# Non-Advertized does not Mean Concealed: Body Odour Changes across the Human Menstrual Cycle

Jan Havlíček\*†, Radka Dvořáková†, Luděk Bartoš‡, & Jaroslav Flegr§

\* Department of Anthropology, Faculty of Humanities, Charles University, Prague, Czech Republic

† Department of Philosophy of Science, Faculty of Science, Charles University, Prague, Czech Republic

‡ Ethology Group, Institute of Animal Production, Prague-Uhříněves, Czech Republic

§ Department of Parasitology, Faculty of Science, Charles University, Prague, Czech Republic

#### Correspondence

Jan Havlíček, Department of Anthropology, Faculty of Humanities, Charles University, Husnikova 2075, 158 00 Prague 13, Czech Republic. E-mail: jan.havlicek@fhs.cuni.cz

Received: October 26, 2004 Initial acceptance: January 22, 2005 Final acceptance: April 15, 2005 (B. Kempenaers)

## Abstract

Females of a number of primate species display their fertile period by behavioural and/or morphological changes. Traditionally, the fertile period in human females has been considered to be concealed. However, this presumption has rarely been tested. One of the possible mechanisms for assessing menstrual cycle phase is through the sense of smell. In this study possible changes in odour across the menstrual cycle were investigated. Samples of body odour were acquired from 12 women (aged 19-27 yr), none of whom were using hormonal contraceptives. Samples were collected using cotton pads worn in the armpit for 24 h, from the menstrual, follicular and luteal cycle phases. Our experimental sample of 42 males (age 19-34 yr) repeatedly rated these odour samples for their intensity, pleasantness, attractiveness and femininity. Raw subjective smell ratings from each man were transformed to z-scores. Subsequently, these z-scores were tested by the general linear mixed-model analysis (PROC MIXED, SAS) with the female's ID nested within the subject's ID as a random factor to account for the repeated measures of the subjects. Significant changes across the cycle were found for ratings of pleasantness  $[F_{(2,689)} = 702; p = 0.001]$ , attractiveness [F(2,546) =6.35; p = 0.002] and intensity [F(2,530) = 3.57; p = 0.028]. Odour from women in the follicular (i.e. fertile) phase was rated as the least intense and the most attractive. Subsequent post hoc analysis revealed significant differences in intensity, pleasantness and attractiveness between the menstrual phase and the follicular phase, and in pleasantness and attractiveness between the menstrual and luteal phases. Significant difference between the follicular and the luteal phase was found only for attractiveness. Our results suggest that men can potentially use smell as a mechanism for monitoring menstrual cycle phase in current or prospective sexual partners. Therefore, the fertile period in humans should be considered non-advertized, rather than concealed.

#### Introduction

The visual appearance of females of various primate species changes considerably across their menstrual cycle. These changes usually take place in the anogenital region and are commonly called sexual swellings. Sexual swellings are related to ovulation (e.g. Deschner et al. 2003), correlate with female sexual proceptivity (e.g. Wallis 1992) and are found to be attractive to males (Hrdy & Whitten 1987).

Traditionally, human females are different from species which possess 'sexual swelling', with human

ovulation considered to be concealed (cryptic, hidden). From this perspective, there is supposedly a lack of any cues to female ovulation, with no systematic changes in female attractiveness across the cycle. A number of hypotheses have tried to explain the functions or evolutionary causes of this phenomenon. It has been suggested that concealed ovulation evolved to reduce competition between males and thus to allow greater cooperation, which may have been necessary for survival of small hunter-gatherer groups (Daniels 1983); to promote paternal care (Strassmann 1981) or paternity confusion (Benshoof & Thornhill 1979) and thus reduce the risk of infanticide (Hrdy 1979). Burley (1979) stressed that ovulation is concealed from females themselves. She proposed that there was a selective disadvantage for women who were aware of their fertile period, and subsequently avoided sex during that time to escape life-threatening and painful childbirth. Lovejoy (1981) argued that signs of fertility are not concealed but rather extended to the whole cycle in order to constantly maintain male sexual interest.

Despite many hypotheses to explain the absence of ovulation signs, there is a distinct lack of experimental studies (i.e. the absence of systematic changes in attractiveness across the cycle). Moreover, all of the above-mentioned hypotheses have focused on visual signs of ovulation. However, the proximate causes of ovulation are changes in hormonal levels, and body odour is arguably more closely connected to changes in hormonal levels than visual appearance is. Thus, one can expect body odour attractiveness to be a potential cue to female fertility status.

The results of the four previous studies to examine changes in female body odour attractiveness across menstrual cycle are contradictory. Thornhill & Gangestad (1999) asked men to rate the attractiveness of women's body odour. Half of the women were in their follicular phase while the other half were in the luteal phase of their cycle. There was no significant difference in the attractiveness between the two groups. Singh & Bronstad (2001) collected T-shirts (worn for three consecutive nights and afterwards kept in a freezer) from women in their follicular phase and from the same women in their luteal phase. The T-shirts from the follicular phase were rated as significantly more attractive than those from the luteal phase. In the third study, the authors found a positive correlation between the estimated probability of conception and the odour of the T-shirt (Thornhill et al. 2003). Recently, Kuukasjärvi et al. (2004) reached a similar conclusion: odour attractiveness peaks around the time of presumed ovulation. On the contrary, such changes were not found in the sample of T-shirts worn by women using hormonal contraception (Kuukasjärvi et al. 2004).

This raises several questions. First, T-shirts were used as stimuli in all the previously mentioned studies. This method, however, does not examine the specific odour source responsible for changes in attractiveness across the cycle. Therefore, the main aim of our study was to specifically test whether axillary odour attractiveness increases during the follicular phase. Secondly, it is also not clear whether the changes across the cycle are due to either variation in the intensity of the odour or in more qualitative characteristics. For this reason, not only were changes in the subjective rating of attractiveness assessed, but also changes in intensity, pleasantness and femininity across the cycle. Thirdly, no previous study has addressed whether the increase in odour attractiveness during the follicular phase is higher compared with inter-individual variability in odour attractiveness. Fourthly, the results of the former studies are restricted to comparison between the follicular and luteal phases. No data are available on axillary body odour during menstrual phase; therefore, in the current study we also monitored female subjects during this time. This is a biologically relevant issue as men who regard their sexual partners as less appealing during her menstrual phase may avoid sexual intercourse during this time and thus decrease a potential health risk in their female partners.

## **Materials and Methods**

## Subjects

Subjects were enrolled via e-mail or personally by one of the experimenters (JH). They were asked to voluntarily participate in an experiment dealing with odour changes across the menstrual cycle. Fifty-one male students of the Charles University (Prague, the Czech Republic) repeatedly rated odour samples. Male raters who smoke were not excluded from the analyses in order to increase external validity of our results. Nine men did not complete the whole protocol and were excluded from the analyses. The final sample of raters thus consisted of 42 males (age 19-34 yr;  $\overline{x} = 24.4$ ; SD = 3.7). Nineteen females in total acted as sample donors. None of them were using hormonal contraceptives (i.e. the pill) during the time of the experiment and all had regular menstrual cycles (24-30 d). In order to acquire data across the whole cycle, experiments (sampling and rating) were carried out once a week for five

consecutive weeks. Thus, all female subjects began participating during different phases of their cycle. This fact excludes possible bias caused by the differences among particular rating days (e.g. by changes in weather). Conversely, this meant that the set of samples from each woman could not be evaluated by all raters, who were sometimes unable to attend at the required time. This resulted in a relatively high drop-out rate of subjects. Unequal sampling was therefore adjusted statistically. We acquired stimuli (body odour) from all three phases of menstrual cycle (menstrual, follicular, luteal) from 12 women (age 20–27 yr;  $\bar{x} = 23.6$ ; SD = 2.4). Only females who provided samples from all three phases were included in the analyses.

#### Menstrual Cycle Assessment

During the first session, each woman was asked about the date of onset of her last period of menstrual bleeding and the usual length of the cycle. All subjects reported having a regular menstrual cycle. Cycle length was estimated according to the onset of the next period of menstrual bleeding, which was reported to us during the course of the study. The day of onset of menstrual bleeding was considered to be the day 1 of their cycle. Menstrual cycle was divided into three phases: (1) menstrual phase (day 1-6), (2) follicular phase (day 7-14) and (3) luteal phase (day 15-28). The above-mentioned days (in parentheses) are valid for the 28-d cycle: in case of a different length of the cycle, the end of follicular phase was computed as F = L - 14, where F was the last day of the follicular phase and L the length of the cycle (modified after Thornhill & Gangestad 1999). In five women, only one date of onset of menstrual bleeding was available, therefore we used the reported usual length of the cycle instead. As it is unlikely that the random error introduced by our method of menstrual cycle estimation spuriously generates any significant relationship, the results we obtained would probably underestimate rather than overestimate actual effects (Thornhill et al. 2003).

## **Odour Sampling Procedure**

Cotton pads (7.5 cm in diameter) were used for collecting odour samples, a method used in several of the previous studies (e.g. Chen & Haviland-Jones 1999; Ackerl et al. 2002). Subjects fixed cotton pads in their armpits with unscented paper plaster and wore them for 24 h. We propose that, compared with using T-shirts, this method of odour sampling,

considerably decreases the possibility of contamination by compounds of exogenous origin. Each participant received instructions and restrictions in a written form. They were instructed to refrain from: (1) using perfumes, deodorants, antiperspirants, aftershave and shower gels, (2) eating meals containing garlic, onion, chilli, pepper, vinegar, blue cheese, cabbage, radish, fermented milk products, marinated fish, (3) drinking alcoholic beverages or using other drugs, (4) smoking, (5) sexual activity and sleeping in the bed of the partner the day before and on the day of wearing the pads. The restrictions are an expanded version of those used in most behavioural studies (e.g. Wedekind & Füri 1997; Chen & Haviland-Jones 1999; Rikowski & Grammer 1999; Platek et al. 2001; Singh & Bronstad 2001; Ackerl et al. 2002; Thornhill et al. 2003).

Cotton pads, plaster, an opaque jar for storing the pads and an instruction sheet were provided to female subjects 2 d before the rating session. Subjects started to wear pads the following morning and wore them for 24 h in total. The next morning, they placed the pads in the opaque jar and returned them to the experimenters. To avoid a possible effect of refrigeration on the stimuli, olfactory rating of the samples started within an hour of collection.

#### **Rating Procedure**

Ratings were conducted in a quiet, ventilated room. Raters were asked to come for the session approximately at the same time each week in order to avoid possible temporal changes of rated odours. A withinsubject design was used (i.e. each week, all men rated odours collected from the same women). Stimuli (pads) were encased in a 250-ml opaque jar labelled by a three-number code, which was changed throughout the sessions. Each subject rated 12 stimuli in a randomized order on seven-point scale for its: (1) intensity, (2) pleasantness, (3) sexual attractiveness and (4) femininity. Both ends of each scale were anchored by verbal descriptions (e.g. very unpleasant and very pleasant). The ratings were written down immediately after sniffing each stimulus, but the time spent by sniffing was not restricted.

#### **Statistical Analysis**

In order to eliminate the effect of individual rating habits (i.e. subjective scale use), raw ratings were transformed to z-scores. The z-scores of particular ratings were calculated as z = (x - M)/SD, where 'x' was the particular subjective rating (e.g. pleasantness),

M and SD were mean rating and standard deviation, respectively, of a variable (e.g. pleasantness) rated by the particular subject. Subsequently, these z-scores were tested using a multivariate general linear mixed model (GLMM) with intensity or pleasantness or sexual attractiveness or femininity as the dependent variable. To overcome unequal sampling and to account for the repeated measures of the subjects repeatedly rating odour samples, and of the samples obtained from the same female across different phases of the menstrual cycle, all analyses were performed using a Mixed model analysis with the female's ID nested within the subject's ID (female ID (subject ID)) as a random factor, using PROC MIXED (SAS, version 9.1). The significance of each fixed effect in the mixed GLMM was assessed by the F-test, on sequential dropping of the least significant effect, starting with a full model. Independent variables were classes (cycle phase, week) and continuous variable (order of presentation). In unbalanced designs with more than one effect, the arithmetic mean for a group may not accurately reflect response for that group, since it does not take other effects into account. Therefore, where appropriate, we used least-square means instead. Least-square means are, in effect, within-group means appropriately adjusted for the other effects in the model. Least-square means (further referred as 'adjusted means') were computed for each class and differences between classes were tested by t-test. For multiple comparisons, we used the Tukey-Kramer adjustment.

Associations between intensity and other characteristics (i.e. pleasantness, attractiveness and femininity) were estimated by fitting a random coefficient model using PROC MIXED as described by Tao et al. (2002) with fixed effects pleasantness, attractiveness and femininity (and all other factors as above). With this model, we calculated predicted intensity values and plotted them against selected fixed effect values with predicted regression lines for each site of the sample collection. Then, we calculated correlation coefficient between intensity and selected fixed effect values. Analogically, we estimated gradually all characteristics as intensity. The particular characteristic being a dependent variable, while the rest of the characteristics plus all other factors entering the model as fixed effects. As in the previous model, all factors and interaction terms were tested, but are not reported unless statistically significant.

#### Results

First, we tested how the subjects perceived the odour pleasantness (attractiveness, intensity and femininity) in individual phases of the menstrual cycle. Confounding variables (week of testing, order of presentation and female individuality) were included in the analyses. GLMM analyses revealed highly significant effects of female ID and menstrual cycle phase on pleasantness, attractiveness and intensity. Interactions between female ID and menstrual cycle phase were found to be significant for ratings of pleasantness and intensity. There was also a significant effect of the week of testing on intensity. The significant effects on femininity were female ID and presentational order. For all rated variables (e.g. pleasantness), the effect of the individual female (female ID) was higher then the changes across the cycle (Fig. 1; for detailed results see Table 1). The odour of women in the follicular phase was rated as



**Fig. 1:** Adjusted means of body odour pleasantness for individual subjects in the menstrual phase, the follicular phase and the luteal phase. Error bars show standard errors

 Table 1: Degrees of freedom, F-values, and p-values for predictors

 (fixed effects) associated with dependent variable used in a model

		Degrees of freedom			
Model for dependent variable	Fixed effect	Num. df	Den. df	F-value	Pr > F
Pleasantness	Female	11	689	32.15	<0.0001
	Phase	2	689	7.02	0.001
	Female * Phase	22	689	2.66	<0.0001
Attractiveness	Female	11	166	29.74	<0.0001
	Phase	2	546	6.35	0.0019
Intensity	Female	11	211	34.44	<0.0001
	Female * Phase	22	530	7.23	<0.0001
	Phase	2	547	3.57	0.0288
	Week	4	560	2.49	0.0422
Femininity	Order	1	665	8.56	0.0035
	Female	11	179	7.89	<0.0001

the least intense, the most pleasant and the most attractive (Fig. 2). Subsequent post hoc analysis showed significant differences in intensity, pleasantness and attractiveness between the menstrual and the follicular phase and in pleasantness and attractiveness between the menstrual and the luteal phase. The difference in attractiveness between follicular and luteal phase did not reach formal level of statistical significance in a two-tailed test (p = 0.08). However, if treated by the more appropriate onetailed test (a peak of attractiveness in the follicular phase was expected according to our a priori hypothesis) the results reached statistical significance



**Fig. 2:** Adjusted means of axillary odour attractiveness, pleasantness and intensity in the menstrual phase (black bars), the follicular phase (grey bars) and the luteal phase (white bars). Error bars show standard errors. Asterisks above the bars indicate level of significance in one tailed test (for details see text). \*Significance at the <0.05 level; \*\*at the <0.01 level; \*\*\*at the <0.001 level; ns, not significant at the >0.05 level

Subsequently, we analysed the relationships between rated variables using a mixed-model analysis with doubly repeated measurements as described above. The best-fit model of attractiveness included pleasantness and femininity (Fig. 3). The best-fit model of pleasantness as the dependent variable included attractiveness and intensity (Fig. 4). The best-fit model of intensity included pleasantness and femininity (Fig. 5). The best-fit model of femininity included attractiveness, intensity (Fig. 6), interaction between pleasantness and intensity and order of presentation.

#### Discussion

Our results show that both the pleasantness and attractiveness ratings given to axillary odours were lowest during menstruation and peaked in the follicular phase when the probability of conception is highest. The opposite pattern was seen for odour intensity (i.e. it was most intense during the menstrual phase and the least intense during the follicular phase). It was demonstrated for the first time that axillary odour itself may carry information



**Fig. 3:** Predicted values for attractiveness (y-axis) associated with pleasantness (+, full line) and femininity ( $\triangle$ , dashed line) (x-axis). Both axes show *z*-scored subjective ratings



 Attractiveness Intensity 3 Femininity (predicted values of 2 z-scored subjective rating) 1 0 -1 -2 -3 -3 0 2 3 -2 -1 z-scored subjective rating

**Fig. 4:** Predicted values for pleasantness (y-axis) associated with attractiveness ( $\bigcirc$ , full line) and intensity ( $\blacklozenge$ , dashed line) (x-axis). Both axes show z-scored subjective ratings



**Fig. 5:** Predicted values for intensity (y-axis) associated with pleasantness (+, full line) and femininity ( $\triangle$ , dashed line) (x-axis). Both axes show z-scored subjective ratings

about women's fertility status. These findings confirm the results of Singh & Bronstad (2001) who, using a T-shirt method, found the attractiveness to be significantly higher during the follicular phase compared with the luteal phase. However, from the study of Singh & Bronstad (2001), it is not clear whether all women wore T-shirts in their follicular

86

**Fig. 6:** Predicted values for femininity (y-axis) associated with attractiveness ( $\bigcirc$ , full line) and intensity ( $\blacklozenge$ , dashed line) (x-axis). Both axes show z-scored subjective ratings

phase first or whether the order of collection was randomized. It is well documented that attractiveness correlates negatively with the intensity of odour, which becomes lighter with the length of storage. Therefore, if it is true that the T-shirts from the follicular phase in Singh & Bronstad's (2001) study were collected first, the supposed differences between the follicular and the luteal phase could be in fact an effect based on different lengths of storing. Moreover, during the rating session, boxes with the T-shirts worn during the follicular phase were labelled F and those worn during the luteal phase L. The authors declare that none of the subjects were aware of the meaning of the markings, but the possibility of a low but systematic bias cannot be excluded.

In spite of a similar pattern of results between our study and that of Singh & Bronstad's (2001), differences between the follicular and the luteal phase in our study reached formal level of statistical significance only by using a one-tailed test. The lower statistical difference between the follicular and luteal phase could be due to the relatively small sample size. Another reason could be our broader definition of the follicular phase (day 7–14) compared with that of Singh & Bronstad (2001) (day 13–15). It is possible that body odour attractiveness increases between days 7 and 14, peaking around the time of ovulation. Thus the attractiveness in the early

follicular phase can be similar to that in the luteal phase. This possibility is supported by a relatively fast transitory decrease (24 h) in the asymmetry of the soft body tissue leading up to ovulation (Manning et al. 1996; Scutt & Manning 1996).

A recent study by Kuukasjärvi et al. (2004) also supports our findings. Their target sample (T-shirt donors) consisted of women both not using hormonal contraception and those who were. In the sample of women not using hormonal contraception, quadratic regression between male ratings of odour attractiveness and day of menstrual cycle peaked around the time of presumed ovulation. A non-significant trend (p = 0.07) was found when T-shirts were rated by women. This may be due to the relatively fewer number of female raters (n = 12) compared with males (n = 31). No relationship between the day of the menstrual cycle and odour attractiveness was found for T-shirts worn by women using hormonal contraceptives. A potential issue in an otherwise elaborated study is the method selected for the transformation of data on days of the menstrual cycle. The authors used a formula: 28/cycle length  $\times$  day of menstrual cycle. It is known that the length of the luteal phase is relatively stable and in cycles different from 'an ideal 28-d cycle' the length of the follicular phase fluctuates (Stern & McClintock 1998). Therefore, the formula used may introduce a relatively high rate of error; we believe, however, not one that is systematic. Moreover, the authors do not report whether their target subjects had a regular cycle or if they excluded women with very long cycles (maximum of 42 d). In both cases, it is disputable whether such cycles are ovulatory.

Other evidence of body odour changes across the cycle was provided by Thornhill et al. (2003). They asked the women to wear T-shirts and computed the probability of conception based on Jöchle's work (1973). Using correlational analysis, the authors found a positive association between conception risk and body odour attractiveness (r = 0.33, p = 0.02). It should be noted, however, that the method used for fertility risk assessment has been seriously questioned by the results of several other studies (Dunson et al. 1999; Wilcox et al. 2000). Moreover, Poran (1995) found that pair-bonded males prefered the body odour of their partners collected during the late follicular phase compared with the luteal phase. However, as Singh & Bronstad (2001) pointed out, from Poran's paper it is not clear whether subjects were allowed to use perfumes during the body odour collection. The use of perfumes (both the amount, and the type of perfume used) can change across the cycle and thus bias the natural body odour changes results.

The above-mentioned findings contradict those of Thornhill & Gangestad (1999) who did not find any differences between body odour attractiveness in the follicular and the luteal phase. However, this could be due to the differences in experimental design. Our results show that the inter-individual variability is much higher compared to the intra-individual changes across the cycle. Thus, we can expect that the between-subjects design used by Thornhill & Gangestad (1999) lacks the statistical power to detect rather subtle odour changes across the cycle. On the contrary, the main disadvantage of a within-subject design (i.e. repeated-measures design) is the relatively high drop-out rate of subjects. In our study, 12 of 19 women completed the whole protocol across their menstrual cycle.

The negative correlation between pleasantness and the intensity of odour suggests that the changes in pleasantness across the cycle can be, to some extent, explained as changes in odour intensity rather than odour quality. This effect was also observed in earlier studies concerning gender identification by smell (Doty et al. 1978, 1982) in which more intense smells were usually judged to be masculine. Nevertheless, our results cannot be fully explained by changes in intensity as they are statistically weaker compared with changes in attractiveness or pleasantness. Moreover, the intensity was a significant preonly for pleasantness and not for dictor attractiveness. Similarly, in the above-mentioned study of Kuukasjärvi et al. (2004), there was no correlation between odour attractiveness and intensity. Therefore, we may expect that both changes in odour intensity and quality constitute subjectively perceived changes in odour attractiveness and pleasantness.

Axillary odour is probably not the only odour cue to ovulation. Another potential source of relevant olfactory information could be changes in vaginal odour. It is known that the peak of pleasantness corresponds with the late follicular (ovulatory) phase (Doty et al. 1975; Keith et al. 1975). However, the pattern of changes in individual women was highly heterogeneous. The hedonic changes in perception of the vaginal odour can be due to the changes in relative concentration of short aliphatic acids (Michael et al. 1975). On the contrary, other authors did not confirm fluctuation of short aliphatic acids across the cycle (for review, see Huggins & Preti 1981). Vaginal inspection (oral sex practices) is relatively inter-culturally widespread behaviour. In spite of that, we suggest that due to bipedality, the axillary odour is a relatively more important source of information in humans.

Recently, it was found that the changes in attractiveness across the cycle are not restricted to odour cues but can also be detected visually. Facial images of women taken during their follicular phase were found to be more attractive compared with images of the same women taken during their luteal phase (Roberts et al. 2004). There are also several other lines of indirect evidence supporting the view that ovulation is not as hidden as previously assumed. Women become more symmetrical (Manning et al. 1996), their waist-hip ratio is lower (Kirchengast & Gartner 2002) and their skin becomes lighter (Symons 1995) around the time of ovulation. All mentioned characteristics are known to be important markers of attractiveness (e.g. Singh 1995; Scheib et al. 1999).

The changes in attractiveness across the cycle perceived on the basis of particular cues (e.g. axillary odour) are generally rather subtle. Nevertheless, in natural situations, they are perceived multimodally and thus their final reliability can be much higher than can be estimated from laboratory experiments under reductionistic conditions.

Pair-bonded males can use both olfactory and visual cues to monitor a woman's fertility status and thus avoid possible cuckoldry by other males. Gangestad et al. (2002) reported that pair-bonded males are more attentive and more proprietary near their partners' ovulation. From an evolutionary perspective, it would be also advantageous for casual partners to be attracted to women when conception is most probable. However, it is not known whether primary partners are more sensitive to the menstrual cycle changes of their mates compared with casual partners. Furthermore, there are no data regarding the role of previous experience (e.g. being pair-bonded, or co-habiting) for tracking changes across the cycle. The relatively high inter-individual variability in attractiveness, compared with the rather subtle menstrual cycle changes, suggests that the significance of body odour cues of fertility for unfamiliar males is rather low. Conversely, it could be argued that in ancestral hunter-gatherer conditions (i.e. relatively small groups), even potential casual partners were acquainted with women in their group and thus could track menstrual cycle changes.

In spite of the potential ability of males to track systematic changes across the cycle, woman can behaviourally adjust (i.e. suppress/promote) cycledependent changes according to her partner status (i.e. single/pair-bonded). Paired but unaccompanied women not using hormonal contraceptives were observed at a discotheque to be dressed in a more sexually provocative way when they were in the most fertile period. They wore shorter and tighter skirts with more skin exposed. This pattern was not observed among single women (Grammer & Renninger 2004).

On the basis of the phylogenetic analyses, it is suggested that human ancestors possessed moderate sexual swellings (Sillen-Tullberg & Møller 1993). Why this feature has disappeared in the course of evolution in the modern human is debated (e.g. Pawlowski 1999). Concentration on the lack of this particular feature led most theorists to the incorrect conclusion that there are no cues to the fertility state of the female. Nevertheless, experimental data suggest that such cues exist. However, such cues should not be misinterpreted as signals of ovulation. We propose that the cues used by males for monitoring women's cycles are rather a byproduct of physiological changes across the cycle. Based on the available data, we suggest that males cannot pinpoint ovulation but that cues based on the menstrual cycle phase allow them to assess female fertility in a probabilistic manner. Therefore, it would be more appropriate to substitute the rather confusing term 'concealed ovulation' with the more suitable term 'non-advertized ovulation'.

## Acknowledgements

We would like to thanks to all participants for their effort and time they spent by taking part in the study and to express our gratitude to Jindra Jileckova and Mark Sergeant for their considerable help with language corrections. This research was supported by the GA UK 323/2002 grant, by the Czech Ministry of Education (grant no. 0021620828) and by the Czech Ministry of Agriculture (MZE0002701402).

## **Literature Cited**

- Ackerl, K., Atzmueller, M. & Grammer, K. 2002: The scent of fear. Neuroendocrinol. Lett. **23**, 79–84.
- Benshoof, L. & Thornhill, R. 1979: The evolution of monogamy and loss of estrus in humans. J. Soc. Biol. Struct. 2, 95—106.
- Burley, N. 1979: Evolution of concealed ovulation. Am. Nat. **114**, 835–858.
- Chen, D. & Haviland-Jones, J. 1999: Rapid mood change and human odors. Physiol. Behav. **68**, 241–250.

Daniels, D. 1983: The evolution of concealed ovulation and self-deception. Ethol. Sociobiol. **4**, 69–87.

Deschner, T., Heistermann, M., Hodges, K. & Boesch, C. 2003: Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. Anim. Behav. **66**, 551–560.

Doty, R., Ford, M., Preti, G. & Huggins, G. R. 1975: Changes in the intensity and pleasantness of human vaginal odours during the menstrual cycle. Science **190**, 1316—1317.

Doty, R. L., Orndorff, M. M., Leyden, J. & Kligman, A. 1978: Communication of gender from human axillary odours: relationship to perceived intensity and hedonicity. Behav. Biol. **23**, 373–380.

Doty, R., Green, P. A., Ram, C. & Yankell, S. L. 1982: Communication of gender from human breath odours: relationship to perceived intensity and pleasantness. Horm. Behav. **16**, 13–22.

Dunson, D. B., Baird, D. D., Wilcox, A. J. & Weinberg, C. R. 1999: Day-specific probabilities of clinical pregnancy based on two studies with imperfect measures of ovulation. Hum. Reprod. 14, 1835—1839.

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. Lond. B – Biol. Sci. **269**, 975–982.

Grammer, K. & Renninger, L. 2004: Disco clothing, female sexual motivation, and relationship status: is she dressed to impress. J. Sex Res. **41**, 66–74.

Hrdy, S. B. 1979: Infanticide among animals – review, classification, and examination of the implications for the reproductive strategies of females. Ethol. Sociobiol.
1, 13—40.

Hrdy, S. B. & Whitten, P. L. 1987: Patterning of sexual activity. In: Primate Societies (Smuts, B. S., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T., eds). Univ. Chicago Press, Chicago, IL, pp. 370–384.

Huggins, G. R. & Preti, G. 1981: Vaginal odours and secretion. Clin. Obstet. Gynecol. 24, 355–377.

Jöchle, W. 1973: Coitus-induced ovulation. Contraception 7, 523—565.

Keith, L., Draunieks, A. & Krotoszynski, B. K. 1975:
Olfactory study: human pheromones. Archiv. Gynakol.
218, 203—204.

Kirchengast, S. & Gartner, M. 2002: Changes in fat distribution (WHR) and body weight across the menstrual cycle. Collegium Antropologicum 26, 47–57.

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 contraceptives and receiver sex. Behav. Ecol. **15**, 579—584. Lovejoy, C. O. 1981: The origin of man. Science **211**, 341—350.

Manning, J. T., Scutt, D., Whitehouse, G. H., Leinster, S. J. & Walton, J. M. 1996: Asymmetry and the menstrual cycle in women. Ethol. Sociobiol. 17, 129–143.

Michael, R. P., Bonsall, R. W. & Kutner, M. 1975: Volatile fatty acids, "copulins", in human vaginal secretions. Psychoneuroendocrinology **1**, 153–163.

Pawlowski, B. 1999: Loss of oestrus and concealed ovulation in human evolution. Curr. Anthropol. 40, 257—276.

Platek, S. M., Burch, R. L. & Gallup, G. G. 2001: Sex differences in olfactory self-recognition. Physiol. Behav. 73, 635—640.

Poran, N. S. 1995: Cyclic attractivity of human female odours. Adv. Biosci. 93, 555–556.

Rikowski, A. & Grammer, K. 1999: Human body odour, symmetry and attractiveness. Proc. R. Soc. Lond. B – Biol. Sci. **266**, 869–874.

Roberts, S. C., Havlicek, J., Flegr, J., Hruskova, M., Little, A. C., Jones, B. C., Perrett, D. C. & Petrie, M. 2004:
Female facial attractiveness increases during the fertile phase of the menstrual cycle. Proc. R. Soc. Lond. B – Biol. Sci. Suppl., Biology Letters 271, S270—S272.

Scheib, J. E., Gangestad, S. W. & Thornhill, R. 1999:
Facial attractiveness, symmetry and cues of good genes.
Proc. R. Soc. Lond. B – Biol. Sci. 266, 1913—1917.

Scutt, D. & Manning, J. T. 1996: Symmetry and ovulation in women. Hum. Reprod. **11**, 2477–2480.

Sillen-Tullberg, B. & Møller, A. P. 1993: The relationship between concealed ovulation and mating system in anthropoid primates: a phylogenetic analysis. Am. Nat. 141, 1—25.

Singh, D. 1995: Female health, attractiveness, and desirability for relationships: role of breast asymmetry and waist-to-hip ratio. Ethol. Sociobiol. **16**, 465–481.

Singh, D. & Bronstad, P. M. 2001: Female body odour is a potential cue to ovulation. Proc. R. Soc. Lond. B – Biol. Sci. **268**, 797–801.

Stern, K. & McClintock, M. K. 1998: Regulation of ovulation by human pheromones. Nature **392**, 177–179.

Strassmann, B. I. 1981: Sexual selection, paternal care, and concealed ovulation in humans. Ethol. Sociobiol. 2, 31–40.

Symons, D. 1995: The Evolution of Human Sexuality. Oxford University Press, Oxford.

Tao, J., Littel, R., Patetta, M., Truxillo, C. & Wolfinger, R.2002: Mixed Model Analyses Using the SAS System Course Notes. SAS Institute Inc., Cary, NC.

Thornhill, R. & Gangestad, S. W. 1999: The scent of symmetry: a human sex pheromone that signals fitness? Evol. Hum. Behav. **20**, 175–201.

Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., McCollough, J. K. & Franklin, M. 2003: Major histocompatibility complex genes, symmetry, and body scent attractiveness in men and women. Behav. Ecol. 14, 668–678.

- Wallis, J. 1992: Chimpanzee genital swelling and its role in the pattern of sociosexual behavior. Am. J. Primatol. 28, 101–113.
- Wedekind, C. & Füri, S. 1997: Body odour preferences in men and women: Do they aim for specific MHC combi-

nations or simply heterozygosity? Proc. R. Soc. Lond. B – Biol. Sci. **264**, 1471–1479.

Wilcox, A. J., Dunson, D. & Baird, D. D. 2000: The timing of the "fertile window" in the menstrual cycle: day specific estimates from a prospective study. Br. Med. J. **321**, 1259–1262.