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Factors affecting the urine-marking activity in water voles *Arvicola amphibius* (Rodentia, Cricetidae)

Galina G. Nazarova*, Ludmila P. Proskurnjak & Ekaterina I. Yuzik

ABSTRACT. Water voles inhabiting Western Siberia in spring, after the snow melts, leave wintering stations and occupy the banks of rivers, ditches, and swamps. During this period, urine-marking behavior can be of great importance for initiating reproduction and maintaining the social relationships in population. We studied the urine marking rates under laboratory conditions in winter and spring months to understand the role of urine signals in the intraspecies communication. We hypothesized that the number of urine scent marks depends on the season of the year, sex, the vaginal cytology in females, and blood testosterone level in males. Urine marking rates were evaluated in an unfamiliar clean cage. The results we obtained have confirmed the hypothesis. In spring, urine-marking activity increases, with males have more urine marks than females. In May, there was a positive correlation between blood testosterone levels, body mass (r = 0.626, p = 0.022), and anogenital distance (r = 0.701, p = 0.008), which reflects the size of testes. A positive relationship was found between the testosterone levels in blood measured in May and the average monthly number of urine marks left by the males (r = 0.577, p = 0.039). In females, at the beginning of the reproductive season, an increase in urine-marking activity was noted in individuals with a high content of keratinized epithelial cells in vaginal smear, i.e., physiologically ready for mating (r = 0.624, p = 0.013). We concluded that increased urine scent marking behavior during the spring month helps to synchronize reproduction.

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Факторы, влияющие на маркировочную активность водяных полевок *Arvicola amphibius* (Rodentia, Cricetidae)

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РЕЗЮМЕ. Водяные полевки, обитающие в Западной Сибири, весной, после таяния снега, переселяются с мест зимовки в обводненные биотопы. В этот период маркировка территории мочой может иметь большое значение для инициации размножения, установления и поддержания социальных связей в популяции. Для понимания роли хемосигналов мочи во внутривидовой коммуникации мы оценили частоту маркировки мочой в зимние и весенние месяцы в лабораторных условиях. Предположили, что количество мочевых меток зависит от сезона года, пола, клеточного состава вагинального мазка, отражающего физиологическую готовность самок к спариванию, и уровня тестостерона в крови самцов. Количество мочевых меток оценивали, помещая животное в незнакомую чистую клетку. Полученные результаты показали, что весной частота маркировки мочой увеличивается, а самцы оставляют больше мочевых меток, чем самки. В мае отмечена положительная корреляция между уровнем тестостерона в крови самцов, массой тела (r = 0.626, p = 0.022) и аногенитальным расстоянием (r = 0,701, p = 0.008), отражающем размеры семенников. Обнаружена положительная связь между уровнем тестостерона в крови самцов в мае и среднемесячным количеством моче-

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вых меток за весенний период ($r = 0.577$, $p = 0.039$). У самок маркировочная активность в начале репродуктивного сезона повышалась с увеличением относительного содержания числа ороговевших эпителиальных клеток во влагалищном мазке, отражающем готовность к спариванию ($r = 0.624$, $p = 0.013$). Таким образом, повышение маркировочной активности в весенние месяцы связано с половым созреванием и может способствовать синхронизации размножения.

КЛЮЧЕВЫЕ СЛОВА: маркировочная активность, моча, пол, сезон, половое созревание, рост, тестостерон.

Introduction

Urine scent marking behavior is an environmentally controlled and content-dependent form of communicative behavior which has several main functions: mate attraction, territorial defense, self-advertisement, and kin recognition (Hurst & Rich, 1999; Roberts, 2007; Arakawa *et al*., 2008). Urine volatile compounds and proteins of lipocaline family play an important role in realization of the above functions and organization of social life in murid rodents (Pelosi & Knoll, 2022). Various chemosignals in urine of conspecifics can affect the timing of puberty and the maintenance of pregnancy in female rodents, and therefore, can affect the population size and dynamics (Petrulis, 2013).

Quantitative aspects of scent-marking behavior have been studied in many rodent species, and the obtained results indicate that the frequency of scent marking and the spatial distribution of scent marks can be under seasonal control, as well as the hormonal state and reproductive conditions of animals (Ferkin, 2018). A temporal variation in the frequency of fecal and urine marking, consistent with the period of reproductive activity, has been shown in seasonal breeding mammals (water voles: Woodroffe *et al*., 1990; wolves: Asa *et al*., 1990; Eurasian beavers: Rosell & Bergan, 2000; gerbils: Gromov, 2015). Identifying the internal and external factors explaining the differences in the scent-marking activity is important for understanding the evolution and biological significance of this form of behavior in different mammalian species. Moreover, understanding the driving causes of urine-marking behavior may have implication for reducing the risk of zoonotic infections, because urine excretes are not only the source of odoriferous substances used for chemical communication, but also are the source of infectious agents, such as hantavirus or leptospira (Gelling *et al*., 2012; Han *et al*., 2015). Contact with contaminated urine, either directly or indirectly through the soil or water can lead to transmission of zoonotic diseases. Undoubtedly, animal behavior plays an important role in pathogen cycling in the environment and influences the likelihood of human infection (Herrera & Nunn, 2019).

Our research aims to elucidate the factors responsible for urine scent marking behavior in water vole, which have not been studied so far. Water voles undergo cyclic population outbreaks and crashes in Western Siberia and in peak years become the major agricultural pests (Panteleev, 1970). One of the most striking ecological peculiarities of water voles living in a strongly seasonal environment is the seasonal migration from wet to dry habitats in autumn and to the opposite direction in spring. In winter, water voles have solitary lifestyles (Potapov *et al*., 2004). In spring, after snow melting, they occupy banks of rivers, ditches, marshes free from conspecifics. In such ecological condition scent-marking behavior seems to be of great importance for creating individual "odor-signal field" (Eisenberg & Kleiman, 1972) which is necessary for initiation of reproduction and maintaining the social-spatial relationships among members of population. Chemical communication signals and social cues proved to play a particularly important role in the regulation of reproduction in water voles (Evsikov *et al*., 1995, 1997). During the breeding season, lasting from April to September, voles use the latrines to indicate their presence in a territory (Stoddart, 1970). Latrine counts serves as the indicator of reproductive activity of animals (Woodroffe *et al*., 1990). According to results of field studies addressed to investigate the space use, male home ranges are several times larger than that of females. Home ranges of males overlap extensively with one another and with home-ranges of several females (Panteleev, 1971). Males with higher than average body mass are able to monopolize larger numbers of receptive females, than males with lower body mass (Evsikov *et al*., 1999). These data indicate the existence of intrasexual competition between males for access to females, in the outcome of which female mate choice (intersexual selection) may play an important role. Females can discriminate dominant from subordinate males by odor cues, preferring the odor of dominant male, which appear to be more reproductively successful (Evsikov *et al*., 1995).

It has been established that proteins of male urine with molecular weight of 15–25 kDa or volatile molecules bound by these proteins are important in male-male chemical communication in the water vole (Nazarova *et al*., 2016). Urinary protein excretion depends on season, sex, and male reproductive condition (Nazarova & Proskurnyak, 2013; Nagnan-Le Meillour *et al*., 2019). It is still not known whether the increasing concentration of urine protein in spring months is accompanied by temporally related changes in urine marking activity. It has been demonstrated that in mammals scent marking may be a response to variety of environmental stimuli, not limited to conspecific odors (Eisenberg & Kleiman, 1972). It may be under photoperiodic and hormonal control, as has been shown in

Syrian hamsters (Caldwell *et al*., 2008) and other rodent species (Brown, 1978; Lisk & Nachtigall, 1988; Petrulis, 2013).

In the present study we investigated the seasonal changes in urine marking behavior of males and females tested in a clean arena. We hypothesized that urine marking behavior depends on the month of the year, sex, vaginal cytology in females, and androgen status of sexually matured males.

Materials and methods

Ethical note

The study was conducted in accordance with the Declaration of Helsinki and met the guideline requirements of the order of the Russian High and Middle Education Ministry (No. 742 issued on 13 November, 1984) and by the Federal Law of the Russian Federation (No. 498-FZ issued on 19 December, 2018). Experimental procedures and protocols were approved by the Institutional Animal Care and Use Committees (Protocol 2020-02, 2021-01). After the experiments, voles were kept in the laboratory for other research projects.

Animals and rearing conditions

We used laboratory-born water voles (13 males, 15 females). Laboratory colony was founded in 1984 by voles captured in Novosibirsk region (55.8333° N, 80.0000° E). Every two to three years, the colony was replenished with wild individuals to prevent inbreeding. Voles were weaned at 21 days of age, and thereafter housed singly in stainless steel cages (25 × 25 × 48 cm) under a natural photoperiod, at 18–21°C. Food (carrot, grains, oat sprouts, fresh grass) and water were provided *ad libitum*. Hay was used as a nesting material. Under the mesh floor of the cages were trays filled with sawdust (1 cm thick). Voles were sexually inexperienced when the experiment began.

Body mass and reproductive conditions

Body mass was measured with a digital balance (model Scout Ohaus, weighing accuracy of 0.1 g) at monthly intervals (from January to May) just after testing. As an external index of puberty onset in females we used vaginal opening. Vaginal cytology was evaluated microscopically, immediately after collection of vaginal wall cells and preparing of an unstained, wet mount preparation. We describe cytological picture based on relative counts of leucocytes, round nuclear and cornified epithelial cells (Nazarova *et al*., 2007), using numeric classification: 0 — absence or few epithelial cells in a smear: 25 — predominance of leucocytes or nucleated epithelial cells; 50 — the number of all types of cells in approximately equal proportions; 75 — predominance of cornified epithelial cells. Vaginal smears were taken only from females with an open vagina. For females with closed vagina, the proportions of cornified epithelial cells assume to be zero (Evsikov *et al.,* 1989).

Reproductive conditions of males were estimated by anogenital distance (AGD), measured from the anterior base of the penis to the center of the anus. Anogenital distance can serve as a prognostic trait for determining the testes mass and readiness of males to mate (Nazarova, 2011). Males with anogenital distance less than 23 mm are not capable to mating (copulations and inseminations). The proportion of males capable of mating increases with increasing anogenital distance and remains relatively constant after AGD exceeded 26 mm. Therefore, we used AGD ≥ 27 mm to differentiate males roughly in two groups: sexually mature, immature.

Scent marking tests

Animals were tested in a monthly interval (January–April) from 11.00 to 13.00. To avoid the stress associated with handling, the animal was transferred from the home cage to the experimental cage, carefully driving it into a tubular trap. In total, four trials were carried out with each animal. Scent marking tests began by placing the experimental vole into a clean cage (25 × 25 × 48 cm) lined with filter paper. To prevent the introduction of human scents, we used latex gloves. Scent marking behavior was allowed for 30 min, and then the animal was returned to his home cage. The experimental cage and gloves were thoroughly cleaned between trials with both water and 75% ethanol.

Analysis of urine marks

The filter paper was examined under ultraviolet illumination (Blacklight Blue UV lamp, 20 W, 365 mm, Model ESL-312-20/BLB/E27 CHINA) in a dark room to record the number of urine marks deposited by the vole (Desjardins *et al*., 1973), which appeared as bluish spots. To identify each mark, we traced its outline on the paper substrate with a pencil. We counted all colored urine marks.

Blood collection and testosterone measurement

Blood was collected from the retro-orbital sinus under topical ophthalmic anesthetic (proparacaine) in May, one month after the experimental exposure, to determine testosterone concentration in serum by the immunoassay method. The blood samples were centrifuged for 15 minutes at 3000 rpm and the serum was stored at −20°C until assayed.

Serum testosterone concentration was measured by the ELISA (#X-3972, Vektor-Best, Novosibirsk, Russia). The sensitivity of assay was 0.2 nmol/l, and the intra-assay coefficient of variation was less than 8%. The testosterone assay was validated for *A. amphibius* by testing for parallelism using serial doubling dilutions of unextracted serum over the dilution range (1:1 to 1:64) (Nazarova *et al*., 2021). The concentration of testosterone was determined from the calibration curve after measuring the optical density of the solution in wells at 450 nm in the PowerWave XS2 spectrophotometer.

Statistical analysis

Data was analyzed by using SPSS Statistics for Windows, ver. 16.0. Normality of the data was tested by Kolmogorov-Smirnov tests and log transformations, ln(n+1), were applied when necessary. For statistical analyses, we used general linear mixed model (GLMM) to assess effects of sex and calendar month (fixed factors) on body mass, and for testing whether

anogenetal distance in males (AGD) was affected by the month of the year (fix factor) and body mass (covariate). To account for non-independence of data due to repeated measurements from the same individual we include animal identity as a random factor.

To assess sex and monthly patterns of urination, we carried out a GLMM with amount of urine scent marks as a response variable, month and sex as fixed factors, individual identity as a random intercept. Body mass was used as covariate. To evaluate the influence of reproductive state, this analysis has been performed separately for each sex. Body mass and proportion of cornified cells in vaginal smears (for females) were used as covariates. Comparison of differences between groups was performed by using the Bonferroni test.

Correlations between scent mark frequency and characteristics of reproductive function were assessed using Spearman's rank tests. For compare of frequencies we used Pearson's Chi-squared test.

Means are given with standard error of the mean (X ± SEM). For all analyses, a *p*-value below 0.05 was considered to be significant.

Results

Growth and sexual maturation

Linear mixed model revealed statistically significant influence of the month of the year ($F_{3,81} = 85.717$, $p < 0.001$), sex ($F_{1,26} = 6.031$, $p = 0.021$), and individual identity ($Z = 3.338$, $p = 0.001$) on body mass. Plots of the body mass against months are presented in Fig. 1.

Acceleration of growth in spring months was associated with sexual maturation, as evidenced by increasing anogenital distance in males and proportion of females with open vagina (Fig. 2). We found that AGD depends on the month of the year ($F_{3,38.5} = 11.553$, $p < 0.001$), and the body mass ($F_{1,15.3} = 46.859$, $p < 0.001$; $\beta = 0.063 \pm 0.009$, $p < 0.001$). The influence of individual identity was not significant ($Z = 1.159$, $p = 0.246$).

In January and February, all females had closed vagina. Vagina opening began in March and ended in April that was associated with changes in vaginal cytology. In March, only 20.0% of females with open vagina had predominantly cornified epithelial cells in vaginal smears. In April, there were 80.0%, $\chi^2 = 5.934$, $df = 1$, $p = 0.015$.

Seasonal changes in the frequency of scent marking

We found statistically significant influence of the month of the year ($F_{3,89} = 5.051$, $p = 0.003$) and sex ($F_{1,27.4} = 6.238$, $p = 0.019$) on the amount of urine marks deposited by voles. The dependence of urine-marking activity on body mass ($F_{1,46.4} = 0.658$, $p = 0.421$) or individual identity ($Z = 1.382$, $p = 0.167$) were insignificant.

Fig. 3 illustrates seasonal dynamics of scent-marking activity in males and females. The amount of urine marks in March were significantly higher, than in January (Bonferroni post hoc test: $p = 0.002$) and February (Bonferroni post hoc test: $p = 0.025$). In average, males deposited significantly more scent marks than did females ($\beta = 0.748 \pm 0.299$, $p = 0.019$).

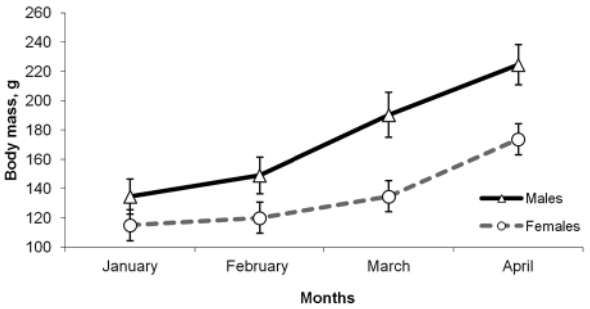

Fig. 1. Body mass growth in males (triangles) and females (circles). Mean ± SEM with all data points shown.

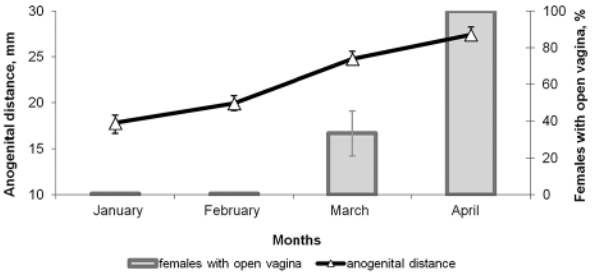

Fig. 2. Vaginal opening in females (bars) and anogenital distance in males (line) in different months. Mean ± SEM with all data points shown.

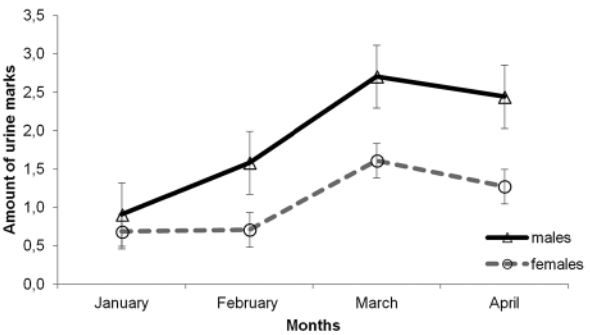

Fig. 3. The amount of urine marks (natural logarithm transformed data) in males (triangles) and females (circles) tested in different months of the year. Mean ± SEM with all data points shown.

Sexual maturation and urine marking in females

In April, urine-marking activity in females was influenced by vaginal cytology, evaluated by the proportion of cornfield epithelial cells in vaginal smears. Spearman's rank correlation between the amount of urine marks and the proportion of cornified epithelial cells was statistically significant ($r_s = 0.624$, $n = 15$, $p = 0.013$).

Sexual maturation and urine marking in males

The results of GLMM with the month of the year and reproductive condition (AGD ≥ 27 mm: yes, no) as a fixed factors, body mass as covariate, and individual identity as a random intercept evidenced that urine-marking activity in males depend only on the month of the year (month of the year: $F_{3,38.3} = 4.023$, $p = 0.014$; reproductive condition: $F_{1,45.2} = 0.800$, $p = 0.376$; body mass: $F_{1,17.4} = 0.321$, $p = 0.578$; individual identity: $Z = 0.955$, $p = 0.340$).

In May, there were positive correlations between blood testosterone level and body mass ($r = 0.626$, $p = 0.022$), blood testosterone level and AGD ($r = 0.701$, $p = 0.008$). To evaluate the relation between hormonal status of males and their urine-marking activity, data on the numbers of urine marks in different tests were individually averaged. As a result, a positive correlation was found between the blood testosterone level and the mean number of urine marks deposited by males ($r = 0.577$, $p < 0.039$).

Discussion

Our results demonstrated that the quantity of urine marks left by water voles in an unfamiliar territory is sex-dependent. In males it is higher than in females, which likely indicates the androgen-dependence of urine-marking behavior and its significance in sexual selection (Gosling & Roberts, 2001; Roberts, 2007). Urine chemosignals can prime the physiology and social behavior of potential mates (Petrulis, 2013; Nazarova *et al*., 2016). Additionally, quantitative characteristics of urine-marking behavior can determine the female mate choice (Thonhauser *et al*., 2013).

The quantity of urine scent marks depends on calendar months. It increases in spring, when (in natural conditions) water voles occupy free territories and start breeding. This finding indicates that urine-marking activity seems to be of greater importance during the period of reproductive activity, compared to the period of reproductive rest. As shown by other authors, water voles leave urine and fecal marks at the boundaries of their individual territory only during the breeding season (Woodroffe *et al*., 1990). Analysis of literature related to scent-marking phenomenon revealed that seasonal differences in the frequency of scent marking exist in other rodent species. Thus, Gromov (2015) demonstrated that scent-marking activity in gerbils reached a maximum in spring and early summer.

Our results suggest that seasonal changes in the amount of urine marks are tightly linked to the process of sexual maturation. In females, the increase of amount of urine marks is accompanied by raising the proportion of cornified epithelial cells in vaginal smears, which reflect female sexual receptivity. Dependence of female scent-marking activity on physiological conditions has been shown in mice (Coquelin, 1992), rats (Birke, 1978, 1984; Matochik *et al.*, 1992), Syrian hamsters (Fischer & McQuiston, 1991), red-backed voles (Rozenfeld & Denoël, 1994), meadow voles (Ferkin & Johnston, 1993), and other mammals (Johnson, 1973; Asa *et al*., 1990; Coombes *et al*., 2018). Increasing the frequency of urine scent marking in receptive females can help attract males and encourage competition between males, thereby increasing the likelihood of mating with high-quality individuals (Fischer & Brown,1993: Coombes *et al.*, 2018).

Odoriferous substances of urine can convey information about female potential fertility (Lai *et al*., 1996). Water vole males can discriminate females with different reproductive potency by odor cues. Females' odor attractiveness to opposite sex is a consistent individual characteristic, which is positively connected with future reproductive success. Virgin sexually mature females with a higher index of odor attractiveness for males produced more offspring during the reproductive season (Nazarova, 2001). Therefore, female scent marking can be involved in competing signaling for potential mates (Stockley *et al*., 2013).

Interestingly, we found a positive correlation between the monthly means of individual urine-marking frequency in males and the blood testosterone level measured in May. There were also positive correlations between blood testosterone level, body mass, and AGD. Thus, urine-marking activity before starting reproduction is associated with future androgen status of sexually mature individuals. These results are consistent with those obtained in mice: urine scent marking rate in sexually immature males is the best predictor of their dominant status as adult (Collins *et al*., 1997).

To conclude, our data demonstrate that urine scent marking in water voles is sexually dimorphic. In males it is higher than in females. The urine-marking activity significantly enhanced in spring months compared to winter months. The frequency of urine marking seems to be a behavioral predictor of androgen status of males and sexual receptivity in females. We believe that increased urine scent marking during the spring months helps to synchronize reproduction.

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