ACTA THERIOLOGICA
Vol. 34, 22: 315—324, 1989

Precopulatory Isolating Mechanisms Between the House and Mound-Building Mouse

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Kotenkova E. V., Osadchuk A. V. & Lyalyukhina S. I., 1989: Precopulatory isolating mechanisms between the house mouse and mound-building mouse. Acta theriol., 34, 22: 315—324, [With 3 Tables]

The reaction to olfactory signals of individuals of their own species and a closely related one was investigated in *Mus musculus* Linnaeus, 1758 and *Mus hortulanus* Nordmann, 1840. Mice of both species readily distinguished conspecific animals from individuals of related species, as well as from individuals of other rodents, by odour. In sexual relations, the possibility of information between representatives of these closely related species of mice was demonstrated. The presence of an estrous conspecific female induced a significant increase in the blood plasma testosterone level in males compared with controls with no females. Females of closely related species did not activate the hypophyseal-testicle system. Thus, responses to olfactory signals may serve as precopulatory isolating mechanisms between house and mound-building mice both at the behavioural (search and identification of mates) and physiological level (direct contact with a potential mate).

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1. INTRODUCTION

At present, at least five species of mice are distinguished in Europe on the basis of morphological and biochemical traits (Sage, 1981; Marshall & Sage, 1981; Bonhomme *et al.*, 1984). Most of the USSR is occupied by a single species *Mus musculus*. In Caucasus and Trans-Caucasus, a hybrid zone may exist between different biochemical groups *M. m. musculus*, *M. m. bactrianus* and *M. m. domesticus* (Mezhzherin & Kotenkova, 1989). In Primorski Territory another hybrid zone may exist between *M. m. musculus* aud *M. m. castaneus* (Frisman *et al.*, 1988). In the Ukraine and Moldavia two species live sympatrically, the house mouse *M. m. musculus* and the mound-building mouse, *Mus hortulanus* (Mez-

hzherin, 1987). The ecology of *M. hortulanus* and *M. m. musculus* differs substantially. The former, inhabitants of agrocoenoses, live in open biotopes and are never encountered in dwellings. In the autumn the animals construct little mounds with reserves of food and remain there for the winter (Valkh, 1927; Naumov, 1940). *M. hortulanus* and *M. m. musculus* are distinguished by morphological, ecological, physiological and ethological properties (Naumov, 1940; Sokolov *et al.*, 1985; Meshkova *et al.*, 1986) and the study of protein polymorphism showed that they are genetically isolated (Bonhomme *et al.*, 1984; Mezhzherin, 1987).

According to previously obtained data, successful hybridization in the laboratory is possible of *M. hortulanus* with *M. m. musculus* from natural populations and laboratory *M. m. domesticus* with the production of viable and completely fertile F_1 and F_2 hybrids of both sexes (Bulatova *et al.*, 1986; Lavrenchenko *et al.*, 1989). A study of meiosis in hybrids showed that natural house mice and laboratory animals must be differentiated when discussing reproductive isolation and, consequently, taxonomic interrelationships of mice (Bulatova *et al.*, 1986). In the meiosis of four hybrid males from *M. m. domesticus* × *M. hortulanus*, metaphase plates contained a normal number of bivalents $n=20$. During diakinesis of both hybrids *M. m. domesticus* × *M. hortulanus*, plates with 21-meiotic patterns predominated, including 19 bivalents and 2 univalents. Irregularities of the cytological pattern of meiosis in hybrids of first generation indicate serious noncorrespondence of chromosome sets of mound and laboratory mice, which, however, does not have a bearing on cytogenetic species differences between mound-building and laboratory mice. The phenomenon of intensification of genetic anomalies, including disruption of segregation of meiotic chromosomes, sterility of male hybrids, chromosome breaks, *etc.*, was detected in *Drosophila* under the name hybrid disgenesis during crosses of individuals from natural populations with laboratory lines of the same species (Bregliano *et al.*, 1980). Observations of meiosis in hybrids of mound-building and laboratory mice together with the facts presented suggest that this phenomenon may also occur in mammals (Bulatova *et al.*, 1986).

Genetical isolation in nature (Bonhomme *et al.*, 1984; Mezhzherin, 1987) makes it possible to assume the existence of reliable precopulatory isolating mechanisms between the *M. m. musculus* and *M. hortulanus*, which is discussed here.

The present experiments were carried out as part of more extensive studies on the behaviour and communication of closely related forms of *Mus* (Sokolov *et al.*, 1985; 1988; Meshkova *et al.*, 1986). The objectives of the present study were: to test the behavioral and endocrine responses

of two related species *M. m. musculus* and *M. hortulanus* to stimuli of the same and different species; to examine olfactory discrimination as a potential mechanism in sexual preference and isolation in the two species concerned.

2. MATERIAL AND METHODS

2.1. Experiment 1

In the experiments we used adult males and adult females trapped in April 1982 and April and October 1983 in the vicinity of Kirovograd and Kishinev as well as their offspring born in the laboratory: 18 males and 23 females *M. hortulanus* were caught manually by digging up mounds; 30 males and 20 females *M. m. musculus* were trapped in dwellings; F_1 10 males were born in the laboratory (synanthropic sympatric form); 3 males and 3 females of *Cricetulus migratorius*. Eight males and 6 females *M. m. musculus* were trapped in Moscow (allopatric form).

All animals were fed a standard diet of oats, bread, curds and vegetables. The animals were kept singly in glass cages (35×20×20 cm) with a mesh lid. The animals were studied every other day, during a period of maximum activity from 2100 to 0100 h. A plastic feeding dish (12 cm in diameter) was placed upside down at one end of the cage, and two plastic petri dishes (40 mm in diameter) were placed on it. Round openings (25 mm in diameter) were made in the lids of the petri dishes. The dishes were covered with fine stainless steel mesh, over which the lids with openings were placed. The mesh prevented direct contact of the animal with the source of odour. The feeding and petri dishes were kept in the dwelling chambers permanently. Before the experiment cellophane squares, with urine from one sexually mature mouse, unknown to the experimental animals, was preliminarily applied, and placed in the dishes. A stopwatch with an accuracy to 0.1 sec was used to record the total time spent by the animals on investigating the odour sources during the first one to two activity periods after emergence from the nest. The behavioral responses of the mice with respect to dishes with odour were also recorded. Urine was collected from individuals when they were picked up in the hands approximately 0.5—1 h before the beginning of the experiment. The females were in dioestrous except for some experiments.

The results were treated statistically according to two-tailed Wilcoxon's signed--ranks test (Sokal & Rohlf, 1969).

2.2. Experiment 2

The second experiment was designed to study sexual activation of males in the presence of estrous females of various origins. House mice for these experiments were individuals caught from various places in Moscow and Kishinev, as well as their offspring born in the laboratory. Mound-bilding mice were caught in Kishinev and in the Odessa region.

The tests were conducted as follows: a clean acrylic plastic cage (25×25×15 cm) was partitioned into two compartments by a meshwork, and a male mouse, previously isolated for 3—5 days in a standard plastic cage, was placed in one of the compartments. On the next day, an estrous female was placed for 40 minutes in the other compartment. At the end of this time period, the male was decapitated and its testosterone level in the peripheral blood plasma was determined radioimmunologically (radioimmunological sets of CEA-IRE-Sorin, France).

We used these tests to determine the testosterone levels induced in males of either mouse species, by the presence of estrous females of their own species, the other mouse species, and of the northern red-backed vole, control males were treated similarly, but had confronted no female. The females used in these experiments were injected with hormones (0.12 ml 0.2% estrogen bensoate and in 36—48 hours 0.06 ml 1% progesterone) to induce estrous.

The results were treated statistically according to Student *t* test (Lacin, 1980).

3. RESULTS

3.1. Olfactory Discrimination of Urine House and Mound-building Mice

The results of the experiments are presented in Tables 1 and 2. House and mound-building mice differentiated well between conspecifics, other

Table 1

Pairwise comparisons of times spent by mice sniffing at urine of conspecifics and individuals of other species.

Experimental mice [1]	Origin of urine [1]	Time of sniffing $\bar{x}\pm SD$ (sec) [2]	N times "preferred" [3]	N replicates [4]	Significance (Wilcoxon--two sample test)
Mbm 5 ♂♂, 9 ♀♀	♀ Mbm	7.8∓1.4	12	17	$p<0.01$
	♀ Cm	5.9∓1.4	2		
Hm 5 ♂♂, 9 ♀♀	♀ Mbm	5.0∓0.8	8	29	NS
	♀ Cm	5.4∓0.7	8		
Mbm 8 ♂♂	♀ Mbm	10.3∓2.0	17	25	$p<0.01$
	♂ Hm (s)	4.0∓0.6	4		
Mbm 8 ♂♂	♀ Mbm	16.4∓3.1	15	17	$p<0.01$
	♀ Hm (s)	7.5∓1.3	1		
Mbm 6 ♂♂, 8 ♀♀	♂ Hm (a)	5.5∓0.7	5	30	NS
	♂ Hm (s)	5.3∓0.7	6		
Hm 11 ♂♂	♂ Mbm	5.3∓0.6	10	46	$p<0.05$
	♂ Hm (s)	6.9∓1.0	25		
Hm 11 ♂♂	♀ Mbm	4.1∓0.5	7	33	$p<0.05$
	♀ Hm (s)	6.0∓0.9	18		
Hm 11 ♂♂	♀ Hm (a)	6.5∓0.8	9	20	NS
	♀ Hm (s)	6.6∓0.7	12		

[1] Mbm — mound-building mouse, Hm — house mouse, Cm — *Cricetulus migratorius*, s — sympatric with *M. hortulanus*, a — allopatric. [2] Average time of sniffing at each urine type. [3] Number of times each urine type was sniffed for a longer period than the other type. [4] in the same experiment.

species and closely related forms by odour. They investigated the odour of conspecific urine significantly longer than that from a different species in any pair combinations with only one exception. No significant difference was noted in the response of male *M. hortulanus* to olfactory signals of conspecific and house mice females in estrous. There were no significant sex differences in the time of sniffing of the same odour sources and in some case the responses of males and females were similar. In mound-building mouse urine collected from conspecifics elicited significantly longer investigation as compared with that of sympatric house mice. Mound-building mice exhibited no discrimination between the urine of sympatric and that of allopatric populations. In the house mice from Kirovograd and Kishinev the urine from conspecifics was "preferred" to that of mound-building mice. The differences in the responses of the house mice to the urine from the Kirvograd and Moscow trapped mice were not statistically significant. The responses of the Moscow trapped mice to all the odours under study were identical to those obtained from the Kirovograd mice. (These data are not presented in Table 1).

Table 2

Pairwise comparisons of time spent by mice sniffing at urine of conspecific and heterospecific males and females. e — female in estrus. Symbols as in Table 1.

Experimental mice [1]	Oringin of urine [1]	Time of sniffing $\bar{x}\pm SD$ (sec) [2]	N times "preferred" [3]	N replicates [4]	Significance (Wilcoxon--two sample test)
Hm 10 ♂♂	♂ Hm	6.2∓1.3	5	28	$p<0.01$
	♀ Hm (e)	9.7∓1.1	18		
Hm 10 ♂♂	♂ Mbm	4.9∓0.8	2	26	$p<0.05$
	♀ Mbm (e)	6.3∓1.1	14		
Mbm 10 ♂♂	♂ Mbm	5.3∓1.0	4	23	$p<0.01$
	♀ Mbm (e)	9.1∓1.5	15		
Mbm 10 ♂♂	♀ Hm	6.0∓1.0	2	25	$p<0.05$
	♂ Hm (e)	9.8∓1.9	12		
Hm 12 ♂♂	Mbm (e)	5.2∓1.1	2	14	$p<0.01$
	♀ Hm (e)	11.7∓2.2	10		
Mbm 12 ♂♂	♀ Mbm (e)	4.9∓1.0	10	24	NS
	♀ Hm (e)	7.9∓2.5	10		

Males of house mice and mound-building mice were capable of distinguishing a female in estrous from a male according to odour regardless of which form served as the urine donors. Males of house mice investigated the odour of conspecific females longer than those of another species when both female urine donors were in estrous.

There were differences in behavioral responses of *M. hortulanus* to

the odour of urine of con- and heterospecifics. They often removed the Petri dish tops and carried them to their nests. Occasionally mound-building mice licked and gnawed the urine containing cellophane squares. In mound-building mice the urine from conspecifics elicited these behavioral patterns more significantly than that of house mice (in response to conspecific urine 25; urine of other species 6; $p<0.05$).

3.2. Species-specific Sexual Activation of the Hypophyseal-testicle System

Males confronted to an estrous conspecific female had a significant increase in the testosterone level in the blood plasma, as compared with control males (Table 3). Females of a closely related species evoked no activation of the hypophyseal-testicle system, while the presence of a northern red-backed vole decreased the testosterone level, which was presumably an indication of stress. Hence, sexual activity of males induced by the presence of female is a species-specific response.

Table 3

Blood plasma testosterone level (μg/ml) in house mice (Hm) and mound-building mice (Mbm) in controls (C) and in those under sexual activation.

No.	Experimental ♂♂	Nature of effect	Avg. testosterone level	N ♂♂	t	Significance
1	♂ Hm	♀ Hm	2.5∓0.39	13	3.18	1 *vs* 2 $p<0.01$
2	♂ Hm	♀ Mbm	1.2∓0.12	12	1.87	1 *vs* 3 *n5*
3	♂ Hm	C	1.6∓0.32	13	4.39	1 *vs* 4 $p<0.001$
4	♂ Hm	♀ Rv	0.7∓0.17	5	2.59	2 *vs* 4 $p<0.05$
5	♂ Mbm	♀ Mbm	2.5∓0.30	9	2.57	3 *vs* 4 $p<0.02$
6	♂ Mbm	♀ Hm	1.5∓0.21	9	2.72	5 *vs* 6 $p<0.02$
7	♂ Mbm	C	1.6∓0.20	8	2.44	5 *vs* 7 $p<0.05$

4. DISCUSSION

Olfactory cues have been shown to act as reproductive isolating mechanisms in a number of rodents, *e.g. Clethrionomys, Peromyscus* and others (Godfrey, 1958; Moore, 1965; Kotenkova, 1989). Laboratory mice discriminate between the odours of urine of conspecifics and *Rattus norvegicus* (Sokolov *et al.*, 1979). The present experiments, in which auditory, visual and tactile cues were excluded, indicate that house and mound-building mice can distinguish conspecifics by olfactory cues only. Finally, our tests suggested that the odours of *M. m. musculus* and *M. hortulanus* differ strongly. It is possible that, on the basis of odour these species "choose" their mate's species.

It has been suggested that the ethological isolation between close species is significantly more pronounced in the sympatric zone than in allopatric regions of the range. Data confirming this hypothesis have been obtained for a number of rodents (McCarty, 1964; Smith, 1965, *etc.*). In certain species of *Peromyscus*, a pronounced difference in the reaction to olfactory signals of representatives of the same and a closely related species in the sympatric region has been noted. However, no such difference was observed in allopatrically distributed populations. Thus, one of the mechanisms of isolation may be a reaction to olfactory signals (Doty, 1972, 1973). In our experiments no such pattern was detected: synanthropic house mice from the sympatric zone with m. b. mice and those living allopatrically reacted in the same way to all the paired combinations of odour presented. But house mice can distinguish odours of individuals from different demes (Cox, 1980).

According to our data information exchange between house mice and m. b. mice is possible, at least in the sphere of sexual relationships. It was found that house mice and mound-building mice are capable of distinguishing a female in estrous from a male according to odour regardless of which form served as the urine donors. And yet the animals investigated the odour of conspecific females longer than heterospecific females when both female urine donors were in estrous. Only in males of the m. b. mice was such a reaction not detected.

There are data in the literature indicating the possibility of a partial information exchange between representatives of closely related species, for example between two species of guinea pigs (Beauchamp *et al.*, 1979) and rats (Sokolov *et al.*, 1983).

Earlier, on the basis of experiments on reactions to olfactory signals, it was shown that in laboratory mice selectivity in the selection of the odour of sexual partners is characteristic only of females (Mainardi *et al.*, 1965). In our experiments a pronounced difference was detected in the experiments on odour of conspecific and heterospecific males and females. Possibly, in males of laboratory mice the selectivity in the selection of sexual partners could be lost as a result of "domestication".

Actually, the main criterion according to which we judged the reaction of animals to olfactory signals was the difference in the time of their investigation. In this work we shall not discuss the resolving power of this procedure in detail. Let us note only that our data, obtained on laboratory mice, as well as the results of experiments with golden hamsters (*Mesocricetus auratus*), indicate its limited applicability and the difficulty of interpreting the data obtained (Johnston, 1981; Koten-

kova, 1989). In view of this, our hypothesis needs additional experimental verification.

There is evidence available in the literature that in contrast to closely related species, conspecifics elicit in rodent certain physiological responses, which appear to be determined by primer pheromones (Bronson, 1974). The species-specificity of physiological responses may serve as an additional isolatory barrier (Perrigo & Bronson, 1983).

Thus, responses to olfactory signals may serve as mechanisms of precopulational isolation between house and mound-building mice both at the behavioural (search and identification of mates) and physiological level (direct contact with a potential mate).

Another mechanism of isolation between house and mound-building mice is partial biotopic and seasonal isolation (during the cold season). Probably, during the symbiotopy of these species, the mechanism of ethological isolation acquires primary importance. It should be considered that the main task facing the animals is to find a sexual partner of their form, rather than to avoid encounters with an animal of the opposite form. Thus, selection "should be directed not so much toward interspecies isolation as toward intraspecies integration" (Nikol'skii, 1983). Such integration of individuals of the same species can occur as a result of their reaction to the species-specific odour, and by no means only in the reproductive period.

Acknowledgements: We are grateful to Academician V. Sokolov for consultations A. Mikhailenko of the Moldavian Plague Control Station and V. I. Soloviev and and assistance in performing the present study and also to the zoologist I. T. Rusev of the Odessa Plague Control Station for assistance in capturing mice for the experiments.

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Received 10 September 1988, Accepted 31 March 1989.

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PRZEDKOPULACYJNE MECHANIZMY IZOLACYJNE MIĘDZY *MUS MUSCULUS MUSCULUS* I *MUS HORTULANUS*.

Streszczenie

Badano rozróżnianie zapachowe u dwóch sympatrycznych gatunków myszy: *Mus m. musculus* i *Mus hortulanus*. Stwierdzono, że osobniki obydwu gatunków bardzo dobrze rozróżniają za pomocą węchu osobniki swojego własnego gatunku od osobników drugiego gatunku (Tabela 1). Samce obydwu gatunków rozróżniają przy pomocy zapachu moczu samce i samice swojego gatunku, a także gatunku blisko spokrewnionego (Tabela 2). Samce przetrzymywane w obecności samic swojego gatunku będących w rui wykazywały znaczny wzrost poziomu testosteronu w osoczu krwi, podczas gdy obecność samic drugiego gatunku takiej reakcji nie powodowała. Tak więc reakcje na bodźce zapachowe mogą działać jako mechanizmy izolacji przedkopulacyjnej zarówno na poziomie behawioralnym (poszukiwanie i rozpoznawanie partnerów) jak i fizjologicznym (bezpośredni kontakt z potencjalnym partnerem).