $q(1)+(1-q)(4)=q(2)+(1-q)(3)$. There are many different ways of interpreting them – e.g. males are promiscuous 1/2 of the time, and committed 1/2, or for any potential mate, males randomise over which strategy to use (similar remarks can be made for females). These differences in interpretation are not relevant here, however; the only one interpretation that must be excluded is that of seeing 1/2 of males as being promiscuous, and 1/2 as being committed – see section IV for more on this.

[17] This can also be spelled out using extensive-form games or by appealing to more than two players; however, doing so brings up no new issues from the ones raised in the text.

[18] This point also affects the approach of Buss (1988), where the mate-attraction tactics of one sex are said to be influenced by the preferences of the other: this makes sense only if it is assumed that the sexes *already have* evolved sexual preferences – which requires an *interactive* evolutionary account of this in its turn.

[19] Of course, since (as argued above) Buss does not present any game theoretic model whatsoever, it is not even clear what the predictions are that these data *ought* to match. However, the point here is just that even if Buss's predictions did turn out to be justifiable game theoretically, and even if – contra Buller (2005) – they really did match his data, this would not necessarily vindicate SST.

[20] Note that this is related to, but still different from, the issue of 'cad / dad' conditional strategies mentioned earlier. The point here is not that the fitness value of any male strategy depends on what other males are playing, but that for *non-adaptive* reasons, males might be polymorphic in their sexual strategies.

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Appendix: A Model of Short-Term Mating Under Uncertainty

Assume that males can send a costly signal that signifies commitment (prolonged courtship displays, say); assume also that it costs 2 units of fitness to send this signal if the male is actually promiscuous, and nothing if he is committed. Assume further that females can observe this signal, but cannot observe whether the male is following a promiscuity strategy or not. Given this, the task of the males can be taken to be to choose whether to *signal* and whether to be *promiscuous*, and the task of the females to choose whether to *accept* a male (who may or may not have signalled) for mating purposes.

In line with Buss assumptions, assume next that the fitness payoffs of the different possible outcomes are as follows (with subscripts indicating whether the payoff accrues to the male (M) or the female (F)):

F_M (Mating Occurs | Male is Promiscuous) = 4; F_M (Mating Occurs | Male is Committed) = 3;
F_F (Mating Occurs | Male is Promiscuous) = 0; F_F (Mating Occurs | Male is Committed) = 3;
F_M (No Mating Occurs) = F_F (No Mating Occurs) = 1

Note that these values are – purposively – very similar to the ones in figure 2: males are assumed to achieve their highest possible fitness by being promiscuous, and females are assumed to achieve their highest possible fitness by having a partner that is committed. Assume further – again following Buss's lead – that females are more likely to accept a mate if the male in question has signalled commitment than if he has not:

(i) P (Female Accepts | Male has signalled) > P (Female Accepts | Male has not signalled)

Then the expected fitness of the different male strategies is as follows:

(ii) EF_M (Male is Promiscuous & Male has signalled)

= P (Female Accepts | Male has signalled) (4)

+ (1 - P (Female Accepts | Male has signalled)) (1) – 2

(iii) EF_M (Male is Promiscuous & Male has not signalled)

= P (Female Accepts | Male has not signalled) (4)

+ (1 – P (Female Accepts | Male has not signalled)) (1)

(iv) EF_M (Male is Committed & Male has signalled)

= P (Female Accepts | Male has signalled) (3)

+ (1 – P (Female Accepts | Male has signalled)) (1)

(v) EF_M (Male is Committed & Male has not signalled)

= P (Female Accepts | Male has not signalled) (3)

+ (1 – P (Female Accepts | Male has not signalled)) (1)

An important point to note about these expected values is that by assumption (i), it must be that (iv) > (v) – so that *if* males commit, they will do so with signalling. Further, it must also be that (iv) > (ii), as this only requires that

(vi) 2 > P (Female Accepts | Male has signalled), which will always be true by the axioms of the probability calculus. More interestingly, note that (ii) > (iii) holds if and only if

(vii) P(Female Accepts | Male has signalled) – P(Female Accepts | Male has not signalled) > 2/3,

i.e. if the difference is large between the probability that females accept an offer when there is a signal and the probability that they accept an offer when there is no signal.

From the point of view of the females, the situation is as follows. The fitness of their strategies is given by:

(viii) EF_F (Female Accepts | Male has signalled)
= P (Male is Committed | Male has signalled) (3)
+ (1 – P (Male is Committed | Male has signalled)) (0)

(ix) EF_F (Female Accepts | Male has not signalled)
= P (Male is Committed | Male has not signalled) (3)
+ (1 – P (Male is Committed | Male has not signalled)) (0)

(x) EF_F (Female does not Accept) = 1

Now (viii) > (ix) if and only if

(xi) P(Male is Committed | Male has signalled) > P(Male is Committed | Male has not signalled).

Further, (viii) > (x) if and only if

(xii) P (Male is Committed | Male has signalled) > 1/3.

This leads to the key concerning the solution of this model: under what conditions are (vii), (xi), and (xii) consistent? That is, when is it the case that the females' beliefs about the males' strategies (given the signals sent by them) fit to what the males are actually doing? While giving a general answer to this question is somewhat complex, for present purposes it is enough to note that *one* possible solution has it that all males commit and signal, and that females accept all offers. For then:

(xiii) P (Female Accepts | Male has signalled) = 1.

If – plausibly – females are furthermore very unlikely to accept offers without a signal – i.e. if

(xiv) P (Female Accepts | Male has not signalled) $\in$ [0, 1/3],

then (vii) will be true. Furthermore, (xi) and (xii) will be true as well, as:

(xv) P (Male is Committed | Male has signalled) = 1

(this is due to the fact that all males commit and signal, and that the probability of P (Male is Committed | Male has not signalled) can be set arbitrarily in the range [0, 1)).

Note that this is a strict (Bayesian) Nash Equilibrium: male mutants switching to playing promiscuous but continuing to signal get a payoff of (4) – (2) = (2), which is less than what the committing majority get (3). Finally, males who do not signal will get a payoff of 1, which is also lower than the signalling commitment equilibrium. Females, too, cannot profit from switching strategies – in particular, accepting fewer offers leads to losses in fitness, as those accepting all offers get a payoff of (3), while those accepting fewer offers only get a payoff between 3 and 1 (depending on how many offers they reject).

The point of all this is to show that Buss may be right in saying that males do best by being promiscuous in absolute terms (as they can then get a payoff of 4 – the highest possible), *and* he may be right in saying that females do best by caring about male promiscuity (as they can get a payoff of 3 – the highest possible for them); *moreover* it may be the case that females cannot tell if males are promiscuous (and so have to rely on the signal sent by them). Still, Buss may be wrong in saying that male promiscuity is an adaptation: if the situation in the EEA was as described in this game, evolutionary consideration might in fact suggest that what evolved is male *commitment*, not male *promiscuity*, for this, too, is part of a Nash Equilibrium of the game between the two sexes.

Player 1 / Player 2	Left	Right
Up	4, 1	0, 0
Down	2, 2	3, 3

[Figure 1: Payout Matrix for an Evolutionary Game]

Males / Females	Don't Care	Care
Promiscuous	4, 1	0, 0
Committed	2, 2	3, 3

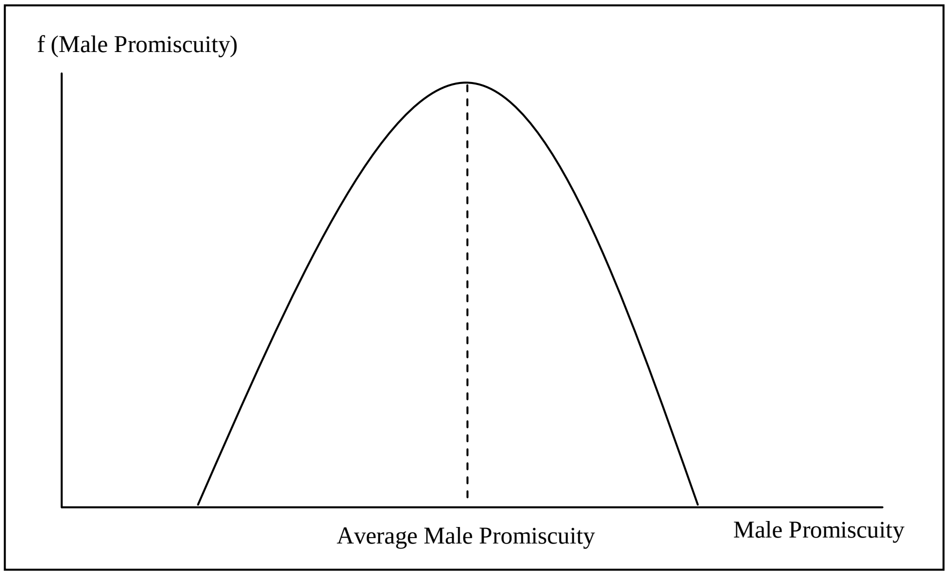
[Figure 2: Payout Matrix for an Evolutionary Game Consistent with Buss's Reasoning]

Males / Females	Don't Care	Care
Promiscuous	4,1	1,2
Committed	2,4	3,3

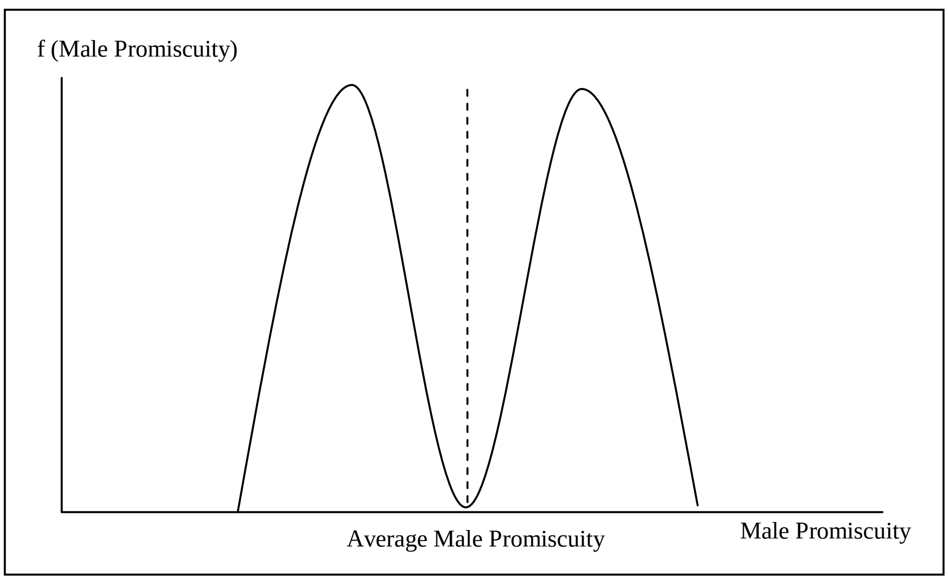
[Figure 3: Payout Matrix for an Evolutionary Game concerning Sexual Strategies with a Stable State in Mixed Strategies]

Males / Females	Don't Care At All	Care A Bit	Care Considerably	Care A Lot
Promiscuous (Pure Short-Term)	x_1, y_1	x_2, y_1	...	x_4, y_1
Much Promiscuity, Some Commitment (Part Long-Term / Part Short-Term 1)	x_1, y_2	...	...	...
Some Promiscuity, Much Commitment (Part Long-Term / Part Short-Term 2)	...	...	...	...
Committed (Pure Long-Term)	x_1, y_4	...	...	x_4, y_4

[Figure 4: Payout Matrix for an Evolutionary Game Involving Complex Strategies with both Short-Term and Long-Term Components]



[Figure 5: Single-Peaked Distribution of Short Term Male Promiscuity]



[Figure 6: Multi-Peaked Distribution of Short Term Male Promiscuity]