

Review

Human oestrus

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For several decades, scholars of human sexuality have almost uniformly assumed that women evolutionarily lost oestrus—a phase of female sexuality occurring near ovulation and distinct from other phases of the ovarian cycle in terms of female sexual motivations and attractiveness. In fact, we argue, this long-standing assumption is wrong. We review evidence that women's fertile-phase sexuality differs in a variety of ways from their sexuality during infertile phases of their cycles. In particular, when fertile in their cycles, women are particularly sexually attracted to a variety of features that likely are (or, ancestrally, were) indicators of genetic quality. As women's fertile-phase sexuality shares with other vertebrate females' fertile-phase sexuality a variety of functional and physiological features, we propose that the term oestrus appropriately applies to this phase in women. We discuss the function of women's non-fertile or extended sexuality and, based on empirical findings, suggest ways that fertile-phase sexuality in women has been shaped to partly function in the context of extra-pair mating. Men are particularly attracted to some features of fertile-phase women, but probably based on by-products of physiological changes males have been selected to detect, not because women signal their cycle-based fertility status.

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1. OVERVIEW

Scholars have long thought that the nature of human sexuality provides key insights into hominin evolution, not only of human mating adaptations but also, more broadly, the importance of biparental care in human evolution, human foraging patterns, prominent aspects of the human life course, the general nature of human social organization and even reasons for hominin encephalization—indeed, virtually every core feature of adaptive complexes arisen in hominins (e.g. Alexander & Noonan 1979; Symons 1979; Alexander 1990; Miller 2000).

For close to half a century, evolution-minded theories of human sexuality have typically been built around a foundational 'fact': during the course of their evolution, women lost a distinct phase of fertile sexuality in their reproductive cycles, typically referred to as 'oestrus' in non-human mammalian species (see Etkin 1964; Jolly 1972; Alexander & Noonan 1979; Burley 1979; Spuhler 1979; Symons 1979; Alexander 1990). Behaviourally, oestrus has been thought to entail enhanced proceptivity and receptivity to males when females are fertile. In its stead, women evolved to exhibit 'continuous' sexuality—a sexual nature that changes, if at all, in only minor ways across the cycle, such that women are near-equally sexually proceptive throughout it. Typically, scholars have thought loss of oestrus functions to conceal ovulation.

Recent evidence and theory indicates that this fact is fiction. Women have not lost oestrus. Although women are continuously receptive, their sexuality is not accurately characterized as continuous. Rather, women possess 'dual

sexuality,' consisting of a phase of oestrus and a phase of extended (non-fertile) sexuality in their cycles. Loss of oestrus in humans serves no function, as it simply has not occurred, though there is an important sense in which women have evolved to conceal cycle fertility (or, in our terms, their oestrus).

In this review, we focus on evidence and theory supporting these claims. We distinguish the oestrous phase of women's cycles from their phase of extended sexuality. We also briefly comment on women's concealed oestrus. A forthcoming book expands upon these and related arguments (Thornhill & Gangestad in press).

2. THE PHENOMENON OF OESTRUS

A dictionary definition of oestrus is 'the periodic state of excitement in the female of most mammals, excluding humans, that immediately precedes ovulation and during which the female is most receptive to mating; heat' (*American Stedman's Medical Dictionary*, 2002). The term derives from the Greek word for a botfly that excites cows when they lay eggs on their hide, and was first adopted to refer to the sexual excitement during heat by 1890 (according to the Oxford English Dictionary, in *Billings' Medical Dictionary*). This dictionary definition generally reflects scientific usage, particularly of the concept of behavioural oestrus (indeed, medical dictionaries seek to distil scientific usage; see Nelson 2000). (Some usages of the term, however, also include female attractiveness to males as a component of oestrus. Particularly in this regard, some authors do not apply the term to all non-human primates (see §7).) This characterization of behavioural oestrus is, in our view, flawed or incomplete in three ways.

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(a) Behavioural oestrus is not typically characterized by generalized sexual excitement or motivation

It makes little sense that females possess special adaptation to indiscriminately seek copulations from males. Males differ in their ability to offer genetic benefits to offspring or material benefits to female mates. Females should hence be choosy, not indiscriminate, when making mate choices during the fertile phase of their reproductive cycles. Empirically, evidence suggests that, indeed, females are typically choosy when fertile, often favouring males who, in theory, would make good sires through delivery of intrinsic good genes or compatible genes (e.g. house mouse: Potts *et al.* 1991, Williams & Lenington 1993; pronghorn antelope: Byers *et al.* 1994; pademelon: Radford *et al.* 1998; American bison: Wolff 1998; the Asian elephant: Schulte & Rasmussen 1999; pygmy loris: Fisher *et al.* 2003; snow vole: Ludue-Larena *et al.* 2003; guinea-pig: Hohoff *et al.* 2003; rhesus macaque: Waitt *et al.* 2003; meadow vole: Spritzer *et al.* 2005; red deer: Charlton *et al.* 2007). Recent evidence on a close relative of humans, the common chimpanzee, illustrates this point. Females are more sexually receptive and initiate sex with more males *outside* of the period of peak fertility than during their most fertile period (Stumpf & Boesch 2005). Sex during the period of infertile sex appears to function to reduce male aggression towards offspring by confusing paternity, which females do by having sex with most, any resident male. At peak fertility, by contrast, females are choosier—they both initiate less sex with other males and are receptive to fewer males' advances—and their preferences tend to converge on the same males, ones who may offer the best genes for offspring.

Exceptions, in which females possess oestrous adaptations to assure conception *per se*, should be limited to unusual circumstances in which females' encounter rate with males is severely limited or they are faced with strong constraints on time to find sperm. For instance, gravid túngara frogs (who must lay soon after egg maturation) will accept sperm from lower quality males (but still prefer sperm from high-quality males when offered choice; Lynch *et al.* 2005, 2006). In general, sexual selection favours males who possess adaptation to seek out and find fertile females. Hence, rarely should female reproduction be sperm limited in natural circumstances (see Thornhill & Gangestad (in press) for a fuller discussion; see also Pagel 1994).

(b) A scientifically proper application does not restrict oestrus to mammals

We argue that it makes little theoretical sense to restrict the concept of oestrus to mammals. All vertebrates possess receptors for oestrogen (itself named for being the 'gen' (or generator) of oestrus). These receptors hence evolutionarily debuted in an ancestor common to all vertebrates and became linked to female-specific reproductive capacitation in the ancestor to jawed vertebrates (gnathosomes) ca 400 Myr ago (Thornton 2001). Moreover, oestrogen's effects on female sexuality may be homologous across (nearly) all vertebrates and function, in some ways, similarly. (Nonetheless, other reproductive hormones, such as progesterone and testosterone (phylogenetically almost as old as oestrogen; Thornton *et al.* 2003), also play important roles in modulating female sexuality in these species. Also, the precise roles played by different hormones may vary across species.) For instance, females of many bird species

exhibit mating preferences during their fertile period different from their preferences that characterize the period preceding peak fertility, and this fertile phase possesses homologies with mammalian fertile phases. Application of the term oestrus to all vertebrate females who possess a distinct fertile sexuality recognizes the homologies that they share. Scientifically, it is the most appropriate and defensible use of this term (see Thornhill & Gangestad in press).

(c) Women possess oestrus

As we review, women possess a distinct fertile sexuality that is, in fact, functionally homologous with as well as functionally similar to oestrus observed in other vertebrate species (see also Tarín & Gómez-Piquer 2002).

3. CHANGES IN WOMEN'S SEXUAL PREFERENCES ACROSS THE REPRODUCTIVE CYCLE

Similar to other mammal species, human females are fertile during a brief window of their cycles, from several days prior to the day of ovulation up until the day of ovulation itself (e.g. Wilcox *et al.* 1995). If, in fact, women possess a fertile-phase sexuality that is distinct from their sexuality outside the fertile phase, female preferences (e.g. features they find most sexually attractive) should change across the cycle. If fertile-phase sexuality was shaped by the benefits of obtaining sires who offer genetic benefits to offspring, women should particularly prefer male features indicative of genetic benefits to offspring when fertile. Finally, cycle shifts should be particular to women's evaluations of men's sexual attraction (e.g. their 'sexiness') rather than dimensions related to long-term mateship compatibility (Penton-Voak *et al.* 1999).

(a) Preferences do shift

Over 20 studies, most in the past decade, show that female preferences clearly do shift. We summarize findings on purported fitness indicators in table 1. At mid-cycle, normally ovulating, non-pill using women particularly prefer a number of masculine male traits perceived through a variety of sensory modalities: the scent of social dominance; facial masculinity; bodily masculinity; masculine vocal qualities; masculine behavioural displays; and tall height. They also prefer traits associated with body symmetry (an indicator of developmental instability): scents associated with symmetry and facial features associated with body symmetry. Many of these effects appear to be robust, even if some effects are of modest size and questions about mediators remain. (For instance, what is the chemical(s) responsible for women's preference for the scents of symmetry and social dominance mid-cycle? Women are more attracted to certain androgen-related scents when mid-cycle, but the one published study examining preferences for the scent associated with high testosterone levels found no effect.) Masculine traits and traits associated with symmetry may have been indicators of intrinsic good genes ancestrally. (Intrinsic good genes have additive effects on fitness and hence could benefit the offspring of any female; see Jennions & Petrie 2000, Kokko *et al.* 2003.)

Evidence on whether symmetrical faces themselves are more attractive to women when they are mid-cycle is mixed. Possibly, facial symmetry itself is not a cue that individuals use to assess intrinsic good genes (Gangestad & Thornhill 2003). But Little *et al.* (2007b),

Table 1. Demonstrated variation in female preferences for purported indicators of good genes across the cycle. ('+' indicates that a significant effect (an overall preference or preference for a short-term mate at 0.05 level of statistical significance using a directed test) was detected. '-' indicates that no such effect was detected. (In no case was a significant effect in the unpredicted direction detected. Hence, minus signs connote null effects.) The interaction effect refers to finding a greater shift for ratings of attractiveness in a short-term relationship (men's sexiness) than long-term relationship. '0' means that the effect was not examined in the study. A few studies also examined differences in preferences as a function of whether women were in long-term committed relationships or single. This table does not report these effects.)

trait	study	positive finding?	interaction w relat. context
<i>masculine features</i>			
scent of social dominance	Havlicek <i>et al.</i> (2005)	+	0
scent of androstenone	Grammer (1993)	+	0
	Hummel <i>et al.</i> (1991)	+	0
scent of testosterone	Rantala <i>et al.</i> (2006)	-	0
masculine face	Penton-Voak <i>et al.</i> (1999) study 1	+	0
	Penton-Voak <i>et al.</i> (1999) study 2	+	+
	Penton-Voak & Perrett (2000)	+	0
	Johnston <i>et al.</i> (2001)	+	+
	Scarborough & Johnston (2005)	-	-
	Jones <i>et al.</i> (2005a)	+	0
facial features associated with high testosterone	Roney & Simmons 2008	+	0
masculine body	Little <i>et al.</i> (2007a)	+	+
	Gangestad <i>et al.</i> (2007)	+	+
masculine voice	Puts (2005)	+	+
	Feinberg <i>et al.</i> (2006)	+	0
dominant behaviour	Gangestad <i>et al.</i> (2004)	+	+
	(see also Gangestad <i>et al.</i> 2007)		
tall height	Pawlowski & Jasienska (2005)	+	+
dark (masculine) skin	Frost (1994)	+	0
<i>correlates of symmetry</i>			
scent of symmetry	Gangestad & Thornhill (1998)	+	0
	Thornhill & Gangestad (1999)	+	0
	Rikowski & Grammer (1999)	+	0
	Thornhill <i>et al.</i> (2003)	+	0
facial features associated with body symmetry	Thornhill & Gangestad (2003)	+	0
facial symmetry	Koehler <i>et al.</i> (2002)	-	-
	Koehler <i>et al.</i> (2006)	-	-
	Cardenas & Harris (2007)	-	0
	Little <i>et al.</i> (2007b), study 1	+	0
	Little <i>et al.</i> (2007b), study 2	+	+
<i>purported mental fitness indicators</i>			
creative talent (versus wealth)	Haselton & Miller (2006)	+	+
intelligent appearance	Gangestad <i>et al.</i> (2007)	-	-
<i>compatible genes</i>			
scent of MHC dissimilarity	Thornhill <i>et al.</i> (2003)	-	0

who did find a preference shift in two studies, discussed reasons why effects may not have been found in other research. Evidence is mixed too with respect to purported fitness indicators such as creative talent and intelligent appearance, and the one study examining a feature of compatible genes (major histocompatibility complex (MHC) dissimilarity) found no effect (but see Garver-Apgar *et al.* 2006). (See also DeBruine *et al.* (2005) who found that, during the luteal phase, women are particularly attracted to self-resembling faces of both men and women and also discuss additional selection pressures that shaped changes in preferences as a function of fertility and hormonal status.) More research examining variation across the cycle in preferences for these measures is needed.

(b) Preference shifts are not general

Women do not find all positive traits sexier mid-cycle. Traits particularly valued in long-term mates (e.g. promise

of material benefits) appear to be preferred as strongly by infertile women as by fertile women (e.g. Thornhill *et al.* 2003). In one study (Gangestad *et al.* 2007), women rated the attractiveness of men shown on videotapes. Independent samples of women rated men on a variety of qualities desirable in mates. Whereas fertile-phase women were particularly sexually attracted to men perceived as arrogant, intrasexually confrontative, muscular and physically attractive, no cycle shifts were observed in women's attraction to men seen to be successful financially, intelligent or kind and warm. Men who appeared to be sexually faithful were less sexually attractive to fertile-phase women; put otherwise, fertile women are particularly attracted to men who appear that they would not be faithful (probably because they possess features women find attractive in sex partners).

Women are also particularly attracted to healthy looking faces during the infertile luteal phase and, more

generally, when women experience relatively high progesterone levels (Jones *et al.* 2005a,b). Possibly, this preference shift is a by-product of selection favouring avoidance of unhealthy persons during pregnancy.

(c) Preference shifts are particular to evaluations of men's sexiness

No study to date has detected fertile-phase shifts in women's evaluations of men as good long-term partners. Rather, shifts in preferences are particular to women's ratings of men's sex appeal (or, as it is sometimes phrased, men's attractiveness as a 'short-term partner'; table 1).

Considered together, the findings are consistent with the proposal that women's oestrous preferences function to enhance the genetic quality of offspring through sire choice. Naturally, we cannot be certain that masculine qualities and features associated with developmental stability were associated with genetic quality ancestrally, but we know of no adequate alternative explanation of these preferences. The view that the preferences function to acquire genes for offspring constitutes a defensible 'inference to the best explanation' (e.g. Sterelny & Griffiths 1999).

(d) Women's fertile-phase sexuality is appropriately referred to as oestrus

Female vertebrate oestrus typically entails adaptations that possess this same function (reviewed by Thornhill & Gangestad *in press*). Moreover, components of the physiological machinery (hormonal and neural) possessing this function are broadly shared by vertebrates. Aspects of women's oestrus, then, are homologous with oestrus in other vertebrates. From a broad comparative and phylogenetic perspective, then, women's fertile-phase sexuality constitutes oestrus.

4. WOMEN'S EXTENDED SEXUALITY

(a) The function of extended sexuality

In addition to possessing oestrus, some vertebrate species are also sexually receptive or proceptive outside of their fertile phase (e.g. Rodriguez-Girones & Enquist 2001); they possess 'extended sexuality,' motivation or interest in sex that is not directly conceptive (though, in theory, it typically evolved owing to its reproductive benefits, i.e. it reflects adaptation, not by-product). The explanation of extended sexuality most conceptually coherent while also receiving empirical support argues that it reflects adaptation to obtain material benefits, typically male delivered (e.g. Rodriguez-Girones & Enquist 2001; Wakano & Ihara 2005; see also Stacy 1982).

This function is illustrated by many Old World primates. Hrdy (1981) proposed that females may protect offspring from infanticide (or more mild forms of harm) imposed by resident males in a primate troop by confusing paternity. If a female has sex with all adult males in a troop during a reproductive cycle, not allowing any one to exclude possibility of paternity, it may benefit no male to harm her offspring. A female can simultaneously maintain control over paternity and receive the benefits of paternity confusion if most promiscuous outside of the fertile phase (i.e. during extended sexuality) while maintaining choosiness at peak fertility. (This assumes that males themselves cannot perfectly discriminate a female's fertile phase from her

infertile phases.) As noted earlier, Stumpf & Boesch (2005) observed precisely this pattern in common chimpanzees.

The purported function of extended sexuality in these species is, ultimately, to obtain material benefits from males. In the logic of evolutionary economics, actions that reduce male-imposed harm yield male-delivered benefits.

(b) Women exhibit extreme extended sexuality

Few, if any females, match the degree to which women's sexuality is extended into infertile phases of the reproductive cycle. A recent study of over 20 000 women of reproductive age in 13 developing countries detected no systematic changes in frequency of sexual intercourse with regular partners across the cycle, aside from a drop during menses (Brewis & Meyer 2005; cf. Wilcox *et al.* 2004). These women had sex with partners as frequently during the luteal phase as during their fertile phases. Women are sexually receptive and proceptive during other non-fertile periods of life as well: across anovulatory cycles; during adolescence; when pregnant; and when lactating.

Women's extended sexuality too appears to function to obtain male-delivered benefits. Unlike close primate relatives, however, extended sexuality in human females appears to function to enhance the flow of material benefits delivered by primary partners within pair bonds. Whether men's subsidization of women's and offspring diet serves a function of parental effort or mating effort has been widely debated (e.g. Kaplan *et al.* 2000; Hawkes 2004). Although an argument is beyond the scope of this review, recent evidence points to a role for parental effort (e.g. Marlowe 2003). Extended sexuality may enhance the flow of material benefits from partners in two different ways. First, receptivity during extended sexuality may enhance a partner's assessment of paternity (assuming, again, that male ascertainment of female fertility status is imperfect). Second, males may deliver benefits as a function of sexual access (Symons 1979; Hill 1982; Buss 2003). Females in many biparentally investing bird species appear to have a fertile sexuality as well as extended sexuality (e.g. Birkhead & Møller 1992). As in humans, these two periods are partially characterized by adaptations that have different functions. Indeed, the effects summarized in table 1 constitute evidence that sexuality during the two phases have been shaped, in part, by different costs and benefits (see also below and Thornhill & Gangestad *in press*). The phases are not discrete; rather, changes in women's preferences are graded shifts probably regulated by changes in the levels of reproductive hormones.

5. THE ROLE OF EXTRA-PAIR COPULATION

(a) Oestrus in species with biparental care

As distant vertebrate ancestors of women possessed oestrus (see above), women's oestrus did not evolve in the context of biparental care. Nonetheless, components of women's oestrus may have been altered by selection subsequent to the evolution of biparental investment in hominins. In biparentally investing species, reproductive benefits achieved through oestrus can be, in principle, partly garnered through extra-pair copulations (EPCs). Reproducing females possess primary investing partners, which vary in the extent to which they possess indicators of genetic fitness. When females paired with mates not possessing these indicators are sexually attracted to and

mate with other males during oestrus, they may receive genetic benefits to offspring through EPC. In these species, then, several additional predictions about oestrus follow. First, females on average should be more attracted to males other than primary partners during oestrus than infertile phases. Second, shifts in attraction to extra-pair males should be moderated by the qualities of the male primary partner: females with partners lacking indicators of genetic fitness should be most attracted to extra-pair males during oestrus. Females whose primary partners possess these indicators should evidence little or no shift.

In some biparental species of birds, these predictions have been confirmed: western bluebirds (Dickinson 1997, 2001); hooded warblers (Neudorf *et al.* 1997); wheatears (Currie *et al.* 1999); collared flycatchers (Sheldon *et al.* 1999, Michl *et al.* 2002); superb fairy wrens (Double & Cockburn 2000); raptors (Mougeot 2004); and common yellowthroats (Pedersen *et al.* 2006). Akçay & Roughgarden (2007) recently meta-analysed 121 studies testing claims that female birds EPC to obtain genetic benefits. Over 40% of the studies yielded support, whether assessing benefits of intrinsic good or compatible genes. As some null results occur even when true effects exist, these results are consistent with the possibility that female EPC in birds often, even if not always, functions to obtain genetic benefits.

(b) Women's extra-pair sexual interests during oestrus

In women, too, these predictions receive support. Two studies that had women report sexual attraction in the past 2 days twice in a month—once when fertile and once during the luteal phase—revealed substantial increases in women's attraction to extra-pair men during oestrus, but detected no change in women's attraction to their primary partners (Gangestad *et al.* 2002, 2005). (Using a different design, Pillsworth *et al.* (2004) did not replicate this pattern. Bellis & Baker (1990), however, found that women's rates of EPC increased mid-cycle, whereas in-pair copulation rates did not. Perhaps relatedly, Jones *et al.* (2005a) found that women reported themselves to be less committed to their partners when fertile in their cycles, when compared with during the luteal phase).

Several studies have documented moderators of these effects. (i) Gangestad *et al.* (2005) found that male primary partners' fluctuating asymmetry (FA) moderated the effect: women paired with relatively asymmetrical men experienced greater increases in attraction to extra-pair men when fertile, compared with women paired with relatively symmetrical men. By contrast, women paired with symmetrical men experienced greater shifts towards attraction to their own partners than women paired with asymmetrical men. (ii) Two studies found that women mated with sexually unattractive men (as rated by these women themselves) experienced greater increases in attraction to extra-pair men, compared with women mated with sexually attractive men (Haselton & Gangestad 2006; Pillsworth & Haselton 2006). (iii) Although most studies have focused on purported indicators of intrinsic good genes, one study examined the effects of the purported compatibility of male genes with female genes to produce fit offspring. MHC alleles code for cell surface markers used by the immune system to detect foreign pathogens. Purportedly, offspring

benefit from being heterozygotic and hence obtaining two different alleles at these loci from parents. Male–female pairs who do not share alleles at MHC loci hence possess compatible genes. Garver-Apgar *et al.* (2006) found that MHC sharing (proportion of alleles at three loci also possessed by the primary partner) predicted cycle shifts in women's attraction to extra-pair men. Women paired with men with whom they shared relatively many alleles were more attracted to extra-pair men when fertile. By contrast, women paired with men with whom they shared no alleles showed no tendency to become more attracted to extra-pair men when fertile. Moreover, men's FA and MHC sharing have independent effects on cycle shifts in women's attraction to extra-pair men (Garver-Apgar *et al.* 2006, fn 4).

6. MEN'S COUNTER-ADAPTATIONS

(a) Sexually antagonistic coevolution

As women's attraction to men other than primary partners during oestrus conflicts with the reproductive interests of primary partners, sexually antagonistic coevolution of male adaptations in response to female adaptations may be expected. In many bird species, primary partners engage in paternity assurance tactics, such as mate guarding and frequent copulation. For some species, investigators have documented increases in the intensity of these tactics when female partners are fertile (e.g. house martins: Riley *et al.* 1995; kestrels: Korpimäki *et al.* 1996; Montagu's harrier: Arroyo 1999; bearded vultures: Bertran & Margalida 1999; Seychelles warblers: Komdeur *et al.* 1999; European barn swallows: Saino *et al.* 1999; Australian magpie-larks: Hall & Magrath 2000; northern mockingbirds: Bodily & Neudorf 2004; New Zealand stitchbirds: Low 2005).

Similar effects have been documented in humans. Women report that their partners engage in greater amounts of proprietary or related behaviours (e.g. vigilance of partners' whereabouts) when they are fertile (Gangestad *et al.* 2002; Haselton & Gangestad 2006), and reports from male partners yield similar effects (Garver-Apgar *et al.* in preparation). Moreover, men whose proprietary behaviours increase most dramatically during partners' fertile period are paired with women whose extra-pair sexual attraction increases most emphatically during oestrus (Gangestad *et al.* 2002; Haselton & Gangestad 2006; Garver-Apgar *et al.* in preparation; see also Pillsworth & Haselton 2006), which suggest that a conflict of interest over women's attention to extra-pair men during oestrus drives men's increased attention to partners during oestrus. Other work indicates that men's perceptions of other men may change across the cycle as a function of their partners' fertility. Burriss & Little (2006) found that men tend to perceive dominant men as even more dominant when their partners are mid-cycle, an effect that may reflect adaptation to enhance awareness of threats from potential competitors when partners are fertile.

(b) Extra-pair paternity rates

In human populations, extra-pair paternity (EPP) rates are typically low (less than 5%) but variable (in places, more than 10%; Anderson 2006; see also Simmons *et al.* 2004). These rates do not imply a lack of sexually antagonistic coevolution surrounding females' EPC. When males invest heavily in offspring, strong selection

may lead to the evolution of costly counter-adaptations relatively effective at maintaining low EPP rates. By contrast, when the costs of EPP to male partners are relatively low, male counter-adaptations that evolve may be both less costly and less effective, leading to higher rates of EPP (see also Møller 2000). Because sexually antagonistic adaptations pertaining to female EPC can occur despite persistently low rates of female EPC, the question of whether these adaptations exist in any species is distinct from the question of whether sperm competition has been an important selective force in that species (cf. Simmons *et al.* 2004).

This point is illustrated by many raptor species, in which paternal investment importantly affects offspring success. Males hunt across wide ranges, taking them far from nests when foraging. EPP rates are typically low (less than 5%, and often less than 2%), but by no means imply a lack of sexually antagonistic selection. Males engage in costly anti-cuckoldry tactics, returning to the nest to copulate with female partners up to a dozen times a day, on average (see Mougeot 2004). In Montagu harriers, these rates have been observed to increase when females are fertile (Arroyo 1999; see also Mougeot 2004).

In some species, loss of paternal investment due to male detection of non-paternity (in conjunction with low genetic diversity, e.g. Møller 2003) may be sufficient to keep EPP rates low, despite a lack of costly male paternity assurance behaviours (e.g. some island birds such as purple sandpipers: Pierce & Liffield 1998; great spotted and middle spotted woodpeckers: Michalek & Winkler 2001; Capricorn silvereye: Robertson *et al.* 2001; Monteiro's hornbill: Stanback *et al.* 2002). In such species, females may evolve to lose a distinctive period of oestrus. As documented in our review, humans do not appear to be one of these species.

7. CUES TO OESTRUS

Men apparently detect cues of women's oestrus, whether physiological or behavioural. Women's scent appears to be more attractive to men during their fertile phase than the luteal phase (Doty *et al.* 1975; Poran 1994; Singh & Bronstad 2001; Thornhill *et al.* 2003; Kuukasjärvi *et al.* 2004; Havlicek *et al.* 2006; for a negative finding, see Thornhill & Gangestad 1999). Their faces may become more attractive when they are fertile (Roberts *et al.* 2004). Fertile women dress more attractively (Haselton *et al.* 2007) or provocatively (Grammer *et al.* 2004). In one study, the tips received by women working as lap dancers increased nearly \$100 per shift when they were fertile, compared with the luteal phase (Miller *et al.* 2007).

A signal is a perceptible cue that has evolved owing to benefits achieved through communication to other individuals (conspecifics or members of other species). If the cues men use to detect women's oestrus are signals, then women benefit(ed) from men's (or others') detection of them, leading to their evolution. It is highly unlikely that ancestral women benefited from men's detection of oestrous cues. First, in general, females should not pay large costs to signal fertility status, except in rare cases (e.g. Pagel 1994). Selection strongly operates on males to detect fertile phases, which they typically achieve by detecting by-products of the physiological changes in females associated with fertility (e.g. by-products of

changing levels of oestrogen; Nelson 2000), for which females pay no costs of signalling. Second, in humans in particular, it makes little sense that females would benefit through male detection of fertility status, in the light of mounting evidence for sexually antagonistic coevolution of adaptations leading to conflicts during oestrus. (We note, in this context, that a variety of psychological features associated with oestrus may also be by-products of adaptations rather than directly selected; see Jones *et al.* 2005a.)

In fact, women have probably evolved to conceal their oestrus. Concealment need not imply a complete lack of fertility cues. Females' bodies change during oestrus, and the by-products of these changes 'leak' information about their fertility status. Concealment instead implies a reduction in the intensity of these cues selected owing to the value of suppressing information about fertility status to conspecifics (notably, male partners). Concealment is unlikely to be perfect, as a coevolutionary race between females and males leads men to be increasingly sensitive to small cues, while complete suppression of cues by females is constrained by the costs of that suppression on reproduction itself (e.g. fertility depends on changes in oestrogen; see Ellison 2001). Males of virtually any non-human primate species can probably detect the fertility status of females through use of scent cues (e.g. Dixson 1998) much better than men can detect the women's fertility status. (Hence, female primates that lack sexual swellings do not typically possess 'concealed ovulation'; cf. Sillén-Tullberg & Møller 1993; see Thornhill & Gangestad *in press.*) That men can do so at all, we suggest, persists due to positive selection on men for detection, and despite selection on females to conceal reliable cues of oestrus.

8. SUMMARY

Until recently, women have been thought to possess no distinctive sexuality during the fertile phase of their menstrual cycle. Abundant evidence now indicates that they do. This sexuality is appropriately referred to as oestrus. The function of oestrous sexual proceptivity is not to obtain sperm from any male. Rather, oestrous females should be discriminating and prefer to mate with good sires for offspring. Women's sexual preferences for certain male traits probably connoting male genetic quality (or ones that did so ancestrally) appear to be enhanced when women are fertile in their cycles. Women's oestrus shares functional and physiological homologies with the oestrus of not only other mammals but also female vertebrates in general. Oestrus, we propose, debuted *ca* 400 Myr ago.

That women's preferences change across their cycles appears non-controversial at this point. More controversial is the claim that, similar to some bird species in which both sexes exert substantial efforts to enhance offspring quality, aspects of women's oestrus were shaped by the possibility of obtaining reproductive benefits in the context of EPC. On average, women experience greater sexual attraction to particular extra-pair men, but not their own partners, during oestrus, and the effect is pronounced when women's primary partners lack purported indicators of intrinsic or compatible good genes. Some of the best evidence that sexually antagonistic coevolution pertaining to women's EPC has led to fertility-dependent adaptations are provided by the examination of male counter-adaptations

to enhance paternity as primary partners. Men engage in mate-retention tactics more frequently during oestrus, and particularly when their partners experience increased attraction to men other than their primary partners during oestrus. Women may engage in actual EPC very infrequently, despite oestrous changes in their sexuality, precisely because men have evolved counter-adaptations to reduce the costs of cuckoldry and women are sensitive to those costs.

The fact that women possess oestrus raises important unanswered questions. Although many changes across the cycle in women and their partners have been documented, many more may await uncovering. The precise endocrine mechanisms that regulate these changes remain largely unknown. Research to date implicates oestrogen, progesterone and testosterone (e.g. Puts 2006; Welling *et al.* 2007; Garver-Apgar *et al.* in press; Roney & Simmons 2008). Lancaster & Kaplan (in press) raised the possibility that prolactin and oxytocin, whose levels are heightened when women lactate, suppress or alter oestrous sexuality in women, thereby reducing its effects (e.g. on extra-pair sexual interest) in women with young offspring (on one possible effect of prolactin, see Puts 2006; cf. Garver-Apgar *et al.* in press). As research to date has largely examined oestrous effects in nulliparous young women, studies investigating the nature of oestrus in other populations are especially needed.

Most fundamentally, the discovery of women's oestrus has penetrating and potentially revolutionary implications for a proper conceptualization of human mating. New theoretical frameworks that recognize this discovery are needed; we have sketched the outlines of some conjectures here (see also Thornhill & Gangestad in press). The field can look forward to new, exciting avenues of research on human mating that will surely follow.

REFERENCES

- Akçay, E. & Roughgarden, J. 2007 Extra-pair paternity in birds: review of the genetic benefits. *Evol. Ecol. Res.* **9**, 855–868.
- Alexander, R. D. 1990 *How did humans evolve? Reflections on the uniquely unique species*. Ann Arbor, MI: Museum of Zoology, The University of Michigan. Special publication no. 1.
- Alexander, R. D. & Noonan, K. M. 1979 Concealment of ovulation, parental care, and human social evolution. In *Evolutionary biology and human social behavior: an anthropological perspective* (eds N. A. Chagnon & W. G. Irons), pp. 436–453. Scituate, MA: North Duxbury Press.
- Anderson, K. G. 2006 How well does paternity confidence match actual paternity? Evidence from worldwide non-paternity rates. *Curr. Anthropol.* **47**, 513–520. (doi:10.1086/504167)
- Arroyo, B. E. 1999 Copulatory behavior of semi-colonial Montagu's Harriers. *Condor* **101**, 340–346. (doi:10.2307/1369997)
- Bellis, M. A. & Baker, R. R. 1990 Do females promote sperm competition? *Anim. Behav.* **40**, 997–999. (doi:10.1016/S0003-3472(05)81008-5)
- Bertran, J. & Margalida, A. 1999 Copulatory behavior of the bearded vulture. *Condor* **101**, 164–168. (doi:10.2307/1370459)
- Birkhead, T. R. & Møller, A. P. 1992 *Sperm competition in birds: evolutionary causes and consequences*. New York, NY: Academic Press.
- Bodily, R. Y. & Neudorf, D. L. H. 2004 Mate guarding in northern mockingbirds (*Mimus polyglottos*). *Texas J. Sci.* **56**, 207–214.
- Brewis, A. & Meyer, M. 2005 Demographic evidence that human ovulation is undetectable (at least in pair bonds). *Curr. Anthropol.* **46**, 465–471. (doi:10.1086/430016)
- Burley, N. 1979 The evolution of concealed ovulation. *Am. Nat.* **114**, 835–858. (doi:10.1086/283532)
- Burriss, R. P. & Little, A. C. 2006 Effects of partner conception risk phase on male perception of dominance in faces. *Evol. Hum. Behav.* **27**, 297–305. (doi:10.1016/j.evolhumbehav.2006.01.002)
- Buss, D. M. 2003 *The evolution of desire: strategies of human mating*. New York, NY: Basic Books.
- Byers, J. A., Moodie, J. D. & Hall, N. 1994 Pronghorn females choose vigorous mates. *Anim. Behav.* **47**, 33–43. (doi:10.1006/anbe.1994.1005)
- Cardenas, R. A. & Harris, L. J. 2007 Do women's preferences for symmetry change across the cycle? *Evol. Hum. Behav.* **28**, 96–105. (doi:10.1016/j.evolhumbehav.2006.08.003)
- Charlton, B. D., Reby, D. & McComb, K. 2007 Female red deer prefer the roars of larger males. *Biol. Lett.* **3**, 382–385. (doi:10.1098/rsbl.2007.0244)
- Currie, D., Krupa, A. P., Burke, T. & Thompson, D. B. A. 1999 The effect of experimental male removals on extra-pair paternity in the wheatear, *Oenanthe oenanthe*. *Anim. Behav.* **57**, 145–152. (doi:10.1006/anbe.1998.0960)
- DeBruine, L. M., Jones, B. C. & Perrett, D. I. 2005 Women's attractiveness judgments of self-resembling faces change across the menstrual cycle. *Horm. Behav.* **47**, 379–383. (doi:10.1016/j.yhbeh.2004.11.006)
- Dickinson, J. L. 1997 Male detention affects extra-pair copulation frequency and pair behaviour in western bluebirds. *Anim. Behav.* **53**, 561–571. (doi:10.1006/anbe.1996.0331)
- Dickinson, J. L. 2001 Extrapair copulations in western bluebirds (*Sialia mexicana*): female receptivity favors older males. *Behav. Ecol. Sociobiol.* **50**, 423–429. (doi:10.1007/s002650100381)
- Dixon, A. F. 1998 *Primate sexuality: comparative studies of the prosimians, monkeys, apes, and humans*. Oxford, UK: Oxford University Press.
- Doty, R. L., Ford, M., Preti, G. & Huggins, G. R. 1975 Changes in the intensity and pleasantness of human vaginal odors during the menstrual cycle. *Science* **190**, 1316–1318. (doi:10.1126/science.1239080)
- Double, M. & Cockburn, A. 2000 Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. *Proc. R. Soc. B* **267**, 465–470. (doi:10.1098/rspb.2000.1023)
- Ellison, P. T. 2001 *On fertile ground: a natural history of reproduction*. Cambridge, MA: Harvard University Press.
- Etkin, W. 1964 Types of social organization in birds and mammals. In *Social behavior and organization among vertebrates* (ed. W. Etkin), pp. 256–298. Chicago, IL: University of Chicago Press.
- Feinberg, D. R., Jones, B. C., Law Smith, M. J., Moore, F. R., DeBruine, L. M., Cornwell, R. E., Hillier, S. G. & Perrett, D. I. 2006 Effects of menstrual cycle and trait estrogen level on masculinity preferences in the human voice. *Horm. Behav.* **46**, 215–222. (doi:10.1016/j.yhbeh.2005.07.004)
- Fisher, H. S., Swaisgood, R. R. & Fitch-Snyder, H. 2003 Countermarking by male pygmy lorises (*Nycticebus pygmaeus*): do females use odor cues to select mates with high competitive ability? *Behav. Ecol. Sociobiol.* **53**, 123–130.
- Frost, P. 1994 Preference for darker faces in photographs at different phases of the menstrual cycle: preliminary assessment of evidence for a hormonal relationship. *Percept. Mot. Skills* **79**, 507–514.

- Gangestad, S. W. & Thornhill, R. 1998 Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proc. R. Soc. B* **265**, 927–933. (doi:10.1098/rspb.1998.0380)
- Gangestad, S. W. & Thornhill, R. 2003 Fluctuating asymmetry, developmental instability, and fitness: toward model-based interpretation. In *Developmental instability: causes and consequences* (ed. M. Polak), pp. 62–80. Cambridge, UK: Cambridge University Press.
- Gangestad, S. W., Thornhill, R. & Garver, C. E. 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. B* **269**, 975–982. (doi:10.1098/rspb.2001.1952)
- Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E. & Christensen, P. N. 2004 Women's preferences for male behavioral displays shift across the menstrual cycle. *Psychol. Sci.* **15**, 203–207. (doi:10.1111/j.0956-7976.2004.01503010.x)
- Gangestad, S. W., Thornhill, R. & Garver-Apgar, C. E. 2005 Women's sexual interests across the ovulatory cycle depend on primary partner developmental instability. *Proc. R. Soc. B* **272**, 2023–2027. (doi:10.1098/rspb.2005.3112)
- Gangestad, S. W., Garver-Apgar, C. E., Simpson, J. A. & Cousins, A. J. 2007 Changes in women's mate preferences across the ovulatory cycle. *J. Pers. Soc. Psychol.* **92**, 151–163. (doi:10.1037/0022-3514.92.1.151)
- Garver-Apgar, C. E., Gangestad, S. W., Thornhill, R., Miller, R. D. & Olp, J. J. 2006 MHC alleles, sexually responsiveness, and unfaithfulness in romantic couples. *Psychol. Sci.* **17**, 830–835. (doi:10.1111/j.1467-9280.2006.01789.x)
- Garver-Apgar, C. E., Cousins, A. J., Thornhill, R. & Gangestad, S. W. In preparation. Intersexual conflict across women's ovulatory cycle.
- Garver-Apgar, C. E., Gangestad, S. W. & Thornhill, R. In press. Hormonal correlates of women's mid-cycle preference for the scent of symmetry. *Evol. Hum. Behav.*
- Grammer, K. 1993 5- α -androst-16-en-3 α -on: a male pheromone? A brief report. *Ethol. Sociobiol.* **14**, 201–207. (doi:10.1016/0162-3095(93)90006-4)
- Grammer, K., Renninger, L. & Fischer, B. 2004 Disco clothing, female sexual motivation, and relationship status: is she dressed to impress? *J. Sex Res.* **41**, 66–74.
- Hall, M. L. & Magrath, R. D. 2000 Duetting and mate-guarding in Australian magpie-larks (*Grallina cyanoleuca*). *Behav. Ecol. Sociobiol.* **47**, 180–187. (doi:10.1007/s002650050009)
- Haselton, M. G. & Gangestad, S. W. 2006 Conditional expression of women's desires and male mate retention efforts across the ovulatory cycle. *Horm. Behav.* **49**, 509–518. (doi:10.1016/j.yhbeh.2005.10.006)
- Haselton, M. & Miller, G. F. 2006 Women's fertility across the cycle increases the short-term attractiveness of creative intelligence compared to wealth. *Hum. Nat.* **17**, 50–73. (doi:10.1007/s12110-006-1020-0)
- Haselton, M. G., Mortezaie, M., Pillsworth, E. G., Bleske-Recheck, A. M. & Frederick, D. A. 2007 Ovulation and human female ornamentation: near ovulation, women dress to impress. *Horm. Behav.* **51**, 40–45. (doi:10.1016/j.yhbeh.2006.07.007)
- Havlicek, J., Roberts, S. C. & Flegr, J. 2005 Women's preference for dominant male odour: effects of menstrual cycle and relationship status. *Biol. Lett.* **1**, 256–259. (doi:10.1098/rsbl.2005.0332)
- Havlicek, J., Dvorakova, R., Bartos, L. & Flegr, J. 2006 Non-advertized does not mean concealed: body odour change across the human menstrual cycle. *Ethology* **112**, 81–90. (doi:10.1111/j.1439-0310.2006.01125.x)
- Hawkes, K. 2004 Mating, parenting, and the evolution of human pairbonds. In *Kinship and behavior in primates* (eds B. Chapais & C. M. Berman), pp. 443–473. Oxford, UK: Oxford University Press.
- Hill, K. 1982 Hunting and human evolution. *J. Hum. Evol.* **11**, 521–544. (doi:10.1016/S0047-2484(82)80107-3)
- Hohoff, C., Franzin, K. & Sachser, N. 2003 Female choice in a promiscuous wild guinea pig, the yellow-toothed cavy (*Galea musteloides*). *Behav. Ecol. Sociobiol.* **53**, 341–349.
- Hrdy, S. B. 1981 *The woman that never evolved*. Cambridge, MA: Harvard University Press.
- Hummel, T., Gollisch, R., Wildt, G. & Kobal, G. 1991 Changes in olfactory perception during the menstrual cycle. *Experientia* **47**, 712–715. (doi:10.1007/BF01958823)
- Jennions, M. D. & Petrie, M. 2000 Why do females mate multiply? A review of the genetic benefits. *Biol. Rev.* **75**, 21–64. (doi:10.1017/S0006323199005423)
- Johnston, V. S., Hagel, R., Franklin, M., Fink, B. & Grammer, K. 2001 Male facial attractiveness: evidence for hormone-mediated adaptive design. *Evol. Hum. Behav.* **22**, 251–267. (doi:10.1016/S1090-5138(01)00066-6)
- Jolly, A. 1972 *The evolution of primate behavior*. New York, NY: MacMillan.
- Jones, B. C., Little, A. C., Boothroyd, L., DeBruine, L. M., Feinberg, D. R., Law Smith, M. J., Cornwell, R. E., Moore, F. R. & Perrett, D. I. 2005a Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Horm. Behav.* **48**, 283–290. (doi:10.1016/j.yhbeh.2005.03.010)
- Jones, B. C. *et al.* 2005b Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proc. R. Soc. B* **272**, 347–354. (doi:10.1098/rspb.2004.2962)
- Kaplan, H., Hill, K., Lancaster, J. & Hurtado, A. M. 2000 A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* **9**, 156–185. (doi:10.1002/1520-6505(2000)9:4<156::AID-EVAN5>3.0.CO;2-7)
- Koehler, N., Rhodes, G. & Simmons, L. W. 2002 Are human female preferences for symmetrical male faces enhanced when conception is likely? *Anim. Behav.* **64**, 233–238. (doi:10.1006/anbe.2002.3063)
- Koehler, N., Rhodes, G., Simmons, L. W. & Zebrowitz, L. A. 2006 Do cyclic changes in women's face preferences target cues to long-term health. *Soc. Cogn.* **24**, 641–656. (doi:10.1521/soco.2006.24.5.641)
- Kokko, H., Brooks, R., Jennions, M. D. & Morley, J. 2003 The evolution of mate choice and mating biases. *Proc. R. Soc. B* **270**, 653–664. (doi:10.1098/rspb.2002.2235)
- Komdeur, J., Kraaijeveld-Smit, F., Kraaijeveld, K. & Edelaar, P. 1999 Explicit experimental evidence for the role of mate guarding in minimizing loss of paternity in the Seychelles warbler. *Proc. R. Soc. B* **266**, 2075–2081. (doi:10.1098/rspb.1999.0890)
- Korpimäki, E., Lahti, K., May, C. A., Parkin, D. T., Powell, G. B., Tolonen, P. & Wetton, J. H. 1996 Copulatory behaviour and paternity determined by DNA fingerprinting in kestrels: effects of cyclic food abundance. *Anim. Behav.* **51**, 945–955. (doi:10.1006/anbe.1996.0098)
- Kuukasjärvi, S., Eriksson, C. J. P., Koskela, E., Mappes, T., Nissinen, K. & Rantala, M. J. 2004 Attractiveness of women's body odors over the menstrual cycle: the role of oral contraception and received sex. *Behav. Ecol.* **15**, 579–584. (doi:10.1093/beheco/arl050)
- Lancaster, J. B. & Kaplan, H. S. In press. The endocrinology of the human adaptive complex. In *Endocrinology of social relationships* (eds P. G. Gray & P. T. Ellison). Cambridge, MA: Harvard University Press.

- Little, A. C., Jones, B. C. & Burriss, R. P. 2007a Preferences for masculinity in male bodies change across the menstrual cycle. *Horm. Behav.* **31**, 633–639. (doi:10.1016/j.yhbeh.2007.03.006)
- Little, A. C., Jones, B. C., Burt, D. M. & Perrett, D. I. 2007b Preferences for symmetry in faces change across the menstrual cycle. *Biol. Psychol.* **76**, 209–216. (doi:10.1016/j.biopsycho.2007.08.003)
- Low, M. 2005 Factors influencing mate guarding and territory defence in the stitchbird (hihi) *Notiomystis cincta*. *New Zeal. J. Ecol.* **29**, 231–242.
- Ludue-Larena, J. J., López, P. & Gosálbez, J. 2003 Male dominance and female chemosensory preferences in the rock-dwelling snow vole. *Behaviour* **140**, 665–681. (doi:10.1163/156853903322149496)
- Lynch, K. S., Rand, A. S., Ryan, M. J. & Wilczynski, W. 2005 Plasticity in female mate choice associated with changing reproductive states. *Anim. Behav.* **69**, 689–699. (doi:10.1016/j.anbehav.2004.05.016)
- Lynch, K. S., Crews, D., Ryan, M. J. & Wilczynski, W. 2006 Hormonal state influences aspects of female mate choice in the Túngara Frog (*Physalaemus pustulosus*). *Horm. Behav.* **49**, 450–457. (doi:10.1016/j.yhbeh.2005.10.001)
- Marlowe, F. W. 2003 A critical period for provisioning by Hadza men: implications for pair bonding. *Evol. Hum. Behav.* **24**, 217–229. (doi:10.1016/S1090-5138(03)00014-X)
- Michalek, K. G. & Winkler, H. 2001 Parental care and parentage in monogamous great spotted woodpeckers (*Picoides major*) and middle spotted woodpeckers (*Picoides medius*). *Behav.* **138**, 1259–1285. (doi:10.1163/15685390152822210)
- Michl, G., Torok, T., Griffith, S. C. & Sheldon, B. C. 2002 Experimental analysis of sperm competition mechanisms in a wild bird population. *Proc. Natl Acad. Sci. USA* **99**, 5466–5470. (doi:10.1073/pnas.082036699)
- Miller, G. F. 2000 *The mating mind: how sexual choice shaped the evolution of human nature*. New York, NY: Anchor Books.
- Miller, G. F., Tybur, J. & Jordan, B. 2007 Ovulatory cycle effects on tip earnings by lap dancers: economic evidence for human estrus? *Evol. Hum. Behav.* **28**, 375–381. (doi:10.1016/j.evolhumbehav.2007.06.002)
- Møller, A. P. 2000 Male paternal care, female reproductive success, and extrapair paternity. *Behav. Ecol.* **11**, 161–168. (doi:10.1093/beheco/11.2.161)
- Møller, A. P. 2003 The evolution of monogamy: mating relationships, paternal care and sexual selection. In *Monogamy: mating strategies and partnerships in birds, humans and other mammals* (eds U. H. Reichard & C. Boesch), pp. 29–41. Cambridge, UK: Cambridge University Press.
- Mougeot, F. S. 2004 Breeding density, cuckoldry risk and copulation behaviour during the fertile period in raptors: a comparative analysis. *Anim. Behav.* **67**, 1067–1076. (doi:10.1016/j.anbehav.2003.10.011)
- Nelson, R. J. 2000 *An introduction to behavioral endocrinology*, 2nd edn. Sunderland, MA: Sinauer Associates, Inc.
- Neudorf, D. L., Stutchbury, B. J. M. & Piper, W. H. 1997 Covert extraterritorial behavior of female hooded warblers. *Behav. Ecol.* **8**, 595–600. (doi:10.1093/beheco/8.6.595)
- Pagel, M. 1994 Evolution of conspicuous estrous advertisement in old-world monkeys. *Anim. Behav.* **47**, 1333–1341. (doi:10.1006/anbe.1994.1181)
- Pawlowski, B. & Jasienska, G. 2005 Women's preferences for sexual dimorphism in height depend on menstrual cycle phase and expected duration of relationship. *Biol. Psychol.* **70**, 38–43. (doi:10.1016/j.biopsycho.2005.02.002)
- Pedersen, M. C., Dunn, P. O. & Whittingham, L. A. 2006 Extraterritorial forays are related to a male ornamental trait in the common yellowthroat. *Anim. Behav.* **72**, 479–486. (doi:10.1016/j.anbehav.2006.02.010)
- Penton-Voak, I. S. & Perrett, D. I. 2000 Female preference for male faces changes cyclically—further evidence. *Evol. Hum. Behav.* **21**, 39–48. (doi:10.1016/S1090-5138(99)00033-1)
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. & Minamisawa, R. 1999 Female preference for male faces changes cyclically. *Nature* **399**, 741–742. (doi:10.1038/21557)
- Pierce, E. P. & Liffield, J. T. 1998 High paternity without paternity—assurance behavior in the purple sandpiper, a species with high paternal investment. *Auk* **115**, 602–612.
- Pillsworth, E. G. & 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. (doi:10.1016/j.evolhumbehav.2005.10.002)
- Pillsworth, E. G., Haselton, M. G. & Buss, D. M. 2004 Ovulatory shifts in female sexual desire. *J. Sex Res.* **41**, 55–65.
- Poran, N. S. 1994 Cycle attractivity of human female odors. *Adv. Biosci.* **93**, 555–560.
- Potts, W. K., Manning, C. J. & Wakeland, E. K. 1991 Mating patterns in seminatural populations of mice influenced by MHC genotype. *Nature* **352**, 619–621. (doi:10.1038/352619a0)
- Puts, D. A. 2005 Mating context and menstrual phase affect women's preferences for male voice pitch. *Evol. Hum. Behav.* **26**, 388–397. (doi:10.1016/j.evolhumbehav.2005.03.001)
- Puts, D. A. 2006 Cyclic variation in women's preferences for masculine traits: potential hormonal causes. *Hum. Nat.* **17**, 114–127. (doi:10.1007/s12110-006-1023-x)
- Radford, S. L., Croft, D. B. & Moss, G. L. 1998 Mate choice in female red-necked pademelons, *Thylogale thetis* (Marsupialia: Macropodidae). *Ethology* **104**, 217–231.
- Rantala, M. J., Eriksson, C. J. P., Vainikka, A. & Kortet, R. 2006 Male steroid hormones and female preference for male body odor. *Evol. Hum. Behav.* **27**, 259–269. (doi:10.1016/j.evolhumbehav.2005.11.002)
- Rikowski, A. & Grammer, K. 1999 Human body odour, symmetry and attractiveness. *Proc. R. Soc. B* **266**, 869–874. (doi:10.1098/rspb.1999.0717)
- Riley, H. T., Bryant, D. M., Carter, P. E. & Parkin, D. T. 1995 Extrapair fertilizations and paternity defense in house martins, *Delichon urbica*. *Anim. Behav.* **49**, 495–509. (doi:10.1006/anbe.1995.0065)
- Roberts, S. C., Havlicek, J., Flegr, J., Hruskova, M., Little, A. C., Jones, B. C., Perrett, D. I. & Petrie, M. 2004 Female facial attractiveness increases during the fertile phase of the menstrual cycle. *Proc. R. Soc. B* **271**, S270–S272. (doi:10.1098/rsbl.2004.0174)
- Robertson, B. C., Degnan, S. M., Kikkawa, J. & Moritz, C. C. 2001 Genetic monogamy in the absence of paternity guards: the Capricorn silvereye, *Zosterops lateralis chlorocephalus*, on Heron Island. *Behav. Ecol.* **12**, 666–673. (doi:10.1093/beheco/12.6.666)
- Rodriguez-Girones, M. A. & Enquist, M. 2001 The evolution of female sexuality. *Anim. Behav.* **61**, 695–704. (doi:10.1006/anbe.2000.1630)
- Roney, J. R. & Simmons, Z. L. 2008 Women's estradiol predicts preference for facial cues of men's testosterone. *Horm. Behav.* **53**, 14–19. (doi:10.1016/j.yhbeh.2007.09.008)
- Saino, N., Primmer, C. R., Ellegren, H. & Møller, A. P. 1999 Breeding synchrony and paternity in the barn swallow (*Hirundo rustica*). *Behav. Ecol. Sociobiol.* **45**, 211–218. (doi:10.1007/s002650050555)

- Scarborough, P. S. & Johnston, V. S. 2005 Individual differences in women's facial preferences as a function of digit ratio and mental rotation ability. *Evol. Hum. Behav.* **26**, 509–526. (doi:10.1016/j.evolhumbehav.2005.03.002)
- Schulte, B. A. & Rasmussen, L. E. L. 1999 Signal receiver interplay in the communication of male condition by Asian elephants. *Anim. Behav.* **57**, 1265–1274. (doi:10.1006/anbe.1999.1092)
- Sheldon, B. C., Davidson, P. & Lindgren, G. 1999 Mate replacement in experimentally widowed collared flycatchers (*Ficedula albicollis*): determinants and outcomes. *Behav. Ecol. Sociobiol.* **46**, 141–148. (doi:10.1007/s002650050603)
- Sillén-Tullberg, B. & Møller, A. P. 1993 The relationship between concealed ovulation and mating systems in anthropoid primates—a phylogenetic analysis. *Am. Nat.* **141**, 1–25. (doi:10.1086/285458)
- Simmons, L. W., Firman, R. C., Rhodes, G. & Peters, M. 2004 Human sperm competition: testis size, sperm production, and rates of extra-pair copulations. *Anim. Behav.* **68**, 297–302. (doi:10.1016/j.anbehav.2003.11.013)
- Singh, D. & Bronstad, P. M. 2001 Female body odour is a potential cue to ovulation. *Proc. R. Soc. B* **268**, 797–801. (doi:10.1098/rspb.2001.1589)
- Spritzer, M. D., Meikle, D. B. & Solomon, N. G. 2005 Female choice based on male spatial ability and aggressiveness among meadow voles. *Anim. Behav.* **69**, 1121–1130. (doi:10.1016/j.anbehav.2004.06.033)
- Spuhler, J. N. 1979 Continuities and discontinuities in anthropoid-hominid behavioral evolution: bipedal locomotion and sexual receptivity. In *Evolutionary biology and human social behavior: an anthropological perspective* (eds N. A. Chagnon & W. Irons), pp. 454–461. North Scituate, MA: Duxbury Press.
- Stacy, P. B. 1982 Female promiscuity and male reproductive success in social birds and mammals. *Am. Nat.* **120**, 51–64. (doi:10.1086/283969)
- Stanback, M., Richardson, D. S., Boix-Hinzen, C. & Mendelsohn, J. 2002 Genetic monogamy in Monteiro's hornbill, *Tockus monteiri*. *Anim. Behav.* **63**, 787–793. (doi:10.1006/anbe.2001.1975)
- Sterelny, K. & Griffiths, P. E. 1999 *Sex and death: an introduction to the philosophy of biology*. Chicago, IL: University of Chicago Press.
- Stumpf, R. M. & Boesch, C. 2005 Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte d'Ivoire. *Behav. Ecol. Sociobiol.* **57**, 511–524. (doi:10.1007/s00265-004-0868-4)
- Symons, D. 1979 *The evolution of human sexuality*. Oxford, UK: Oxford University Press.
- Tarin, J. J. & Gómez-Piquer, V. 2002 Do women have a hidden heat period? *Hum. Reprod.* **17**, 2243–2248. (doi:10.1093/humrep/17.9.2243)
- Thornhill, R. & Gangestad, S. W. 1999 The scent of symmetry: a human sex pheromone that signals fitness? *Evol. Hum. Behav.* **20**, 175–201. (doi:10.1016/S1090-5138(99)00005-7)
- Thornhill, R. & Gangestad, S. W. 2003 Do women have evolved adaptation for extra-pair copulation?. In *Evolutionary aesthetics* (eds E. Voland & K. Grammer), pp. 341–368. Heidelberg, Germany: Springer.
- Thornhill, R. & Gangestad, S. W. In press. *The evolutionary biology of human female sexuality*. New York, NY: Oxford University Press.
- Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., Knight, J. & Franklin, M. 2003 MHC, symmetry, and body scent attractiveness in men and women. *Behav. Ecol.* **14**, 668–678. (doi:10.1093/beheco/arg043)
- Thornton, J. W. 2001 Evolution of vertebrate steroid receptors from an ancestral estrogen receptor by ligand exploitation and serial genome expansions. *Proc. Natl Acad. Sci. USA* **98**, 5671–5676. (doi:10.1073/pnas.091553298)
- Thornton, J. W., Need, E. & Crews, D. 2003 Resurrecting the ancestral steroid receptor: ancient origin of estrogen signaling. *Science* **301**, 1714–1717. (doi:10.1126/science.1086185)
- Wakano, J. Y. & Ihara, Y. 2005 Evolution of male parental care and female multiple mating: game-theoretical and two-locus diploid models. *Am. Nat.* **166**, E32–E44. (doi:10.1086/431252)
- Waits, C., Little, A. C., Wolfensohn, S., Honess, P., Brown, A. P., Buchanan-Smith, H. M. & Perrett, D. I. 2003 Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. *Proc. R. Soc. B* **270**, S144–S146. (doi:10.1098/rsbl.2003.0065)
- Welling, L. L. M., Jones, B. C., DeBruine, L. M., Conway, C. A., Law Smith, M. J., Little, A. C., Feinberg, D. R., Sharp, M. A. & Al-Dujaili, E. A. S. 2007 Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Horm. Behav.* **52**, 156–161. (doi:10.1016/j.yhbeh.2007.01.010)
- Wilcox, A. J., Weinberg, C. R. & Baird, D. D. 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. (doi:10.1056/NEJM199512073332301)
- Wilcox, A. J., Baird, D. D., Dunson, D. B., McConaughy, D. R., Kesner, J. S. & Weinberg, C. R. 2004 On the frequency of intercourse around ovulation: evidence for biological influences. *Hum. Reprod.* **19**, 1539–1543. (doi:10.1093/humrep/deh305)
- Williams, R. J. & Lenington, S. 1993 Factors modulating preferences of female house mice for males differing in T-complex genotype—role of T-complex genotype, genetic background, and estrous condition of females. *Behav. Genet.* **23**, 51–58. (doi:10.1007/BF01067553)
- Wolff, J. O. 1998 Breeding strategies, mate choice, and reproductive success in American bison. *Oikos* **83**, 529–544. (doi:10.2307/3546680)