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Experimental Hybridization and Breeding Intensity of House (*Mus musculus wagneri*) and Mound-Building (*Mus spicilegus*) Mice: Effect of Early Experiences and the Maternal Environment

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Abstract—Cross-fostering of pups was used as a method for estimating the effect of early experiences and the maternal environment on the breeding success and fertility in con- and heterospecific pairs in two mouse species: house (*M. m. wagneri*) and mound-building (*M. spicilegus*). During experimental hybridization of these species, the breeding success depended both on the species identity of sexual partners themselves (con- or heterospecific) and on the species identity of the fostering female (con- or heterospecific fostering female). It was found that the intensity of reproduction (the ratio of breeding pairs to nonbreeding ones) in mixed pairs of house and mound-building mice is lower than in control ones consisting of members of the same species. It was demonstrated that in different variants of crossings (both in con- and heterospecific), the proportion of pups that did not survive to 40 days of age is significantly higher in pairs, in which at least one of the partners was fostered by a female of another species. This can be caused by a discrepancy between parental behavior and species-specific parental behavior, which disrupts the interaction between educators and pups. This can cause an increase in the mortality of pups. This study demonstrated the importance of early postnatal social experiences (postnatal social ontogenesis) and the maternal environment in the formation of species-specific patterns of behavior in adult individuals of closely related species of house mice.

Keywords: cross-fostering, evolution, breeding, mortality, *Mus musculus* s. l.

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INTRODUCTION

According to the biological concept of species, the formation of reproductive isolation between closely related forms underlies the speciation. Several studies, including a whole series of our works, are devoted to the functioning and formation of the mechanisms of reproductive isolation in house mice of the *Mus musculus* s. l. group of species in the process of evolution (Sokolov et al., 1990; Kotenkova and Naidenko, 1999; Heth et al., 2001; Smadja and Ganem, 2008; Kotenkova, 2014). We substantiated the validity of our proposed hypothesis explaining the functioning of the mechanisms of precopulatory isolation in sympatric (that is, quite reliably isolated in nature) closely related species of house mice (Ambaryan et al., 2010; Kotenkova, 2014). The next step in our development of this problem was to study the formation of the mechanisms of isolation in the process of ontogenesis and, first of all, the role of learning (imprinting, classical conditioning), which is widespread in different animal species and can be important in the course of evolutionary processes (Verzijden et al., 2012; Witte et al., 2015). Imprinting at an early age of phenotypic traits (such as visual, acoustic, olfactory) of parents and/or brothers and sisters leads to the fact that the animal can distinguish the members of their own species from other closely related species and recognize the gender of conspecific individuals (Owens et al., 1999; Verzijden et al., 2008; Maras and Petrulis, 2008; Kotenkova, 2017). A number of field and laboratory studies confirmed the essential importance of different forms of learning in the evolutionary process, their influence on sexual selection, development of reproductive isolation, and divergence of populations (Laland, 1994; Owens et al., 1999; Aoki et al., 2001; Svensson et al., 2010; Verzijden et al., 2012).

A large number of works are devoted to the study of the effect of early experience, conditions of existence and education at an early age on subsequent development, breeding, behavior in different animal species, including human (see reviews Sloboda et al., 2011; Kotenkova et al., 2017; Gromov, 2020). The question of how epigenetic effects (for example, imprinting and other forms of learning during early postnatal ontogenesis) can influence the choice of sexual partner and adult preferences is of special interest. Mature rodents (including the members of closely related species of house mice) usually prefer conspecific individuals as sexual partners, as well as choose the odor of members of the opposite sex of their own species compared to the odors of heterospecifics (see review, Kotenkova, 2014). In most mammals, parents (first of all nursing females) are the main component of the social environment in early period of postnatal ontogenesis. Therefore, cross-fostering of offspring by lactating females of different species is the main approach to estimate the significance of early experience and maternal environment for subsequent formation of different types of behavior and reactions to the odors of con- and heterospecific individuals (particularly, in rodents). Thus, it was demonstrated in the study of Quadagno and Banks (1970) (which was carried out on individuals of the house mouse (*M. musculus* (L. 1758)) and the northern pygmy mouse (*Baiomys taylori* (Thomas 1887)) that cross-fostering between these two species influences not only behavioral reactions related to reproduction and social preferences, but also exploratory behavior in the open field in cross-fostered individuals. We used the same approach to study the effect of early olfactory experience on the assortativity of responses to olfactory signals and modification of neuronal responses in olfactory bulbs in adult individuals of their own and closely related sympatric species in house and mound-building (*M. spicilegus* (Petenyi 1882)) mice. It was found that early experiences during postnatal ontogenesis associated with a change in the maternal environment lead to modification of behavioral and neuronal responses to con- and heterospecific odors in adult individuals in three closely related taxa of house mice. Males of these taxa fostered by their own mothers demonstrated a pronounced preference for the odor of the members of their own species, including conspecific females in the state of estrus, as compared with the odor of heterospecific females (Sokolov et al., 1984, 1984a; Kotenkova et al., 1989), specific patterns of activation in the sensory epithelium of the vomeronasal organ and neuronal activation in the additional olfactory bulb only in response to the odor of receptive females of their own, but not closely related species, were detected in males of house and mound-building mice (Voznesenskaya et al., 2010). The cross-fostering changed the assortativity of choice of con- and heterospecific odors in house and mound-building mice. *M. spicilegus* fostered by *M. musculus* females preferred the odor of females of the educator species (Kotenkova et al., 2018). *M. m. wagneri* (Eversmann 1848) fostered by *M. spicilegus* and *M. spicilegus*, nursed by *M. m. wagneri*, did not show a preference for the odor of females of their own or the nursing species. The neuronal activation in the additional olfactory bulb in males fostered by heterospecific females was opposite as compared with males fostered by conspecific females (Kotenkova et al., 2019). Thus, the maternal environment, including the odor, has a greater influence on the level of the MRI signal in the additional olfactory bulb in sexually mature males than the genetic relationship between the recipient and the odor donor. Fostering by a female of another species also caused significant changes in neuronal activation in the main olfactory bulb in males. The data provided prove the presence of a significant effect of early experience on the specificity of the reaction to the odors of sexual partners in two mouse species. Previously, the effect of fostering conditions in these species on other forms of behavior has not been studied.

In the laboratory, successful hybridization of house (*Mus musculus musculus*) and mound-building mice with the production of viable and fertile hybrids (males and females) F_1 and F_2 is possible. During the experimental hybridization, the breeding intensity and fertility of females in mixed pairs decrease as compared with the control pairs consisting of members of the same species (Lavrenchenko et al., 1994), which indicates the presence of postcopulatory mechanisms of isolation.

The aim of this study was to identify the presence or absence of the influence of cross-fostering on subsequent breeding success in two mouse species: house (*M. m. wagneri*) and mound-building (*M. spicilegus*). We tested the working hypothesis, according to which fostering by heterospecific females will have a more significant effect on the subsequent breeding success of cross-fostered individuals than fostering by adoptive females of their own species.

MATERIALS AND METHODS

During the years 2016–2019, to estimate the results of the breeding intensity, pairs (male and female) consisting of the members of the same or different species of house mice fostered either by their own mother or by another female of their species or by a heterospecific adoptive mother were formed (Table 1). House mice of two taxa (*M. m. wagneri* and *M. spicilegus*) were used. Animals of generations F_3–F_4 were obtained from animals caught in nature (*M. m. wagneri* were caught in Astrakhan oblast (46°20′ N, 48°0′ E); *M. spicilegus*, in Rostov oblast (47°23′ N, 39.70′ E)). Cross-fostering of pups to lactating females of another taxon or adoptive mothers of their own species (control) was carried out at the age 5–6 days. The choice of this time period is substantiated by data of previous research, in which it was demonstrated that the sensitive period for imprinting of the odors in mice begins two weeks after the birth and corresponds to a sharp increase in the number of dendrites in the olfactory system from the 11th day to the 20th day of ontogenesis (Hinds, J.W. and Hinds, P.L., 1976; Panhuber et al., 1988; Wang et al., 1993; Voznessenskaya et al., 1995). Males were separated from the females 2–3 days before the birth of pups. At the same time, the litters were swapped entirely, regardless of the number of pups and the sex composition; however, both males and females were in each of the transferred litters. The pups were kept with females up to the age of four weeks in a room in which there were both house and mound-building mice. Then they were divided, forming same-sex groups, in which young animals were kept until maturity. Twelve variants of pair formation of potential sexual partners of two species of house mice were used (Table 1). Pairs of house mice (male and female) were formed out of sexually mature individuals at the age 40 and 90 days for a period of 3–6 months. In the case of the death of one of the partners in a pair, it was replaced by a new one or the experiment was interrupted for this pair. During this time, the number of received litters, born pups, their mortality during the first 40 days after birth were calculated every 2–3 days. In addition, the ratio of the number of pairs, from which the offspring was obtained, to the total number of pairs formed was determined. Animals were kept under standard conditions with a natural light mode throughout the year in plastic cuvettes 265 × 180 × 420 mm in size with a cover out of metal mesh. The grain mixture consisting of oat and sunflower seeds, specialized mixed fodder for rodents of domestic production, as well as carrot served as a feed. Water was given ad libitum. Animal trapping and maintenance rules and conditions, as well as the experimental procedures, did not violate the rules for conducting scientific research using experimental animals approved by the order of the Presidium of the Academy of Sciences of the USSR of April 2, 1980, no. 12000–496 and the order of the Ministry of Higher Education of the USSR of September 13, 1984, no. 22. When analyzing the data, the following proportions were determined: (1) number of pairs that gave offspring in relation to total number of formed pairs; (2) number of pups that did not survive to 40 days in relation to the total number of born pups. The indices obtained were used when carrying out statistical intergroup comparisons. In statistical analysis, processing, χ^2 test with pairwise comparisons of proportions using the Marasquilo procedure was used. The validity of the significance of differences in proportions by the χ^2 test was estimated using the Monte Carlo simulation. The number of statistical trials of the test was 5000. The level of significance in pairwise comparisons $\alpha = 0.05$. When comparing the proportions of the number of pairs that gave birth to offspring in relation to those that did not breed, those variants of crossings in which the number of formed pairs was at least four were selected in the analysis. When comparing the proportions of the number of pups that did not survive to 40 days of age, those variants of crossings in which the total number of pups in three breeding pairs was at least twenty were selected in the analysis. The statistical analysis was carried out in the XLSTAT 2019 2.2 program.

RESULTS

In a significant number of cases, the proportion of the number of breeding pairs was significantly higher in the variants of crossings of conspecific partners (χ^2 test: test statistics (χ^2)—51.982, $P < 0.0001$, Tables 1 and 2) as compared with heterospecific ones. This is true for the comparisons of the following variants of crossings (conspecific variant/heterospecific): *M. m. wagneri* male fostered by another female of its own species × *M. m. wagneri* female (no. 2) (5, 9, 11); *M. spicilegus* male × *M. spicilegus* female fostered by *M. m. wagneri* (no. 10) (5, 9, 11); *M. spicilegus* male fostered by *M. m. wagneri* female × *M. spicilegus* female (no. 8) (5, 9, 11), *M. m. wagneri* male × *M. m. wagneri* female fostered by *M. spicilegus* female (no. 6) (5, 9, 11), *M. m. wagneri* male × *M. m. wagneri* female (no. 1) (9, 11), and *M. m. wagneri* male fostered by *M. spicilegus* female × *M. m. wagneri* female (no. 4) (11). In all of the above heterospecific variants of crossings, one of the sexual partners was fostered by a female of another species. In one of conspecific variants of crossings, the female that fostered each of the partners was their native mother in the compared variants (no. 1). In other variants of conspecific crossing, another conspecific (no. 2) or heterospecific female (nos. 4, 6, 8, 10) was a mother that fostered one of the partners. There were no significant differences in the proportion of the number of pairs that gave offspring when comparing the variants of *M. m. wagneri* crossing, in which the pups were fostered either by their mother (no. 1) or by the adoptive mother of their species (no. 2), as well as in heterospecific female (nos. 4, 6).

In three variants of crossings, in two of which both partners were fostered by their own mother (1, 7), while in the third variant one partner was fostered by its own, while another by an alien, but conspecific female (no. 2), the mortality of pups was lower than in the variants of crossings in which one of the partners was fostered by a heterospecific female (χ^2 test: test statistics (χ^2) 98.719, $P < 0.0001$, Tables 1 and 3). In particular, the mortality was lower in variant 1 (conspecific variant, in which both partners are fostered by their own mother) than in variant nos. 8 and 10, while the mortality was lower in variant 7 (heterospecific variant, in which both partners were also fostered by their own mother) than in variant 8. In the combination in which one of the partners (female) was fostered by itsown mother, while the male was fostered by an alien, but conspecific mother (no. 2) is greater the mortality was significantly lower than in the variant no. 8. Thus, the conspecificity of the female that fostered the partners (moreover, both in conspecific (nos. 1, 2) and heterospecific variant of crossings (no. 7)), could con-

Table 1. Variants of crossing of sexual partners of different forms of house mice and reproduction rates in different variants of crossings

No.	Variant of crossing	Number of pairs	Number of breeding pairs	Proportion of the number of breeding pairs, %	Number of pups born	Number of dead pups	Proportion of the number of pups not surviving to 40 days of age, %
1	♂ *M. m. wagneri* × ♀ *M. m. wagneri*	25	23	92	160	5	3.12
2	♂ *M. m. wagneri*, fostered by alien female of its own species × ♀ *M. m. wagneri*	8	8	100	186	23	12.37
3	♂ *M. m. wagneri*, fostered by alien female of its own species × ♀ *M. spicilegus*	7	2	28.57	10	0	0
4	♂ *M. m. wagneri*, fostered by ♀ *M. spicilegus* × ♀ *M. m. wagneri*	10	8	80	124	19	15.32
5	♂ *M. m. wagneri*, fostered by ♀ *M. spicilegus* × ♀ *M. spicilegus*	8	2	25	10	0	0
6	♂ *M. m. wagneri* × ♀ *M. m. wagneri*, fostered by ♀ *M. spicilegus*	5	5	100	81	15	18.52
7	♂ *M. spicilegus* × ♀ *M. m. wagneri*	9	3	33.33	73	12	16.44
8	♂ *M. spicilegus*, fostered by ♀ *M. m. wagneri* × ♀ *M. spicilegus*	5	5	100	82	43	52.44
9	♂ *M. spicilegus*, fostered by ♀ *M. m. wagneri* × ♀ *M. m. wagneri*	9	2	22.22	4	0	0
10	♂ *M. spicilegus* × ♀ *M. spicilegus*, fostered by *M. m. wagneri*	5	5	100	206	50	24.27
11	♂ *M. spicilegus* × ♀ *M. m. wagneri*, fostered by *M. spicilegus*	5	0	0	0	0	0
12	♂ *M. spicilegus*, fostered by alien female of its own species × ♀ *M. m. wagneri*	4	2	50	17	0	0

Table 2. Pairwise comparisons of proportions of the number of bred pairs with different combinations of crossings (Marascuilo procedure)

Comparisons of variants of crossings	Value of criterion statistic	Critical value of statistics (*r*)	Significance of differences
1–12	0.420	1.135	No
2–1	0.080	0.241	No
2–3	0.714	0.757	No
2–4	0.200	0.561	No
2–5	0.750	0.679	**Yes**
2–6	0.000	0.000	No
2–7	0.667	0.697	No
2–8	0.000	0.000	No
2–9	0.778	0.615	**Yes**
2–10	0.000	0.000	No
2–11	1.000	0.000	**Yes**
2–12	0.500	1.109	No
3–1	0.634	0.795	No
3–4	0.514	0.943	No
3–5	0.036	1.017	No
3–6	0.714	0.757	No
3–7	0.048	1.029	No
3–8	0.714	0.757	No
3–9	0.063	0.975	No
3–10	0.714	0.757	No
3–11	0.286	0.757	No
3–12	0.214	1.343	No
4–1	0.120	0.611	No
4–6	0.200	0.561	No
4–11	0.800	0.561	**Yes**
4–12	0.300	1.243	No
5–1	0.670	0.720	No
5–4	0.550	0.881	No
5–6	0.750	0.679	**Yes**
5–7	0.083	0.973	No
5–8	0.750	0.679	**Yes**
5–9	0.028	0.916	No
5–10	0.750	0.679	**Yes**
5–11	0.250	0.679	No
5–12	0.250	1.300	No
6–1	0.080	0.241	No
6–11	1.000	0.000	**Yes**
6–12	0.500	1.109	No
7–1	0.587	0.737	No
7–4	0.467	0.895	No
7–6	0.667	0.697	No
7–8	0.667	0.697	No
7–9	0.111	0.929	No

Table 2. (Contd.)

Comparisons of variants of crossings	Value of criterion statistic	Critical value of statistics (*r*)	Significance of differences
7–10	0.667	0.697	No
7–11	0.333	0.697	No
7–12	0.167	1.310	No
8–1	0.080	0.241	No
8–4	0.200	0.561	No
8–6	0.000	0.000	No
8–11	1.000	0.000	**Yes**
8–12	0.500	1.109	No
9–1	0.698	0.660	**Yes**
9–4	0.578	0.832	No
9–6	0.778	0.615	**Yes**
9–8	0.778	0.615	**Yes**
9–10	0.778	0.615	**Yes**
9–11	0.222	0.615	No
9–12	0.278	1.268	No
10–1	0.080	0.241	No
10–4	0.200	0.561	No
10–6	0.000	0.000	No
10–8	0.000	0.000	No
10–11	1.000	0.000	**Yes**
10–12	0.500	1.109	No
11–1	0.920	0.241	**Yes**
11–12	0.500	1.109	No

* Here and below, the numbering of combinations of bringing together is given according to Table 1.

tribute to a decrease in the mortality of pups in the first 40 days after the birth. The level of mortality of pups was maximal in the variant of crossings of conspecific partners *M. spicilegus* in which males fostered by *M. m. wagneri* female. The comparison with other variants of crossings demonstrated that the mortality in this variant was significantly higher than in conspecific variants (4, 6, 10). In all these variants of crossings, one of the partners was fostered by a heterospecific female.

DISCUSSION

We demonstrated that two factors influence the breeding success during the experimental hybridization of two species of house mice: the species affiliation of sexual partners (con- or heterospecifics) and fostering conditions for males and females, that is, they were fostered by a female of their own or a closely related species. We consider the possible reasons leading to such results.

As was already noted in the Introduction, during the experimental forced crossing, the breeding intensity and fertility of females in mixed pairs of house and mound-building mice are lower than in the control ones consisting of the members of one species. In previous studies, the following results were obtained in the variants of crossings of *M. musculus* and *M. spicilegus*: when crossing *spicilegus* male × *musculus* female, seven out of 13 formed pairs gave offspring (12 litters, 45 pups); *musculus* female × *spicilegus* male, three out of nine pairs bred (six litters, 20 pups) (Lavrenchenko et al., 1994); that is, these data are quite comparable with our results according to the proportion of the number of breeding heterospecific pairs. In meiosis in four hybrid males of direct and reciprocal variants of crossing, metaphase plates contained a normal number of bivalents ($n = 20$) (Lavrenchenko et al., 1994), which can indicate a normal course of meiosis in hybrids. In the experiments, we tried to reveal not only the effect of postcopulatory isolating mechanisms on the breeding intensity, but also to estimate the effect of cross-fostering of pups on the reproductive success. However, there were no significant differences in the proportion of the number of pairs that gave offspring

Table 3. Pairwise comparisons of proportions of the number of pups not surviving to an age of 40 days with different combinations of crossings (Marascuilo procedure)

Combination of bringing together	Value of criterion statistic	Critical value of statistics (r)	Significance of differences
1–6	0.154	0.161	No
2–1	0.092	0.099	No
2–4	0.030	0.143	No
2–6	0.062	0.175	No
2–7	0.041	0.176	No
2–8	0.401	0.214	**Yes**
2–10	0.119	0.136	No
4–1	0.122	0.125	No
4–6	0.032	0.191	No
7–1	0.133	0.161	No
7–4	0.011	0.192	No
7–6	0.021	0.217	No
7–8	0.360	0.249	**Yes**
7–10	0.078	0.187	No
8–1	0.493	0.202	**Yes**
8–4	0.371	0.227	**Yes**
8–6	0.339	0.249	**Yes**
10–1	0.211	0.117	**Yes**
10–4	0.089	0.156	No
10–6	0.058	0.186	No
10–8	0.282	0.223	Yes

when comparing the variants of crossings of *M. m. wagneri* in which the sexual partners used in the experiments on experimental hybridization were fostered by a female of another species (*M. spicilegus*) as compared with those variants in which they were fostered by conspecific females. In our experiments, we found no effect of early experience on this index in *M. m. wagneri*. The factor of conspecificity of sexual partners was of paramount importance, despite the fact that, as already noted in the Introduction, fostering by females of a closely related species in house and mound-building mice can change the behavioral and neuronal responses to con- and heterospecific odors to the opposite (Kotenkova et al., 2018, 2019).

The role of species-specific peculiarities of the sexual behavior in reproductive precopulatory isolation in rodents is not the same. It was demonstrated that potential sexual partners of closely related species can both mate successfully and exhibit individual elements of sexual behavior in relation to each other, sometimes there is a reduced activity of males during mating, while in some cases copulation is impossible due to the difference in the stereotype of behavior (Zorenko, 2013; Kotenkova, 2014). According to the results of our previous studies on the stereotype of sexual behavior, house and mound-building mice differ significantly, which can prevent mating of the representatives of these two species. In other words, differences in sexual behavior in these species can be one of the mechanisms of one of reproductive isolation (Ambaryan et al., 2019). But, as is known, even reliably isolated species in nature are crossed during the forced experimental hybridization, which is true not only for house and mound-building mice (Meier et al., 1981, 1996; Malygin, 1983; Koval'skaya et al., 2014).

However, estimation of the number of pups reaching 40 days of age in different variants of crossings demonstrated a significant effect of the conditions of fostering of parents (by con- and heterospecific females) on the survival of their offspring. It can be assumed that a lower survival rate in pairs consisting both of con- and heterospecific partners is caused by a violation of parental behavior in the case of fostering of at least one member of the pair by a female of another species. Previously, it was demonstrated that, in two closely related species *Peromyscus leucopus* (Rafinesque 1818) and *P. maniculatus* (Wagner 1845), the survival rate of pups in conspecific pairs, if the male was fostered by parents of another species, was lower than in pairs, in which the female received a heterospecific fostering (Hawkins and Cranford, 1992). We obtained similar results: the maximal proportion of the death of pups (52%) was observed in the crossing variant no. 8 (*M. spicilegus* male fostered by *M. m. wagneri* female × *M. spicilegus* female). This proportion was much lower (15%) in variant no. 4 (*M. m. wagneri* male fostered by *M. spicilegus* female × *M. m. wagneri* female), although no significant differences were found during the comparison. The proportion of mortality of pups in pairs that included females fostered by heterospecifics (nos. 6 and 10) was also relatively high. Further studies are needed to identify the reasons that lead to violations of parental behavior. It is possible that such violation was associated with insufficient manifestation of grooming of parents in relation to offspring when fostered with heterospecifics. A number of studies show the special importance of this form of behavior of parents in relation to the offspring, including for the manifestation of parental behavior by adult individuals (Gromov, 2013, 2020). However, it is necessary to note that females of meadow voles (*Microtus pennsylvanicus* (Ord 1815)) fostered in family pairs of prairie voles (*M. ochrogaster* (Wagner 1842)) demonstrate a higher level of caring for offspring and are more likely to show grooming in relation to the pups than females fostered by an alien female of its own species (McGuire, 1988). The same ratios are also typical for cross-fostered (by a female of prairie voles) males of this species that more often make contact with their pups and stay with them longer in the nest than males fostered by another female of its species. In this case, a pattern of parental behavior, which changed under the influence of early experiences in *M. pennsylvanicus* individuals during the period of fostering in heterospecific familial pairs, probably contributed to an increase in the care for their own offspring in cross-fostered adult individuals of this species. The same mechanism of the effect of "social ontogeny" (Campbell and Hauber, 2009) (or, in other words, associated social interactions) was also noted in studies on birds (zebra finches (*Taeniopygia guttata* (Vieillot 1817)) and Japanese finches (*Lonchura striata* (L. 1766)). According to the results of studies (ten Cate, 1984; ten Cate et al., 1984), the number of behavioral interactions (which varied experimentally in the study, and only in relation to the conspecific parent) between the chicks of male zebra finches and a conspecific parent in a mixed heterosexual pair, consisting of male or female zebra finches and Japanese finches, determined the sexual preferences in males fostered in such pairs in relation to con- and heterospecific females. It was found that a decrease or elimination of behavioral contacts with a conspecific parent contributed to a shift in the preferences of adult males from conspecific female to heterospecific female. Thus, species-specific and sexual preferences of adult individuals are formed not only on the basis of phenotypic traits (visual characteristics, acoustic or olfactory signals), but also on the basis of a set of behavioral interactions between parents and pups during social ontogenesis or fostering of pups. It can be assumed that the more complex the social organization and social interactions in the breeding groups of a species, the more significant the role of behavioral interactions and social ontogenesis in the formation of species-specific preferences of adult individuals.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. The conditions for the capture and keeping animals, as well as experimental procedures, did not violate the rules for conducting scientific research using experimental animals approved by the order of the Presidium of the Academy of Sciences of the USSR of April 2, 1980, no. 12000–496 and the order of the Ministry of Higher Education of the USSR of September 13, 1984, no. 22.

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