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NO TIME TO EAT: AN ADAPTATIONIST ACCOUNT OF PERIOVULATORY BEHAVIORAL CHANGES

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ABSTRACT

A comprehensive review of women's dietary behavior across the menstrual cycle suggests a drop in caloric intake around the time of ovulation; similar patterns occur in many other mammals. The periovulatory nadir is puzzling, as it is not explicable in terms of changes in the energy budget. Existing explanations in the animal literature operate wholly at the proximate level of analysis and hence do not address this puzzle. In this paper, I offer an ultimate explanation for the periovulatory feeding nadir, arguing that the decrease in the set point for satiation during the fertile period of the female cycle is an adaptation produced by natural selection in order to reduce the motivational salience of goals that compete with those directly or indirectly pertaining to mating. In support of this explanation, I adduce evidence of: a) periovulatory reductions in other ingestive behaviors, and b) periovulatory increases in motor activity and the psychological concomitants thereof.

CONSIDERABLE ATTENTION has been dedicated to the study of changes in human dietary behavior over the course of the menstrual cycle. The vast majority of this research has focused upon late luteal phase increases in consumption. With a few notable exceptions (e.g., Lyons et al. 1989; Dye and Blundell 1997), investigators have dedicated little or no attention to an equally striking if somewhat more muted pattern, the reduc-

tion in food consumption that occurs around the time of ovulation. This paper explores patterned changes in eating and other behaviors during the periovulatory period. I begin by presenting data, gleaned from published sources, that demonstrate the existence of a periovulatory feeding nadir. I then show that the nadir is not explicable in terms of energetic homeostasis, nor can it be explained in terms of the influence of other activities on

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feeding, and is not likely to be an accidental by-product of hormonal changes at ovulation. Reviewing evidence of patterned changes in motor activity and related psychological states, I argue that the periovulatory feeding nadir is best viewed as the product of an adaptive mechanism that reduces motivational conflicts between those behaviors that subserve bodily maintenance and those that subserve mating. In short, natural selection has taken account of the fact that, during the fertile period, females have better things to do than eat.

EVIDENCE OF THE PERIOVULATORY NADIR

Using the PubMed, Biosis, PsychInfo, WorldCat, and Melvyl electronic databases, and following a snowball citation strategy, I searched for studies that contain caloric intake data recorded during at least three points in the menstrual cycle, including the period at or near ovulation. This search produced nineteen publications, sixteen of which present comparable quantitative results. Because these sixteen investigations were conducted in pursuit of diverse research goals, they vary considerably with regard to the parsing of the menstrual cycle, making meta-analysis impossible. Data gleaned from these studies are therefore presented in graphic form for inspection in Figure 1; methods, durations, and subject profiles for each study are described in Table 1. To enhance comparability, in those cases where investigators examined both a special population (e.g., sufferers of premenstrual dysphoria, smokers) and a control group, only data from the controls were included.

Although the effect varies in magnitude, ten of the sixteen studies in Figure 1 (1–6, 8–10, 15) present considerable evidence of a drop in caloric intake at or near ovulation. Two studies (12 and 14) reveal a much smaller decline at ovulation. One study (13) shows no difference between the late follicular, ovulatory, and late luteal periods; another study (16) shows a similar pattern but with ovulatory intake being slightly lower than pre- and postovulatory; and two studies (7 and 11) indicate a slight peak at ovulation. Hence, ten studies support the existence of a periovulatory nadir, two supply weaker confirmation, and four provide contrary evidence. Note that

while the sixteen studies vary with regard to the rigor of the methods used (see Table 1), this variation does not correspond with confirmation or disconfirmation of the existence of a periovulatory nadir, making it unlikely that the favorable distribution of results is a consequence of a preponderance of weak studies in the literature.

In addition to the work summarized in Figure 1, three additional studies report results that are relevant but not directly comparable. Examining nutrient intake across the cycle, Abraham et al. (1981) asked 23 Australians to keep daily food logs and menses records. Describing cyclic variation in protein intake as representative of their findings for all nutrients examined, the authors present results that reveal a clear periovulatory nadir. Bäuml (1989) collected food logs and daily weight measurements from 8 Germans. Apparent random variation in intake led the author to suspect that subjects had failed to keep accurate dietary records. Bäuml therefore used body weight fluctuations as an index of changes in food intake, as cyclic variation in weight and intake are significantly correlated (Pelkman et al. 2001). The result indicates an intake nadir four days before ovulation. Lastly, Alberti-Fidanza et al. (1998) asked 8 Italians to keep dietary logs, and used scheduled blood tests to assess hormone levels. Although a comprehensive account of findings is not presented, the authors note, "The greatest difference in energy intake, kcal 122 (MJ 0.51) = 8%, was observed between the II and III Groups of days (respectively 6th, 7th and 8th and 13th, 14th and 15th) predominantly due to the lower consumption of bread at 13th-15th" (1998:152). This statement strongly implies that the authors recorded a periovulatory nadir.

In sum, of the sixteen studies that contain comparable quantitative results, twelve indicate a periovulatory drop in food intake, and of the three studies containing less well-quantified results, all suggest the same pattern.

IS THE PERIOVULATORY NADIR SIGNIFICANT?

Overall, the results presented above suggest that human food consumption is reduced

around the time of ovulation. Nevertheless, given the frequently small magnitude of the effect, skeptics might question the significance of this phenomenon—after all, minor perturbations of behavior, however patterned, hardly call for extensive investigation. It is therefore important to note that research to date almost certainly underestimates the extent to which humans are prone to reduce food consumption around ovulation. All of the above studies were conducted in modern Western nations, societies characterized by a superabundance and an enormous variety of food. One consequence of the ready availability of huge quantities of food is that patterns of consumption are profoundly influenced by a wide variety of factors unrelated to immediate bodily needs, including personal habits, cultural norms and beliefs, and standardized portions of purchased foods (cf. Bernstein et al. 1981; de Castro 1991; Wan-sink 1996; de Castro et al. 1997; Rolls et al. 2000; McConahy et al. 2002; Young and Nestle 2002). Similarly, because dietary variety increases meal size (Rolls et al. 1984), the cornucopia available to the Western diner likely affects intake. As demonstrated by the fact that obesity looms as a leading public health problem in the West (a circumstance unprecedented in human history), these factors conspire to dampen the influence of endogenous elements on human feeding behavior (cf. Young and Nestle 2002). Seen in this light, the fact that Western women exhibit *any* periovulatory nadir at all indicates that the phenomenon is probably quite robust. If, in contrast to the contemporary Western case, food is both relatively hard to come by and of limited variety, individuals are unlikely to eat when they are not hungry, suggesting that the periovulatory nadir will be significantly more pronounced among women living under conditions more similar to our species' environment of evolutionary adaptedness.

THE PUZZLE OF THE PERIOVULATORY NADIR

The periovulatory nadir is puzzling. To appreciate why, consider another marked feature of caloric intake across the menstrual

cycle: a wide variety of studies report a luteal phase peak in consumption (reviewed in Buffenstein et al. 1995; Dye and Blundell 1997; see also Danker-Hopfe et al. 1995; Alberti-Fidanza et al. 1998; Li et al. 1999; Paolisso et al. 1999; Allen et al. 2000; Pelkman et al. 2001; but see also Chappell and Hackney 1997), a pattern that is evident in many of the studies summarized in Figure 1. Increased luteal phase caloric intake may be compensatory in nature, as the basal metabolic rate increases in the luteal phase (Webb 1986; Ferraro et al. 1992; Eck et al. 1997; Allen et al. 2000; but see also Paolisso et al. 1999), plausibly due to the energetic costs of constructing and maintaining the endometrium (Strassmann 1996). Alternately, luteal phase increases in intake may constitute anticipatory preparation for the demands of a possibly ensuing pregnancy (cf. Drewett 1973). In contrast to these multiple (and nonmutually exclusive) explanations, energetic homeostasis cannot explain the periovulatory drop in food intake. If, across the entire cycle, caloric intake was significantly determined by the metabolic demands of the endometrium, then, given that the preliminary rebuilding of the endometrium begins in the early follicular phase, we would expect a gradual increase in caloric intake from the early follicular through the luteal phase, rather than a sudden dip around ovulation. Similarly, the heightened probability of conception around the time of ovulation suggests that, if the prospect of the upcoming increased caloric demands of pregnancy affects intake, there should be a gradual increase in consumption from the late follicular through the luteal phase, rather than a dip in the middle thereof. Lastly, because caloric intake in general reflects daily gross energy expenditure, patterned changes in intake might reflect patterned changes in expenditure. Animal models suggest, however, that rather than a drop in expenditure around ovulation, there is an increase that results in a net energy deficit (Wade 1976). As will be discussed at length, the periovulatory period is marked by an increase in motoric activity, hence a simple match between expenditure and intake cannot explain the periovulatory nadir in food consumption.

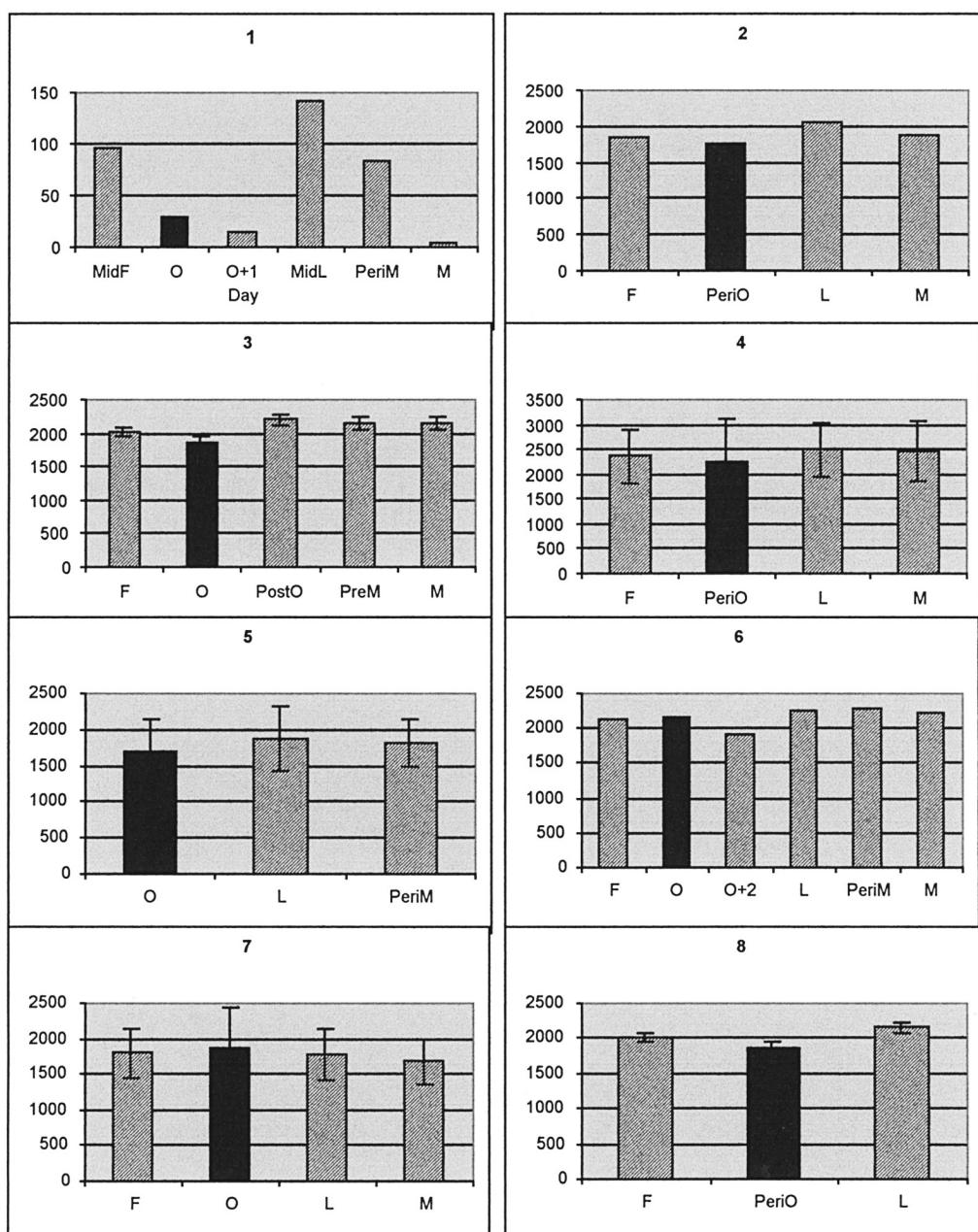


FIGURE 1. CHANGES IN CALORIC INTAKE ACROSS THE MENSTRUAL CYCLE

Data for the ovulatory or periovulatory period are shown in black. Chart 1 shows residual energy intake in KCals/Day; all other Charts show mean intake in KCal/Day. MidF = middle of follicular phase; O = ovulation; O + # = number of day(s) postovulation; MidL = middle of luteal phase; PeriM = perimenstrual period; M = menses; F = follicular phase; PeriO = periovulatory period; L = luteal phase; PostO = postovulatory period; PreM = premenstrual period; Early L = early luteal phase; Late L = late luteal phase; Mid-L = middle luteal phase; Late F = late follicular phase; Mid-F = middle follicular phase; Early F = early follicular phase; Pre-O = preovulatory period; Post-O = postovulatory period.

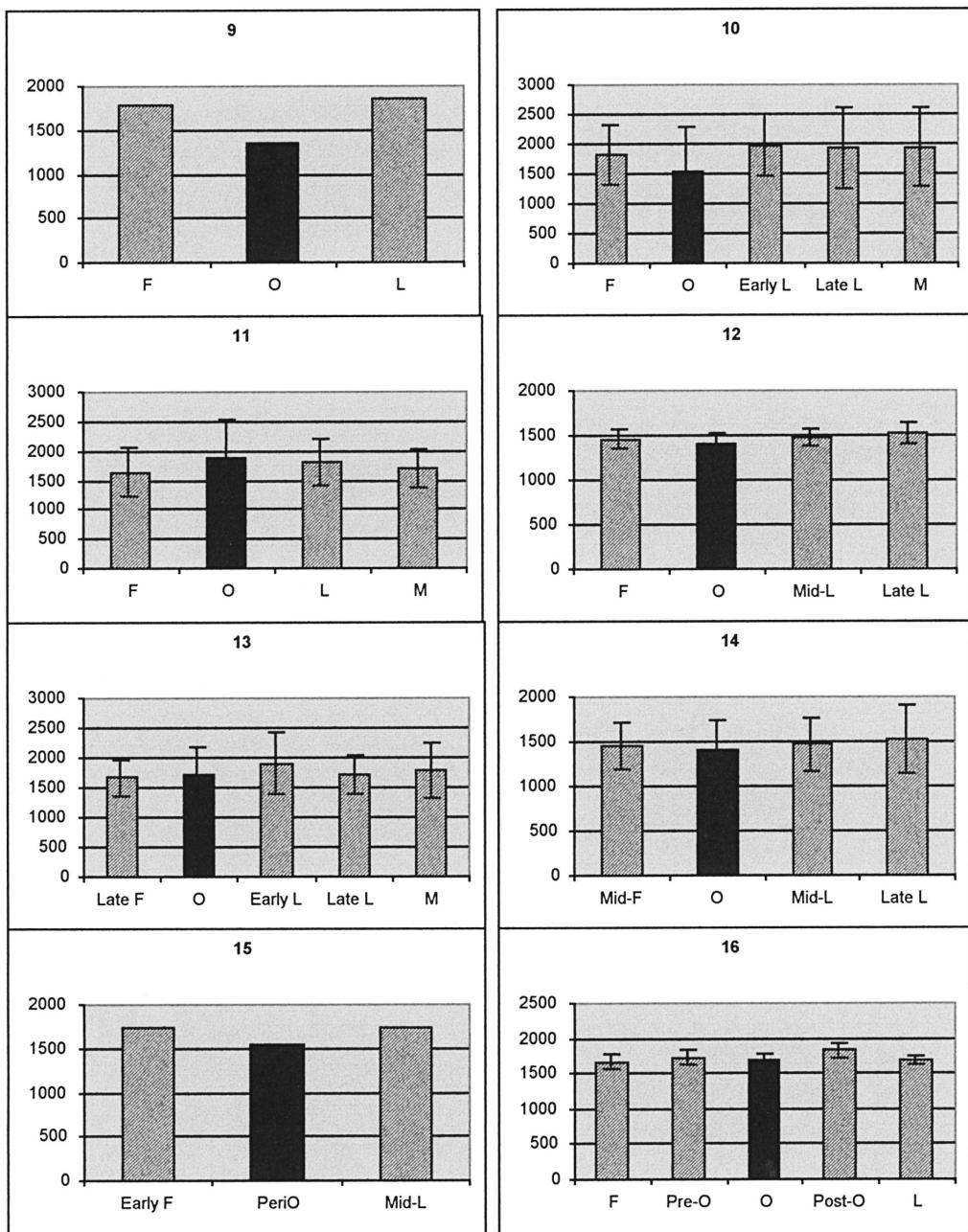


TABLE 1
Sources of data presented in Figure 1

Chart	Subjects	Methods	Duration	Reference
1	23 North Americans, age 22–41, healthy, nonsmoking, no oral contraceptive (OC) use, no severe premenstrual syndrome	Lab weighing of all food and uneaten portions; self-reported onset of menses, standardized to 28 day cycle	At least one full cycle (two studies, durations = 42 and 56 days)	Lissner et al. 1988
2	7 North Americans, age 24–43, healthy by medical history and labs, not obese, no current OC, medication, or dieting; cycle length 23–35 days	Tape-recorded record of diet and activity; foods weighed prior to eating, plate waste weighed after, daily oral temperature	One full cycle	Gong et al. 1989
3	18 Australians, age 17–35 (mean 23.6), normal weight, not taking OC for at least 2 months, healthy, not dieting, no psychiatric or eating disorders; cycle of 23–34 days for past 6 months	Self-weighing of all foods and liquids, daily log; daily urine collection with lab analysis of LH levels	35 days	Lyons et al. 1989
4	9 North Americans, nonsmoking, normal weight, age 23–35, history of regular menstrual cycles, no dieting, OC, or regular medication for 1 year prior, full physical examination, parasite check	Confined to research unit, fixed and unchanging amount of physical activity per day; all food and liquids provided by staff; unbeknownst to subjects, precise amount and contents of all foods and liquids consumed determined after each meal or snack by staff; onset of menses recorded	52 days	Fong and Kretsch 1993
5	26 North Americans, normal weight, no eating disorders, age 22–39, regular menses during past 6 months, no tobacco, OC, or medication use, not pregnant	Self-recorded food intake using supplied forms; daily temperature upon awakening; self-recorded exercise type and duration; weekly lab visits with blood analysis for LH, FSH, progesterone, estradiol	One cycle	Johnson et al. 1994
6	16 Germans, age 21–48, regularly menstruating, no OC use	Daily weighed food self-report and basal temperature	At least one full cycle	Danker-Hopfe et al. 1995
7	15 North Americans, age 18–35, nulliparous, no tobacco or OC use, no dieting or eating disorders; cycle 26–30 days, BMI 19–25 kg/m ²	Daily food intake record, ovulation prediction kit (luteinizing hormone detector)	One full cycle	Eck et al. 1997
8	16 Italians, lean, not pregnant, lactating, diabetic, or glucose intolerant, free of illness, not using tobacco, OC, or drugs, not dieting, stable body weight for previous 6 months; cycle length 26–30 days	Daily weighed food record plus (comparative) retrospective questionnaire; daily rectal temperature	One full cycle	Paolisso et al. 1999
9	9 North Americans, mean age 29.8, regular cycles 26–41 days, normal weight-for-height, no substantial weight fluctuations in previous 6 months, no dieting, OC, or medications; no recent stressful events	Daily food record, including weighing for nonstandardized items; daily oral temperature	One full cycle	Sophos 1983

10	15 North Americans, age 18–35 (mean = 26), regular cycle of 23–35 days, no oral or implant contraceptive use, no dieting, smoking, gynecological problems, or regular medication use; not pregnant within last year, not nursing	Daily food logs with random telephone monitoring for accuracy; oral temperature, home ovulation prediction kit	One full cycle	DeBon 1992
11	15 North Americans, age 18–35 (mean = 19.9), good health, regular cycle of 26–30 days, BMI 19–25 kg/m ² , nulliparous, no eating disorders, medications, smoking, or gynecological problems	One practice cycle, one study cycle; daily food records, home ovulation prediction kit	One full cycle	Bennett 1994
12	19 North Americans, mean age 27.7, not taking OC for at least 2 months, not pregnant or lactating, no psychiatric illness, dieting, or gynecological problems; regular menstrual cycles less than 35 days, normal BMI	One practice cycle, one test cycle; daily food records following training using models; data collected for four days per phase; onset of menses recorded	One full cycle	Haken-Virapen 1990
13	10 North Americans, age 18–45 (mean = 33.2), no medical or psychiatric illness, regular cycles of 25–31 days, no hormonal or psychoactive medications for two months prior, normal BMI, no eating disorders or significant negative mood differences across cycle	Food diary following training with models; basal temperature	5–9 weeks	Virts 1997
14	19 North Americans, age 18–45 (mean = 27.7), healthy, no medical or psychiatric problems, no medications or OC, not pregnant during previous 3 months, regular cycles (average = 28.7 days), normal BMI	Daily food diaries following training with models for two consecutive days during each of four phases; onset of menses recorded	Two full cycles	Neuhaus 1990
15	5 North Americans, age 19–25 (mean = 22); cycle length 29–45 (mean = 34.6), healthy, modest alcohol intake, no smoking or OC	Daily food diaries, onset of menses recorded	1–2 cycles	Adams 1985
16	67 North Americans, mean age = 24.4; cycle length 28–30 days (mean = 29.7), no recent stresses, medications, or OC, modest caffeine intake, not pregnant, normal BMI	Semi-cross-sectional design using once weekly 24-hour food diary and record of current menstrual status and date of onset of last menses; subjects unaware of research objectives	Six weeks	Wall 1987

THE PERI-ESTRUS NADIR IN ANIMALS

Human feeding behavior is profoundly determined by cultural constructions of diet, gastronomy, and the meaning of eating (cf. Caplan 1996; Rozin et al. 1999). Similarly, cultural models influence experience and behavior across the menstrual cycle (cf. Fitzgerald 1990; Lu 2001). It is therefore not inconceivable that ideational factors somehow shape human feeding behavior around ovulation. Granted, the fact that the same pattern appears in samples of North American, Italian, German, and Australian women suggests that culture is not a primary determinant of the periovulatory nadir. Because these societies are all related, however, available results do not allow us to rule out such a possibility. More persuasive, therefore, is the observation that the same pattern occurs in a wide variety of other mammals: a peri-estrus nadir in food intake occurs in chacma baboons (Bielert and Busse 1983), rhesus macaques (Czaja 1975; Rosenblatt et al. 1980; Mello et al. 1986; Kemnitz et al. 1989), owl monkeys (Rauth-Widmann et al. 1996), dogs (Houpt et al. 1979), pigs (Friend 1973; Rollin et al. 1989), goats (Forbes 1971), sheep (Tarttelin 1968; Michell 1979), deer (Wong and Parker 1988), cows (Raun et al. 1967), guinea pigs (Czaja and Goy 1975), and rats (Tarttelin and Gorski 1971; Drewett 1974; Blaustein and Wade 1976; Eckel et al. 2000).

COMPETING BEHAVIORS DO NOT EXPLAIN THE NADIR

Naturalistic observations of common chimpanzees (Matsumoto-Oda and Oda 1998), chacma baboons (Saayman 1970; Bielert and Busse 1983), tonkean macaques (Aujard et al. 1998), black-tailed deer (Wong and Parker 1988), and Richardson's ground squirrels (Michener and McLean 1996) all reveal marked changes in females' activity budgets during the peri-estrus period. More time is spent moving from one location to another and, often, less time is spent feeding. This raises the possibility that the periovulatory nadir is a consequence of a sudden increase in competing demands on the individual's time. While I will argue that cyclical changes in the immediately relevant fitness goals are indeed central to the ultimate explanation

for the periovulatory nadir, multiple lines of evidence indicate that the nadir is not directly caused by the impingement of other activities on time available for feeding. First, it is highly implausible that time constraints affect caloric intake among Western women. The ready availability of prepared foods makes the time demands associated with feeding remarkably low; note, for example, that two of the studies reporting marked nadirs employed professionally prepared foods (Lissner et al. 1988; Fong and Kretsch 1993). Second, rodent studies reveal that the estrus drop in food consumption occurs independently of changes in activity levels: when rats are provided with an exercise wheel, their locomotion increases markedly at estrus; however, the depression in food intake occurs whether the wheel is present or not (Eckel et al. 2000).

PROXIMATE CAUSES OF THE NADIR AND THE BY-PRODUCT HYPOTHESIS

Rather than being a result of a time allocation conflict, there is substantial evidence that the periovulatory nadir is produced by discrete neuroendocrine mechanisms. Experimental manipulations (ovariectomy and/or the use of exogenous hormones) reveal that estrogen and/or estradiol are directly linked to the periovulatory feeding nadir in baboons (Bielert and Busse 1983), rhesus macaques (Czaja and Goy 1975; Kemnitz et al. 1989), owl monkeys (Rauth-Widmann 1989, cited in Rauth-Widmann 1996), dogs (Houpt et al. 1979), cows (Muir et al. 1972), rats (Wade and Zucker 1970; Tarttelin and Gorski 1971; Blaustein and Wade 1976), golden hamsters (Morin and Fleming 1978), and guinea pigs (Czaja and Goy 1975). Although the specific pathways may be multiplex (see Buffenstein et al. 1995; Geary 1998), a growing corpus of evidence indicates that estradiol exerts its effect on feeding behavior in part by potentiating the activity of cholecystokinin (CCK), a peptide released from the small intestine during meals that is a principal determinant of satiation (see Geary 2001). The periovulatory nadir in food intake is thus in part the product of a mechanism that reduces meal size by lowering the satiation threshold.

It is possible that, rather than serving an adaptive purpose, the potentiation of CCK's

satiating influence is an accidental consequence of some feature of estradiol; perhaps inevitable design constraints or issues of path dependence have preserved a by-product effect over time. The by-product explanation is weakened, however, by the observation that ovulation is accompanied by parallel declines in other ingestive behaviors. In rats (Tarttelin and Gorski 1971; Eckel et al. 2000), pigs (Friend 1973; Rollin et al. 1989), sheep (Tarttelin 1968; Michell 1979), cows (Macfarlane 1967), and, apparently, humans (Fong and Kretsch 1993), water intake exhibits the same cyclic changes as food intake. Although food intake and water intake are generally behaviorally linked (Engell 1988; Mathis et al. 1996), the periovulatory reduction in water intake is not a secondary consequence of the reduction in food intake, but rather reflects changes independent of those responsible for the decrease in feeding. Specifically, there seems to be a periovulatory increase in the osmotic threshold for thirst (Rollin et al. 1989; but see also Vokes et al. 1988). Estrogen appears to directly modulate the effects of the dipsogenic peptide angiotensin (Jonklaas and Buggy 1984; Kucharczyk 1984). In harmony with changes in water intake, sodium intake exhibits a similar cyclic nadir in sheep (Michell 1975), pigs (Rollin et al. 1989), and rats (Danielsen and Buggy 1980), apparently again due to the interaction of estrogen and angiotensin (Danielsen and Buggy 1980). Hence, estrogen and estradiol lower both the satiation threshold for food and the satiation thresholds for water and salt. Because the pathways whereby these effects occur are independent of one another, it is unlikely that they are merely accidental by-products; reducing one ingestive behavior might be an accident, but independently simultaneously reducing a second ingestive behavior smacks of adaptive design. Moreover, evidence from other facets of ingestive control mechanisms supports the conclusion that the timing of these changes is not accidental.

Across mammals, estrogen and estradiol are key proximal determinants of female reproductive behavior (Pfaff 1980). The fact that hormones which promote reproductive behavior also dampen ingestive behavior is wholly consistent with larger patterns in the neurophysiological mechanisms that regulate

these two forms of activity. For example, in rats, stimulation of the 5-HT_{1A} serotonin receptor inhibits lordosis (Uphouse et al. 1992) and facilitates feeding (Curzon 1990). Conversely, blocking activity at the 5-HT_{2C} receptor inhibits lordosis (Wolf et al. 1999) and hence, presumably, stimulation of the 5-HT_{2C} receptor facilitates lordosis (see also Ahlenius 1993); stimulation of this receptor also inhibits feeding (Vickers et al. 1999). Stimulation of the 5-HT_{2C} receptor causes oxytocin release (Bagdy 1996); exogenous oxytocin decreases feeding (Arletti et al. 1989) and increases female sexual receptivity (Benelli et al. 1994). Finally, blocking the effects of neuropeptide Y prolongs receptivity (Clark 1992), facilitates lordosis, and decreases feeding (Marin-Bivens et al. 1998). The proximate mechanisms responsible for complementary changes in ingestive and sexual behavior thus exhibit the sort of convergent complexity associated not with by-products but rather with adaptations—features produced by natural selection in the service of a specific ultimate goal. That goal, I suggest, stems from the fact that time is a limited resource.

BEHAVIORAL CHANGES DURING THE FERTILE PERIOD

BEHAVIORAL CHANGES IN ANIMALS

In all of the nonhuman animals discussed above, in keeping with the increased possibility of conception, the period around ovulation is characterized by a substantial increase in sexual activity, with females becoming both more proactive and more receptive toward mature males. In most mammals, females are most likely to conceive if they maximize the amount of time dedicated to mating activities during the fertile window. I propose that the proximate mechanisms described above serve the ultimate function of reducing the conflict between foraging activities and reproductive activities. Finding food, water, and salt takes time. By lowering the thresholds for ingestive satiation, the mechanisms described above reduce the quantity of food and water sought, thus reducing the time dedicated to foraging, thereby freeing up more time for mating activities.

Skeptics might object that, for many mammals, copulation does not take very long;

hence time constraints would not seem likely to play a role in relative reproductive success. Copulation is merely the punctuation mark at the end of the mating process, however. For many mammals the most time-consuming facet of mating is not copulation but mate seeking. As noted earlier, naturalistic studies of chimpanzees, baboons, macaques, and squirrels all reveal that, as the fertile period approaches, females move around more, often expanding their typical day ranges; the same is also true of kangaroo rats (Behrends et al. 1986). More carefully controlled laboratory studies indicate that increased locomotion is a hallmark of estrus or its approach in rats (Eckel et al. 2000), golden hamsters (Moline and Albers 1988), ferrets (Donovan 1985), cows (Arney et al. 1994), pigs (Flowers 1997), and owl monkeys (Rauth-Widmann et al. 1996). Indeed, the increase in locomotion is so marked that it can be used as a reliable index of the fertile period for purposes of animal husbandry (Kiddy 1977; Maatje et al. 1997). Presumably, peri-estrus increases in movement function to enhance the likelihood of encountering a desirable mate, a goal that has been clearly demonstrated in controlled studies of sheep (Ortman 2000) and deer (Wong and Parker 1988). Laboratory experiments indicate that, like a mirror image of the peri-estrus decline in feeding, the increases in locomotion are a direct consequence of the changing hormonal milieu, as administration of exogenous estrogen or estradiol induces locomotory increases in mice (Garey et al. 2001), rats (Wade and Zucker 1970), Syrian hamsters (Widmaier and Campbell 1980), golden hamsters (Takahashi and Menaker 1980), and owl monkeys (Rauth-Widmann 1989, cited in Rauth-Widmann 1996).

BEHAVIORAL CHANGES IN HUMANS

Do humans exhibit the sorts of cyclic changes in behavior described above? First, human sexual behavior is remarkably plastic. Nevertheless, although women engage in both proceptive and receptive sexual behavior across the menstrual cycle, increases in sexual activity, sexual desire, and sexual satisfaction are frequently reported to occur around ovulation (Hedricks 1994; Regan

1996; Clayton et al. 1999). Second, although results are mixed, there is substantial evidence that, like other female mammals, women exhibit spontaneous changes in motor activity around the time of ovulation.

The first attempt to systematically examine changes in motor activity across the menstrual cycle was that of Billings (1934): 6 women, age 16 to 33, wore pedometers every day for one or two cycles. Reasoning that they were free from the demands of normal life, Billings employed psychiatric inpatients as subjects. Five subjects showed postmenstrual peaks in locomotion (one with an ovulatory nadir), and one subject showed both ovulatory and postmenstrual peaks. These results differ from those reported for nonhuman animals, but Billings's study is highly problematic, as subjects suffered from such disorders as schizophrenia, depression, "agitation," and "stupor," the vicissitudes of which likely affected locomotory behavior.

Morris and Udry (1970) applied pedometer measurements to 26 healthy North Americans ("typical age" = 30), who had regular cycles and were not using oral contraceptives. Subjects, the majority of whom participated for three or more complete menstrual cycles, went about their daily lives. Pooling results and plotting them onto a standardized 28 day cycle, consistent with the results from animal studies, Morris and Udry report a significant midcycle peak in locomotion; additional peaks occur at the beginning and end of the cycle. While promising, these results cannot be taken as definitive, as the use of a standardized cycle is somewhat problematic (see Hedricks 1994).

In a third pedometer study, Chrisler and McCool (1991) used daily oral temperature readings to generate a more accurate division of each subject's cycle. Seven North American undergraduates, participating for six weeks, served as subjects; no information is provided on age, weight, health, menstrual regularity, or oral contraceptive use. No significant differences in activity level were detected between phases. The apparently poor subject screening and limited study duration make this result difficult to interpret, however, particularly given that the phase/activity association approached

statistical significance. Unfortunately, the data cannot be revisited as they have since been destroyed (J Chrisler, personal communication).

Stenn and Klinge (1972) employed an actometer worn on the nonpreferred arm 24 hours a day. Subjects were 7 North Americans who were physically and psychiatrically normal, age 21 to 31, nulliparous, had regular menstrual cycles of 27 to 35 days, and were not taking oral contraceptives or medications. Oral temperature was measured daily. Subjects participated for between 1 and 5 complete cycles. Stenn and Klinge report considerable intersubject variation, with no overarching patterns across subjects from measurements recorded 24 hours a day. Since ancestral humans were likely sedentary at night in order to avoid predators, however, an evolutionary perspective suggests that patterned changes in activity should occur primarily during the day. Looking only at daytime movements, two subjects show absolute peaks just prior to the midcycle thermal shift, one subject shows a relative peak just prior to the shift with a second peak in the luteal phase, one subject shows a dramatic absolute peak several days after the shift, two subjects show gradual increases across the whole cycle, and one subject shows a nadir at the shift. Hence, four out of seven subjects show peaks in daytime arm movement around the time of ovulation, two out of seven subjects do not show marked changes, and only one subject shows low levels of activity at ovulation.

Investigating changes in energy expenditure across the menstrual cycle, Howe, Rumpler, and Seale (1993) examined 12 North Americans, age 21 to 45, of normal body weight. As confirmed by blood hormone assays, during the menstrual, periovulatory, and late luteal phases, subjects spent 24 hours in an enclosed calorimeter. Although some activities were scheduled, subjects were also able to move about freely. In contrast to findings in the animal literature, Howe, Rumpler, and Seale report that a significantly lower percentage of time was spent in movement during the periovulatory phase than during the menstrual and luteal phases (the authors do not describe how activity was recorded). It is unclear how confinement in a calorimeter

might affect women's spontaneous behavior, however. If women's changing proximate goals largely revolve around simple motor patterns, then confinement in a calorimeter should not affect activity, in which case these results contradict the hypothesis that ovulation is accompanied by increases therein. If women's proximate goals involve higher-order subjective experiences, however (e.g., an increase in wanderlust or a desire to see new faces), then the calorimeter method may not be ecologically valid for the question at issue. Confinement during the periovulatory phase could, for example, lead to dejection and a corresponding *decrease* in activity.

While less precise than the mechanical measurement of movement or the observation of confined subjects, daily logs provide another means of examining activity over the menstrual cycle. In two of the studies of dietary behavior summarized in Figure 1, investigators employed daily logs as a means of estimating motoric energy expenditure (a factor to be controlled for, from their perspective). Eck et al. (1997) report a (nonsignificant) subpeak in activity related energy expenditure at ovulation, with a second peak during menstruation. Johnson et al. (1994) report a marked peak in exercise related energy expenditure at ovulation. This pattern did not reach significance, however, presumably due to substantial intersubject variation.

In a lengthy and detailed five month study, Altmann, Knowles, and Bull (1941) examined 10 normal weight North Americans, age 22 to 36, with cycle lengths of 23 to 61 days. Rectal temperature readings were taken daily, and subjects visited a lab daily at a fixed time. Vaginal smears were taken for microscopic evaluation of cycle related histological changes, and the electrical potential was measured between fingertips immersed in salt water (this study predated the use of blood hormone assays to parse the menstrual cycle). Extensive interviews regarding the subject's current thoughts, feelings, and activities were conducted daily. The authors report prominent peaks in physical activity at or near ovulation in 85.3% of recorded cycles and in the late luteal phase in 71.8% of recorded cycles. Intriguingly, the two peaks are qualitatively distinct, as the periovulatory peak is typically

associated with a positive mood, often with feelings of elation (cf. Henderson and Whissell 1997; Smith et al. 1998), while the premenstrual peak is associated with tension (cf. Frackiewicz and Shiovitz 2001); in a number of subjects the premenstrual peak in activity strikingly revolves around housecleaning activities (cf. Wang 1923 on cyclic changes in, respectively, running and nest building in the female rat).

ECOLOGICAL VALIDITY AND THE NATURE OF MOTIVATIONAL CHANGES

To summarize the above results, some investigators find a substantial periovulatory peak in locomotion and related motor activity, others report a less robust pattern, and some fail to find the effect at all. Considerable variation in both the methods used to measure activity and the techniques employed to parse the menstrual cycle make it difficult to compare investigations. Perhaps even more significant is that all of these studies were conducted in modern societies, a context that may obscure the effect at issue. As Billings correctly pointed out in 1934, the habits, obligations, and routines of daily life in a modern society likely confound any changes in activity levels that stem from endogenous processes. Most of us lead very scheduled lives, and this extends both to physical activity in general (how much of your daily locomotion is a product of exogenous demands?) and to exercise in particular (aerobics classes, tennis matches). Moreover, as I noted in discussing the Howe, Rumpler, and Seale calorimeter study (1993), investigators have employed methods that may not address the question at issue here.

It is possible that women experience a desire to "stretch their legs" at ovulation; i.e., a direct impetus for increased locomotion. The Johnson et al. finding that exercise increases periovulatorily is consistent with this possibility, as is the finding that women who exercise feel substantially more vigorous at ovulation than do sedentary women, a difference that reverses itself later in the cycle (Mahoney and Smith 1997; but see also Hackney et al. 1991). Given human psychological complexity, however, it is likely that such highly proximal motives would not be the

sole factors selected to drive midcycle changes in behavior; even in infrahuman species it is clear that locomotion is not an end in itself, as animals engage in goal directed behavior when given the opportunity to do so. Hence, rather than experiencing subjective states linked only to motor activity, women may well experience changes such as "cabin fever," a desire to get out and see the world, to meet new people, and so on. Evidence consistent with this proposal comes from a study of volunteering behavior among 117 North American undergraduates (Doty and Silverthorne 1975). During class, students were asked to provide various information, including menstrual cycle length and date of recent menses. Some days later experimenters solicited volunteers for experiments. Social security numbers allowed the investigators to match volunteers with the data collected earlier and thus to calculate volunteers' current menstrual cycle phase. Women in the periovulatory phase were significantly more likely to volunteer for experiments than were women in other phases, suggesting that ovulation is indeed accompanied by increasing interest in new experiences and/or a desire to meet new people.

Note that, in contrast to behavior in the artificial setting created by Doty and Silverthorne (1975), the naturally occurring behaviors that have been measured to date are such that a modern lifestyle is likely to obscure the influence of any cyclical motivational changes. First, locomotion is a poor index of such changes since, in many Western locales, subjects who wish to visit new areas are more likely to use vehicular transport than they are to walk. Second, if higher-order subjective changes motivate behavioral changes across the cycle, a modern environment may radically attenuate motor activity because books, television, movies, and the Internet provide virtual experiences that (spuriously) satisfy desires to temporarily change one's surroundings and interact with new people. Seen in this light, given that all studies to date have been conducted in contexts that diverge drastically from the conditions in which ancestral foraging women acted, it is striking that the evidence of human periovulatory behavioral changes is as robust as it is.

In addition to entailing changes in motivational patterns, the claim that human ovulation is associated with increased ranging behavior suggests that navigational abilities should also exhibit regular variation across the menstrual cycle. A sizeable corpus of research has documented significant sex differences in human spatial cognition (reviewed in Harrison 2000; Silverman et al. 2000; see also Saucier et al. 2002). A robust feature of this pattern is greater male reliance on an "internal compass" and greater female reliance on landmarks. Addressing this dimorphism, Silverman and Eals (1992) argue that a sex-based division of labor in ancestral foragers selected for complementary spatial abilities. Hunting, a predominantly male activity, requires the ability to follow game for long distances across the landscape, concentrating on the prey while still maintaining knowledge of the distance and direction to base camp. In contrast, gathering, a predominantly female activity, requires the ability to recall the locations of fixed resources, move efficiently between them, and return thereafter to base camp. Harrison (2000) tested both young and elderly women using a realistic virtual wayfinding task. In young women, comparing those on their second or third day of menstruation (when estrogen is low) with those two days prior to ovulation (when estrogen is high), Harrison found that the latter group exhibited a significantly more malelike pattern, relying far less on landmarks for navigation. Similarly, among postmenopausal women, those receiving hormone replacement therapy that contained a sizeable estrogen component were less dependent on landmarks than were women not taking replacement hormones. Harrison concludes that estrogen shifts female spatial reasoning to a more malelike pattern. This suggests that, compared to other phases of the menstrual cycle, during the periovulatory period women are better equipped to travel in a malelike fashion; i.e., to range farther from home and pursue mobile rather than fixed objectives. This is exactly the result that we should expect if natural selection has shaped the mind so as to enhance mating opportunities during the fertile period—whereas

men pursue game, periovulatory women pursue men.

THE QUESTION OF FUNCTIONALITY

I have argued that, like other mammals, humans possess psychological mechanisms that would have led ancestral females to spend less time foraging and more time in activities that can lead to mating. In keeping with the highly altricial nature of our offspring, however, extended mating relationships are almost certainly the norm for humans (cf. Murdock 1967; van den Berghe 1988). This raises the question of the need for such mechanisms: if, over the course of our species' history, a woman's mate has generally been readily at hand, why would natural selection maintain complex psychological mechanisms that presumably evolved in solitary mammals for the purpose of increasing the likelihood of encountering a mate during the fertile period? To begin with, note that many of the animals discussed earlier live in sizable social groups containing many adult males. In such species an indiscriminate female interested only in finding a willing mate would not need to substantially decrease her foraging and increase her movements, and this is particularly true in the many species possessing advertised estrus. The fact that marked behavioral changes nevertheless occur in these animals therefore suggests that the psychological mechanisms which initially served simply to facilitate contact with males have been exapted in social species and put to a related purpose: decreased female foraging and increased female movements during or just before the fertile window likely facilitate "shopping" for alternatives to those current or potential mates who are readily at hand. Numerous potential benefits of such female choice have been proposed including good genes, offspring heterogeneity, infanticide prevention, and increased male investment (reviewed in Small 1993; Barash and Lipton 2001).

In theory, "shopping" for alternative mates can provide fitness benefits to women that are similar to those thought to underlie nonhuman female extra-pair copulations (reviewed in Greiling and Buss 2000). Consistent with this perspective, periovulatory changes in

women's olfactory (Gangestad and Thornhill 1998) and visual (Frost 1994; Penton-Voak et al. 1999) preferences, and their sexual interest in extra-pair males (Gangestad et al. 2002), all suggest a design for seeking good genes during the fertile phase, and some authors claim a periovulatory increase in extra-pair copulations (Bellis and Baker 1990). Although both practical and ethical obstacles make it difficult to accurately measure rates of human extra-pair paternity, it is likely that, in all but the most patriarchal societies, such conceptions are not rare (Barash and Lipton 2001). Indeed, the existence of both: a) male physiology suggestive of a history of sperm competition, and b) panhuman psychological mechanisms that motivate men to attempt to regulate the sexual behavior of their partners suggests that female extra-pair copulation has constituted a significant selection pressure on males over the course of human history (reviewed in Greiling and Buss 2000; Barash and Lipton 2001). Hence, rather than constituting nonfunctional vestiges inherited from ancient solitary mammals, it is likely that psychological mechanisms motivating a periovulatory nadir in feeding and a periovulatory peak in ranging behavior were maintained (and perhaps refined) in humans because of the fitness advantages that ancestral women could reap by shopping for mating alternatives.

CONCLUSION

I have argued that the periovulatory nadir in human feeding is best understood as the product of evolved mechanisms that reduce the satiation threshold in one goal system (foraging) in the service of allowing time for the pursuit of another goal (mating). Together with the recognition that modern societies may constitute a source of evolutionary disequilibrium, this hypothesis generates a number of discrete testable predictions, as follows:

1) Because a readily available and virtually inexhaustible supply of food is likely to exaggerate the influence of cultural and other exogenous factors on meal size, the periovulatory nadir in feeding should be more marked in societies where food is less abundant.

2) Because both vehicular transport and virtual travel via print and electronic media are likely to reduce the periovulatory peak in locomotion, cyclical changes in this and related motor activities should be more pronounced in societies where women, though able to travel relatively freely, lack ready access to such technology.

3) Because locomotory activity is probably motivated by higher-order subjective changes, interest in new experiences, feelings such as "wanderlust" and "cabin fever," and a desire to meet new people (particularly men) should peak around ovulation.

4) Because the periovulatory nadir is potentially costly in that it can create a temporary energetic deficit, if the utility of the nadir derives from the time that it frees up for mating relevant activities, then for a given individual there should be a correlation between the value of the latter and the extent of the former. Accordingly, holding constant physiological variables such as age, health, cycle regularity, and body mass index, and also holding constant environmental variables such as access to vehicular transport and mass media, across subjects, the magnitude of the periovulatory feeding nadir should correlate with the extent of increases in locomotory activity and/or the psychological concomitants thereof (see #3, above).

BROADER IMPLICATIONS

Because the actions entailed by various fitness-enhancing objectives are often incompatible with one another, a crucial feature of adaptive behavior is the ability to prioritize goals. In many species, the cyclical nature of fecundability has led to the evolution of mechanisms that regularly rearrange the priority of various goals so as to maximize the likelihood of optimal matings during the fertile period. Traditionally, theorists have (implicitly or explicitly) conceptualized this reprioritization as consisting of: a) a rise in the prominence of a specific motivation or drive (i.e., an increase in libido), and/or b) a change in the salience and/or hedonic valence of some cue (i.e., heightened attention and attraction to primary and second-

ary sex characteristics). While this view is undoubtedly correct, the evidence regarding periovulatory changes in ingestion indicates that cyclical reprioritization is achieved not only by increasing the motivational salience of one goal or cue, but also by actively decreasing the motivational salience of goals or cues that entail competing behaviors. It is possible that natural selection frequently produces such coordinated enhancement and depression of mechanisms that serve incompatible objectives. For example, the same time allocation conflict between foraging and mating that forms the core of my argument here may also provide an ultimate explanation for the reduction in male libido that occurs during dramatic dietary constriction (cf. Keys et al. 1950). Furthermore, it is likely that such coordinated enhancement and depression is not limited to questions of time allocation. For example, in male mice, exposure to the odor of a novel estrus female increases locomotory and searching activities, behaviors that are at odds with predator

avoidance strategies. Kavaliers, Choleris, and Colwell (2001) recently demonstrated that brief exposure to such odors also causes reductions in: a) aversion to predator odors, b) defensive analgesic responses to predator odors, and c) hormonal stress reactions to predator odors. Apparently, because of the overwhelming fitness value of reproduction, the incompatibility between mate-finding behavior and predator avoidance is resolved in favor of the former through a downregulation of mechanisms that subserve the latter. These observations suggest that a useful heuristic in the investigation of any given adaptive behavior, psychological state or goal may be to first consider what other behaviors, states, or goals are incompatible with the target, and then explore the influence of the former upon the latter and vice versa.

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