

Die folgende Beobachtung verringert wieder den Abstand zwischen *A. sylvaticus* aus Europa und *A. sylvaticus* aus Asien. Der Unterschied zwischen beiden im IPO-Allel ist hier nicht absolut. In einer *A. sylvaticus*-Population aus den Nordalpen wurde inzwischen einmal auch das für *A. flavicollis* typische Allel entdeckt (GEMMEKE unpubl.). Damit ist gezeigt, daß die ursprüngliche Form auch bei *A. sylvaticus* in Europa noch nicht völlig eliminiert ist.

Zusammenfassung

Eine Untersuchung der Karyogramme der *Apodemus*-Arten aus Nepal (Abb. 1 und 2) stützt die Annahme, daß *Apodemus sylvaticus* von dort in die Untergattung *Sylvaemus*, *A. gurkha* aber in die Untergattung *Alsomys* gehört.

Ein proteinelektrophoretischer Vergleich der Waldmäuse *A. sylvaticus* aus Nepal ergab deutliche Unterschiede zu *A. sylvaticus* aus Europa, aber Übereinstimmung mit *A. sylvaticus* aus dem Iran (Tab. 1 und 2). Ob die Waldmäuse aus Nepal wirklich zu *A. sylvaticus* gehören, muß danach vorerst offen bleiben.

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Relative brain size in Muridae with special reference to *Colomys goslingi*

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Abstract

Calculated the brain size in 18 species of Muridae either directly from brain weights (12 species) or indirectly from cranial capacity measurements (12 species incl. *Colomys goslingi*). In six species data from both sets are presented. In *Colomys* (a predator in limnetic ecosystems) relative brain size (encephalization) and foramen magnum size are larger than in terrestrial Muridae of equal body weight. The differences are similar to those found when comparing water adapted with terrestrial Insectivora. Comparative brain studies are in preparation.

Introduction

Colomys goslingi, the african velvet or forest brook rat, is evidently a predator in limnetic ecosystems, as DIETERLEN and STATZNER (1981) have shown recently. Species with similar habits are found in the Insectivora families Tenrecidae (*Limnogale mergulus*; Potamogalinae: *Micropotamogale lamottei*, *M. ruwenzorii* and *Potamogale velox*), Soricidae (e.g. *Neomys fodiens*) and Talpidae (*Desmana moschata*, *Galemys pyrenaicus*). All of these species have large brains when compared with their purely or mainly terrestrial relatives. Within their brains there is a reduction in size of the structures of the olfactory system and an enlargement of the medulla oblongata, both of which are especially pronounced in *Potamogale*. As a consequence of the large medulla oblongata the foramen magnum also was found to be relatively large.

The enlargement of the medulla oblongata in *Potamogale* is due to a marked development of the trigeminal system, especially of the nucleus of the spinal trigeminal tract. The trigeminal nerves, which also are extremely thick, innervate the strongly developed vibrissae of the muzzle. The vibrissae are considered to be vibration receptors adapted for detecting prey under water. In *Colomys* they seem to be "the only sense organ used in detecting the prey" in waters (DIETERLEN and STATZNER 1981). In predators in limnetic ecosystems the trigeminal system is thought to replace the olfactory system and to become the main sensory system used in the search for food in water (STEPHAN and SPATZ 1962; STEPHAN 1967; BAUCHOT and STEPHAN 1967, 1968, 1970).

Since we do not have well preserved brains of *Colomys* we cannot make exact measurements for comparative quantitative studies. However, an indication of the size of the brain can be obtained from cranial capacity measurements, and the size of the medulla oblongata can be inferred from the cross sectional area of the foramen magnum. By comparing these data with those of terrestrial Muridae we are able to evaluate, whether *Colomys* shows differences from other Muridae similar to those shown by the water adapted Insectivora from other Insectivora.

Material and methods

The cranial capacities (CrC) and foramen magnum areas (FMA) were measured in 10 skulls of *Colomys goslingi* and compared with corresponding measurements in other murid species with similar body weights (*Hybomys univittatus*, *Lemniscomys striatus*, *Praomys natalensis*). The average data and the standard error of the mean (SEM) are given in Table 1. In order to make well founded allometric comparisons similar measurements were made on skulls of especially small-bodied (*Micromys minutus*, *Leggada minutoides*) and large-bodied murids (*Thamnomys venustus*, *Oenomys hypoxanthus*, *Dasymys incomtus*, *Pelomys fallax*, *Rattus norvegicus*, *Malacomys longipes*), and brain weight and body weight data were collected from 12 species (Table 2).

For CrC and FMA measurements skulls, which came from specimens close to the average body weight of the given species, were selected. Average body weights were calculated from the large collections of the Staatliches Museum für Naturkunde, Stuttgart. The CrC measurements were made by introducing fine dust shot into the cranial cavity through the foramen magnum, weighing the skull before and after introducing the dust shot, and by dividing the weight difference by 5.6121, which was found to be the weight in grams per cubic centimeter dust shot. The FMA measurements were made from enlarged photos of the foramen magnum by planimetry and/or by cutting out and weighing the photographic paper (STEPHAN et al. 1981).

Table 1
Data on body weights, cranial capacities, and foramen magnum areas in *Colomys goslingi* and three terrestrial species of African Muridae of similar body weight

	Sex	n	Body weight (BoW) g	SEM g	%	Cranial capacity (CrC) mm ³	SEM mm ³	%	Foramen magnum area (FM/A) mm ²	SEM mm ²	%
<i>Colomys goslingi</i>	mm	5	58.8	2.4	4.1	1299	40.6	3.1	23.1	1.1	4.9
	ff	5	57.6	9.9	17.1	1349	67.1	5.0	22.9	1.7	7.3
	mm+ff	10	58.2	6.8	11.7	1324	58.5	4.4	23.0	1.3	5.8
<i>Lemniscomys striatus</i>	mm	5	58.0	3.2	5.5	1012	52.4	5.2	16.2	1.0	6.2
	ff	5	49.0	5.2	10.6	932	46.6	5.0	16.2	0.7	4.4
	mm+ff	10	53.5 (-8.1%)	6.2	11.7	972 (-26.6%)	62.9	6.5	16.2 (-29.6%)	0.8	5.1
<i>Hybomys univittatus</i>	mm	5	54.4	5.6	10.2	1092	71.9	6.6	18.6	0.7	3.7
	ff	5	59.2	4.6	7.8	1126	39.9	3.5	18.8	0.9	4.9
	mm+ff	10	56.8 (-2.4%)	5.4	9.6	1109 (-16.2%)	57.7	5.2	18.7 (-18.7%)	0.8	4.1
<i>Praomys natalensis</i>	mm	5	71.6	8.8	12.2	900	26.9	3.0	15.6	1.1	6.7
	ff	5	54.4	4.6	8.4	848	71.9	8.5	16.6	1.5	9.2
	mm+ff	10	63.0 (+8.2%)	11.2	17.8	874 (-34.0%)	58.2	6.7	16.1 (-30.0%)	1.3	8.2

Body weights, brain weights and foramen magnum areas, expected values on the regression lines, indices, and percentage deviation of the indices from *Colomys*

When individuals with unknown body weights are included, the average body weights are set in brackets. * brain weights converted from cranial capacities; + values combined from brain weights and converted cranial capacities

Species	n	Body weight (BoW) g (2)	Brain weight (BrW) mg (3)	Expected brain weight (EBrW) mg (4)	Br.W./EB.W. · 100 (EI) (5)	Percentage deviation from <i>Colomys</i> (6)	Foramen magnum area (FMA) mm ² (7)	Expected foramen magnum area (EFMA) mm ² (8)	FMA/EFMA · 100 (FI) (9)	Percentage deviation from <i>Colomys</i> (10)	FMA/CrC mm ² /cm ³ (11)
1 <i>Colomys goslingi</i>	10 ¹	58.2	1372*	1041	131.9	0	23.0	18.1	127.2	0	17.4
2 <i>Micromys minutus</i>	3	5.5	267	251	106.4	-19.3					
	10 ²	6.1	282*	267	105.6	-19.9	8.7	9.0	96.8	-23.9	32.0
	13	5.95	278+	263	105.7	-18.5					
3 <i>Apodemus flavicollis</i>	10	30	750	698	107.5	-18.5					
4 <i>Apodemus sylvaticus</i>	282 ³	19.4	590	536	110.0	-20.3					
5 <i>Thamnomys venustus</i>	1	(82.5)	1350	1284	105.1	-20.3					
	8 ¹	82.5	1284*	1284	100.0	-24.2	20.9	20.1	103.8	-18.4	16.9
	9	(82.5)	1291+	1284	100.5	-23.8					
6 <i>Oenomys hypoxanthus</i>	3	(92)	1150	1371	83.9	-36.4					
	8 ¹	92	1166*	1371	85.0	-35.6	18.9	20.8	90.7	-28.7	16.8
	11	(92)	1162+	1371	84.7	-35.8					
7 <i>Dasymys incommis</i>	8 ¹	102.5	1574*	1464	107.5	-18.5	22.8	21.5	105.8	-16.8	15.0
8 <i>Pelomys fallax</i>	1	121	1460	1618	90.2	-31.6					
	8 ¹	110	1406*	1527	92.1	-30.2	17.9	22.0	81.3	-36.1	13.2
	9	111	1412+	1536	91.9	-30.3					
9 <i>Lemniscomys striatus</i>	2	53	1050	983	106.8	-19.0					
	10 ¹	53.5	1007*	989	101.8	-22.8	16.2	17.6	92.0	-27.7	16.7
	12	53.4	1014+	988	102.6	-22.2					
10 <i>Hybomys univittatus</i>	10 ¹	56.8	1149*	1025	112.1	-15.0	18.7	17.9	104.2	-18.1	16.9
11 <i>Mus musculus</i>	312 ⁴	18	430	513	83.9	-36.4					
12 <i>Leggada sp.?</i>	5	7.7	288	307	93.7	-29.0					
13 <i>Leggada minutoides</i>	8 ¹	10.4	327*	368	88.8	-32.7	10.4	10.6	98.1	-22.9	32.9
14 <i>Rattus norvegicus</i>	354 ⁵	291	2270	2746	82.7	-37.3					
	5 ²	(291)	2248*	2746	81.9	-37.9	28.0	29.8	94.0	-26.1	12.9
	359	(291)	2270+	2746	82.7	-37.3					
15 <i>Praomys natalensis</i>	10 ¹	63.0	906*	1091	83.0	-37.1	16.1	18.5	86.9	-31.7	18.4
16 <i>Malacomys longipes</i>	9 ¹	98	1825*	1425	128.1	-2.9	26.9	21.2	126.6	-0.5	15.3
17 <i>Lophuromys sikapusi</i>	5	63.5	1200	1097	109.4	-17.1					
18 <i>Acomys dimidiatus</i>	28 ⁶	50.5	884	955	92.5	-29.9					

¹ skulls from Staatliches Museum für Naturkunde, Stuttgart. - ² skulls from Senckenberg Museum, Frankfurt. - ³ data of 241 individuals are from KLEMMT (1960). - ⁴ data of 2 individuals are from WEBER (1896), 3 from WELCKER and BRANDT (1903), 6 from HRDLICKA (1905), and 298 from NORD (1963). - ⁵ data of 266 individuals are from DONALDSON and HATAI (1911), 50 from EBIKER (1972), 22 from GOLDBECKER (1972), and 6 from KRUSKA (1975). - ⁶ all data are from KRETSCHMANN (1966); animals are bred under laboratory conditions.

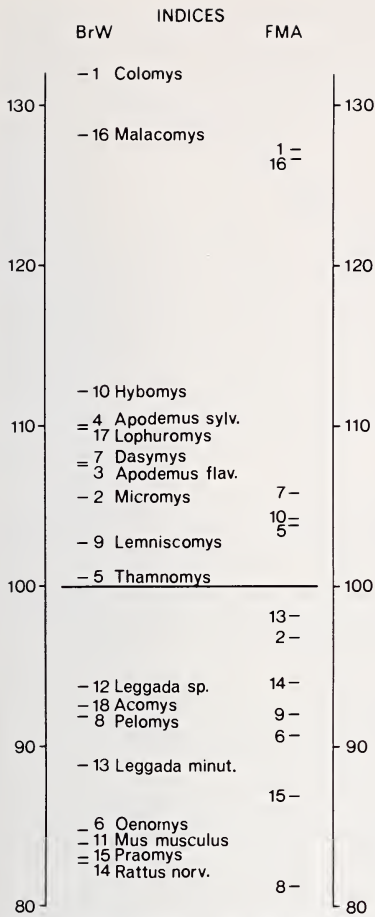


Fig. 2. Diagrammatic representation of the encephalization indices (EI) of 18 murid species (left hand scale) and foramen magnum indices (FI) of 12 murid species (right hand scale). The indices are percentage deviations from the regression lines, all points of which represent 100%. (Numbers as in Table 2)

the species and would not exist if all species had exactly the same body weights. The differences are largest in *Praomys* and *Lemniscomys*, where the average body weights are 8.2 % higher and 8.1 % lower than that of *Colomys* (see Table 1).

Foramen magnum area

When the terrestrial species of about the same body weight as *Colomys* are compared with *Colomys* there is a deficit in the foramen magnum area (FMA) of -18.7 % in *Hybomys*, -29.6 % in *Lemniscomys* and -30.0 % in *Praomys* (Table 1). For the regression line analysis the four species were supplemented by eight species with clearly differing body weights (see column 7 in Table 2).

gravity of the brain) to convert them into brain weights. Brain weights obtained in this way correspond well with the actual brain weights, as was found by STEPHAN et al. (1981) for 83 species of Chiroptera and by us in this study for 6 species of Muridae from which we have both brain weights and cranial capacities (+ in column 3 of Table 2 and in Fig. 1). However, this correlation between brain weight and cranial capacity may be confined to the relatively small-sized animals (e.g. bats and murids) and may not be valid for large species with large brains (e.g. ungulates). The regression line resulting from all 18 species has the formula:

$$\log \text{ brain weight} = 1.953 + 0.603 \cdot \log \text{ body weight}$$

The coefficient of correlation is 0.975.

All three regression lines are relatively similar both in slope and y-intercept. For the following analyses we have used the common regression line of the combined material (Fig. 1). For the following comparisons this line is given a value of 100. The relative distances of the various species from this line (= encephalization indices, EI; see column 5 in Table 2 and Fig. 2) and their percentage deviation from *Colomys* (column 6 in Table 2) are given for all 18 species which were used to construct the common regression line of the Muridae.

Only *Malacomys* is close to *Colomys*. All other species have distinctly lower EI values than *Colomys* and the percentage deficits (column 6 in Table 2) are distributed between -15.0 % in *Hybomys* and -37.3 % in *Rattus*. When comparing the deficits of *Hybomys*, *Lemniscomys* and *Praomys* with those of the direct comparison of the cranial capacities (see above) they are in *Hybomys* -15.0 % (versus -16.2 %), in *Lemniscomys* -22.2 % (versus -26.6 %), and in *Praomys* -37.3 % (versus -34.0 %). The differences are due to the differences in the body weights between

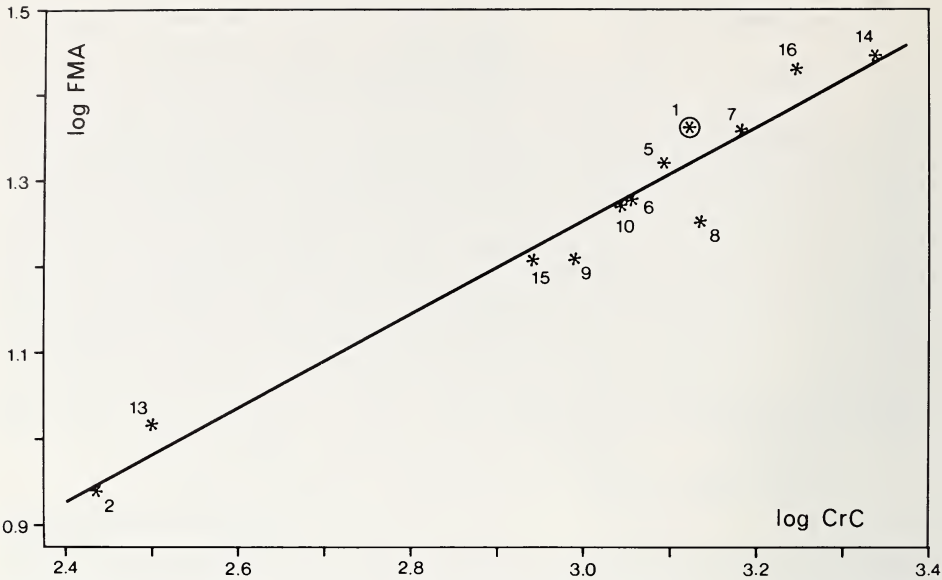


Fig. 3. Plot of log cranial capacity (CrC in mm^3) and log foramen magnum area (FMA in mm^2) for 12 species of Muridae. The regression line has the formula $\log \text{FMA} = -0.372 + 0.542 \cdot \log \text{CrC}$. The coefficient of correlation is 0.976. ⊗ = *Colomys goslingi*. (Numbers as in Table 2)

The formula of the regression line of these 12 species is:

$$\log \text{foramen magnum area} = 0.710 + 0.310 \cdot \log \text{body weight}$$

The coefficient of correlation is 0.921.

The relative distance of each species from this line (= foramen magnum index, FI) is given in column 9 of Table 2 and in Figure 2, and the percentage deviation from *Colomys* in column 10 of Table 2. Again only *Malacomys* is close to *Colomys*. All other species have lower FI values than *Colomys* and the percentage deficits (column 10 in Table 2) are distributed between -16.8% in *Dasymys* and -36.1% in *Pelomys*. When comparing the deficits of *Hybomys*, *Lemniscomys* and *Praomys* with those obtained from the direct FMA comparison (see above), they are in *Hybomys* -18.1% (versus -18.7%), in *Lemniscomys* -27.7% (versus -29.6%) and in *Praomys* -31.7% (versus -30.0%). Again the differences are due to differences in the body weights.

In general, the distances of *Malacomys* and *Colomys* from the other species appear to be similar in the foramen magnum indices and in the encephalization indices (compare both parts of Figure 2). In order to investigate whether or not *Colomys* has an disproportionately large FMA in relation to its brain size, we plotted FMA against CrC in a double logarithmic scale and made a regression analysis (Fig. 3). The coefficient of correlation is 0.952. The slope is 0.542 or, when plotting FMA against $\text{CrC}^{2/3}$ (thus equalizing the dimensions of both axes) it is 0.813. According to this slope, which is distinctly smaller than 1, the FMA in species with small brains is relatively larger than in those with large brains. The same results are obtained when FMA is compared with CrC size in each of the investigated species (column 11 in Table 2). The two species with the lowest body and brain size (*Micromys minutus* and *Leggada minutoides*) have the highest values (32.0 and $32.9 \text{ mm}^2/\text{cm}^3$) whereas the species with the largest body and brain size (*Rattus norvegicus*) has the lowest value ($12.9 \text{ mm}^2/\text{cm}^3$).

When the regression line in Figure 3 is given a value of 100 the highest positive deviations are found in *Malacomys* (110.1), *Colomys* (110.0), and *Leggada minutoides*

(108.1), whereas the highest negative deviations are found in *Pelomys* (84.4) and *Lemniscomys* (91.6). All other species are close to 100. Thus, in *Colomys*, the FMA is relatively large when related to brain size. This relatively large FMA is, however, not exceptional as several other species such as *Malacomys* and *Leggada* also have relatively large FMA's.

Discussion

The brain weight of *Colomys* was indirectly inferred from cranial capacities. The validity of such a procedure was checked in 83 species of bats (STEPHAN et al. 1981) and is verified in the present paper by data on 6 species of Muridae, from which both brain weights and cranial capacities are available. In four of the six species the converted brain weights are slightly lower than the measured ones (*Thamnomys*, -4.9 %; *Lemniscomys*, -4.1 %; *Pelomys*, -3.7 %; *Rattus*, -1.0 %), whereas in the other two (*Micromys*, +5.6 %; *Oenomys*, +1.4 %) they are slightly higher. As in the 83 bat species, the 6 murid species had similar values for measured brain weights and for those converted from cranial capacities.

All these species are, however, either aerial or purely terrestrial and the question arises, whether or not such a direct correspondence also exists for water adapted forms. According to investigations on *Potamogale velox* the conversion factor from cranial capacity to brain weight is 1.113 instead of 1.036 (specific gravity of the brain) as found in bats and terrestrial rodents. In *Potamogale* this difference is expected to be the consequence of the large size of the medulla oblongata and of the proximal parts of the spinal cord (caused by the extremely developed spinal trigeminal nucleus; STEPHAN and SPATZ 1962). The spinal cord is always cut so that the part attached to the brain forms a square (seen from below). The extracranial caudal parts of the medulla oblongata and the proximal parts of the spinal cord left with the brain are in *Potamogale*, and may be in other water adapted species, of a larger percentage of the total brain than in terrestrial and aerial species. Thus, cranial capacity measurements of water adapted species may underestimate brain size since relatively larger parts of the total brain (as recorded by brain weight) may be outside of the skull.

According to our investigations on Insectivora the adaptation to predatory life in limnetic ecosystems is always accompanied by an enlargement of the medulla oblongata. Therefore, it can be expected, that *Colomys* also has a large medulla oblongata. The results of our FMA measurements are compatible with such an expectation, but not conclusive. A final decision only can be obtained from comparative investigations on the brain composition.

If we accept a relatively large medulla oblongata in *Colomys*, it can be expected, that in *Colomys* (1) the brain weight is larger than that resulting from a conversion factor of 1.036, and (2) the EI is somewhat higher than given in Table 2. When the conversion factor of *Potamogale* ($1.113; = 1.036 \cdot 1.074$) is used, the brain weight of *Colomys* would be 1474 mg ($1372 \cdot 1.074$) instead of 1372 mg as given in Table 2, and the EI 141.7 instead of 131.9. However, *Potamogale* seems to be more strongly adapted to water than is *Colomys* and, therefore, we expect the average brain weight of *Colomys* to be anywhere between 1372 and 1474 mg, and the EI between 131.9 and 141.7.

The similarly high position of *Malacomys* both in cranial capacity and foramen magnum size needs further attention. It is of interest that *Malacomys* also is found near waters and in swamps (WALKER 1964) and its diet is at least in part animal food. "Termites, crickets, slugs, snails, caterpillars, crabs and a toad are recorded animal foods" (KINGDON 1974). However, according to DIETERLEN *Malacomys* may be found also far away from water, and its hunting strategies in water are clearly different from those of *Colomys*. Not the vibrissae but the hands seem to be used by *Malacomys* in detecting prey in shallow water.

With reference to these differences a comparative investigation of the composition of the brains (nearly equal in relative size, see Fig. 2) would be of great interest.

In conclusion, there are good indications that *Colomys*, which is a predator in limnetic ecosystems, has a larger brain and may have a larger medulla oblongata than do terrestrial species of Muridae. A final confirmation as well as an answer to the question, whether or not there is also a reduction of the olfactory structures, as is generally found in water adapted mammals, can only be obtained from investigations of brain components. Brain collection and quantitative investigations are in preparation.

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Zusammenfassung

Relative Hirngröße bei Muriden mit besonderer Berücksichtigung von Colomys goslingi

Die Hirngröße von 18 Arten von Muriden wurde teils direkt aus Hirngewichten (12 Arten) oder indirekt aus Messungen der Hirnschädelkapazität (12 Arten inkl. *Colomys goslingi*) erschlossen. 6 Arten waren mit Daten in beiden Gruppen vertreten. Bei *Colomys* (einer im Süßwasser jagenden Art) sind relative Hirngröße (Encephalisation) und Foramen magnum größer als bei terrestrischen Muriden gleichen Körpergewichts. Die Unterschiede ähneln jenen, wie man sie beim Vergleich an das Wasserleben angepaßter Insectivora mit terrestrischen Insectivora findet. Vergleichende Hirnuntersuchungen sind in Vorbereitung.

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The influence of the sexual cycle on the olfactory sensitivity of wild female house mice (*Mus musculus domesticus*)

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Abstract

Studied was the influence of the sexual cycle of the olfactory sensitivity of wild female house mice (*Mus musculus domesticus*), using a two-choice training apparatus. Large fluctuations in olfactory sensitivity related to the sexual cycle were shown with the odourant geraniol (C₁₀H₁₇OH). During proestrus the mice recognized a concentration of 5×10^8 molecules geraniol/cm³ air, while in metestrus they did not even respond to a concentration of 5×10^{11} molecules/cm³.

Introduction

The sense of smell plays a major role in social behaviour of house mice. For example, the sexual cycle of female mice may be accelerated when exposed to a male odour (WHITTEN 1958). Olfactory contact with strange males can even lead to a depression of gravidity (BRUCE 1959, 1962; DOMINIC 1966).

While olfactory sensitivity in males is constant over a long period of time, the females' varies in relation to the sexual cycle (SCHMIDT 1979). The results from these electrophysiological experiments and behavioral studies with rats (PIETRAS and MOULTON; PHILLIPS 1974 and VALLOWE 1975) differ greatly. Thus, studies with trained wild mice need to be conducted to determine wheater these differences are a result of methods employed.

Material and methods

Nine female mice, approximately four months old, whose parents were caught in the wild, were used in this experiment. A two-choice training apparatus consisting of transparent plexiglass half-tubes was used. The gaseous odour was pumped via a nozzle into one of the tunnels, while filtered air entered the other tube. The location of the olfactory stimulus was randomly distributed. Three experimental animals were trained to reject the odour while the other six were trained to choose the olfactory marked side. The animals were punished with an electric shock each time they responded incorrectly. Each correct response was rewarded with food (for details of this method, see SCHMIDT 1979). Vaginal smears were done every day after the mice completed 30 trials in order to determine the stage of the sexual cycle of each mouse (ALLEN 1922; ZONDECK and ASCHHEIM 1926).

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