Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Review

Does the contraceptive pill alter mate choice in humans?

Alexandra Alvergne and Virpi Lummaa

Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK

Female and male mate choice preferences in humans both vary according to the menstrual cycle. Women prefer more masculine, symmetrical and genetically unrelated men during ovulation compared with other phases of their cycle, and recent evidence suggests that men prefer ovulating women to others. Such monthly shifts in mate preference have been suggested to bring evolutionary benefits in terms of reproductive success. New evidence is now emerging that taking the oral contraceptive pill might significantly alter both female and male mate choice by removing the mid-cycle change in preferences. Here, we review support for such conclusions and speculate on the consequences of pill-induced choice of otherwise less-preferred partners for relationship satisfaction, durability and, ultimately, reproductive outcomes.

Women's dual sexuality

In humans, female fertility increases gradually before ovulation and rapidly decreases thereafter. Conceiving is only possible during a brief ~6-day period ending on the day of ovulation (i.e. oestrous phase; [1]). However, women engage in and seek copulations throughout their cycles (i.e. extended sexuality [2]). This dual sexuality (conceptive and not conceptive) is suggested to have two distinct functions: one at the fertile cycle phase to obtain genetic benefits for offspring, and the other at the infertile cycle phase to obtain non-genetic material benefits [2]. Such a 'dual strategy' is generally observed in species where females must balance sires' genetic benefits with costs of losing resources provided by their primary partners, owing to intrinsic and/or socio-ecological constraints precluding them from having both genetic and non-genetic material benefits provided by the same mate (Box 1). It is regulated by cycling physiological and subsequent behavioural changes (Box 2), which can interact with mate choice.

It is well documented that women prefer cues of mate non-genetic material benefits and assistance during less fertile periods and cues reflecting mate genetic quality or compatibility during more fertile periods (reviewed in Ref. [3]). Accumulating evidence suggests that ovulation also induces men to find women more attractive during their fertile phase (reviewed in Ref. [4]). Overall, the 'dual strategy' of women's sexuality is likely to have enabled ancestral women to make informed and, ultimately, adaptive decisions regarding with whom to pair and with whom to reproduce to maximize their reproductive success.

Corresponding author: Lummaa, V. (V.Lummaa@sheffield.ac.uk).

The oral contraceptive pill, used by ~100 million women of reproductive age worldwide (http://www.unpopulation.org), changes the hormonal state of the menstrual cycle by mimicking pregnancy (Box 2). Thus, mate preferences and choice could be modified by the use of such a pill (hereafter referred to as 'the pill'; similar reasoning is applicable to any other hormone-based contraceptives, i.e. patch or implants, but empirical data concerning their influence on mate preferences are lacking). Here, we review recent evidence to discuss the possibility that contraceptive pill use in women changes mate preferences in both sexes and affects subsequent mate choice and reproductive outcomes. Modern contraception has improved the quality of life worldwide, by reducing unintended pregnancies and maternal deaths [5] and, by enabling women to postpone childbearing, increased their educational level and subsequent role in modern economy [6,7]. Although we take a purely biological perspective towards pill use, we do not wish to undermine the crucial social and medical positive associates of this contraceptive method, which might act in opposite ways from those discussed here.

Mate preferences vary across the menstrual cycle

Both women's and men's mate choice preferences vary according to the natural menstrual cycle. In women, menstrual cycle phase is related to shifts in preferences for cues suggested to be related to genetic benefits ('genetic quality' indicators) versus non-genetic material benefits ('good dads' indicators) associated with hypothetical mates (Box 2). During the past decade, >75% of studies investigating women's cycling mate preferences have demonstrated that women seek specific characters when fertility is maximal: ovulating women prefer more masculine and symmetrical male features (reviewed in Ref. [3]). Fertile women are also particularly attracted to men showing dominance and intrasexual competitiveness [8], and other possible indicators of genetic quality such as creative intelligence ([9] but see Ref. [10]).

Preferences for indicators of male genetic quality are hypothesized to be particularly enhanced during oestrus because not all women are able to pair-bond with high-quality males, even though all women could engage in extra-pair copulations (EPC) with one (Box 1). Accordingly, the shifts in a woman's mate preferences near ovulation should concern evaluations of genetic benefits, rather than dimensions related to a long-term relationship, such as paternal investment. Given the potential costs associated with EPC, however, preferences for long-term mates probably would not be silenced during oestrus [2]. In support of

0169-5347/$ – see front matter © 2009 Elsevier Ltd. All rights reserved. doi:10.1016/j.tree.2009.08.003 Available online 7 October 2009

Author's personal copy

Box 1. Cycling female preferences: benefits versus costs of extra-pair paternity (EPP)

Accumulating evidence suggests that women show an increased motivation (and rate) for extra-pair copulation (EPC) at mid-cycle (reviewed in Ref. [3]), which is likely to be translated into realised extra-pair offspring because women's in-pair copulation rates do not increase at mid-cycle [55]. Rates of women engaging in EPC that lead to EPP range from 0.8% to 30% across socio-ecological contexts (reviewed in Ref. [14]). Given that humans typically form long-term pair bonds, and a woman's reproductive success does not increase linearly with the number of partners [56], why do women have EPC, why does its rate vary across the menstrual cycle, and why do the preferences for male attributes cycle?

First, men vary in their potential (evolutionary) value as a mate. In maximizing their reproductive success, they face a tradeoff between acquiring mates and caring for their offspring, given that mating effort and parental effort might overlap in time [57]. This depends on the intrinsic value of individuals (e.g. attractiveness) and the social environment (e.g. local level of male–male competition), leading men to vary in their relative investment in mating and parenting efforts. Second, females cannot always choose their preferred long-term partner [58]. In traditional societies, parents often choose the long-term partner for their daughter, a choice that might not match her own preferences. There is also some evidence that women are socially constrained to accept imposed unions. For instance, in human societies where widows must marry their deceased husband's brother, the widow must hand over all the property between partners left to her by the deceased husband to his brother should she refuse [59].

Women might thus have EPC during their fertile phase if they encounter males potentially of superior genetic quality to their social partner, and they can enhance the reproductive success of their offspring by reproducing with such males. Many studies on birds have shown that extra-pair offspring have greater mean size-adjusted mass than the within-pair offspring in the same clutch [60]. Similar results from humans are, however, not available owing to the ethical concerns associated with such research. Nevertheless, the documented EPC during mid-cycle is suggested to improve offspring quality, because women prefer cues of genetic quality in mates for short-term rather than long-term relationships, and when their fertility probability is high (reviewed in Ref. [2]).

The suspicion of infidelity however involves severe costs. First, suspected or actual infidelity is a major source of marital conflict [61,62] and the leading cause of conjugal dissolution cross-culturally [63]. Increased paternity uncertainty owing to perception of female infidelity can also be associated with a reduction in paternal care [64]. Thus, selection is likely to have shaped a woman's mate preferences to be contingent on her fertility status across the ovulatory cycle, balancing between fitness benefits of EPP and the potential cost of losing her primary partner [65].

this, shifts in preferences at peak fertility for male attractiveness or sexiness have only been observed in a short-term relationship context, and no study has detected fertile-phase shifts in a woman's evaluations of men as good long-term partners (reviewed in Ref. [10]). This suggests that the primary context in which preference shifts have been favoured is the potential genetic benefit to offspring through EPC [2].

The benefit of pursuing an EPC to obtain genetic benefits for offspring depends on the genetic quality of the primary mate: with high genetic quality primary partner, the potential benefits of engaging in an EPC might be small. Accordingly, both primary male attractiveness and genetic quality and/or compatibility moderate women's shifts in preference across their cycle and desire for EPC. First, women paired with mates they perceive as unattractive experience a greater shift in their mate preference near ovulation [11,12]. Second, genetic compatibility between partners at the major histocompatibility complex (MHC, loci associated with the immune system for which genetic dissimilarity between partners potentially enhances the immunocompetence of offspring) predicts female sexual relationships depending on their fertility status: MHC sharing negatively predicts a woman's sexual attraction and sexual responsiveness to her current partner and positively predicts her attraction to other men, particularly during the fertile phase of her cycle [13]. Furthermore, a high level of MHC sharing also predicts a woman's reported number of extra-pair partners [13]. This suggests that the documented cycling preferences, conditional on women's and their primary partners' phenotypic attributes, aimed at maximizing offspring reproductive value.

Cycling preferences in women are likely to enable discriminative mate choice at peak fertility for mate genetic quality and/or compatibility. However, the adaptive significance of such cycling preferences in contemporary populations is not straightforward, given the low mean rate of extra-pair paternity (EPP) worldwide among men confident of their paternity ($\sim$3.5% [14]). This implies that, for $>$95% of long-term partners believing to be the genetic father of the offspring, this indeed is the case. Evidence from other species does however suggest that a low rate of EPP is sufficient to select for adaptations in both sexes to control paternity [15]. In an attempt to clarify whether cyclicity in preferences brings reproductive benefits to contemporary women, the presence of cycling preferences cross-culturally, and the link between the strength of the shift in preferences and the costs associated with EPP should be investigated.

Women also shift in their attractiveness to men across their menstrual cycle, and several detectable ovulatory cues in women have been documented [3,16] challenging the traditional view of concealed ovulation [17]. The ovulatory cycle induces changes in the physical properties of women, such as modification of face, odour, or voice pitch [18], to which men are sensitive [19,20]. In addition, the ovulatory cycle contributes to changes in a woman's motivations to appear attractive, and during the fertile phase, women dress more provocatively [21,22], report a higher self-perceived attractiveness [23] and increased sexual desire and fantasies [12]. That a woman's fertility status is detectable by men is also suggested by studies showing that men's guarding of their mates increases when women are more fertile [12,23]. For example, in Trinidad, men with fecund mates undergo higher rates of agonistic interactions with other unrelated men than men with subfecund mates [24]. Finally, a study investigating tip earnings by lap dancers showed that earnings varied across their menstrual cycle (Figure 1) [4]. Such changes are probably a result of multiple factors, including changes in both female physical traits as well as behaviour [3,4,21], and could be indicative of changes in male preference and/or female mate acquisition. The presence of an ovulation peak within women across their cycle considered with regard to their ability to extract money from men suggests that cycling female attractiveness has consequences for potential mate attraction.

Author's personal copy

Box 2. Behavioural and hormonal correlates of oestrus in women

The oestrous phase (near ovulation) is marked by several adaptations suggested to function to obtain genetic benefits for offspring [2]. First, during oestrus, women are more likely to spend energy in mating effort (e.g. Ref. [23]). Moreover, a woman's desire for orgasm and sexual satisfaction increases, whereas food and water consumption is reduced, which might indicate an increased allocation of energy to mating effort at mid-cycle [66]. Second, women are choosier during oestrus and are physically more attractive to men (possibly achieved by responding to products of the physiological changes in females associated with fertility such as variation in oestrogen levels [23]) and they behave more provocatively [21,22], increasing mating opportunities. Concomitantly, women are more likely to resist poor or unwanted mating options (e.g. Refs [67,68]). Third, a woman's preference for mates shifts during oestrus. Ovulating women prefer mate characteristics that are possible cues of genetic benefits and compatibility compared with non-fertile phases of the cycle (reviewed in Ref. [3]). Finally, women are more likely to have EPC during oestrus (Box 1).

In normally cycling women, the menstrual cycle involves changes in the concentration of several hormones, and the ovulatory-cycle fluctuations in behavioural outcomes are related to different hormones or combination of hormones (Figure Ia). During the first phase of the cycle, follicle-stimulating hormone (FSH) stimulates the growth and recruitment of immature ovarian follicles in the ovary. During mid-cycle, luteinizing hormone (LH) surges, causing ovulation. Consequently, progesterone levels increase sharply. If implantation does not occur, progesterone and estrogen levels decrease, causing menstruation. Such fluctuations also lead to various behavioural responses and a woman's preferences for cues of genetic benefits (e.g. masculinity), for example, are regulated through oestradiol concentrations [69].

Hormonally based contraception inhibits the release of FSH and LH and thus softens the normal mid-cycle peak in oestrogen level and elevates progesterone levels (Figure Ib). These hormonal changes prevent ovulation and mimic the hormonal state of pregnancy, which is predicted to modify human female sexuality. In line with this, women using the pill do not appear to exhibit typical oestrous sexuality, but instead display preferences and interests similar to those of women in the non-fertile phases (Table 1, main text). All ovulatory-cycle effects are potentially modified by oral contraceptives. The impact of such oestrous disruption on reproductive success is currently unknown although it is likely that if oestrus is adaptive, then any drug specifically designed to eliminate ovulation and the associated oestrus psychological and physical changes will have maladaptive side-effects.

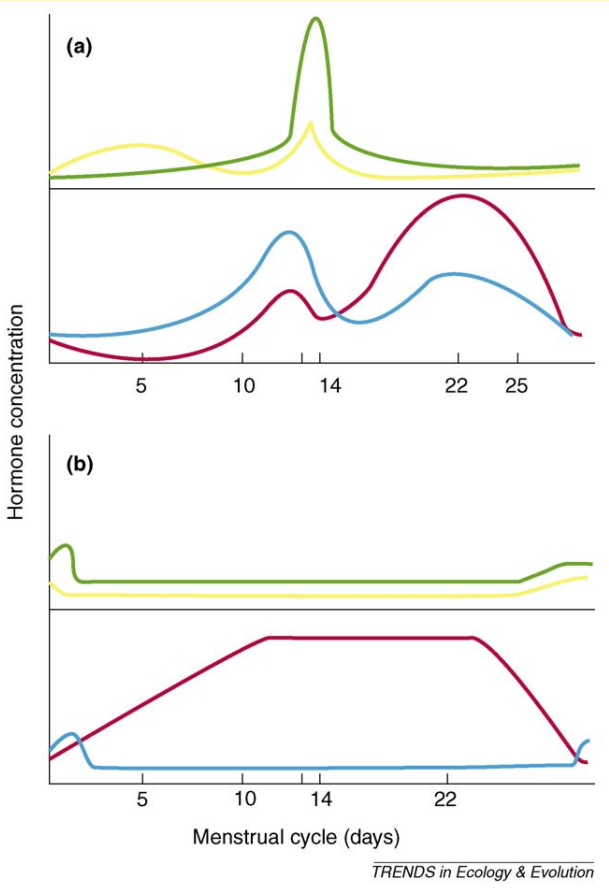

Figure I. Hormonal regulation of the menstrual cycle in **(a)** normally cycling women and **(b)** pill users. By providing a steady daily level of both progestin (a substitute for progesterone; red lines) and oestrogen (blue lines), oral contraceptives prevent gonatropin-releasing hormone (GnRH) secretion from the hypothalamus, blocking a signal to the pituitary gland to produce FSH (yellow lines) and LH (green lines). Because FSH stimulates the ovaries to grow egg follicles and LH triggers ovulation, their absence causes the ovary to be relatively dormant, and no egg is produced to a point where it could be released. Hormonal contraception thus maintains the menstrual cycle at the same late phase of the natural cycle on a continuous basis. Adapted, with permission, from http://www.pbs.org .

Whether the changes leading to women's increased attractiveness near ovulation are the expression of evolved 'signals' of fertility status [25] or simply by-products of changes in women's hormonal status [2] is controversial. Nonetheless, such enhanced attractiveness to men might bring fitness benefits to ovulating women in terms of increased ability to choose or to retain appropriate mates when conception potential is maximal. Indeed, given that for men beauty is among the primary mate selection criteria [26], women are likely to compete in attractiveness. For example, a rival's perceived value, assessed by a woman's rating of other women's facial attractiveness, is decreased when the rater's oestrogen levels are high ([27] but see Ref. [28]), whereas this shift is not observed in post-menopausal women no longer taking part in female-female competition for reproduction [29]. Moreover, evidence from established couples suggests that partnered women compete to keep their mate: the more satisfied women are with their primary partners, the more they shift towards revealing clothing during high versus low fertility [22]. It is thus possible that ovulating women are more successful at gaining desired mates and more likely to realise their adaptive mating preferences, although further studies are needed to explore this.

Importantly, shifting preferences across the menstrual cycle only matter if they are translated into actual mate choice. Cycling preferences have probably been favoured in women when long-term partners have been socially imposed and the tradeoff between mating and parenting effort in men is particularly pronounced (i.e. polygynous systems where males can access multiple wives simultaneously), so that resources were favoured over genetic quality in long-term partners (Box 1). However, in many monogamous societies where women might be more free to choose their partners, it remains to be confirmed whether actual choice of long-term partners corresponds with evolved short-term or long-term mate preferences. Unfortunately, this question has received little attention in

Author's personal copy

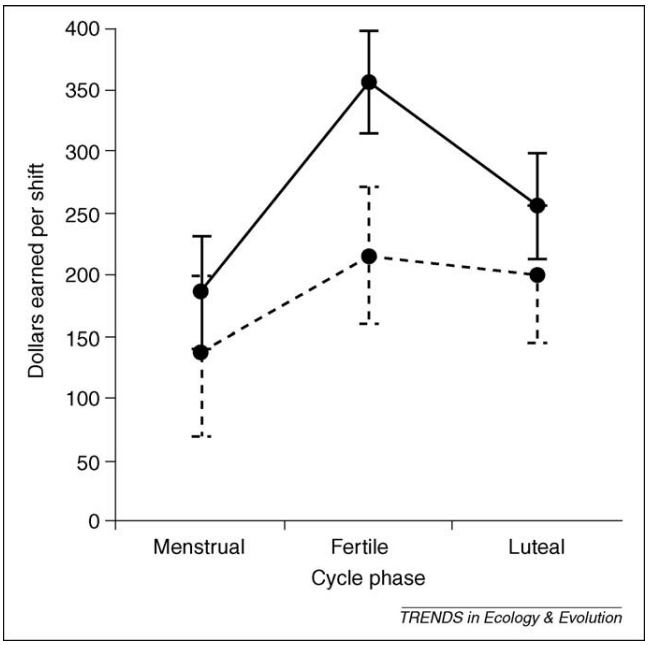

Figure 1. Effects of ovulatory-cycle phase on lapdancer tip earnings per shift in normally cycling women (solid lines) versus women using hormonal contraception (pill users, dashed lines). Over a 60-day period, 18 heterosexual women working as lap-dancers reported day-by-day start or stop of menstruation and their tip earnings from any shift they worked. Normally cycling participants earned ~US$335 per 5-hr shift during oestrus, US$260 per shift during the luteal phase, and US$185 during menstruation. By contrast, pill users showed no rise in earnings during oestrus, suggesting that the use of pill interrupts cycling attractiveness of women to men. Error bars represent 95% confidence intervals. Adapted, with permission, from Ref. [4].

humans. That ideal mate preference might have a role in actual mate choice in modern societies is suggested by evidence that women's preferences for masculine male faces are positively related to the masculinity of both their actual and ideal partner [30]. Moreover, when an odour, smelled on a T-shirt, reminded the rater of his/her mate's or former mate's odour, the rater and the respective T-shirt-wearer shared fewer MHC alleles, again indicating that MHC preferences correlate with actual mate choice [31]. Conversely, one recent study using speed-dating experiments suggested that reported preferences do not correspond to actual mate choice [32]. Future studies are needed to investigate the correlation between mate preference and actual mate choice to establish whether and which preferences (genetic quality or good dad and material benefits) can lead to actual mate choice in various social contexts (i.e. arranged marriage or free choice) to better understand the adaptive value of women's mate preferences.

Pill use and mate preferences

Daily use of the oral contraceptive pill increases and 'smoothens' a woman's levels of oestrogen and progesterone and, by mimicking the hormonal state of pregnancy, results in prevention of ovulation and loss of normal fertility (Box 2). New evidence suggests that the pill, by eliminating oestrus, changes the natural cycling preferences in women for markers of both genetic quality and compatibility in mates (Table 1), as well as natural cycling attractiveness to men (Table 1). As compared with normally cycling women, pill users show no or weaker preferences for facial (Figure 2 [33]) and vocal masculinity [34,35]. For instance, the preferred face shape is more masculine during the high conception-probability phase of the menstrual cycle in non-pill users, but pill users do not show similar preference [35]. Similarly, as compared with non-pill users, pill users express neither the preferences for scents of symmetry (hypothesized to be an honest signal of phenotypic and genetic quality in human males), nor a change in mate scent preferences over the menstrual cycle [36]. Furthermore, whereas normally cycling women express a preference for MHC dissimilarity in mates, pill users prefer odours of MHC-similar men, indicating that pill use might eliminate adaptive preferences for genetic dissimilarity [37]. These results suggest that the use of the pill is related to women favouring less symmetrical, masculine and MHC-dissimilar men, a preference attributed to the pill-induced changes in hormone levels simulating pregnancy (Box 2), and could lead to subsequent preference for individuals likely to support child rearing [31,37].

What is the influence of the pill on the ability of women to attract mates? Given that men prefer ovulating women

Table 1. Effects of oral contraceptive pill use for women's mate preferences and attractiveness[a]

	Trait	Non-pill users	Pill users	Design	Sample size	Refs
Preferences	Symmetry	Increased preferences for scents of symmetrical men at mid-cycle	No preference for either symmetrical or asymmetrical men's scent	B	17 NPU-35 PU	[65]
		Increased preferences for scents of symmetrical men at mid-cycle	No preference for either symmetrical or asymmetrical men's scent	B	16 NPU-66 PU	[72]
	Masculinity	Increased preferences for facial and vocal masculinity at mid-cycle	Weaker change across the cycle	B	307 NPU-112 PU	[35]
		Increased preferences for facial masculinity when paired or when seeking short- term relationship	No change according to the relationship status	B	214 NPU-102 PU	[33]
	MHC scents	Preferences for MHC-dissimilar men	Preferences for MHC-similar men	B	31 NPU-18 PU	[37]
		Preferences for MHC-dissimilar men	Preferences for MHC-similar men	B	32 NPU-26 PU	[31]
		No preferences for either MHC-similar or dissimilar men during fertile phase	Increased preference for MHC-similar men	W	60 NPU-40 PU	[39]
Attractiveness	Voice	Attractiveness ratings by men are increased for women at mid-cycle	No variation in attractiveness ratings by men	B	17 NPU-21 PU	[19]
	General	Attractiveness ratings by men are increased for women at mid-cycle	No variation in attractiveness ratings by men	B	11 NPU-7 PU	[4]
	Body scent	Attractiveness ratings by men are increased for women at mid-cycle	No variation in attractiveness ratings by men	B	42 NPU-39 PU	[38]

[a]Abbreviations: B: between-individual design; NPU: non-pill users; PU: pill users; W: within-individual design.

Author's personal copy

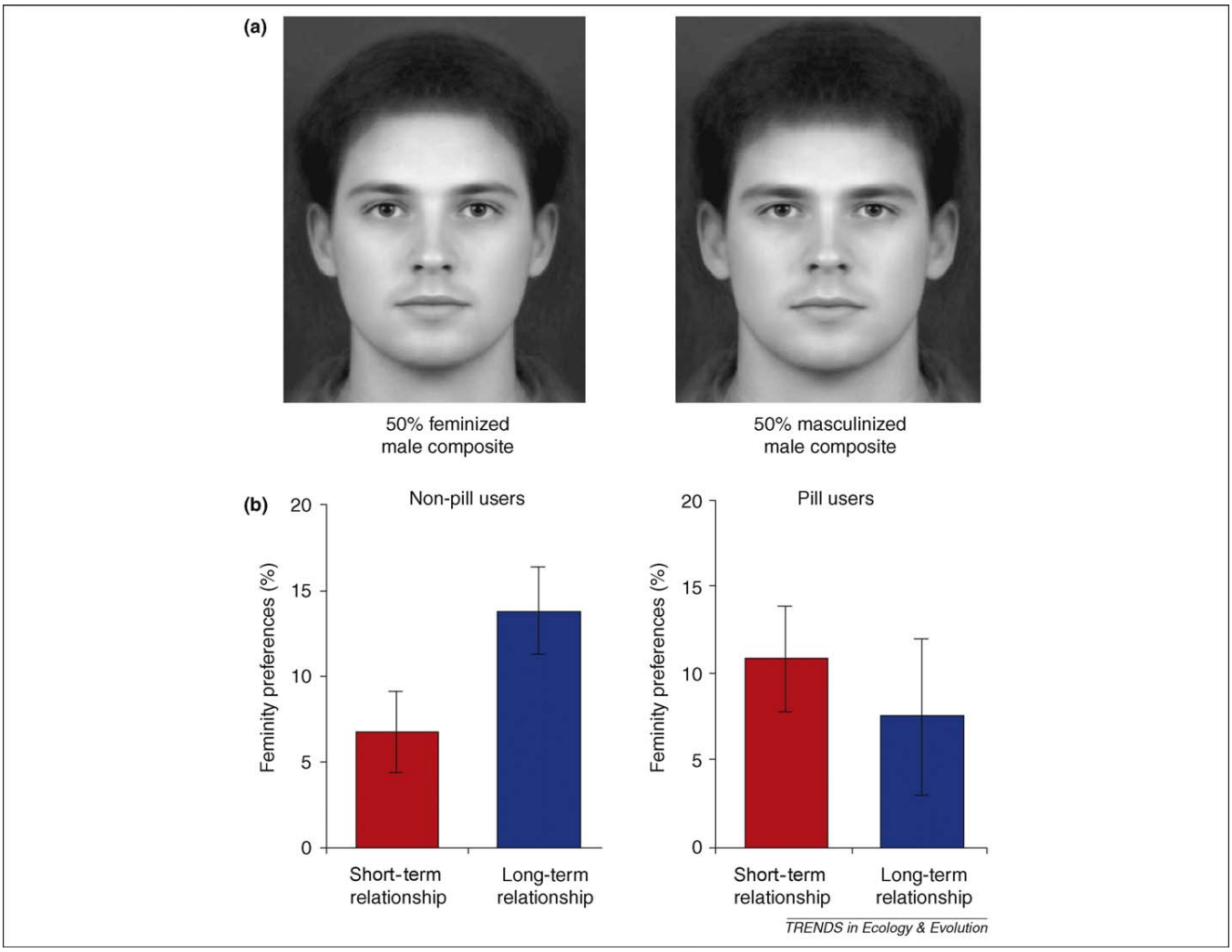

Figure 2. Effect of oral contraceptive pill use on women's facial preferences for short- and long-term relationships (short-term versus long-term preferences are proxy for, e.g. relationship during fertile versus infertile menstrual cycle phase, respectively). **(a)** Each composite image tested for female preferences was formed of ~20 male and 20 female facial images of young adults in a neutral pose. Five different images were presented in random order to participants (158 women aged between 16 and 39 years) recording their preferences for short- and long-term contexts. **(b)** Normally cycling women (non-pill users) preferred less masculine faces in a long-term context compared with a short-term context. Masculinity-related physical traits in men are related to high levels of testosterone [70], which, because of its associated immunosuppressive effects, is thought to be an indicator of genetic quality because it is sustainable only by an individual having high genetic resistance against pathogens [71]. Context-dependent preferences are adaptive if they maximize: (i) non-genetic material benefits (i.e. parental investment and cooperation) in long-term relationships, and (ii) genetic benefits (e.g. immunocompetence) from short-term or extra-pair partners. Such context-dependent preferences were not displayed by pill users, who consistently preferred feminine features in men. Adapted with permission from Ref. [33].

in situations where they can compare the attractiveness of different women, the use of the oral contraceptive pill could influence a woman's attractiveness to men. Kuukasjärvi *et al.* [38] found that pill and non-pill users do not differ in their overall odour attractiveness but, however, unlike in normally cycling women, the attractiveness of the odours of pill users does not depend on their menstrual cycle phase [38]. Thus, oral contraceptives might remove the cyclicity of female attractiveness. Similarly, whereas the voices of normally cycling women become more attractive as the potential for conception increases, this is not observed for pill users [19]. The consequences of such changes in attractiveness for men's preferences and female intra-sexual competition are currently unknown but there is some support for real-life consequences: revisiting the lap-dancing study, normally cycling lap dancers made ~US$20 more per hour in their fertile phase as compared to their luteal phase, whereas pill users did not show any mid-cycle peak in tip earnings (Figure 1; [4]). This is among the most direct current evidence for pill use disrupting women's attractiveness cycle, given that real consumer spending patterns (i.e. tips) probably reflect actual mate choice decision more directly than verbally stated hypothetical attractiveness judgments [4].

Unfortunately, however, the previous studies cannot with confidence directly attribute the differences in preferences in pill users and non-pill users to the pill, and must be interpreted cautiously. First, female cycle phase is often not systematically inferred through physiological measurements but instead self-reports, introducing noise into the data sets. Second, human mate choice studies, although often conducted using elaborate designs, suffer from relatively small sample sizes and, sometimes, potential confounding factors. Nevertheless, the increasing number of consistent findings on the effects of the pill by several research groups using a wide range of methods and

Author's personal copy

outcome measures are intriguing. Third, most studies have not been aimed at directly testing the effect of oral contraceptives on mate preferences; instead, their findings have emerged as secondary results obtained from between-subject designs with regard to the pill users. It thus remains possible that pill users and non-users differ and pill users, for example, have been reported as having more lifetime partners than others [33], indicating that pill and non-pill users possibly vary in their degree of sociosexuality. Whether an increased number of sexual partners is the cause or the consequence of the use of contraception is unknown. Pill and non-pill users might also generally differ in other ways, such as their degree of conscientiousness and openness to experience or their socio-economic status, all of which could interact with cycling mate preferences and choices.

Recently, Roberts *et al.* [39] attempted to eliminate these potential confounds by adopting a within-subject design in which women's mate preferences were assessed before and after they began taking the pill. Women starting the pill showed a significant preference shift towards MHC similarity compared with three months before the pill was taken, a shift that was not observed in the control group of normally cycling women (Figure 3 [39]). This study replicates previous evidence based on between-subject comparisons [31,37], and suggests that contraceptive pill use disrupts disassortative mate preferences in women, leading to a preference for individuals who are similar to relatives. Although the study used a within-subject design, allocation of women towards the pill or the control group was the decision of the participants, for ethical reasons.

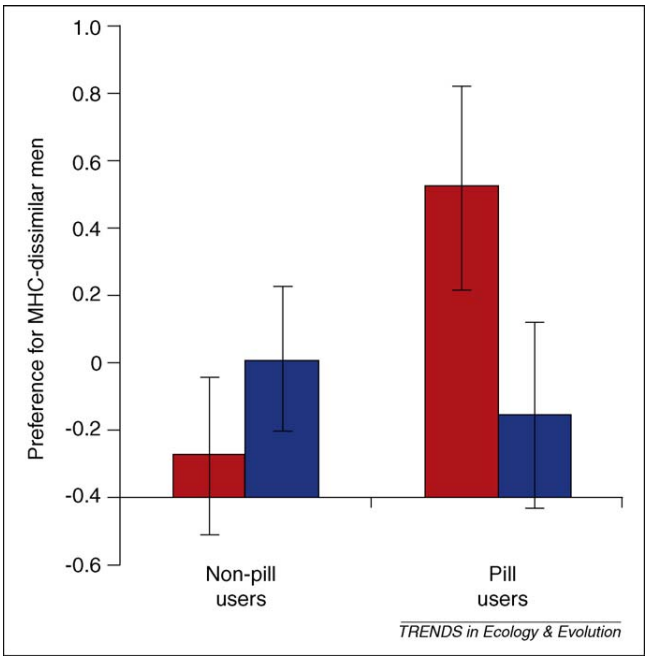

Figure 3. Mean difference in odour desirability ratings for MHC-dissimilar and MHC-similar men by women before (session I; red bar) and during (session II, blue bar) the use of oral contraceptive pill. Positive scores indicate preferences for MHC-dissimilar odours. In session I, none of the women were using the pill, and in session II, 60 had started using the pill whereas 40 had not. A decreasing preference for dissimilarity across the two sessions was observed among the pill-using group and, to a lesser extent, an increasing preference for dissimilarity in the control group. This suggests that pill use disrupts preferences for genetically dissimilar men at MHC loci. Adapted, with permission, from Ref. [39].

The best way to show experimentally an effect of the pill (rather than of pill-related confounds in personality and mating strategy) would be through double-blind placebo-controlled random assignment of women to pill versus non-pill groups, or of random within-subject comparison of active pill versus placebo-pill users. This might be difficult to execute for obvious ethical reasons, although perhaps not impossible if accompanied by condom-use or other non-hormonal additional contraceptive methods for both groups.

Consequences of maladaptive mate choice

The contraceptive pill appears to interfere with natural mate preferences, but it is currently unknown whether this also leads to altered mate choice decisions. Do couples formed while women were taking the pill differ in any way from others, and if so, is the difference a direct effect of the pill? If the effect of the pill is strong enough to modify actual mate choice, what are the consequences for marital stability and fitness of offspring? It must be acknowledged that current evidence suggests such changes in preferences mainly concern short-term partners. However, for women who can have it all (both genetic quality and non-genetic material benefits combined in a single mate), the classic distinction between short- and long-term partners might not hold because a one-night stand with a short-term partner of high genetic quality can be converted into a long-term relationship. In that context, the effect of the pill might be extended to pair-bond formation and production of within-pair offspring. For other women, attributes or quality of the long-term partners might not change as a consequence of the pill use, but the pill might decrease motivations for extra-pair sex at mid-cycle and influence satisfaction and stability of long-term relationships. In any case, the possibility remains that female–female competition for the access to preferred long-term mates could be affected.

We can thus predict that: (i) the use of the pill when choosing a partner for reproduction has consequences for actual mate choice and subsequent offspring survival, health and reproductive prospects; and (ii) commencement or cessation of the pill influences the quality and stability of pre-existing long-term relationships [40], which are not independent of offspring social and physical well-being [41,42].

First, if using the pill while forming relationships leads to a choice of an otherwise less-preferred partner owing to the potentially altered mate preferences discussed above, this could give rise, for example, to decreased genetic compatibility between mates through the choice of MHC-similar mates. One prediction is that offspring of pill users are more homozygous than expected, possibly related to impaired immune function and decreased perceived health and attractiveness [43]. Currently, there are no studies investigating the direct effect of the pill on such outcomes, and whether genetic incompatibility between mates influences offspring reproductive success in humans is also not proven. For example, choosing MHC-similar mates can be associated with spontaneous abortion of foetuses and decreased hererozygosity-related problems in the resulting offspring [44–46]. However, few studies

Author's personal copy

have investigated whether more homozygous foetuses are preferentially aborted; results in outbred populations are inconsistent, and studies in isolated populations with dissassortative mating do not show any deficit in homozygous children (reviewed in Refs [44–47]). In outbred populations, MHC similarity between partners is associated with reduced offspring birthweight [45], which in turn can have long-term effects on offspring health and reproductive success [48,49]. Moreover, MHC similarity between spouses can be associated with the genesis for pre-eclampsia [50]. Finally, reduced genetic compatibility between partners could also influence the time taken to conceive [51].

Investigations into the relationship between the use of pill at pair-bond formation and fertility problems might thus provide insights into the effect of pill use on mate choice and subsequent reproductive outcomes. In addition, offspring health-related, physical or behavioural traits could also be affected, if the pill leads to a choice of otherwise less-preferred partners. For example, if pill users mate with less masculine men and masculinity is heritable [52], then their children are also likely to express less masculine phenotypes, potentially influencing attractiveness, behaviour and reproductive strategies. However, studies aimed at testing these possibilities are currently lacking.

Second, if mate preferences altered by the pill, such as odour or facial perception, play a part in maintaining attraction to partners, relationship satisfaction, stability and duration could ultimately be affected. Does starting to take the pill influence the stability of an already existing pair-bond? This could happen if cyclicity in female attractiveness and behaviour [4,21–23] helped to maintain partner attraction; more importantly, ultimately women might prefer different male characters when using the pill. Alternatively, if a woman who began a long-term relationship while taking the pill subsequently stops taking it to conceive, is the woman's attraction to her partner reduced?

Studies that compare divorce rates or marital satisfaction across societies that differ by the prevalence of pill use but are similar in, for example, social tolerance for divorce and use of contraceptives might prove helpful in understanding whether marital dissatisfaction owing to the effect of the pill on mate choice could influence the duration and the stability of long-term relationships. Such approaches could be supplemented with investigation of large-scale individual-level longitudinal datasets now available for a range of societies, including detailed information on partners, reproductive events and various psychological and social outcomes across several decades, that could be linked to medical records or questionnaire data on pill use at different time periods. Such retrospective studies on women who have gone on or off the pill before or during a long-term relationship would enable investigating how pill use impacts women's mating decisions.

Conclusion

There is emerging evidence that the use of the pill by women can disrupt: (i) the variation in mate preferences across their menstrual cycle; (ii) their attractiveness to men; and (iii) their ability to compete with normally cycling women for access to mates. Consequently, mate choice studies in humans have routinely recorded pill use during the past decade to control for its confounding effects, but little effort has been invested in understanding the consequences of such effects of the pill. Moreover, some important limitations of previous results must be acknowledged. For example, all but one study are based on between-subjects designs, thus not controlling for possible pre-existing differences in pill and non-pill users (Table 1). We thus suggest the need for further studies using within-individual designs, and investigating whether general differences between pill users and non-users account for the effect of the pill on mate preferences. Whether the influence of pill use on mate preferences then interacts with actual mate choice is an open question: first, supporting evidence that mate preferences in normally cycling women are reflected on the choice of real partners is relatively indirect and second, whether the use of the pill when making pair-bonding decisions leads to choose an otherwise (when normally cycling) less preferred partner is currently unknown. Finally, all of the studies so far have been conducted on Western monogamous societies using mostly university student samples. Whether the pill presents a real evolutionary problem is likely to depend on the social context in which preferences are disrupted; the local importance of short-term preferences for choosing genetic fathers; the overall opportunity for women to choose mates; and the costs of EPP.

Because only short-term but not long-term partner preferences tend to vary with the menstrual cycle (reviewed in Ref. [3]), we predict different effects of the pill on mating decisions depending on the context and the women's opportunities. Consider the effect of using the pill first on a woman whose short-term partner becomes long-term partner with whom offspring are produced (e.g. women who can have both genetic benefits and non-genetic material benefits from the same mate). In this context, the use of oral contraceptives could interfere not only with the ability to attract the preferred man but also cause stronger phenotypic correlations between partners, and/or lead to chosen men being of different phenotypes than those otherwise preferred (i.e. less masculine, symmetrical and genetically different), which could have important long-term consequences for offspring. Then, consider the effect of using the pill on a woman whose short-term and long-term partners differ (e.g. women trading off between genetic benefits in short-term relationships and non-genetic material benefits in long-term relationships). In a long-term context, the pill might not interfere with a woman's preferences but rather with the ability of a woman to compete for, or to retain, her preferred mate resulting from a potentially decreased attractiveness, as compared to normally cycling women. Given that, worldwide, 9% of women aged 15 to 49 who are married or in union use the pill and >50% of women in pair-bond rely on the pill in developed countries such as Germany (http://www.unpopulation.org), understanding how the pill might influence formation of pair-bonds in different social contexts is an important question to resolve.

The ultimate outstanding evolutionary question concerns whether the use of oral contraceptives when making

Author's personal copy

mating decisions can have long-term consequences on the ability of couples to reproduce and the reproductive success of offspring. These questions have not received any attention to date. It is worthy of note that since the approval of the pill as a contraceptive method by the US Food and Drug Administration (FDA) in 1960 and the subsequent rapid export, for example, to Canada (1961), Australia (1961) and Europe (West Germany, 1961, UK, 1961, France, 1967), the potential side-effects on a range of women's psychological attributes and behaviour have never been investigated by FDA or drug companies. Given the centrality of relationship satisfaction and offspring quality in the subjective well-being of women and mothers, drug companies marketing hormonal contraception should be encouraged to institute large-scale clinical trials investigating behavioural and psychological side-effects potentially associated with oral contraceptives, and any possible maladaptive side-effects of pill use on mate choice, attractiveness, relationship satisfaction, divorce probability and offspring health.

Any such effects should be weighed against the multiple benefits that the invention of the pill has brought. This revolutionary contraceptive method has given women unprecedented control over their fertility with the possibility to sample different partners before reproduction, to control their number of children, to reach optimal birth spacing given circumstances or to end reproductive career before menopause if desired, which has had a considerable impact on their social life. For instance, a sharp increase in college attendance and graduation rates for women was observed after the pill was legalized [7]. The ability to control fertility without sacrificing sexual relationships has facilitated women's long-term educational and career plans, and many social scientists consider the widespread use of the pill to be key in creating women's modern economic role (reviewed in Ref. [7]). Furthermore, pill use can bring health benefits by decreasing the risk of ovarian and endometrial cancer later in life by $>$ 40% and 50%, respectively [53], by decreasing the need for induced abortion and surgical sterilization, and by helping to improve the condition of those suffering from pelvic inflammatory disease, dysmenorrhea, premenstrual syndrome, and acne [54].

Pill use is however also associated with risks and disadvantages. For instance, oral contraceptive use might increase breast cancer especially at young age (but current data are conflicting, see Ref. [53]); and when combined with cigarette smoking, pill use is associated with increased rates of cardiovascular diseases. Nevertheless, for example in USA, the risk of death due to the use of the pill in a nonsmoker (1/63 000) is less than the risk of death from pregnancy (1/11 000), suggesting that the health benefits of the pill might generally outweigh its costs [53]. As we have argued, however, the pill might also have a non-negligible impact on mating decisions and subsequent reproduction. If this is the case, pill use will have implications for both current and future generations, and we hope that this review will stimulate further research on this question.

Acknowledgements

We acknowledge Tiina Sepp for the original idea for this paper. We also thank Hannah Dixon, Charlotte Faurie and Jenni Pettay for help with literature; Steve Gangestad, Geoffrey Miller, Ian Rickard, Craig Roberts, Andy Russell, Rhonda Snook and an anonymous referee for helpful discussions or comments on the manuscript. This research was funded by the Kone Foundation and the Royal Society of London.

References

1 Wilcox, A.J. *et al.* (1995) Timing of sexual intercourse in relation to ovulation: effects on the probability of conception, survival of the pregnancy, and sex of the baby. *New Engl. J. Med.* 333, 1517–1521
2 Thornhill, R. and Gangestad, S.W. (2008) *The Evolutionary Biology of Human Female Sexuality*, Oxford University Press
3 Gangestad, S.W. and Thornill, R. (2008) Human oestrus. *Proc. R. Soc. Lond. B* 275, 991–1000
4 Miller, G. *et al.* (2007) Ovulatory cycle effects on tip earnings by lap dancers: economic evidence for human estrus? *Evol. Hum. Behav.* 28, 375–381
5 Nagase, T. *et al.* (2003) Why family planning matters. Population Reports. *Contraception* 68, 125–134
6 Shah, N.M. *et al.* (2001) Trends, patterns and correlates of contraceptive use among Kuwaitis, 1984–1999. *Med. Principles Pract.* 10, 34–40
7 Goldin, C. and Katz, L.F. (2002) The power of the pill: oral contraceptives and women's career and marriage decisions. *J. Polit. Econ.* 110, 730–770
8 Gangestad, S.W. *et al.* (2004) Women's preferences for male behavioral displays change across the menstrual cycle. *Psychol. Sci.* 15, 203–207
9 Haselton, M.G. and Miller, G. (2006) Women's fertility across the cycle increases the short-term attractiveness of creative intelligence. *Human Nature* 17, 50–73
10 Gangestad, S.W. *et al.* (2007) Changes in women's mate preferences across the ovulatory cycle. *J. Pers. Soc. Psychol.* 92, 151–163
11 Pillsworth, E.G. and Haselton, M.G. (2006) Male sexual attractiveness predicts differential ovulatory shifts in female extra-pair attraction and male mate retention. *Evol. Hum. Behav.* 27, 247–258
12 Gangestad, S.W. *et al.* (2002) Changes in women's sexual interests and their partners' mate retention tactics across the menstrual cycle: Evidence for shifting conflicts of interest. *Proc. R. Soc. Lond. B* 269, 975–982
13 Garver-Apgar, C.E. *et al.* (2006) Major histocompatibility complex alleles, sexual responsivity, and unfaithfulness in romantic couples. *Psychol. Sci.* 17, 830–835
14 Anderson, K.G. (2006) How well does paternity confidence match actual paternity? Evidence from worldwide nonpaternity rates. *Curr. Anthropol.* 47, 513–519
15 Moller, A.P. and Cuervo, J.J. (2000) The evolution of paternity and paternal care in birds. *Behav. Ecol.* 11, 472–485
16 Tarín, J.J. and Gómez-Piquer, V. (2002) Do women have a hidden heat period? *Hum. Reprod.* 17, 2243–2248
17 Alexander, R.D. and Noonan, K.M. (1979) Concealment of ovulation, parental care, and human social evolution. In *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective* (Chagnon, N.A. and Irons, W., eds), pp. 436–453, Duxbury Press
18 Bryant, G.A. and Haselton, M.G. (2009) Vocal cues of ovulation in human females. *Biol. Lett.* 5, 12–15
19 Pipitone, R.N. and Gallup, G.G.J. (2008) Women's voice attractiveness varies across the menstrual cycle. *Evol. Hum. Behav.* 29, 268–274
20 Roberts, S.C. *et al.* (2004) Female facial attractiveness increases during the fertile phase of the menstrual cycle. *Proc. R. Soc. Lond. B* 271, 270–272
21 Haselton, M.G. *et al.* (2007) Ovulatory shifts in human female ornamentation: near ovulation, women dress to impress. *Horm. Behav.* 51, 40–45
22 Durante, K.M. *et al.* (2008) Changes in women's choice of dress across the ovulatory cycle: naturalistic ad laboratory task-based evidence. *Pers. Soc. Psychol. Bull.* 34, 1451–1460
23 Haselton, M.G. and Gangestad, S.W. (2006) Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. *Horm. Behav.* 49, 509–518
24 Flinn, M.V. (1988) Mate guarding in a Caribbean village. *Ethol. Sociobiol.* 9, 1–28
25 Pagel, M. (1994) The evolution of conspicuous oestrous advertisement in Old World monkeys. *Anim. Behav.* 47, 1333–1341

Author's personal copy

26 Buss, D.M. (1999) *Evolutionary Psychology, The New Science of the Mind*, Allyn and Bacon
27 Fisher, M.L. (2004) Female intrasexual competition decreases female facial attractiveness. *Proc. R. Soc. Lond. B* 271, 283–285
28 Fisher, M.L. *et al.* (2008) The influence of relationship status, mate seeking, and sex on intrasexual competition. *J. Soc. Psychol.* 148, 493–508
29 Vukovic, J. *et al.* (2009) Circum-menopausal effects on women's judgements of facial attractiveness. *Biol. Lett.* 5, 62–64
30 DeBruine, L.M. *et al.* (2008) Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proc. R. Soc. Lond. B* 273, 1355–1360
31 Wedekind, C. and Furi, S. (1997) Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proc. R. Soc. Lond. B* 264, 1471–1479
32 Todd, P.M. *et al.* (2007) Different cognitive processes underlie human mate choices and mate preferences. *Proc. Natl. Acad. Sci. U.S.A.* 104, 15011–15016
33 Little, A.C. *et al.* (2002) Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proc. R. Soc. Lond. B* 269, 1095–1100
34 Penton-Voak, I.S. (1999) Menstrual cycle alters face preference. *Nature* 399, 741–742
35 Feinberg, D.R. *et al.* (2008) Correlated preferences for men's facial and vocal masculinity. *Evol. Hum. Behav.* 29, 233–241
36 Thornhill, R. and Gangestad, S.W. (2003) Do women have evolved adaptation for extra-pair copulation? In *Evolutionary Aesthetics* (Voland, E. and Grammer, K., eds), pp. 341–368, Springer-Verlag
37 Wedekind, C. *et al.* (1995) Mhc-dependent mate preferences in humans. *Proc. R. Soc. Lond. B* 260, 245–249
38 Kuukasjärvi, S. *et al.* (2004) Attractiveness of women's body odors over the menstrual cycle: the role of oral contraceptives and receiver sex. *Behav. Ecol.* 15, 579–584
39 Roberts, S.C. *et al.* (2008) MHC-correlated odour preferences in humans and the use of oral contraceptives. *Proc. R. Soc. Lond. B* 275, 2715–2722
40 Vollrath, F. and Milinski, M. (1995) Fragrant genes help Damenwahl. *Trends Ecol. Evol.* 10, 307–308
41 Kim, K. and Smith, P.K. (1999) Family relations in early childhood and reproductive development. *J. Reprod. Infant. Psych.* 17, 133–147
42 Kim, K. and Smith, P.K. (1998) Retrospective survey of parental marital relations and child reproductive development. *Int. J. Behav. Med.* 22, 729–751
43 Roberts, S.C. *et al.* (2005) MHC-assortative facial preferences in humans. *Biol. Lett.* 1, 400–403
44 Beydoun, H. and Saftlas, A.F. (2005) Association of human leucocyte antigen sharing with recurrent spontaneous abortions. *Tiss. Antig.* 65, 123–135
45 Reznikoff-Etievant, M.F. *et al.* (1991) HLA antigen-sharing in couples with repeated spontaneous abortions and the birth weight of babies in successful pregancies. *Am. J. Reprod. Immunol.* 25, 25–27
46 Ober, C. *et al.* (1999) Inbreeding effects on fertility in humans: evidence for reproductive compensation. *Am. J. Hum. Genet.* 64, 225–231
47 Choudhury, S.R. and Knapp, L.A. (2001) Human reproductive failure II: Immunogenetic and interacting factors. *Hum. Reprod. Update* 7, 135–160
48 Lummaa, V. and Clutton-Brock, T. (2002) Early development, survival and reproduction in humans. *Trends Ecol. Evol.* 17, 141–147
49 Barker, D.J.P. (1998) *Mothers, Babies and Health in Later Life*, Churchill Livingstone
50 Ooki, I. *et al.* (2008) Studies on the compatibility of HLA-Class II alleles in patient couples with severe pre-eclampsia using PCR-RFLP methods. *Am. J. Reprod. Immunol.* 60, 75–84
51 Havlicek, J. and Roberts, C. (2009) MHC-correlated mate choice in humans: A review. *Psychoneuroendocrinology* 34, 497–512
52 Cornwell, R.E. and Perrett, D.I. (2008) Sexy sons and sexy daughters: the influence of parents' facial characteristics on offspring. *Anim. Behav.* 76, 1843–1853
53 Sherif, K. (1999) Benefits and risks of oral contraceptives. *Am. J. Obstet. Gynecol.* 180, S342–S347
54 Huber, J.C. *et al.* (2008) Non-contraceptive benefits of oral contraceptives. *Expert Opin Pharmacother* 9, 2317–2325
55 Bellis, M.A. and Baker, R.R. (1990) Do female promote sperm competition? Data for humans. *Anim. Behav.* 40, 997–999
56 Brown, G.R. *et al.* (2009) Bateman's principles and human sex roles. *Trends Ecol. Evol.* 24, 297–304
57 Magrath, M.J.L. and Komdeur, J. (2003) Is male care compromised by additional mating opportunity? *Trends Ecol. Evol.* 18, 424–430
58 Jennions, M.D. and Petrie, M. (2000) Why do females mate multiply? A review of the genetic benefits. *Biol. Rev. Cambridge Phil. Soc* 75, 21–64
59 Mandelbaum, D.G. (1938) Polyandry in Kota Society. *Am. Anthropol.* 40, 574–583
60 Freeman-Gallanta, C.R. *et al.* (2006) Genetic similarity, extrapair paternity, and offspring quality in Savannah sparrows (*Passerculus sandwichensis*). *Behav. Ecol.* 17, 952–958
61 Daly, M. and Wilson, M. (1988) *Homicide*, Aldine de Gruyter
62 Daly, M. *et al.* (1982) Male sexual jealousy. *Ethol. Sociobiol.* 3, 11–27
63 Betzig, L. (1989) Causes of conjugal dissolution: a cross-cultural study. *Curr. Anthropol.* 30, 654–676
64 Apicella, C.L. and Marlowe, F.W. (2004) Perceived mate fidelity and paternal resemblance predict men's investment in children. *Evol. Hum. Behav.* 25, 371–378
65 Gangestad, S.W. and Thornhill, R. (1998) Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proc. R. Soc. Lond. B* 265, 927–933
66 Fessler, D.M.T. (2003) No time to eat: An adaptationist account of periovulatory behavioral changes. *Q. Rev. Biol.* 78, 3–21
67 Bröder, A. and Hohmann, H. (2003) Variations in risk taking behavior over the menstrual cycle: an improved replication. *Evol. Hum. Behav.* 24, 391–398
68 Chavanne, T.J. and Gallup, G.G. (1998) Variation in risk taking behavior among female college students as a function of the menstrual cycle. *Evol. Hum. Behav.* 19, 27–32
69 Roney, J.R. and Simmons, Z.L. (2008) Women's estradiol predicts preference for facial cues of men's testosterone. *Horm. Behav.* 53, 14–19
70 Penton-Voak, I.S. and Chen, J.Y. (2004) High salivary testosterone is linked to masculine male facial appearance in humans. *Evol. Hum. Behav.* 25, 229–241
71 Folstad, I. and Karter, A.J. (1992) Parasites, bright males and the immunocompetence handicap. *Am. Nat.* 139, 603–622
72 Thornhill, R. and Gangestad, S.W. (1999) The scent of symmetry: a human sex pheromone that signals fitness? *Evol. Hum. Behav.* 20, 175–201