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The estrous cycle in female wood mice (*Apodemus sylvaticus*) and the influence of the male

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Based on studies of vaginal smears from wild-caught Swedish wood mice, females with three types of estrous cycles were identified: females with a continuous estrus; females with an estrous cycle between 6 and 11 days in length; and females that only rarely showed signs of estrus. We tested the pregnancy rates and how stable the estrus patterns were among the females. Ninety-one percent of the females with a continuous estrus pattern became pregnant, 50% of the females showing a cyclic estrus pattern, and 60% of the females showing an infrequent estrus. However, pregnancy occurred about 2 weeks later in females with an infrequent estrus pattern. Some females changed their estrus pattern after pregnancy, indicating that estrus patterns are not fixed.

1. Introduction

In literature, the estrous cycle of the female wood mouse (*Apodemus sylvaticus*) has been described as similar to the estrous cycle of the house mouse (*Mus musculus*), with a regular periodicity of 4–6 days (Brook 1984, Clarke 1985). However, Brook (1984) found that in captivity, the length of the estrous cycle varied greatly in wood mice from an English breeding population. We checked the variation of the estrous cycle described by Brook (1984) on a wild-caught population of Swedish wood mice.

In small mammals, the production of gametes for fertilization is generally a cyclic process in the females. The estrous cycle culminates when the female ovulates (estrus period). In mice species, the females have spontaneous ovulation with a short inactive luteal phase (Flowerdew 1987). Females in estrus attract males; without male presence, the estrus is wasted and no fertilization occurs. The presence of a male, especially the male pheromones, is important in stimulating a female's sexual activity (Whitten 1956, Bruce 1966, Roger & Beauchamp 1976, Teague & Brandley 1978, Carter *et al.* 1980, Marchlewska-Koj 1981, Bronson & Macmillan 1983, Vandenbergh 1983). The stimulatory effect of male pheromones can be enhanced by tactile cues, such as fighting and chasing (Bronson & Maruniak 1975). Male pheromones stimulate sexual behaviour in the female, but also affect other processes such as ovulation (Marsden & Bronson 1964, Lomas & Keverne 1982, Bronson 1985).

In the present study, we investigated the length of the estrous cycle in a Swedish population of wood mice. We also investigated how the presence of a male affected the estrous cycle and the reproductive success of the females with different estrous cycles.

2. Material and methods

Wood mice were captured near Göteborg, southwest Sweden, with multiple live-catch traps (Ugglan special-type). From the wild-caught females (16–28 g), only adult non-pregnant females were used in the experiment. Females were kept one to a cage for about 4 months before the onset of the study in February. In September, the estrus pattern of 17 young females (10–15 weeks), born in the laboratory during the summer was determined. The room was set to a long-day photo regime (16L:8D), and at a constant temperature (20°C) and humidity. The females were kept in plastic wire-mesh cages (38 × 22 × 15 cm) with the bottom covered by sawdust. A small wooden house was placed in each cage, in which the animal could build its nest with paper as nest-building material. Cages were cleaned once every three weeks or more often if needed. Animals were provided with rat and mouse pellets (1 260 KJ/100g), placed in a wire-mesh trough. Water was ad libitum. The food consumption and body mass of each individual were measured daily using an electronic balance with an accuracy of 0.5 g. Food consumption was measured as the difference between the initial food amount and that left the following morning. The daily waste of food in the sawdust was not measured as the pieces were scattered at the bottom of the cage. Odours from males were present in the room.

2.1. Vaginal smear

The different stages of the estrous cycle were determined with the analysis of vaginal smears. From the number of wild-caught wood mice, 30 non-pregnant females over 16 g were selected and investigated in Studies I–III. Vaginal smears were obtained by using a Pasteur-pipette. The tip of the pipette had been flamed to a smooth, reduced aperture.

A few drops of 0.9% sodium chloride solution was drawn into the pipette and introduced into the vagina. Fluids were then extracted with the pipette and transferred to a microscope slide. The vaginal smear was examined directly at low-power magnification (10 ×) in a light microscope, without being stained. The most common cell types observed were nucleated or cornified (old, non-nucleated) epithelial cells and leucocytes. The number of these cells (cell index) was scored on a scale of 1 = A few cells, 2 = A moderate number of cells, and 3 = A large number of cells. The method and the histological appearance of the vaginal smear have been described in detail by Rugh (1968) and Flowerdew (1987). We did not use the method of looking at the vaginal opening.

2.2. Study I: The estrous cycle

When we made a preliminary investigation of the vaginal smears from a number of wild-caught females, three types of estrus patterns could be distinguished. Ten females from each type were selected for more detailed studies. The length of the estrus and diestrus periods was investigated in each type during 21 days. This was done by collecting daily vaginal smears from each female. The females were given food and water ad libitum.

The estrus pattern of young females (n = 17) born in the laboratory during the summer, were investigated at the age of 10–15 weeks. A vaginal smear was done, and the body mass and food consumption were calculated daily during a period of 2 weeks.

2.3. Study II: Effect of a male presence

Almost all (n = 25) the females used in Study I were also used in Study II. Study II started a month after Study I had been completed. The aim of Study II was to investigate if and how the presence of a male affected the estrous cycle. Six new females with different estrous-cycle types were included in the study. All the female estrus patterns (n = 31) were investigated during 14 days. Males were chosen at random and introduced into each cage with a female. All males used were adults (25–37 g) and had prominent testes with black pigmentation on the posterior scrotal skin. After the introduction of the male, signs of pregnancy were noted, body mass was calculated and vaginal smears were done only three times a week, to minimize disturbance. The pairs were kept in their cages for 45 days.

2.4. Study III: The effect of pregnancy on the female estrous cycle

The pattern of the estrous cycle was also determined for nearly all females from Study II (n = 29) 3 months after they had been separated from the male and their offspring. Body mass and food consumption were measured and vaginal smears collected every day during a 16-day period.

2.5. Statistical analysis

Statistical analysis was performed by the analysis of variance (one-way anova with contrast) after a logarithmic transformation of the data (in SPSS). The contrast (two-sample test) was used when comparing the mean food consumption and body weight, and for the reproductive parameters. Chi-square analysis (Likelihood Ratio) was used for testing the difference in the number of pregnancies between the three groups, the estrus pattern in the young females and the change in the female estrus pattern after pregnancy. We used the Spearman rank correlation test for the correlation of the estrus pattern between mother and offspring, and for the correlation between the mother's body mass and litter size. The criteria for a non-significant test is $P >$ 0.05.

3. Results

3.1. Study I: The estrous cycle in wild-caught female wood mice

The wild-caught females were characterized into three groups of ten females according to the length of the estrus and the diestrus periods, and the number of cells in the vaginal smear. The first group was considered to be in a state of continuous estrus as the duration of the diestrus period was very short (1.4 ± 0.4 days, see Fig. 1) (mean ± *S.E.*), and occurred only at irregular intervals. The mean length of the estrus period was 15.8 ± 1.1 days. Females in the second group had an estrous cycle between 6 and 11 days (9.0 ± 0.6 days). The mean length of the estrus period was 4.9 ± 0.7 days, while the length of the diestrus period was 4.8 ± 0.4 days.

Females in the third group only showed vaginal estrus rarely. The mean length of the diestrus period was 13.3 ± 1.6 days, while the length of the estrus period was 1.3 ± 0.2 days. Females with a continuous estrus pattern showed significantly longer periods of estrus than those in the cyclic estrus group ($df = 12.9$, $F = -8.19$, $P < 0.001$). The infrequent estrus group showed significantly more days of diestrus than the cyclic estrus group ($df = 15.8$, $F = 6.67$, $P < 0.001$). The three groups differed significantly in the number of leucocytes ($df = 14.8$, $F = 8.64$, $P < 0.001$) and cornified epithelial ($df = 14.3$, $F = 6.32$, $P < 0.001$) cells in the vaginal smears. In the continuous estrus group, females had an index (number of cell abundance) of 2.7 ± 0.3 for leucocytes and 2.9 ± 0.2 for cornified epithelial cells. The cyclic estrus group females had an index of 1.9 ± 0.3 and 2.0 ± 0.3, while those in the infrequent estrus group had 1.1 ± 0.2 and 1.0 ± 0.3, respectively.

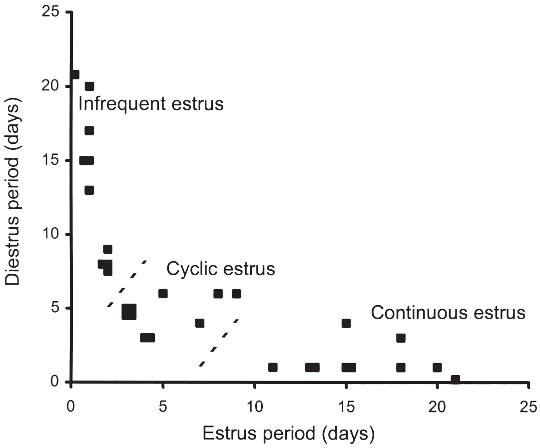

Fig 1. The graph shows the individual maximum length of the estrus and diestrus periods in female wood mice ($n = 30$), measured during a period of 21 days. Data are based on the histological appearance of vaginal smears. The estrus period in the vaginal smear was characterized by a cornified epithelial cells, while the diestrus period was characterized by leucocytes. Based on the data, females were divided into three categories.

Females showing a continuous estrus pattern had a significantly higher food consumption than cyclic estrus females ($df = 27$, $F = 3.14$, $P < 0.004$), who in turn had a significantly higher food consumption than females with an infrequent estrus pattern ($df = 27$, $F = -2.43$, $P < 0.007$; Table 1). Body mass did not differ significantly between the three groups ($df = 2$, $F = 2.86$, $P < 0.07$): continuous estrus: 22.6 ± 0.7 g; cyclic estrus: 22.9 ± 0.8 g and infrequent estrus: 20.5 ± 0.9 g.

3.1.1. The estrous cycle in the young females

The young virgin females showed the same three distinct estrus pattern types as the wild-caught females.

Table 1. Food consumption and body mass in wild-caught and young female wood mice in three different estrus groups. Values are given as mean and *S.E.*

	Continuous	Cyclic	Infrequent
Food consumption (g)			
Wild-caught females	5.3 ± 0.3	4.1 ± 0.3	3.1 ± 0.2
Young females	4.9 ± 0.2	4.5 ± 0.1	3.4 ± 0.1
Body mass (g)			
Wild-caught females	22.6 ± 0.7	22.9 ± 0.8	20.5 ± 0.9
Young females	19.9 ± 0.3	20.3 ± 0.8	18.6 ± 0.9

The continuous estrus females ($n = 4$) showed an estrus pattern between 11 and 14 days in length. Females with cyclic estrus ($n = 5$) had an estrous cycle between 5 and 8 days, and those with infrequent estrus ($n = 8$) between 6 and 14 days. Females from the continuous estrus group showed significantly more days of estrus than those from the cyclic estrus group ($df = 4$, $F = 3.67$, $P < 0.02$). In the infrequent estrus group, females showed significantly more days of diestrus than females in the cyclic estrus group ($df = 5.4$, $F = 2.89$, $P < 0.03$). In the continuous estrus group, 75% of the young females showed the same estrus pattern as their mother. In the cyclic estrus group, the figure was 60%, and in the infrequent estrus group 63%. There was a significant correlation between the estrus type of the young females and the estrus pattern of their mothers ($df = 15$, $r = 0.61$, $P < 0.05$).

Food consumption did not differ significantly between females with continuous and females with cyclic estrus patterns ($df = 5.1$, $F = 1.71$, $P < 0.15$). Females with a cyclic estrus pattern had a significantly higher food consumption than infrequent estrus females ($df = 10.8$, $F = 6.48$, $P < 0.001$; Table 1). There was no significant difference in body weight between the three groups ($df = 2$, $F = 1.42$, $P < 0.27$; Table 1).

3.2. Study II: Prior to the presence of a male

Continuous estrus females had a significantly higher food consumption than cyclic females ($df = 28$, $F = -4.94$, $P < 0.001$), who in turn had a significantly higher food consumption than females with an infrequent estrus pattern ($df = 28$, $F = 3.58$, $P < 0.001$; Table 2). Females with infrequent estrus had a significantly lower body mass than females in the other two groups ($df = 28$, $F = 3.78$, $P < 0.001$; Table 2), whereas body mass did not differ significantly between the other two groups of females ($df = 28$, $F = -0.47$, $P < 0.64$). The mean body mass and food consumption rates of males did not differ among the three groups ($df = 2$, $F = 0.21$, $P < 0.81$) ($df = 2$, $F = 0.03$, $P < 0.97$; Table 2).

3.2.1. Pregnancy, litter size and body mass

Pregnant females that exhibited continuous and cyclic estrus patterns had significantly higher body masses than pregnant females with an infrequent estrus pattern ($df = 18$, $F = -2.34$, $P < 0.03$; Table 3). There was no significant difference in body mass between females with continuous estrus and females with a cyclic estrus pattern ($df = 18$, $F = 0.32$, $P < 0.88$). Not all females became pregnant. Only one continuous estrus female did not become pregnant. Her body mass was 26.4 g. The average body mass of the five non-pregnant females with cyclic estrus was 23.8 ± 0.5 g (mean ± *S.E.*), and for the four non-pregnant females with infrequent estrus, mean body mass was 19.4 ± 1.2 g.

Ninety-one percent of continuous estrus females, 50% of cyclic estrus females, and 60% of infrequent estrus females became pregnant during the study. There were no significant differences in the number of pregnancies between the three groups ($df = 2$, $x^2 = 4.96$, $P < 0.08$; Table 3). Females with infrequent estrus became pregnant

Table 2. Food consumption and body mass of female wood mice exhibiting the three estrus patterns. The females were investigated in the study: in presence of a male (Study II) and after the females became pregnant (Study III). Values are given as mean and *S.E.*

	Study	Continuous	Cyclic	Infrequent
Food consumption (g)				
Females: presence of a male	II	4.9 ± 0.2	3.6 ± 0.1	2.9 ± 0.1
Males: single	II	4.9 ± 0.5	5.2 ± 0.6	4.9 ± 0.5
Females: after pregnancy	III	4.7 ± 0.2	3.5 ± 0.1	2.8 ± 0.1
Body mass (g)				
Females: presence of a male	II	23.7 ± 0.8	23.3 ± 0.7	19.1 ± 1.0
Males: single	II	29.4 ± 0.7	29.6 ± 0.9	28.9 ± 1.0
Females: after pregnancy	III	23.6 ± 1.0	23.7 ± 1.0	20.7 ± 1.0

and had their first litter significantly later than females in the other two groups (*df* = 18, *F* > 3.13, *P* < 0.006, in both cases; Table 3). There was no significant difference between the continuous estrus and cyclic estrus groups (*df* = 18, *F* = – 0.29, *P* < 0.78). Females with cyclic estrus had significantly larger litter sizes than females with infrequent estrus (*df* = 17, *F* = 2.33, *P* < 0.03), whereas there was no difference between the other two groups (*df* = 17, *F* > – 1.14, *P* < 27). There was no correlation between the three different groups and the litter size (*df* = 18, *r* = – 0.24, *P* < 0.16). However, there was a significant correlation between the body mass of the mother (*n* = 20) and its litter size (*r* = 0.56, *P* < 0.01).

3.3. Study III: The effect of pregnancy on the estrous cycle

The majority of the females did not change their estrus pattern (*df* = 2, x^2 = 0.60, *P* < 0.8). One female each in the continuous and cyclic estrus groups died during the latter part of Study II. The number of females that had changed their estrus patterns from Study II were: 2 continuous estrus females (*n* = 10), 3 cyclic estrus females (*n* = 9), and 2 infrequent estrus females (*n* = 10). Two females that showed a continuous estrus pattern in Study II changed to a cyclic estrus pattern. Two out of three females with a cyclic estrus pattern (in Study II) changed to a continuous estrus pattern and one changed to infrequent estrus. Two females showing an infrequent estrus pattern during Study II changed the pattern to continuous estrus and cyclic estrus respectively.

The females' food consumption three months after separation from the males and their litters are shown in Table 2. Continuous estrus females had significantly higher food consumption than cyclic estrus females (*df* = 26, *F* = 3.99, *P* < 0.001), while females with cyclic estrus had significantly higher food consumption than infrequent estrus females (*df* = 26, *F* = 3.94, *P* < 0.001). The body masses of females in the three groups were the same as in Study I. Females with continuous and cyclic estrus still had a significantly higher body mass than females with infrequent estrus (both *df* = 26, *F* > – 2.18, *P* < 0.04). Body mass did not differ between the other two groups (*df* = 26, *F* = – 0.07, *P* < 0.94).

4. Discussion

Based on studies of vaginal smears from wild-caught wood mice, three distinctive types of estrous cycles were identified. The estrous cycles differed in the lengths of the estrus and the diestrus periods, and in the number of leucocytes and epithelial cells in the vaginal smear. One group of females showed a cyclic estrus pattern with an estrous cycle of 6–11 days in length. A second group of females showed more or less continuous estrus (large numbers of grand cornified epithelial cells), with estrus lasting from 11 to 21 days and with a very short diestrus period (1–4 days).

The third group of females showed a more or less constant state of diestrus (7–21 days), with short and infrequent estrus periods (1–3 days). This group showed a very low number of epithelial cells compared with the other two groups. The existence of three categories of females was emphasized by the fact that also young females (10–15 weeks), bred in the laboratory, showed the same patterns as the wild-caught females. The estrus

Table 3. Reproductive parameters of females exhibiting three different estrus patterns in the presence of a male. Values are given as mean and *S.E.*

	Continuous	Cyclic	Infrequent
n	11	10	10
Number of females that became pregnant (n)	10	5	6
Body mass at the end of pregnancy (g)	32.9 ± 1.3	32.3 ± 0.9	27.6 ± 1.5
Increase in body mass during pregnancy (%)	39 ± 4	39 ± 4	45 ± 7
Days until delivery of the first litter	27.4 ± 2.1	28.4 ± 3.1	40.3 ± 2.2
Litter size	3.8 ± 0.3	4.6 ± 0.5	3.2 ± 0.4
Range in litter size	2–5	3–6	2–4

patterns among these young females were supposed to represent the estrous cycle in young virgin females that had just reached puberty and that had not had contact with any male.

The estrous cycles in the Swedish wood mice differed in the pattern and the length from other studies on small rodents (4–6 days cycle) (Brook 1984, Clarke 1985, Flowerdew 1987). Brook discerned four categories of female wood mice (n = 17). One group (about 30%) showed unchanging vaginal smears with a large number of cornified epithelial cells, and large ovaries, corresponding to our continuous estrus group. The second group (about 15%) showed a regular estrous cycle of four to six days. These females had large ovaries, corresponding to our cyclic estrus group. The third group (about 45%) of females had diffuse vaginal smears containing few cells of any sort, corresponding to our infrequent estrus group. These females only had small ovaries. The fourth class (about 10%), mainly showed a non-perforated vaginal opening. The estrus patterns shown by the females in the study of Brook, corresponded well to the three groups seen in the present study, although the length of the estrous cycle in the cyclic estrus group (6–11 days) and the second group (4–6 days) studied by Brook, differed in the number of days.

How stable over season and over the generations are the three estrus strategies? Do they correspond to three different genotypes or do they exist as a consequence of females being exposed to different environmental stimuli? At present, there are no good answers to these questions. At the most, some preliminary judgments can be made on the basis of the results of the present study.

In captivity, the wood mice showed three distinct estrus types despite the fact that the physical and social environments were constant and similar for all females. In the presence of a male, only 68% of the total number of females became pregnant. Pregnancy occurred in all three groups, but females with infrequent estrus gave birth significantly later than those from the other two groups. The delayed pregnancy in this group may be a consequence of the infrequent occurrence of estrus. The low number of young in the infrequent estrus group can be in concordance with their low body mass and food consumption. The litter size varied from 3.2 in infrequent estrus females to 4.6 in continuous estrus females compared with 4.2–5.0 (Eriksson 1980, Brook 1984, Clarke 1985) and 5.3–6.9 (Gurnell & Rennolls 1983, Clarke 1985) in other studies. We expected females with continuous and cyclic estrus to exhibit similar patterns of reproduction and the females with an infrequent estrus pattern to have a low number of pregnancies. This was not the case, however, since there was no significant difference in the number of pregnancies between the three groups. Brook (1984) showed that female wood mice with an infrequent estrus pattern had significantly smaller ovaries than females with continuous or cyclic estrus patterns. The size of the ovaries may indicate a depressed reproductive activity in these females.

In a behavioural observation arena, P. Jonsson and S. Erlinge (unpublished data) found that females with continuous and cyclic estrus patterns exhibited dominant behaviour, whereas females with infrequent estrus were subordinated against the other two groups. Usually, the dominant females in a population have a greater opportunity for reproduction (Stenseth 1983). Our results indicate that having infrequent estrus reduces the reproduction rate as well as the litter size.

We studied young virgin females born in the laboratory during the summer, about 65% of these showed the same estrus pattern as their mother (n = 17). There was a significant correlation between the mother's estrus pattern and her daughter's. Can the estrus pattern be related to the body condition of the mother during pregnancy and nursing? We observed a significant correlation between the body mass of the mother and the litter size. Another interesting question is if the estrus pattern is related to the age of the females. It is possible that the young females more often show an infrequent estrus pattern, while more experienced females may show any type of estrus pattern.

The presence of a male did not change the estrus pattern significantly in any of the three groups. Both females that had been non-pregnant and pregnant, exhibited the same estrus pattern after removal of the male and the young, as they did at the onset of the third study, three months earlier. Seven females changed their estrus pattern, three of which had not become pregnant. The fact that the majority of the females retained their original estrus patterns after being housed together with a male, suggests that it is not the presence of a male that is important for the type of estrus pattern expressed by the female.

In the house mice, the estrous cycles may be absent unless male odours are present (Whitten 1966, Bruce 1970). The presence of a male normally affects the female's reproductive status and her fertility (Whitten 1956, Marsden & Bronson 1964, Bronson 1985). Clarke (1985) showed that the presence of a mature male stimulated young female wood mice to have larger ovaries than females living totally separated from males.

For practical reasons, it is almost impossible to perform a corresponding study on free-living wood mice. We can therefore only speculate on the functional significance of the different estrus patterns in a wild population, and how they affect female fitness during different environmental conditions. The fact that some females switched estrus patterns after exposure to a male, but others did not, suggests some flexibility in the control mechanism. However, the majority of the females maintained the same estrus pattern throughout the study, suggesting some genetic component. We must assume that the same estrus patterns are found among free-living wood mice, and that each pattern is adaptive under certain environmental conditions such as high or low food abundance, or social conditions associated with density and competition.

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