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# Understanding olfactory fertility cues in humans: chemical analysis of women's vulvar odour and perceptual detection of these cues by men

Madita Zetzsche [a,b,*], Marlen Kücklich [a,b], Brigitte M. Weiß [a,b], Julia Stern [c], Andrea C. Marcillo Lara [d,e], Claudia Birkemeyer [d], Lars Penke [f,g,1], Anja Widdig [a,b,1]

[a] Behavioural Ecology Research Group, Institute of Biology, Leipzig University, Talstraße 33, 04103 Leipzig, Germany
[b] Department of Human Behavior, Ecology, and Culture, Max-Planck-Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany
[c] Personality Psychology and Psychological Assessment, Department of Psychology, University of Bremen, Grazer Straße 2c, 28359 Bremen, Germany
[d] Research Group of Mass Spectrometry, Institute of Analytical Chemistry, Leipzig University, Linnéstraße 3, 04103 Leipzig, Germany
[e] Forschungszentrum Jülich GmbH, Institute of Climate and Energy Systems, ICE-3: Troposphere, Wilhelm-Johnen-Strasse, Jülich 52428, Germany
[f] Biological Personality Psychology, Georg Elias Müller Institute of Psychology, Georg August University Göttingen, Goßlerstraße 14, 37073 Göttingen, Germany
[g] Leibniz ScienceCampus Primate Cognition, 37073 Göttingen, Germany

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ABSTRACT

By conveying cues of their current fertility, females can provide valuable reproductive information to conspecifics. Our closest relatives, non-human primates, employ diverse strategies, including olfactory cues from the anogenital region, to communicate information about female fertility. While their shared phylogeny with humans suggests that analogous olfactory cues may have been preserved in modern women, empirical evidence is lacking. In a comprehensive two-fold approach, we investigated fertility-related shifts in the chemical composition of women's vulvar volatiles as well as men's ability to perceive them. We collected vulvar odour from 28 naturally cycling women (students, academic staff members, and citizen of Göttingen) on up to ten days of their menstrual cycle, focusing on fertile days. For 146 vulvar samples (subsample of $n = 16$ women), we assessed whether their volatile profiles varied in relation to female fertility using gas chromatography–mass spectrometry. Simulating a first encounter, 139 men evaluated a total of 274 vulvar odour samples from 28 women, collected on different cycle days. We used hormonal analyses to confirm women's fertile days. We assessed variation in chemical composition and male odour ratings in relation to women's conception probability, temporal distance to ovulation, and ovarian hormone levels. We found no evidence for chemical changes allowing tracking of fertility across the cycle. However, in the immediate assessment (i.e., without tracking), no significant effects were found for any predictors except conception risk. Notably, the significance of the conception risk effect varied depending on the model specification. Further, men's attraction to vulvar odour was not significantly predicted by female fertility. Overall, our data suggests a relatively low retention of chemical fertility cues in vulvar odour of modern women.

## 1. Introduction

In light of the sexual conflict between the sexes, where competition over mating partners, parental investment and other aspects of reproductive dynamics are prevalent, information about their current fertility is highly valuable knowledge females may provide to conspecifics (Parker, 2006). In non-human primates, our closest living relatives, females use various strategies to advertise fertility, such as sexual swelling in *Papio* sp. and *Pan* sp. (Nunn, 1999), vocalisations in yellow baboons (*Papio cynocephalus*: Semple et al., 2002), and chemical cues in common marmosets (*Callithrix jacchus*: Kücklich et al., 2019). In humans, evidence for subtle cues to fertility has been suggested. For instance, when fertile, women's faces or voices are perceived as more attractive, and women dress in a more attractive way (e.g., face: Roberts et al., 2004; Puts et al., 2013; voice: Puts et al., 2013; clothing style: Durante et al., 2008;for a review see Haselton & Gildersleeve, 2011). However, whether human females show cues to fertility is still debated, as more recent, higher-powered studies did not replicate earlier findings, and

* Corresponding author at: Behavioural Ecology Research Group, Institute of Biology, Leipzig University, Talstraße 33, 04103 Leipzig, Germany.
*E-mail address:* madita.zetzsche@uni-leipzig.de (M. Zetzsche).
[1] These authors contributed equally to this work and share last authorship

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men (including romantic partners) do not detect any fertility-related changes across the cycle (e.g., facial attractiveness: Catena et al., 2019; Marcinkowska et al., 2021; odour attractiveness: Roney et al., 2023; general attractiveness perceived by romantic partners: Schleifenbaum et al., 2022; clothing style: Stern et al., 2024).

There is substantial evidence across primate taxa that body odour, particularly anogenital odour, conveys information about female fertility (reviewed in Drea, 2015). This is observed across a variety of primates, including basal species such as lemurs and lorises, as well as later-diverging primates like baboons and macaques, extending to the great apes, including gorillas and chimpanzees, our closest living relatives. Across taxa, evidence suggests that males are capable of perceiving and responding to chemical cues related to female fertility (e.g., certain lemurs, *Lemuridae*: Drea, 2020; common marmosets, *C. jacchus*: Kücklich et al., 2019; baboons, *Papio* spp.: Rigaill et al., 2013; chimpanzees, *Pan troglodytes*: Jänig et al., 2022). While substantial behavioural data about female olfactory fertility cues is available, studies investigating their chemical underpinnings are far less prevalent. Female fertility has been shown to affect chemical richness of vaginal samples in olive baboons (Vaglio et al., 2021). Potentially fertility-related variation in chemical profiles has been shown for anogenital samples in female tamarins (Poirier et al., 2021) and common marmosets (Kücklich et al., 2019), for vaginal secretions of rhesus macaques (Michael et al., 1971, but see Goldfoot et al., 1976) and in the body odour of female chimpanzees (Kücklich et al., 2022; Matsumoto-Oda et al., 2003).

Olfactory fertility cues in the anogenital region hold significant evolutionary importance across strepsirrhine and haplorhine primates. Acknowledging the shared phylogeny between humans and non-human primates, it is important to investigate whether these olfactory fertility cues in the genital area have been preserved or lost in modern women. For instance, modern women may unintentionally emit physical cues of fertility, thereby potentially influencing male perception and mating behaviour, as proposed by the leaky-cue hypothesis (Gangestad & Thornhill, 2008). Potential olfactory fertility cues in humans have largely been investigated in the axillary region, and primarily at the perceptual level. This research showed mixed evidence, with some studies demonstrating effects (Gildersleeve et al., 2012; Havlíček et al., 2006) while others failed to replicate these findings (Mei et al., 2022; Roney & Simmons, 2012; Zetzsche et al., 2024). Furthermore, there is a notable lack of evidence regarding chemical variation in axillary volatile profiles associated with female fertility (Zetzsche et al., 2024).

Odour of the genital area remains largely unaddressed by current research, despite its significant physiological potential for socio-chemical communication of fertility. The vaginal and vulvar tissues are rich in exocrine glands, particularly Bartholin's and Skene's glands, which are prevalent throughout the vulvar region, from the mons pubis to the perineum (Graziottin & Gambini, 2015; Streckfus, 2022). The labia majora contains anogenital sweat and sebaceous glands (van der Putte, 1991). As these glands emit secretions important for socio-chemical communication (Natsch & Emter, 2020), olfactory active substances may be produced across the anogenital area. Additionally, vaginal fluids are influenced by hormonal and fertility fluctuations across the menstrual cycle (Billings et al., 1972; Eschenbach et al., 2000; Streckfus, 2022). For instance, estrogen rise before ovulation coincides with a decrease in vaginal pH (Godha et al., 2017), and cervico-vaginal secretions become more abundant, consistent, and elastic at mid-cycle (Billings et al., 1972; Eschenbach et al., 2000). Thus, physiological changes in the vulvar and vaginal areas towards ovulation may lead to odour variations indicative of a woman's fertile state. A few early studies chemically analysed the volatile composition of vaginal secretions, describing elevated levels of certain organic acids at mid-cycle (Huggins & Preti, 1976; Michael et al., 1975; Preti & Huggins, 1975), although these findings were not replicated in a later study (Huggins & Preti, 1981). These studies had limitations; for example, cycle assessment often relied solely on menstruation dates (Michael et al., 1975), which are inaccurate for determining ovulation and cannot detect anovulatory cycles (Schmalenberger et al., 2021). The statistical approaches were mainly descriptive, focusing on characterising components and interpreting cycle relationships through individual graphs. Most data were based on secretions collected with cotton tampons, which may miss to collect significant odorous substances from the vulvar area. Furthermore, cotton material is limited in its ability to capture the full range of volatile compounds (Birkemeyer et al., 2016; Kücklich et al., 2017). Building on these studies, our research uses advanced statistical methods to better control for confounding effects (Dobson & Barnett, 2001). We precisely determined the exact day of ovulation using urinary ovulation tests and hormonal assessments.

For an olfactory fertility cue to be functional, there must be chemical changes that male conspecifics can perceive and interpret meaningfully. In an initial study, Doty et al. (1975) showed that vaginal secretions shortly before and during ovulation were rated as less intense and slightly more pleasant than those from other cycle phases. In one of the few follow-up studies, vulvar periovulatory odours were rated as more pleasant than samples from the night before menstruation (Cerda-Molina et al., 2013). Notably, more pleasant odours seemed to be generally associated with lower intensity ratings, suggesting a negative correlation between perceived pleasantness and intensity of vulvar odour (Cerda-Molina et al., 2013; Doty et al., 1975). However, these findings were not replicated in a recent study that rigorously investigated male perception of both axillary and vulvar odour (Roney et al., 2023). Previous attempts to combine chemical and perceptual evidence for vulvar odour have focused on substances labelled as 'copulins', which are a mixture of short-chain carboxylic acids suggested to vary with the menstrual cycle (Michael et al., 1975). Williams and Jacobson (2016) found that men exposed to copulins rated women's faces as more attractive than those in the control group, though these findings were not statistically significant. A second study also examined men's sexual behaviour, including motivation, risk-taking, and mating strategy preferences, but found no significant effects from copulin exposure (Williams & Apicella, 2018). This mixed evidence highlights the need for comprehensive research on both the chemical and perceptual aspects of vulvar odour. Despite the evolutionary significance of vulvar fertility cues in non-human primates, research on cyclic shifts in women's vulvar odour remains limited and has yielded mixed results. This lack of empirical data restricts our understanding of whether fertility cues in vulvar odour have been preserved or lost during human evolution. Therefore, we investigated fertility-related variations in both the vulvar volatile profile and men's perceptions of women's vulvar odour. This was part of a large-scale study about olfactory fertility cues investigating both axillar and vulvar odour. Results on axillary odour (collected from the same women as in the current sample) suggested no compelling evidence for ovulatory cycle shifts in women's axillary odour based on chemical and perception data (Zetzsche et al., 2024)

Physiological and endocrine changes are gradual throughout the cycle, and conception probability steadily rises during the fertile window - including the five days leading up to ovulation and the day of ovulation itself (Wilcox et al., 1998). Hence, we anticipate that women's body odour will vary not only between pre-fertile, fertile, and post-fertile days but also within the fertile window itself. To detect odour changes corresponding to this fertility and endocrine gradient, we implemented a sampling design that included pre-fertile and post-fertile days, as well as several days within the fertile window (Fig. 1). Further, we employed test predictors for female fertility that consider multiple potential patterns of odour variation around ovulation.

Changes in volatile composition and odour perception within the fertile window may correspond with the peak in conception risk (i.e., the probability of a single unprotected intercourse leading to conception), which is highest just before ovulation and declines abruptly thereafter (Wilcox et al., 1998). This scenario considers the potential for body odour to reflect sudden shifts in female fertility during the fertile window. To account for the potential influence of hormonal fluctuations throughout the menstrual cycle we assessed estradiol and progesterone

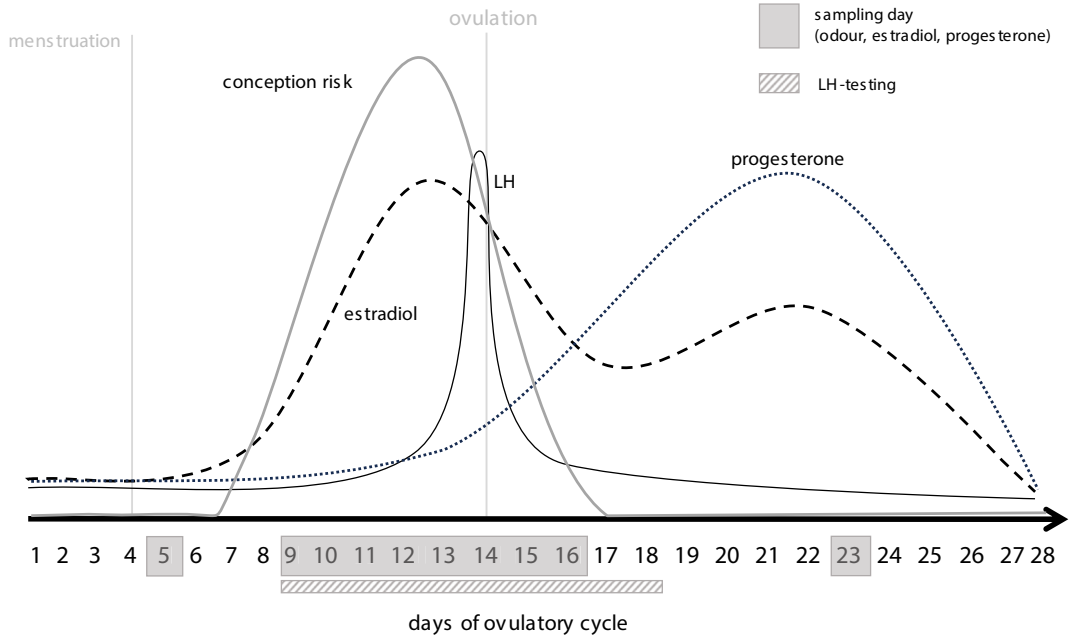


**Fig. 1.** Timing of sample collection across an exemplary menstrual cycle of 28 days. Patterns of conception risk, ovarian hormones, cycle length, and timing of ovulation are idealised for illustration. Depicted are the three hormones relevant to our study. LH = luteinising hormone. Figure adapted from (Zetzsche et al., 2024).

levels. Because humans, like other anthropoid primates but unlike most other mammals, are sexually active throughout the entire cycle, we also considered the possibility that humans may have developed additional mechanisms for guiding mating decisions, such as ovulation as a physiological reference rather than just indicating the peak fertile window. Thus, we included a temporal variable utilising the absolute values relative to the day of ovulation ('distance to ovulation'). An effect in this variable could reveal previously unconsidered processes, aside from variation in conception risk and reproductive hormone levels, that might elicit changes in body odour.

Using gas chromatography–mass spectrometry (GC–MS), we measured the chemical profile of women's vulvar volatiles and assessed changes in the abundance of compounds related to female fertility. Vulvar chemical profiles could vary in a way that requires *continuous monitoring* to decode the corresponding fertility information or in an *immediate* (ad hoc*) assessment*, without the need of tracking such changes throughout the menstrual cycle. While accounting for both scenarios with corresponding data transformations in our chemical study, we assumed vulvar volatiles to vary in accordance with the hormonal fluctuations across the menstrual cycle. To be indicative of the imminent approach of ovulation and ovulation itself, we expected changes in vulvar volatile composition to be most pronounced during the fertile window, i.e., some chemical substances may increase, and others decrease during ovulation compared to other times of the cycle.

For the perceptual study, we aimed to assess whether men's attraction to women's vulvar odour is predicted by female fertility, indicating that men might be able to perceive these potential cycle-related odour shifts. Given the lack of knowledge on how precisely vulvar volatiles track fertility fluctuations, we decided to present vulvar odour in a design resembling a first encounter (resembling mate choice at zero acquaintance) to investigate whether men can infer a woman's current fertile state from a single odour sample. This contrasts with raters comparing multiple samples from the same woman, as would occur within long-term relationships. As we expected the most prominent chemical odour changes during the fertile window, we predicted (i) vulvar odour of days with high conception probability receive higher ratings of attractiveness and pleasantness. (ii) Ratings of attractiveness and pleasantness increase with lower distance to ovulation. (iii) Due to the sharp surge of estradiol levels immediately before ovulation, we assumed a positive association between estradiol and vulvar odour ratings. Given the previously reported negative relationship between progesterone and women's general odour attractiveness (Lobmaier et al., 2018, but see Mei et al., 2022), we predicted higher progesterone levels to correlate with lower odour attractiveness. Consistent with previous studies, (iv) we expected an inverse relationship for intensity ratings.

## 2. General methods

### 2.1. Study setup

Odour collection took place between 2020 and 2021, with male perception tests following between 2021 and 2022. Due to Covid-19, strict protocols were followed (Supplement S1). Five female and three male research assistants, trained by the first author, managed odour collection and ratings, respectively. Written consent was obtained from all participants, and the study was approved by the local ethics committee.

### 2.2. Participants

#### 2.2.1. Odour donors

We collected odour samples from naturally cycling, women, aged 20–30 years, with a regular menstrual cycle (between 21 and 35 days, Creinin et al., 2004) for the past three months, and without hormonal contraception, pregnancy and lactation for the last six months. Donors had to be heterosexual, on a vegetarian or vegan diet for at least one month before sample collection (to avoid the impact of meat on odour quality, Havlíček et al., 2006), be non-smokers, have no chronic or hormonal diseases, and not use medications or recreational drugs regularly (see Havlíček & Lenochova, 2008). Recruitment was conducted via an online database at the University of Göttingen; largely consisting of students and academic staff members. To reduce the risk of anovulatory cycles, we targeted recruitment on women who had demonstrated reliable menstrual cycles in a previous study (Stern, Kordsmeyer and Penke, 2021).

Sixteen participants provided samples for chemical analysis, and odour samples for preference tests were collected from these and 12

additional women, adding to a total of 28 participants (mean age 24.86, *SD* = 3.26). Eighteen women reported to be single, eleven were partnered. Additionally, samples were collected from one more woman whose data was later excluded from further analyses, as detailed below.

#### 2.2.2. Odour raters

Male participants aged 18–40 were recruited based on heterosexual orientation. To ensure normal olfaction, participants were required to be non-smokers without diagnosed olfactory or neurodegenerative disorders, chronic nasal conditions, head trauma, regular medication or recreational drug use (Supplement S8.1). Additionally, olfactory function was confirmed using the medical Sniffin' Stick Screening 12 (Burghart Messtechnik GmbH, Holm, Germany). No participants were excluded based on poor olfactory performance. Demographic data, sexual orientation and raters' compliance with the behavioural restrictions were confirmed using a questionnaire (Supplement S8.3). Odour raters were acquired via the same online participant database as odour donors, bulletins, private contacts, and social media. A total of 139 men (aged 19–40 years, mean = 25.35, *SD* = 4.03) participated as raters, of which 65 were partnered, 67 were single, and seven did not indicate their relationship status.

### 2.3. Sampling schedule and instructions

An introductory meeting was scheduled to verify inclusion criteria, collect demographic data, and confirm sexual orientation of odour donors via questionnaires (Supplement S2.4). Participants received instructions on the study procedure, sampling material, and infection protection. They provided menstrual cycle details for scheduling sample collection using the reverse cycle day method (i.e., assuming that ovulation occurs 15 days prior to the onset of subsequent menstruation, cf. Gildersleeve et al., 2012). Samples were collected before, during, and after the fertile period at ten time points during one menstrual cycle per participant as follows: one session on reverse cycle day 24 (i.e., 24 days prior to the menstrual onset, early follicular phase), eight daily sessions on reverse days 20–13 (comprehensively covering the fertile window), and one session on reverse day six (mid-luteal phase, see Fig. 1).

To accommodate minor cycle variations, we allowed scheduling flexibility of up to five days (Stern et al., 2021). Sample collection was standardised by having participants follow established procedures for behavioural and dietary restrictions (cf. Gildersleeve et al., 2012, Supplement S5.1). Compliance was assessed after each session (Supplement S2.4).

### 2.4. Menstrual cycle assessment

We used highly sensitive urine ovulation strips (10 mIU/ml, purbay® David One Step Ovulation Tests, Runbio Biotech, China) to monitor luteinising hormone (LH) levels and hormonally confirm the day of ovulation for each woman. Participants conducted daily LH tests throughout their estimated fertile window, starting from reverse cycle day 20, concluding after two consecutive negative results followed a positive one. Participants received instructions, performed the tests at home and sent digital photos of each test to the study manager for verification. To estimate cycle length, women reported the onset of their menstruation for the test and subsequent cycle.

Saliva samples were collected via passive drool (1.5–2 ml in SaliCaps, IBL International, Hamburg, Germany) per session, following established protocols (cf. Stern et al., 2021). Contaminated samples (e.g., with blood) were repeated. Within ten minutes of saliva collection, the samples were stored at −80 °C until shipment on dry ice to the Kirschbaum Lab (Technical University of Dresden, Germany), where they were stored at −20 °C until analysis. Saliva was thawed and centrifuged at 3000 rpm for five minutes for a clear supernatant of low viscosity. Estradiol and progesterone levels were measured using chemiluminescence immunoassays with high sensitivity (IBL International, Hamburg, Germany). Mean levels were 4.27 pg/ml for estradiol (*SD* = 2.1, range = 1.57–21.39 pg/ml) and 39.63 pg/ml for progesterone (*SD* = 29.44, range = 11.31–176.63 pg/ml), with intra- and inter-assay coefficients below 9 % for both steroid hormones, which is considered good (Schultheiss & Stanton, 2009).

Ovulation was determined as the day after the first positive LH test, including women with two positive days (*n* = 11). After confirming that the estimated ovulation date aligned with the expected luteal phase range (Crawford et al., 2017), we plotted the ten salivary hormone values relative to ovulation for each participant to assess whether the day of ovulation visually matched the overall hormonal pattern. With dense sampling around the fertile window, we observed increased estradiol levels prior to ovulation. We also assessed decreases in estradiol for women with adequate post-ovulation hormone levels, assigning corresponding conception risk estimates (cf. Stern et al., 2021, Supplement S3.2).

All 29 cycles had a typical range (mean = 30.48 days, SD = 3.31, range = 25–35). One woman was excluded from further analysis, after only negative LH tests and inconclusive hormonal patterns, most likely indicating a non-ovulatory cycle.

### 2.5. General statistical procedures

All statistical analyses were performed using R v. 4.1.3 (R Core Team, 2022). The alpha level was 0.05 in all analyses.

We provide open data and analysis scripts (https://osf.io/d7wpn/?view_only=c4e54e9acb954bba9b21f9c5a0870cf1).

#### 2.5.1. Test predictors

We used the same test predictors for chemical and perceptual data: conception risk, estradiol and progesterone levels, along with the temporal variable 'distance to ovulation' (**Table S4**). Control predictors and model specifications differed between data sets, as detailed in the subsequent sections.

We compared the fit of each full model to a null model that excluded the test predictors but retained control predictors, random effects, and slopes (where applicable), using a likelihood ratio test (LRT; Dobson & Barnett, 2001) to assess the overall significance of the test predictors while avoiding 'cryptic multiple testing' (Schielzeth & Forstmeier, 2009).

We assessed the significance of the individual predictors using LRTs only when the overall full-null model comparison was significant. To mitigate the potential mediation risk between conception risk and cyclic hormones, we adjusted our model approach. In instances where a full-null model comparison was significant but individual predictors were not, we evaluated conception risk as the only test predictor, excluding hormonal predictors and distance to ovulation while maintaining an otherwise identical model structure (Supplement S7.1). Additionally, we conducted a parallel analysis using estradiol and progesterone as the sole test predictors, excluding conception risk and distance to ovulation. Since most related previous studies have tested these predictors individually, this approach also maintains comparability with other research.

Further, since the optimal transformation for cyclic hormones in linear mixed models is still debated, we ran all models using both z- and log-transformations of estradiol and progesterone. For z-transformation, hormone levels were first subject-mean centered and then scaled using z-scores (cf. Stern et al., 2021). To manage negative values due to subject-mean centering, log-transformation was carried out first (cf. Dinh et al., 2023). We performed all statistical analyses using both transformations to ensure that model results were not affected by the choice of transformation. We present the main results in the main text, and a comprehensive description of all analyses and findings in Supplement S7–S11.

## 3. Chemical study

### 3.1. Chemical sample collection

The chemical substances in women's vulvar odour, which our analysis focused on, evaporate easily at room temperature (i.e., semi-volatiles with boiling points between 250 and 400 °C, and volatiles with boiling points below 250 °C, Wypych, 2001) and are directly perceptible by the recipients' main olfactory epithelium (Dulac & Torello, 2003).

A portable, two-channel air pump (BiVOC2, Umweltanalytik Holbach GmbH, Germany) was used to draw ambient air around women's vulva into TD tubes (stainless steel, 0.25 in. × 3.50 in., Supelco, Bellefont, USA) (Kücklich et al., 2019; Weiß, Marcillo et al., 2018). Inside the tube, the compounds present in each sample adhered to polymers, allowing them to be stored until further chemical analysis. We collected 0.5 l of air (flow rate: ~1.5 l/min; Weiß, Marcillo et al., 2018) for each sample. Additionally, we collected and analysed two types of TD tube blanks: analytical blanks (i.e., similar handling and processing as all other samples, without pulling air through the tubes, $n = 27$), and room blanks (i.e., air samples of the testing room at least 60 min before or after participants were present, $n = 12$).

At the lab, odour donors performed odour collection on their own, with detailed guidance provided on handling the equipment during practice trials prior to the actual sampling. For sample collection, the TD tube was positioned approximately 3 cm from the middle of the participant's vulva. We provided participants with a new TD tube if their previous tube was in contact with skin or dropped to the ground. After each session, neutral odour conditions were established by ventilating the test room for 60 min. We collected 158 of the anticipated 160 chemical samples as two participants omitted one test session each.

### 3.2. Chemical analysis

Chemical profiles were measured via gas chromatography–mass spectrometry (GC–MS), a method that separates and identifies the compounds within a given sample. Following GC–MS analysis, the individual compounds in a sample are displayed as peaks in chromatograms, providing insights into the specific volatile compounds present, as well as their relative intensities and retention times (the time taken for a compound to exit the chromatographic column once separated from other components).

GC–MS measurement failed for 12 samples (due to program error overnight), resulting in a total of 146 samples available for further analysis.

Initially, we identified 118 recurring peaks in the chromatograms across all samples, indicating compounds likely derived from vulvar volatiles. Substances identified as contaminants in previous studies using the same TD tubes and analytical techniques ($n = 10$, (Weiß, Marcillo et al., 2018) deemed unlikely to be of human origin were excluded, as were compounds that showed equal or higher intensities in blank (non-human odour control) samples ($n = 5$). This resulted in a total of 103 compounds from vulvar odour considered of likely human origin for statistical testing. Detailed technical information on the chemical analysis is provided in Supplement S6.

### 3.3. Statistical analysis

We examined female fertility in relation to *i)* the overall similarity of whole chemical profiles (Stoffel et al., 2015; Weiß, Kücklich et al., 2018), and *ii)* compound composition between chemical profiles (Kücklich et al., 2019; Weiß, Kücklich et al., 2018) based on 146 vulvar odour samples from 16 women.

We evaluated whether the chemical profiles of vulva samples with the same fertility information (e.g., identical conception risk) were more similar than those with different fertility information. This analysis highlights commonalities in volatile profiles related to varying female fertile states. We did so by assessing the *overall similarity of whole chemical profiles* with regard to female fertility using pairwise Bray-Curtis indices calculated from standardised, log(x + 1)-transformed peak areas (Stoffel et al., 2015) using permutational multivariate analysis of variance (perMANOVA) with distance matrices using the function *adonis2* of the R package 'vegan' (v. 2.6–2, Oksanen et al., 2022).

Vulvar chemical profiles may vary daily during the menstrual cycle to indicate fertility, causing fluctuations between samples from the same woman. *Continuous monitoring* might be needed to decode fertility information through these changes. Alternatively, vulvar volatile profiles could remain stable overall, with only specific substances changing in response to fertility, such as some compounds appearing only during ovulation. This would create profiles specific to a particular fertility trait in an ad hoc assessment, interpretable without monitoring multiple samples. To address both possibilites we ran separate models with two different transformations of relative compound intensity (i.e., peak area). For *continuous monitoring*, we examined changes in the relative abundance of compounds using normalised relative peak areas, centred to a mean of zero and scaled to a standard deviation of one. This adjustment equalises the importance of all compounds within samples in the analysis. To evaluate ad hoc *assessments*, we used log(x + 0.01) to buffer the impact of highly abundant compounds. We mitigated floor and ceiling effects associated with using percentage as a response variable by applying an arcsine transformation.

We evaluated the association between female fertility and vulvar chemical profiles using linear mixed models (LMM) via the function *lmer* of the R package 'lme4' (v. 1.1–28, Bates et al., 2015). All models were fitted with a vectorised multivariate data matrix comprising vulva samples ($N = 146$) and compounds ($N = 103$), with transformed relative peak areas ($146 \times 103 = 15{,}038$) as the response variable. Storage duration of the respective TD sample before GC–MS analysis (in months), the GC–MS batch the tubes were analysed in, and donors' age were included as controls.

To prevent pseudoreplication and heteroscedastic variance (Jamil et al., 2013), we entered samples (matrix rows) and compounds (matrix columns) as random intercepts. Odour donor ID was an additional random factor (see **Table S7.1a**).

The slope estimate's steepness indicates which compounds are most strongly associated with female fertility, i.e. most affected by a test predictor (Weiß, Kücklich et al., 2018). Thus, we fitted the test predictors as random slopes within the random effect compound as our actual test predictors. Accordingly, the corresponding null model was lacking the effects of the test predictor slopes. To obtain reliable *p*-values, we fitted random slopes and interactions maximally (Barr et al., 2013). Model fit and checks are reported in Supplement S7.1.

In robustness analyses, we determined whether volatile composition was affected by odour donors violating the sampling restrictions (medication $n = 4$; perfumed soap $n = 2$; consumption of onion $n = 6$, garlic $n = 5$, alcohol $n = 2$). Details are reported in Supplement S7.1.

### 3.4. Results chemical study

We detected no significant association between the overall similarity of women's whole chemical profiles and female fertility predictors (perMANOVA, $r = 0.02$, $p = 0.976$).

When substances were compared with each other between different samples (normalised response), the chemical composition of women's vulvar profiles was not significantly associated with female fertility predictors (z-transformed hormones: LRT, $\chi 2 = 4.82$, $df = 22$, $p > 0.999$; log-transformed hormones: LRT, $\chi 2 = 2.31$, $df = 22$, $p > 0.999$). When comparing substances relative to the whole sample (log-transformed response), the full-null model comparison was significant for both hormone transformations (**Table 1**). However, none of the test predictors were significantly related to vulvar volatile variation. With a p-value of 0.051, conception risk tended to relate to variation in certain substances

**Table 1**
Results of full-null model comparisons and test predictors of variation in women's vulvar chemical profiles depicting **original** – full data set; **robust**– data subset without donor violations, with N = number most affected substances. *P* values <0.05 are highlighted in bold.

| | | z-transformed hormones (df = 7) | | | | | | log-transformed hormones (df = 7) | | | | | | conception risk as only test predictor (df = 4) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | original | | | robust | | | original | | | robust | | | original | | | robust | | |
| | | $\chi2$ | p | N | $\chi2$ | p | N | $\chi2$ | p | N | $\chi2$ | p | N | $\chi2$ | p | N | $\chi2$ | p | N |
| | mean ± SD | 40.26 | 0.010 | – | 7.33 | 0.998 | – | 35.42 | 0.035 | – | 8.56 | 0.995 | – | -∇ | – | – | – | – | – |
| **conception risk** | 0.09 ± 0.10 | 13.99 | 0.051 | 7 | 2.22 | 0.947 | – | 10.59 | 0.157 | – | 0.96 | 0.995 | – | 26.94 | **<0.0001** | 7 | 1.37 | 0.850 | – |
| **distance to ovulation** | 4.98 ± 3.77 | 6.13 | 0.525 | – | 1.28 | 0.989 | – | 5.02 | 0.657 | – | 1.09 | 0.993 | – | – | – | – | – | – | – |
| **estradiol** | 4.26 ± 2.44 | 2.74 | 0.908 | – | 2.05 | 0.957 | – | 0.60 | 0.999 | – | 0.57 | 0.999 | – | – | – | – | – | – | – |
| **progesterone** | 37.57 ± 25.26 | 8.05 | 0.328 | – | 2.07 | 0.956 | – | 3.39 | 0.847 | – | 1.56 | 0.980 | – | – | – | – | – | – | – |

∇ Conception risk was tested as the only test predictor; hence a full-null model comparison was not necessary.

when estradiol and progesterone were z-transformed, but not when log-transformed.

When conception risk was modelled as the sole predictor, accounting for potential mediating effects of reproductive hormones, this predictor was highly significant (Table 1). We also identified the substances that were most responsive to conception risk in our dataset (Table 2). Estradiol and progesterone individually showed no significant effect (Supplement S7.2).

Overall, results were not consistent across all models in the robustness analyses (Table 1).

## 4. Male odour perception

### 4.1. Odour collection procedure

Women received odourless cotton gauze pads (10 cm × 10 cm) in pre-cleaned 30 ml amber glass vials, disposable gloves and medical adhesive tape (**Table S5.3**), and instructions for pad application (Supplement S2.3). They attached the pads to their underwear covering the vulvar area and wore them overnight for 12 h before each sampling session. Pads were removed the next day at the laboratory and stored at −80 °C within ten minutes of sample collection (Lenochova et al., 2009) in clean glass vials, sealed using airproof polytetrafluoroethylene tape (**Table S5.3**). The average wear time was 12.68 h (SD = 1.92, range = 6–20). We collected 285 out of 290 expected samples, because pads were not returned properly ($n$ = 5). Samples from one woman without confirmed ovulation ($n$ = 10) were excluded, resulting in 274 samples for rating assessment.

### 4.2. Odour rating design and procedure

Each man rated the odour of 24 different women in two corresponding rating sessions over a two-week interval (session A: 10 samples and olfactory performance test, session B: 14 samples). Each session included a 15-min break after half the samples to prevent sensory fatigue. Participants received detailed written information about the procedure, inclusion criteria, infection protection protocols, and behavioural restrictions, including avoiding alcohol or any other recreational drug 12 h prior, and food or drink, except water, one hour before each session to maintain olfactory sensitivity. Raters were informed they would judge different women's vulvar odour.

Odour samples were defrosted at room temperature two hours before each session. Raters were supervised by male experimenters (see Kordsmeyer & Penke, 2019), blinded to fertility condition, and assigned a fixed desk at which they were provided with the first odour sample to be rated. Samples were presented in the opaque glass vials they had been collected and stored in, and were circulated in a clockwise order between desks, ensuring that all raters evaluated each sample in the room. Raters wore cotton gloves and were instructed to avoid exhaling onto the samples. We advised raters to smell the samples in a maximum of two sniffs. Men rated each vulvar sample immediately after smelling using a verbally anchored 11-point Likert scales for 'attractiveness', 'pleasantness', and 'intensity' from −5 (*extremely unattractive/unpleasant/weak*) to +5 (*extremely attractive/pleasant/intense*) on a paper questionnaire (Supplement S8.3). For samples too subtle to assess, raters could select 'I cannot smell this sample'. For analysis, these ratings were numerically transformed to a scale of 1 to 11. After each session, odour samples were resealed and frozen at −80 °C until reuse (defrost frequency: mean = 1.70, SD = 0.96, range = 1–4). In total, 2947 vulvar odour ratings were completed, with 172 (5.8 %) marked as non-perceivable. Each sample was rated by 10.75 men on average ($SD$ = 1.73, range = 5–14). Of the 139 raters, 15 did not return for session B. Individual agreement inter-rater reliabilities (ICC 1,1) were ICC = 0.98 for attractiveness, ICC = 0.90 for pleasantness, and ICC = 0.98 for intensity (Supplement S9.1).

**Table 2**
Most affected substances of conception risk with tentative identification (similarity: [a] > 900, [b] > 800, [c]confirmed with standard), substance class, retention time (RT), slope estimates for the main models tested with indication of the origin and corresponding references (**for details see Supplement S7.2**). Arrows indicate the direction of the effect (↑ = increasing intensities with increasing conception risk, ↓ = decreasing intensities with increasing conception risk).

| Substance | Substance class | RT | z-transformed hormones | log-transformed hormones | Conception risk as single test predictor | Origin | References for origin |
|---|---|---|---|---|---|---|---|
| Acetic acid[a,c] | carboxylic acid | 2.7 | 0.67↑ | 0.55↑∇ | 0.65↑ | pot. End.[1] | Drabińska et al., 2021 |
| Urea-related compound[b] | amide | 10.7 | −0.59↓ | −0.45↓∇ | −0.50↓∇∇ | pot. Metab.[2] | Drabińska et al., 2021; Charpentier et al., 2012 |
| Methylated ketone[a] | ketone | 11.5 | 0.73↑ | 0.62↑∇ | 0.74↑ | pot. End.[1] | Charpentier et al., 2012 |
| Methenamine[a] | heterocyclic compound | 14.8 | −0.69↓ | −0.59↓∇ | −0.64↓ | pot. End.[1] | Filipiak et al., 2014, 2012 |
| Unknown alkane | alkane | 15.4 | 0.61↑ | 0.59↑∇ | 0.67↑ | pot. End.[1] | Kücklich et al., 2019; Schirmer et al., 2010 |
| Unknown amine | amine | 16.4 | 0.79↑ | 0.64↑∇ | 0.75↑ | pot. End.[1] | France et al., 2022; Drabińska et al., 2021 |
| Unknown | unknown | 20.9 | 0.58↑ | 0.48↑∇ | 0.54↑∇∇ | unkn.[3] | |

∇Conception risk was not significant as a test predictor.
∇∇ Compound was not among the compounds most affected in this model.
[1] 'potentially endogenous' (likely of endogenous origin; probably sourced from animals), based on previous animal studies with no known external sources (e.g., plants).
[2] 'potentially metabolised' substances refer to those reported in both animals and external sources (e.g., plants). These compounds could be metabolised by the animal or skin bacteria.
[3] Compounds that we could not identify and for which we could not determine an origin based on the literature were classified as 'unknown'.

### 4.3. Statistical analysis

We investigated the relationship between female fertility and the three rating dimensions—attractiveness, pleasantness, and intensity—by fitting cumulative link mixed models (CLMMs, Agresti, 2002). These models are tailored for ordinal response data such as Likert scale ratings (Bürkner & Vuorre, 2019; Marcinkowska et al., 2021). CLMMs retain the benefits of (G)LMMs by incorporating fixed and random effects predictors. Each rating dimension was analysed separately using the *clmm* function of the R package 'ordinal' (v. 2020-08-22, Christensen, 2019).

Only ratings marked as perceivable were included in the models. Besides the test predictors (**Table S4**), fixed effects control variables included storage duration of the odour sample, defrost frequency at the time of rating, pad wear duration by odour donors, and ages of odour donors and raters. We further included odour donor ID, rater ID, odour sample ID, and rating session ID as random intercepts (**Table S9.1b**), along with maximal random interactions and slopes (Barr et al., 2013). We report model checks and fit in Supplement S9.1.

To facilitate comparisons with previous studies, we assessed conception risk, estradiol and progesterone as sole predictors using identical model structures. Additionally, we assessed whether inter-individual differences in hormonal levels predict vulvar odour attractiveness (see Supplement S9.1). For robustness analyses, we excluded cases where participants violated sampling and rating restrictions to evaluate their impact on scent ratings. An additional robustness analysis confirmed that test predictors did not generally affect odour sample perceptibility (see Supplement S9.2).

### 4.4. Results male odour perception

Samples received an average attractiveness rating of 5.13 ($SD = 2.48$, range = 1–11), a mean pleasantness rating of 5.39 ($SD = 2.45$, range = 1–11), and a mean intensity rating of 5.81 ($SD = 2.89$, range = 1–11). Full-null model comparisons were not significant regardless of the rating dimension, hence male ratings of women's vulvar scents did not significantly vary with any of the test predictors (LRTs, attractiveness: $\chi2 = 0.781$, df = 4, $p = 0.941$; pleasantness: $\chi2 = 2.39$, df = 4, $p = 0.665$; intensity: $\chi2 = 2.01$, df = 4, $p = 0.735$). Models with log-transformed hormones and the robustness analysis confirm these results (Supplement S9.2). When tested individually, neither conception risk, nor estradiol or progesterone showed significant effects for any rating dimension, supporting the findings of our main analyses (Supplement S9.2). Plots of male ratings relative to ovulation and ovarian hormone levels are presented in Figs. 2 **and S9.2**, while inter- and intra-individual fluctuations in vulvar odour ratings illustrate no consistent pattern in Fig. 3.

## 5. Discussion

Using frequent and hormonally confirmed odour samples, our study combined volatile and perceptual analyses to investigate fertility-related shifts in the vulvar odour of women across their menstrual cycle, with a particular focus on the fertile window. For the chemical analyses, we found no evidence of changes that would allow fertility to be tracked across the cycle the immediate assessment (i.e., without tracking), no predictors showed significant effects, except for conception risk. Its significance, however, varied depending on the model specification, indicating an inconclusive link between vulvar chemical profiles and female fertility. This inconsistency suggests that our results may not be robust. Men's attraction to women's body odour was not significantly predicted by female fertility.

We assessed two scenarios regarding how vulvar chemical profiles might indicate female fertility: continuous monitoring (normalised response models) and immediate (ad hoc) assessment via specific substances without tracking changes (log-transformed response models). We found no chemical variation suitable for fertility monitoring over the menstrual cycle, which could be useful in ongoing romantic relationships, as normalised models showed no significant effect. This was also confirmed in robustness analyses.

In contrast, some substances tended to be affected by conception risk for the ad hoc assessment (log-transformed response), showing a trend with z-transformed reproductive hormones and significant results with conception risk as considered as a sole predictor (**Table 1**). However, robustness analyses, excluding samples with odour donor violations, rendered models non-significant (**Table 1**), suggesting possible effects from these violations on chemical profiles or reduced sample size causing non-significance. To address if inconsistencies may have resulted from reduced sample size in the robustness analyses (i.e. 19 excluded samples with violations), six additional analyses were conducted in which 19 randomly picked odour samples were removed from the statistical analyses. No consistent pattern emerged from the additional analyses, which makes it difficult to attribute the difference in results across the different model specifications to any single factor. We thus

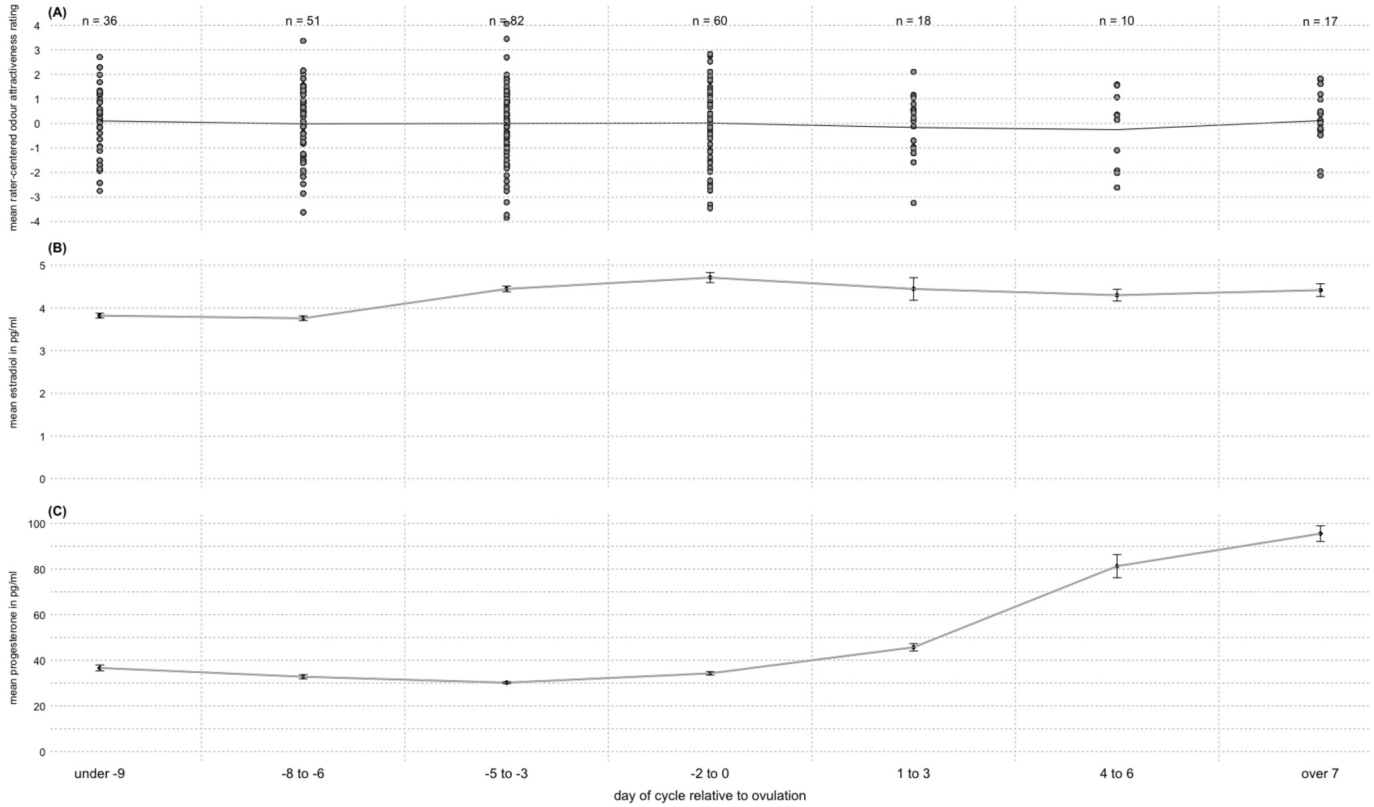


**Fig. 2.** **(A)** Subject-mean-centered and grand-mean standardised odour attractiveness ratings, and average levels of **(B)** estradiol and **(C)** progesterone per cycle day relative to ovulation (day 0 represents the assigned day of ovulation) with n indicating the number of ratings per cycle day interval. For **(A)-(C)**, cycle days were divided into the same 3-day intervals, and the trend lines represent the average odour attractiveness rating and hormone value for each interval. The error bars for both estradiol and progesterone indicate the standard error within each cycle day interval.

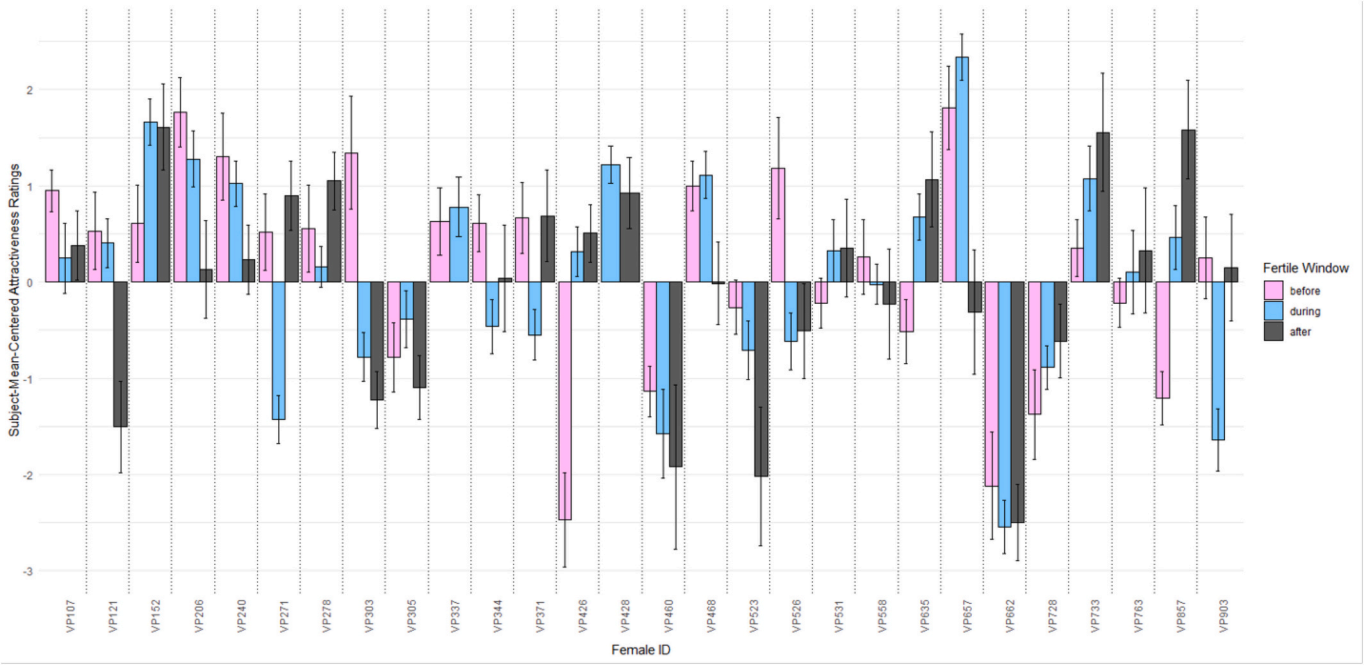


**Fig. 3.** Bar plot depicting inter-individual differences and intra-individual fluctuations in vulvar odour attractiveness ratings, which were subject-mean centered within male raters. Ratings are shown before (pink), during (blue), and after (grey) the fertile window. Error bars represent the standard error within each cycle day interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cannot rule out that the results systematically depended on the number of samples excluded and/or specific types of violations (**Table S7.2c**). At this point, we cannot definitively identify the cause of these inconsistencies.

Nevertheless, since the data tentatively suggest a potential association between conception risk and certain substances, we explored the substances showing the strongest association with conception risk in our data. The different models consistently showed a similar suite of substances responding to conception risk in a similar pattern (**Table 2**). These compounds belonged to diverse chemical classes. An amine, an amide, a carboxylic acid, an alkane, and an unidentified compound increased with conception risk, while a heterocyclic compound and a ketone decreased (**Table 2**)**.** In particular, we observed higher levels of acetic acid, and a urea-related compound associated with higher conception risk. Earlier studies, though not methodologically robust, qualitatively described fertility-related concentration changes in acetic acid (Michael et al., 1975; Preti & Huggins, 1975) in human vaginal secretions. Acetic acid was also included as one of the 'copulins' tested on male perception, but did not convincingly influence male perception or sexual behaviour (Williams & Apicella, 2018; Williams & Jacobson, 2016). None of the other 'copulins' used in these studies - propanoic acid, butanoic acid, methylpropanoic acid, and methylbutanoic acid - were among the compounds found to be associated with conception risk in our study.

We also detected a urea-related compound potentially associated with increased conception risk. Urea, a common excretory product in mammalian odours (Charpentier et al., 2012), has been qualitatively linked to variations in fertility-related concentrations in human vaginal secretions (Huggins & Preti, 1976), suggesting a need for direct investigation in future studies.

In contrast, methenamine likely originates from non-mammalian sources and has primarily been described as a bio-accumulated contaminant expelled through breath in humans (Filipiak et al., 2014, 2012). Given urine excretion's role in eliminating endogenous contaminants in humans (Bonvallot et al., 2018; Li et al., 2023), methenamine might also be excreted via urine and collected as a residue in our samples. To our knowledge, none of the other substances tentatively associated with conception risk in our analyses have been previously linked to cyclical variation in women's body odour.

To further investigate the phylogenetic significance of these compounds, we compared our tentatively identified compounds with olfactory fertility cues in primates. Previous studies have linked changes in acetic acid levels in vaginal secretions to female fertility in rhesus macaques (Keverne & Michael, 1971; but see Goldfoot et al., 1976) and chimpanzees (Matsumoto-Oda et al., 2003). Urea has been observed in circumgenital scent marks of common marmosets (Smith et al., 2001), but has not been associated with female fertility. The other compounds identified in our study (**Table 2**) do not strongly overlap with chemical fertility cues described in non-human primates, suggesting a relatively low retention of these cues in modern women's vulvar volatile profiles.

Compared to other non-domesticated mammals, humans exhibit higher glycogen levels and a dominance of Lactobacilli spp. in the vaginal microbiome, linked to increased starch intake from an agricultural lifestyle (Barker, 2006; Miller et al., 2016; Yildirim et al., 2014). This results in a more acidic vaginal pH (Miller et al., 2016) and higher lactic acid levels in secretions (Petrova et al., 2015). These changes may modify women's vulvar and vaginal volatiles, diverging them from other mammals, including non-human primates. Further studies, ideally with larger sample sizes than the present study, are needed to better understand whether and how information about fertility might manifest in women's vulvar chemical profiles.

This study also aimed to investigate whether men may be able to perceive a woman's fertile state from her vulvar scent after a single exposure. Previous studies suggested men prefer peri-ovulatory vaginal and vulvar odours, finding them more pleasant and less intense than those from other menstrual cycle phases (Cerda-Molina et al., 2013; Doty et al., 1975). Vulvar odours near ovulation have been shown to raise testosterone and cortisol levels, along with elevated sexual motivation in male raters (Cerda-Molina et al., 2013). However, a recent study demonstrated that these hormones and men's sexual motivation remain unaffected by vulvar odour at different fertility states (Roney et al., 2023). Our findings extend this, showing no significant link between female fertility and men's attraction to vulvar odour in a simulated single encounter. Men might detect fertility cues with repeated scent encounters over a menstrual cycle, allowing familiarity development (Higham et al., 2011; Ma & Higham, 2018). Our chemical analysis revealed no consistent changes that could be consistently tracked across the cycle. Even in established romantic relationships, men do not seem to detect women's ovulatory cues (Schleifenbaum et al., 2022). Replication studies covering single and repeated encounters are needed.

Surprisingly, reproductive hormones did not influence vulvar volatile profiles, and no significant effects were observed in the perceptual analysis. Similarly, there was no evidence of hormonal influence on axillary odour perception (Mei et al., 2022; Zetzsche et al., 2024) or volatile composition (Zetzsche et al., 2024). As fluctuations in ovarian hormones are closely linked to variations in conception probability across the menstrual cycle, they should be primary mediators of concurrent odour changes. However, if this is not the case, other factors coinciding with the fertile window may also influence odour changes. For instance, women often eat less during ovulation (reviewed in Hirschberg, 2012). Calorie intake has been shown to affect body odour perception (Fialová et al., 2019) and could potentially also influence volatile composition. The current lack of sufficient studies on this topic highlights the need for future research to directly assess the influence of ovarian hormones.

Nearly all non-human primates primarily walk on four legs, placing the anogenital region near conspecifics' noses for easy odour detection (e.g., scent marking, olfactory inspection). The transition to bipedalism and cultural clothing and hygiene practices practices in modern humans, coupled with intimacy norms prior to genital contact, may make women's vulvar odour less readily interpretable to men, thereby reducing its socio-chemical relevance especially during a first encounter. Social odours might have shifted to the armpits, as they are situated in closer proximity to the nose (Mostafa et al., 2012). Studies suggest men generally find axillary odour more attractive and sexually arousing than vulvar odours (Cerda-Molina et al., 2013; Roney et al., 2023), with ovulating women's scent being perceived as more appealing and pleasant (Gildersleeve et al., 2012; Havlíček & Lenochova, 2006). However, evidence remains inconclusive, as some studies also report null effects for axillary odours (Mei et al., 2022; Roney et al., 2023; Roney & Simmons, 2012). A recent study involving axillary samples from the same women providing vulvar samples in the current research found no compelling evidence for fertility-related chemical shifts (Zetzsche et al., 2024). Male ratings of these axillary and vulvar samples showed no significant correlation between the two body areas on corresponding cycle days (Supplement S10.2). Visual inspection of axillary chromatograms for substances with minor effects in the vulvar samples revealed no patterns linking their abundance to conception risk. Moreover, the relative areas of these substances on corresponding cycle days showed no significant correlation between axillary and vulvar samples (Supplement S10.1). Thus, if vulvar odour were to convey fertility-related information, which our study does not robustly support, it would be even less likely that this information has shifted to axillary volatiles, despite the changing significance of odour sources in communication.

Finally, our study did not strongly support the leaky-cue hypothesis, raising important questions about the role and retention of vulvar chemical fertility cues in modern humans. Given substantial gaps in understanding their chemical composition—especially among non-human primates—and variability in sampling and analytical methods, we advocate for future research to develop consistent methodologies for studying these cues. Incorporating the spandrel hypothesis (Havlíček

et al., 2015), which posits that men may have adapted to discriminate cues of overall fertility among women as a byproduct of their general preference for high estrogen levels, could provide further insights into whether chemical fertility cues are by-products of other evolutionary changes. Systematic behavioural and chemical studies in closely related species, such as great apes, are essential to enhance our understanding of the origin and evolution of chemical fertility cues.

To minimise external influences on odour composition and perception, we standardised odour collection and presentation in a controlled laboratory setting. However, perceiving vulvar scent may require an intimate, possibly sexual, context for an effective response to fertility cues. Changes in secretions during arousal might convey additional information (Farage & Maibach, 2006; Preti, Huggins and Silverberg, 1979), suggesting our study might lack ecological validity to some extent. Similar to other studies, we did not give specific instructions about vulvar hair shaving. Past research noted transient effects of axillary hair on odour perception (Kohoutová et al., 2012). By statistically controlling for odour donor identity, we partially accounted for the effects of vulvar hair presence or absence; however, its influence on vulvar odour warrants further investigation.

We standardised diet, behaviour, and personal hygiene to mitigate factors affecting odour perception (Havlíček & Lenochova, 2008). For example, odour donors followed a vegan or vegetarian diet,likely different to diets from ancestral humans, which might have impacted findings differently from studies without these dietary restrictions. To detect subtle changes around ovulation, we focussed on the fertile window. This approach allowed us to statistically link chemical odour composition to test variables throughout the cycle. Adding more luteal phase samples or sampling across multiple cycles, and controlling for diurnal fluctuation could improve hormonal profile accuracy (Schmalenberger et al., 2021) and address the limited validity of salivary estradiol measurements in traditional immunoassays (Arslan et al., 2023).

## 6. Conclusion

Chemical fertility cues in vulvar odour are observed in females across non-human primates, raising the question whether they might be preserved in modern women. Our hormonally confirmed vulvar odour samples revealed no evidence of chemical changes enabling the tracking of fertility throughout the cycle and provided only inconclusive evidence for chemical variation suitable for immediate assessment. The substances and substance classes identified as most affected by conception risk did not strongly align with those observed in non-human primates. Together this suggests minimal retention of such cues in modern women's vulvar profiles, potentially owing to vaginal microbiome changes, upright gait, and mating patterns of modern humans. Our perceptual evidence further supports this: the lack of association between female fertility and men's attraction to women's vulvar odour indicates a reduced relevance in men for perceiving female fertility compared to many male non-human primates. We strongly recommend further large-scale comparative studies between humans and non-human primates to better understand the potential role of chemical fertility cues and the evolutionary history of human olfactory fertility advertisement.

## CRediT authorship contribution statement

**Madita Zetzsche:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marlen Kücklich:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Brigitte M. Weiß:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Julia Stern:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Formal analysis, Conceptualization. **Andrea C. Marcillo Lara:** Writing – review & editing, Writing – original draft, Software, Resources, Methodology, Investigation, Data curation. **Claudia Birkemeyer:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Funding acquisition. **Lars Penke:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Anja Widdig:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

## Ethics

Both female and male participants provided written, informed consent before participation. The study was was approved by the ethical board of the medical faculty of Leipzig University (#446/18-ek) and all procedures were conducted in accordance with the Code of Ethical Principles for Medical Research Involving Human Subjects (Declaration of Helsinki). The study adhered to a strict infection protection protocol in accordance with the COVID-19 safety regulations approved by the Corona-crisis unit of the University of Göttingen (odour collection approved on 01.06.2020, odour rating approved on 23.03.2021).

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## Declaration of competing interest

None.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.evolhumbehav.2025.106742.

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