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The Influence of Vision and Olfaction on the Homing Ability of the White-Footed Mouse (*Peromyscus leucopus noveboracensis*)

Lynn Mabelle Parsons

College of William & Mary - Arts & Sciences

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THE INFLUENCE OF VISION AND OLFACTION ON THE
HOMING ABILITY OF THE WHITE-FOOTED MOUSE
(PEROMYSCUS LEUCOPUS NOVEBORACENSIS)

A Thesis
Presented to the
Faculty of the Department of Biology
The College of William and Mary in Virginia

In Partial Fulfillment of
The Requirements for the Degree of
Master of Arts

By
Lynn Mabelle Parsons

1976

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Arts

Lynn Mabelle Parsons

Approved, May 1976

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DEDICATION

This manuscript is dedicated to my family and friends in appreciation for their love, their encouragement and their prayers.

I am especially thankful to my parents for instructing me by the example of their lives, and for instilling in me the desire to accept new challenges and then carry them through to completion.

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ABSTRACT

The relative importance of vision and olfaction to white-footed mice while returning after displacement to a trap where previously caught was investigated. Mice were removed from a 12 acre wooded area for six days and then released at two different release points at opposite corners of the study area. Homing was measured by live-trapping during six days after release. Ten trapping periods were conducted over a nine month period. Mice were blinded by bisection of the optic nerve and were made anosmic by nasal injections of zinc sulfate. Both zinc sulfate-injected mice and saline-injected controls were tested in an olfactometer.

The percentage of intact, blind, anosmic and saline-injected mice which homed did not differ significantly from each other. Experience (previous release) at a release site increased the percentage homing. Homing success was distance dependant and the homing percentage was greater from one release site than the other. Blind mice had a significantly poorer ($P < 0.05$) survival during the six days subsequent to release than mice of the other treatments, while the latter did not differ significantly among themselves.

THE INFLUENCE OF VISION AND OLFACTION
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INTRODUCTION

Homing may be defined as the ability of an animal to return to its home range or nest site after being displaced. For small mammals the following possible methods of homing have been suggested: complete random wandering (Murie 1963); random wandering until encountering familiar territory, within which directed movements occur (Griffo 1961); directed movements within familiar territory or the life range of the animal (Robinson and Falls 1965, Fisler 1967); or by navigation ability, allowing directed movements through unfamiliar territory (Burt 1940, Bovet 1972). One or several senses must be utilized in returning to a home area, and then recognizing the home area when it has been reached.

Sheppe (1965) showed that Peromyscus leucopus would not leave islands to which they had been displaced unless they had visual goals toward which to orient. Cooke and Terman (1975) found that blinded P. leucopus did not home as well as intact mice from distances of 336 meters, but did home as well from distances of approximately 50 meters. Other than these studies, very little work has been done investigating the senses utilized by small mammals in the homing process; however, closely related studies have been done with birds, fish and amphibians.

Papi et al. (1972) and Benvenuti et al. (1973) found that olfaction was necessary for homing in homing pigeons. Papi et al. (1972, 1973) postulated that during the first months of life, homing pigeons gather information on smell prevailing in surrounding regions through the winds. Baldacini et al. (1974) found that orientation at release was correct when nostrils were free and exposed to the wind, and they noted (1975) that if wind was deflected while the bird was being held in the home cage, later homing was decreased. Baldacini et al. (1974) found that pigeons could home when either olfactory cues or visual cues were known of the home cage.

Olfaction and vision are also important in the homing of fish. Dodson and Leggett (1974a, 1974b) found that American shad (Alosa sapidissima) located their home river (the Connecticut River) from Long Island Sound by a nonrandom search, and that anosmic fish homed less well than intact fish. In addition, shad that were both blind and anosmic did not home. Khoo (1974) found that both vision and olfaction are important components of home site fidelity for the intertidal fish, Oligocottus maculosus Girard, but these fish when blind homed better than when anosmic. All streams apparently have their own characteristic odor which migratory hime salmon (Oncorhynchus nerka), rainbow trout (Salmo gairdnerii irideus) and carp (Cyprinus carpio) could distinguish (Ueda et al. 1971). Doving et al. (1974), working with char (Salmo alpinus L.), suggested that it

is perhaps fish odors that act as pheromones to help guide homing and that the skin mucous of the fish may be the source of the odorants guiding the fish.

Some of the same results have been obtained in studies of the homing behavior of amphibians. Grubb (1973, 1974, 1975) showed that Bufo woodhousei fowleri, Bufo valliceps, Pseudacris clarki, Pseudacris streckeri, and Rana utricularia in breeding condition could, in an olfactometer, discriminate between the odor of their home pond and the odors of foreign ponds even though the ponds were separated by only a few meters. After two months in the lab, Rana utricularia were retested and were still able to discriminate the home pond odor.

Dole (1972a) found that the Bufo americanus could home under both cloudy and clear skies and Grubb (1970) showed that intact Bufo valliceps moved more on rainy nights than on clear nights, which led him (Grubb 1973) to suggest that there was no evidence of either a nocturnal or diurnal celestial compass for navigation.

Both Barthalamus and Bellis (1972) working with Desmognathus fuscus, a salamander, and Grant et al. (1968) working with the newt Taricha rivularis found that blind animals did not home differently than normal animals; however, anosmic newts were disoriented.

In Bufo americanus and Bufo valliceps, neither blinding nor anosmia alone appreciably altered the ability to home (Dole 1972a, Grubb 1970). Dole (1972b) further showed that anosmic leopard frogs (Rana pipiens) orient

and home even on nights with heavy fog and decreased visibility. However, when Grubb (1970) removed both the senses of smell and vision in Bufo valliceps, he found that they were disoriented and could not home. Dole (1972a) and Grubb (1970) concluded that both visual and olfactory cues were used in homing, and when deprived of one of these senses, the other was utilized.

The purpose of the present study was to continue to study the effect of blindness on homing and also to extend the investigation to the effect anosmia has on the homing ability of Peromyscus leucopus noveboracensis.

THE STUDY AREA

The experiments were conducted on a 4.48 hectare wooded area which has been undisturbed for many years, and is adjacent to the Laboratory of Endocrinology and Population Ecology at the College of William and Mary in Williamsburg, Virginia.

The common trees found on the area were tree of heaven (Ailanthus altissima (Miller) Swingle), beech (Fagus grandiflora Ehrh.), tulip (Liriodendron tulipifera L.), southern red oak (Quercus rubra L.), sycamore (Platanus occidentalis L.), white oak (Quercus alba L.), wild black cherry (Prunus serotina Ehrh.) and red cedar (Juniperus virginiana L.). Wax myrtle (Myrica cerifera L.), privet hedge (Ligustrum sp.) and multiflora rose (Rosa multiflora Thunb.) were common shrubs. Poison ivy (Rhus radicans L.) and honeysuckle (Lonicera japonica Thunberg) form a dense ground cover in open areas. Christmas fern (Polystichum acrostichoides Michx.), English ivy (Hedera helix L.), Indian strawberry (Duchesnea indica Andr.), vetch (Vetch spp.) and many grasses were also present.

Topographical features of the area are given in Figure 1.

Figure 1. Topographical features of the study area.

Key:

RP: Release Point

ARRANGEMENT OF THE GRID

In April and May, 1974, a grid was established on the study area. In each of 12 lines, A--L, there were 12 stations at 20 meter intervals, with the exception of line A with six stations and line B with nine stations (Figure 2). Two mouse live-traps were placed at each station within 2 meters of the station marker.

The aluminum mouse traps were 6.0 cm by 3.6 cm by 25.4 cm and had a wooden floor and treadle. One end of the trap was enclosed by a gravity fall aluminum door and lock, and the other end was covered with $\frac{1}{4}$ inch hardware cloth.

Traps were kept baited with two to four pellets of D & G Laboratory Diet which was inspected approximately every three days and was replaced when missing or moldy. In the late fall and winter when temperatures fell to freezing and below, cotton was placed in the traps. During the entire study, traps were covered with a piece of asphalt roofing about 25 cm by 35 cm to protect them from wind, rain and temperature extremes.

Figure 2. Arrangement of the grid on the study area.

Key

RI: River Point

TRAPPING PROCEDURE

Trapping was conducted from June through December 1974 and from July through September 1975, encompassing ten 13-day trapping periods (Table 1). Daily inspection of the traps began between 0545 and 0730 hours and lasted from 2.5 to 4 hours. All animals were numbered by specific toe removal when first caught, and the number, sex, age, place of capture and reproductive condition (males: testes scrotal or nonscrotal; and females: vaginas perforate or imperforate, notation of pregnancy by palpation, and lactation, if applicable) were recorded daily for each mouse. From July through September 1975, the weight of each animal was measured in the field with a Pesola scale, while previously the weights had been taken in the laboratory when animals were collected. Only Peromyscus leucopus noveboracensis was collected, although field records were kept on other small mammals captured.

During each trapping period, the traps were opened on day one. From day two through day seven, mice which had been captured at least once previously (not necessarily in the same trapping period) were taken to the laboratory where they were housed singly in standard plastic mouse cages with a 3/4 inch layer of wood shavings on

Table 1. Dates of each trapping period

Number of the Trapping Period	Dates	Experimental Treatments Tested
1 (Preliminary)	7/2/74 to 7/14/74	Intact
2	7/23/74 to 8/4/74	Intact
3	8/8/74 to 8/20/74	Intact
4	8/23/74 to 9/4/74	Blinded
5	9/11/74 to 9/23/74	Blinded
6	11/12/74 to 11/24/74	Blinded Saline-Injected
7	12/4/74 to 12/16/74	Saline-Injected
8	7/29/75 to 8/10/75	Intact Saline-Injected Anosmic
9	8/10/75 to 8/22/75	Intact Saline-Injected Anosmic
10	9/12/75 to 9/24/75	Intact Saline-Injected Anosmic

the cage floor. Mice were fed D & G Laboratory Diet and water ad libitum, and a window in the room provided a natural light cycle.

On day seven mice were released on the study area approximately 2.5 hours before sunset at one of two release points, B-2 or K-11. The location of release was determined by dividing the study area into two sub-areas by an imaginary diagonal line from C-11 to L-1 (Figure 2). Each mouse was released in the area opposite to the location of its calculated center of activity (Hayne 1949). Release at B-2 occurred immediately prior to release at K-11.

Five pregnant females which had litters during their stay in the laboratory were not released on the release day, but were kept with the litter. The young were weaned at approximately 21 days and were kept in the laboratory, while the mother was released on the study area at the site of last capture.

The recapture phase of each trapping period was from day eight through day thirteen, and the procedures, which varied with each experiment, will be explained in detail later. Recapture in a trap where previously caught or in an adjacent one was regarded as successful homing.

Because predators disturbed the traps and killed the entrapped mice, it was necessary to place steel traps on the study area. This kept predator disturbance of mouse traps below 10% during most of the year.

PROCEDURES FOR THE EXPERIMENTAL TREATMENT OF MICE

Treatment of Intact Mice

The homing of intact mice was tested during trapping periods two, three, eight, nine and ten (Table 1). These mice were collected, maintained in the laboratory between eight hours and five days (depending upon the day of capture), and then released intact either at release point B-2 or K-11. During the recapture phase, the mice that were caught daily were released immediately at the site of capture.

Treatment of Blinded Mice

The ability of blinded mice to home was tested in trapping periods four, five and six (Table 1). The mice were removed to the laboratory in the same manner as the intact treatment, but on day three through six of the trapping period they were surgically blinded.

The blinding procedure involved anesthetizing each mouse with ether, separating the optic sheath with micro-forceps, locating and severing the optic nerve with micro-scissors, and bathing the area with tetracycline. This surgical procedure was used previously by Cooke and Terman (1975) and found to be successful. The recovery time

after surgery and before release varied from one to four days depending upon the day of surgery. The eyes of all blinded mice developed a glazed, opaque or shriveled appearance, and this was used as the criterion for release. Blinded mice were released in the same manner as intact mice, and during the subsequent recapture phase they were released immediately where captured.

Treatment of Anosmic and Saline-injected Mice

The experiment described below dealt with the influence of olfaction on homing. During trapping periods eight, nine and ten (Table 1), mice were collected and removed to the laboratory in the same manner as the previous treatments. On day three through day six of the trapping period each mouse was anesthetized with Methoxyflurane, placed on its back, and with the aid of a Stereoscopic scope, a 24 gauge hypodermic needle with a blunted and curved 180° tip (Figure 3) was placed in the mouth and inserted dorsal to the soft palate through the nasopharyngeal opening. Immediately the mouse was turned to a head downward position and injected with either 0.2cc of 5.0 mg/ml zinc sulfate in 0.9% saline (anosmic) or 0.2cc of 0.9% saline (control). Once the solution was visible at the external nares, aspiration of the nasal cavity was begun and was continued for the remainder of the injection. The mouse was maintained in a head downward position until consciousness and/or a regular breathing pattern was regained, at which time the mouse was

Figure 3. Illustration of the hypodermic needle used for the zinc sulfate and saline injections.

returned to its original cage. This technique was modified from Alberts and Galef (1971).

Mice were released in the field on day seven of the trapping period which varied from one to four days after the zinc sulfate or saline injection.

PROCEDURE FOR TESTING THE ANOSMIC AND SALINE-INJECTED MICE

Schedule of Testing

All zinc sulfate-injected and saline-injected mice (except eight saline-injected mice injected prior to the development of the olfactometer) were tested in both the olfactometer and the activity cage one day after collection and one day after the injection. Mice which homed after their release on the study area were recaptured, maintained in the laboratory for one day and again given the same set of tests. These animals were then released the next morning at the site of capture.

Description of the Olfactometer

The olfactometer, modified from that of Vandenberg (1973) (Figure 4), consisted of a central plexiglass chamber 15.8 cm by 20.8 cm by 17.0 cm with a sliding plexiglass top and bottom, and two black opaque tunnels at opposite ends of the central chamber. Each of these tunnels was 5.2 cm in diameter and 10.0 cm in length, and the distal end was fitted with screening and a removable odor container. Each tunnel also contained two photoelectric cells at distances of 1.5 cm and 6.5 cm from the central chamber wall. Each photoelectric cell

Figure 4. Olfactometer

Key:

OC: Odor Container Attachment

PC: Photoelectric Cell

All measurements are in centimeters.

was connected to a timer which recorded the number of seconds the mouse spent in each tunnel. The whole olfactometer was placed in a sound insulated environmental cubicle (Lehigh Valley Electronics) measuring 45 cm by 51 cm by 102 cm and equipped with a 16 by 18 cm one-way observation window and an air intake and exhaust blower.

The Olfactometer Test

During the developmental stages of the olfactometer, the responses of P. leucopus noveboracensis to several odor sources, such as conspecific and interspecific male and female urine, Sprecto (an insecticide), cigar butts, food, formaldehyde, and paradichlorobenzene were tested. Since the most consistent avoidance responses were obtained in tests with 0.4 to 0.8 gm of paradichlorobenzene at the end of one tunnel and nothing at the end of the other tunnel, paradichlorobenzene was chosen for the odor stimulus and its location was determined for each test by flipping a coin.

A mouse was placed in the central chamber of the olfactometer and the doors of the cubicle were fastened. A four minute acclimation period was followed by a five minute test, during which the number of entrances into each tunnel was observed and the time spent in each recorded. Extension of at least the head and ears of a mouse into the tunnel was recorded as an entrance.

After each mouse was tested, the floor of the central chamber was wiped clean with a 5% solution of Wescodyne, and the floor and tunnels were wiped with dry paper towel-
ing.

The Activity Cage Test

The activity cage (Lehigh Valley Electronics) consisted of a covered cylinder 70 cm in diameter and 38 cm high. The cylinder had six infra-red photobeams (three on both horizontal, coordinate axes) placed 2.5 cm above the expanded metal floor. Activity along the horizontal axes was measured by the total number of photobeam interruptions.

When the mouse was removed from the olfactometer, it was placed directly in the activity cage, given approximately five minutes of acclimation, and its activity recorded during the subsequent five minute test. Following the tests, the mouse was removed and the aluminum tray beneath the cylinder floor was washed with a 5% solution of Wescodyne.

STATISTICAL ANALYSES

Where appropriate, all data were tested for heterogeneity (R x C Chi Square), and those which lacked heterogeneity were then compared where suitable by chi square and Fisher exact probability tests. The olfactometer, activity cage and distance results were compared by the above tests or by student's t distribution and Mann-Whitney U tests. Probability levels of .05 or less were regarded as significant, but values of .1 or less are indicated.

RESULTS

Homing Related to the Treatment of Mice

Since each treatment extended over several trapping periods, the data were tested for heterogeneity prior to pooling. No significant heterogeneity was found. Subsequent to pooling, comparisons were made by chi square or by Fisher exact probability tests, if appropriate.

To test the influence of vision on homing, the percentage of mice that homed was compared between intact and blinded treatments. Seventy-six intact mice were released, of which 38 homed (50.0%; Table 2), and of 40 blinded mice released, 21 homed (52.5%; Table 2). Thus the homing performance did not differ significantly between intact and blind mice.

To see if homing was impaired with loss of olfaction, comparisons were made between zinc sulfate-injected and saline-injected mice. The following results showed no significant homing differences between the two treatments: 15 zinc sulfate-injected mice homed out of 30 released (50.0%; Table 2), and 17 saline-injected mice homed out of 28 released (60.7%; Table 2).

None of the treatments, when compared with each other, showed a significant difference in the proportion

Table 2. Percentage of mice of each treatment that homed.

Trapping Period	Number Released	Number Homed	Number not Recaptured	Percentage Homed
<u>Intact</u>				
2	24	12	5	50.0
3	30	20	3	66.6
8	9	2	2	22.2
9	7	2	3	28.6
10	6	2	3	33.3
Total	76	38	16	50.0
<u>Blinded</u>				
4	20	12	2	60.0
5	19	9	5	47.4
6	1	0	1	0.0
Total	40	21	8	52.5
<u>Zinc Sulfate-Injected</u>				
8	5	0	3	0.0
9	11	7	0	63.6
10	14	8	1	57.1
Total	30	15	4	50.0
<u>Saline-Injected</u>				
6	6	2	0	33.3
7	2	0	1	0.0
8	6	3	1	50.0
9	11	9	0	81.8
10	3	3	0	100.0
Total	28	17	2	60.7

of mice homing. In fact, in all treatments the percentage of mice that homed was very similar.

Olfactometer Results

Comparisons of the responses of zinc sulfate-injected and saline-injected mice in the olfactometer were made to detect any differences in olfactory capabilities during the sequence of tests. The number of seconds in each of the two tunnels with their corresponding odors was measured.

Prior to injection with either zinc sulfate or saline, over three-fourths of all mice spent more time in the neutral tunnel compared to that with the para-dichlorobenzene odor. However, one day after injection only about half of the mice of each treatment spent a greater amount of time in the neutral tunnel (55.2% for zinc sulfate-injected; 45.0% for saline-injected mice; Table 3). After having homed, significantly more saline-injected than zinc sulfate-injected mice preferred the neutral tunnel ($P=0.02$; exact test; Table 3).

When the mean number of seconds spent in each tunnel was compared before injection, mice of both groups spent significantly more time in the neutral tunnel ($P<0.025$ or less; student's t test; Table 4). On the day after injection the time spent in each tunnel did not differ significantly for mice of either treatment. When the treatments were compared, they did not differ in the time spent in either tunnel before the injection and on

Table 3. Number of mice spending more time in either of the two tunnels of the olfactometer.

Treatment	Neutral Tunnel	Tunnel with Paradichloro-benzene	Neither Tunnel
<u>Prior to Injection:</u>			
ZnSO ₄ -Injected *	16	5	1
Saline-Injected	14	4	2
<u>One Day After Injection:</u>			
ZnSO ₄ -Injected	16	13	1
Saline-Injected	9	11	0
<u>One Day After Homing:</u>			
ZnSO ₄ -Injected	7	7	0
Saline-Injected	12	1	0
* Zinc sulfate-injected mice when used in several replications were not retested prior to injection after the first replication.			

Table 4. Mean number of seconds spent in each tunnel by zinc sulfate-injected and saline-injected mice.

Treatment	Time of Test:		
	Pre-Injection Mean $\pm$ SE	Post-Injection Mean $\pm$ SE	Post-Homing Mean $\pm$ SE
<u>Time Spent in the Neutral Tunnel:</u>			
ZnSO ₄	168.95 $\pm$ 27.68 (N=22)	159.04 $\pm$ 25.50 (N=30)	114.25 $\pm$ 30.89 (N=14)
Saline	167.17 $\pm$ 27.06 (N=20)	121.25 $\pm$ 30.46 (N=20)	209.31 $\pm$ 25.28 (N=13)
<u>Time Spent in the Paradichlorobenzene Tunnel:</u>			
ZnSO ₄	72.80 $\pm$ 24.02 (N=22)	111.18 $\pm$ 25.20 (N=30)	107.55 $\pm$ 34.80 (N=14)
Saline	53.81 $\pm$ 21.02 (N=20)	130.44 $\pm$ 29.55 (N=20)	16.63 $\pm$ 8.59 (N=13)

the day after.

When tested after homing, saline-injected mice spent significantly more time in the neutral tunnel ($P < 0.002$; Mann-Whitney U test; Table 4); whereas for the zinc sulfate-injected mice, the time spent in one tunnel did not differ significantly from the time spent in the other. Comparisons between the two treatments after homing showed that zinc sulfate-injected mice spent significantly more time in the paradichlorobenzene tunnel ($P < 0.05$; Mann-Whitney U test; Table 4) and less time in the neutral tunnel ($P < 0.05$; student's t test; Table 4) than did the saline-injected mice.

For both treatments and during all tests, the number of entrances into the neutral tunnel was not significantly different from the number of entrances into the tunnel with paradichlorobenzene (Table 5).

Activity Cage Results

Because of a heterogeneity of variance among the activity results ($P < 0.01$; Bartlett's test), all data were compared with a non-parametric, Friedman two-way analysis of variance by ranks and showed an overall significant difference in the activity ($P < 0.001$; Table 6).

Specific Mann-Whitney U tests showed the following results. The activity levels of zinc sulfate-injected mice did not differ significantly from saline-injected mice at any test. One day after injection, activity was

Table 5. Number of entrances into each tunnel.

Treatment and Time of Test	Entrances into Neutral Tunnel	Entrances into Paradichlorobenzene Tunnel
<u>Zinc Sulfate-Injected</u>		
Pre-injection	33	32
Post-injection	8	9
Post-homing	15	12
<u>Saline-Injected</u>		
Pre-injection	35	36
Post-injection	12	8
Post-homing	22	13

Table 6. Mean activity levels of zinc sulfate-injected and saline-injected mice.

Treatment	Time of Test:		
	Pre-Injection Mean $\pm$ SE	Post-Injection Mean $\pm$ SE	Post-Homing Mean $\pm$ SE
ZnSO ₄	67.81 $\pm$ 10.66 (N=22)	21.76 $\pm$ 5.91 (N=30)	39.07 $\pm$ 7.54 (N=14)
Saline	69.15 $\pm$ 2.20 (N=20)	29.95 $\pm$ 6.01 (N=20)	55.61 $\pm$ 10.35 (N=13)

significantly less than before injection ($P = 0.02$ for saline-injected and $P < 0.001$ for zinc sulfate-injected mice; Table 6) and significantly less than after homing ($P < 0.05$ for saline-injected and $P = 0.0029$ for zinc sulfate-injected mice; Table 6). The activity levels before injection and after homing did not differ significantly for saline-injected mice, but zinc sulfate-injected mice showed a significantly greater activity prior to injection than after homing ($P = 0.048$; Table 6).

Duration of Anosmia

Five anosmic mice were used in two consecutive trapping periods and, therefore, activity and olfactometer results after injection in one trapping period were compared to pre-injection results of the next. The tests were conducted 25 to 28 days apart.

Activity of anosmic mice prior to injection at the second trapping period did not differ significantly from their activity level after homing at the previous trapping period (Table 10).

Olfactometer results of the zinc sulfate-injected mice when tested 25 to 28 days after having homed showed that mice spent more time in the neutral than in the paradichlorobenzene tunnel ($0.05 < P < 0.1$; student's t test; Table 10). When tested at the time they homed, mice showed no significant difference in the amount of time spent in each tunnel. The amount of time spent

Table 7. Comparison of activity cage and olfactometer results for zinc sulfate-injected mice in two consecutive trapping periods.

Test Results After Having Homed in Trapping Period 9	Test Results Before Injection in Trapping Period 10
Mean $\pm$ SE	Mean $\pm$ SE
<u>Activity Cage</u>	
36.00 $\pm$ 11.11	17.20 $\pm$ 5.96
<u>Time Spent in Neutral Tunnel (seconds)</u>	
167.14 $\pm$ 69.09	193.96 $\pm$ 47.32
<u>Time Spent in the Paradichlorobenzene Tunnel (seconds)</u>	
118.26 $\pm$ 71.24	55.52 $\pm$ 44.20

in the neutral tunnel was not significantly different between the two times of testing, and the same was true of the amount of time spent in the paradichlorobenzene tunnel.

There were also three saline-injected mice released in two consecutive trapping periods; however, the times between the trapping periods varied for the three mice (4, 5 and 26 days). Therefore, accurate comparisons between these and anosmic mice could not be made.

Effects of Variables

Experience

In order to evaluate the influence of previous experience on homing success, mice were compared relative to the following categories of experience: 1) no previous release on the study area, 2) a previous release at the same release point, 3) a previous release at the opposite release point and 4) a previous release at both release points.

A significantly greater percentage of all mice (combined irrespective of treatment) that had been released previously at the same release point homed than mice that had never been released previously on the study area ($P < 0.001$; chi square test; Table 8). The other categories of experience showed no significant homing differences; however, due to small sample sizes, significance may not have been detected.

The experience effect was then tested separately for each treatment. Among intact mice only, a previous release at the same release point significantly increased the percentage homing when compared to intact mice with no previous release on the study area ($P < 0.01$; chi square test; Table 8). No other comparisons of experience in

Table 8. Experience and treatment related to the percentage of mice that homed.

Experience and Treatment	Number Released	Number Homed	Percentage Homing
<u>Never Released Previously on the Study Area:</u>			
Intact	59	24	40.7
Blinded	15	5	33.3
ZnSO ₄	14	5	35.7
Saline	19	10	52.6
Total	107	44	41.1
<u>Released Previously at the Same Release Point:</u>			
Intact	14	12	85.7
Blinded	18	12	66.7
ZnSO ₄	10	6	60.0
Saline	5	4	80.0
Total	47	34	72.3
<u>Released Previously at the Opposite Release Point:</u>			
Intact	3	2	66.7
Blinded	3	1	33.3
ZnSO ₄	4	3	75.0
Saline	2	1	50.0
Total	12	7	58.3
<u>Released Previously at Both Release Points:</u>			
Intact	0	--	----
Blinded	4	3	75.0
ZnSO ₄	2	1	50.0
Saline	2	2	100.0
Total	8	6	75.0

intact mice were significant, although some could not be made because of a lack of mice with experience at both release points. No significant homing differences with respect to experience were found among the other treatments (Table 8).

Blinded and anosmic mice combined ($P < 0.05$; chi square test; Table 8) and intact and anosmic mice combined ($P < 0.005$; chi square test; Table 8) showed the same experience effects on homing as noted above. All other experience comparisons with these two groups showed no significant homing differences.

Site of Release

Since the two different release points were at opposite ends of the study area, and mice released at each of them would be required to orient along different compass bearings, I examined the homing success from both points. Blinded, anosmic and saline-injected mice did not differ significantly in homing performances related to location of release. However, the intact mice released at B-2 homed significantly better than those released at K-11 ($P < 0.025$; chi square test; Table 9; Figure 2). More specifically, a greater proportion of intact mice that had never been released previously on the study area homed from B-2 than from K-11 ($0.05 < P < 0.1$; chi square test; Appendix A). The remaining intact mice when compared relative to their previous release experience

Table 9. Homing Differences from the two release points
(all mice irregardless of experience).

<u>Release at B-2</u>				<u>Release at K-11</u>			
Treat- ment	Number Released	Number Homed	% Homed	Treat- ment	Number Released	Number Homed	% Homed
Intact	35	23	65.7	Intact	41	15	36.6
Blinded	25	15	60.0	Blinded	15	6	38.7
ZnSO ₄	11	4	34.8	ZnSO ₄	19	11	57.9
Saline	13	9	69.2	Saline	15	8	51.8

showed no significant homing differences between the two release points.

Homing Comparisons Through Day Three of the Recapture Phase

Since by day six the homing performances among treatments did not differ significantly and since homing was essentially completed by day three, for each treatment the homing percentages were compared on each of the first three days of the recapture phase.

The homing performance of saline-injected mice was better than intact mice by days two and three ($0.05 < P < 0.1$; chi square test; Appendix B), but no other significant treatment differences were found (Figure 5).

When the experience effect on homing was compared among treatments, a higher proportion of saline-injected mice with no release experience on the study area homed than blinded mice of the same experience by days two ($P=0.1$; exact test) and three ($P=0.055$; exact test; Appendix B: Figure 6).

Distance

For each mouse the distance from its center of activity to its release point was measured and ranged from 95 to 274 meters. The relationship between distance and homing success was determined by noting the percentage of mice which homed at 20 meter intervals of distance (Table 10; Appendices C, D, E, F). To eliminate

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1 mile for the

- Intact (N = 76)
- Blind (N = 40)
- ▲ Zinc-Sulfate (N = 30)
- Saline (N = 28)

Figure 6. Daily homing percentages of mice never released previously on the study area for the six day recapture period.

- Intact (N=59)
- Blind (N=15)
- ▲ Zinc-Sulfate (N=14)
- Saline (N=19)

Table 10. Percentage of mice that homed at each 20 meter interval of homing distance (all mice never released previously).

Distance (meters)	Number Released	Number Homed	Percentage Homing
15-34	1	0	0.0
35-54	1	0	0.0
95-114	1	1	100.0
115-134	4	1	25.0
135-154	2	2	100.0
155-174	12	4	33.3
175-194	28	14	50.0
195-214	22	10	45.5
215-234	14	4	28.6
235-254	15	4	26.7
255-274	7	4	57.1

the experience factor, only mice never released previously on the study area were compared.

For comparison purposes, mice were divided into two groups: with theoretical homing distances less than 194 meters (the median homing distance) and greater than 194 meters. When data from the inexperienced mice were combined (irrespective of treatment) there was a higher homing frequency at distances less than 194 meters ($0.05 < P \leq 0.1$; chi square test; Table 11), but when each treatment was tested separately, the homing frequencies did not differ significantly between the two distance categories.

After release some mice re-established their home range instead of homing. With two mice, this resulted in theoretical homing distances of 15 to 54 meters (Table 10; Appendix C) in a subsequent trapping period.

Survival

Survival was measured by the number of mice recaptured on or after day six of the recapture period. When the treatments of mice were compared for survival ability over the six day recapture period, survival was significantly higher among intact mice than blinded mice ($P < 0.05$; chi square test; Table 12), but no significant differences among other treatments were found.

Experience at the release point had no significant effect on survival when animals of the same treatment, but

Table 11. For each treatment, the percentage that homed less than 194 meters and greater than 194 meters (all mice never released previously).

<u>Less Than 194 Meters</u>				<u>Greater Than 194 Meters</u>			
Treat- ment	Number Released	Number Homed	Percent- age Homing	Treat- ment	Number Released	Number Homed	Percent- age Homing
Intact	22	12	54.5	Intact	37	12	32.2
Blinded	8	3	37.5	Blinded	7	2	28.6
ZnSO ₄	6	3	50.0	ZnSO ₄	8	2	25.0
Saline	13	7	53.8	Saline	6	3	50.0
Total	59	25	42.4	Total	58	19	32.8

Table 12. Survival of intact, blinded, zinc sulfate-injected and saline-injected mice for the six day recapture period (irregardless of experience).

Trapping Period	Number Released	Number Survived	Percentage Survived
<u>Intact</u>			
2	24	17	70.8
3	30	26	86.7
8	9	7	77.8
9	7	3	42.9
10	6	2	33.3
Total	76	55	72.4
<u>Blinded</u>			
4	20	12	60.0
5	20	8	40.0
6	1	0	0.0
Total	41	20	48.8
<u>Zinc Sulfate-Injected</u>			
8	5	1	20.0
9	11	10	90.9
10	14	10	71.4
Total	30	21	70.0
<u>Saline-Injected</u>			
6	6	2	33.3
7	2	1	50.0
8	6	4	66.7
9	11	9	81.8
10	3	2	66.7
Total	28	18	64.3

different experiences, were compared (Table 13). Sample sizes were small in some experience categories, and although differences may have existed, they were not evident when tested.

Age

Mice were categorized as adults, subadults or juveniles according to pelage coloration. A juvenile had a predominantly gray pelage; a subadult had a gray, dorsal band with brown lateral bands and an adult had a predominantly brown pelage. Most of the mice involved in the experiments were adults; therefore, few comparisons could be made with other age classes. Where comparisons were possible (adults of all treatments, and intact and blind subadults), no significant homing differences between age classes or between treatments within the same age class were noted (Table 14).

Sex

When the homing performance of all males was compared to that of all females, no significant differences were noted for any treatment (Table 15).

Table 13. Treatment and experience related to survival
 (A=never released previously on the study area,
 B=released previously at the same release point,
 C=released previously at the opposite release
 point, D=released previously at both release points).

Treatment and Experience	Number Released	Number Survived	Percentage Survived
<u>Intact</u>			
A	59	39	66.1
B	14	13	92.9
C	3	3	100.0
D	0	--	----
<u>Blinded</u>			
A	16	6	37.5
B	18	9	50.0
C	3	2	66.7
D	4	4	100.0
<u>Zinc Sulfate-Injected</u>			
A	14	9	64.3
B	10	6	60.0
C	4	4	100.0
D	2	2	100.0
<u>Saline-Injected</u>			
A	19	9	47.4
B	5	4	80.0
C	2	2	100.0
D	2	2	100.0

Table 14. Age of mice related to the percentage that homed.

Treatment	Age	Number Released	Number Homed	Percentage Homing
<u>Intact</u>				
	Adults	66	34	51.5
	Subadults	10	4	40.0
<u>Blinded</u>				
	Adults	33	17	51.5
	Subadults	6	3	50.0
	Juveniles	1	1	100.0
<u>Zinc Sulfate-Injected</u>				
	Adults	30	15	50.0
<u>Saline-Injected</u>				
	Adults	28	17	60.7

Table 15. Homing performance of males compared to females (irregardless of experience).

<u>Males</u>				<u>Females</u>			
Trapping Period	Number Released	Number Homed	Percent- age Homed	Trapping Period	Number Released	Number Homed	Percent- age Homed
<u>Intact</u>				<u>Intact</u>			
2	19	10	52.6	2	5	2	40.0
3	23	17	73.9	3	7	3	42.9
8	6	1	16.7	8	4	1	25.0
9	4	2	50.0	9	2	0	0.0
10	4	1	25.0	10	2	1	50.0
Total	56	31	55.4	Total	20	7	35.0
<u>Blinded</u>				<u>Blinded</u>			
4	17	10	58.8	4	3	2	66.7
5	13	8	53.8	5	6	1	16.7
6	0	--	----	6	1	0	0.0
Total	30	18	60.0	Total	10	3	30.0
<u>Zinc Sulfate-Injected</u>				<u>Zinc Sulfate-Injected</u>			
8	4	0	0.0	8	1	0	0.0
9	6	4	66.7	9	5	3	60.0
10	10	6	60.0	10	4	2	50.0
Total	20	10	50.0	Total	10	5	50.0
<u>Saline-Injected</u>				<u>Saline-Injected</u>			
6	2	0	0.0	6	4	2	50.0
7	0	--	----	7	2	0	0.0
8	5	2	40.0	8	1	1	100.0
9	8	6	75.0	9	3	3	100.0
10	3	3	100.0	10	0	--	----
Total	18	11	61.1	Total	10	6	60.0

DISCUSSION

The results of this study showed that neither loss of vision nor loss of olfaction in Peromyscus leucopus noveboracensis had significant effects on the frequency of homing compared to intact and saline-injected controls. Comparable studies with small mammals are almost nonexistent, except for the studies by Cooke and Terman (1975) and Sheppe (1965) discussed in the introduction.

Both vision and olfaction have been shown to have important roles in normal growth in adult male rats (Sorrentino et al. 1971), in mating behavior in male rats (Larsson 1972), and in the arousal of intermale aggression in mice (Haug 1971, Edwards et al. 1972, Jones and Nowell 1973). They also are important in recognition of territorial boundaries by Mus musculus (Mackintosh 1973) and gerbils, Meriones anguiculatus (Thiessen and Dawber 1972), as well as in territorial marking in gerbils, M. anguiculatus (Wallen and Glickman 1975, Thiessen et al. 1971).

Since both vision and olfaction are important senses, but since neither blinding alone nor anosmia alone disrupts homing, perhaps there is a compensation factor involved in the homing of small mammals, as Dole (1972a) and Grubb (1970) have suggested for amphibians. Deprivation

of sight may be compensated for by utilization of olfaction and vice versa. The next step in the study with Peromyscus, then, is to eliminate both vision and olfaction to determine whether homing still occurs.

It is possible that in this study the mice were released in an area with which they had become familiar or imprinted during juvenile dispersal and/or by spontaneous movements out of their home range, as Layne (1957) and Debusk and Kennerly (1975) have suggested from other studies.

The size of the home range of P. l. noveboracensis is approximately 0.25 to 0.80 acres (Blair 1940, Burt 1940, Ruffer 1961); the average cruising distance is 53 yards (48.4 meters) (Burt 1940) and the approximate distance of juvenile dispersal is from 165 to 300 meters (Nicholson 1941). Spontaneous movements outside the home range have been shown to occur by Murie and Murie (1931), Blair (1943), Howard (194) and Stickel (1968). Thus while homing, environmental cues could have been perceived, remembered and followed (Griffo 1961, Murie 1963, Furrer 1973).

If familiarity of a life range is involved in successful homing, then memory of the necessary cues and the permanence of cues is very important. Griffo (1961) showed that P. gossypinus after having successfully homed and being held in captivity for 12 weeks showed no decline in homing success, but how long memory lasts in P. l.

noveboracensis is unknown.

The importance of area familiarity to homing has been recently shown by Furrer (1973), who found that P. maniculatus when released outside of the life range were disoriented. Further, Debusk and Kennerly (1975) concluded from their homing studies of the cotton rat (Sigmodon hispidus) that homing in unfamiliar territory may be by navigation or simple wandering, but neither means was adequately demonstrated in their study, nor in the present study.

Experience at a release point increased the percentage of mice that homed, probably due to improved orientation by greater familiarity with the area. However, previous releases at the opposite release point or both release points did not significantly improve homing, but the sample size was perhaps too small to detect significance. Improved homing with experience was found in Peromyscus (Murie 1963, Furrer 1973) and in Microtus (Robinson and Falls 1965).

The experience effect was more evident in the homing of intact and saline-injected mice when their combined data were compared to that from blind and anosmic animals combined. Blind and anosmic mice were unable to use either visual or olfactory cues, respectively, for homing; and this hindrance may have deleted the advantage of previous experience, since certain previously learned cues could not be utilized. When all of the separate treatments were compared, only the intact, experienced mice

showed a significantly greater homing frequency with experience. However, saline-injected controls, having both visual and olfactory senses, also should have shown significantly better homing with experience; although, because of small sample sizes, significance may not have been detected.

The percentage of inexperienced, intact mice that homed was less than that for inexperienced, anosmic mice until day four after release, so despite the lower activity level of anosmic mice in the activity cage, homing did not seem to be hindered.

A significantly lower percentage of inexperienced, blinded mice homed compared to inexperienced, saline-injected mice by days two and three of the recapture period. In addition, the percentage of inexperienced, blinded mice that homed during the first three days of the recapture phase was also lower than the other treatments, although not significantly. Perhaps this is explained by the limiting effect of blindness, even though the ultimate percentage of homing was not different for any treatment.

The release point K-11 in the present study lies S 66° W of release point B-2 (Figure 2). Results showed that intact mice with no experience on the study area homed significantly better from east to west than from west to east. Blind and saline-injected mice also showed better homing from east to west, but anosmic mice showed better homing from west to east; in these treatments, though, the differences were not significant. Further,

there were no differences between the two release points regarding the distances mice were required to home.

The prevailing wind direction for approximately seven hours after release on six of the nine release days was from the northwest, west or southwest (Table 16) (exceptions were trapping periods two, six and ten). Thus, all treatments except anosmic may have oriented by odors transferred by the winds. There may be a limited amount of wind several centimeters from the ground in the undergrowth, but perhaps the semi-arboreal existence of P. l. noveboracensis (Baker 1968) facilitated determination of long distance olfactory cues, if such a phenomenon exists.

Homing success related to direction was investigated for trapping periods two and ten in which the wind direction was from the northeast and the southeast. From the previous suggestion of wind borne odor orientation, it would be expected that homing success during these trapping periods would be greater from a west to east direction; however, the frequency of inexperienced saline-injected, intact and blinded mice that homed was still greater from the east to west (Table 17, Table 18).

As a further test of the influence of wind direction, the frequency of homing against the wind was compared to that in the same direction as the wind. For intact, blinded and saline-injected mice combined, wind direction had no significant effects on homing. Their frequency

Table 16. Prevailing wind direction for seven hours after the release of mice on the release day (from the Ft. Eustis Meteorological Station).

Trapping Period	Date of Release	Wind Direction
2	July 29, 1974	SE (150°)
3	August 14, 1974	SW (210°)
4	August 29, 1974	SW (220°)
5	September 17, 1974	NW (280°)
6	November 18, 1974	Calm
7	December 9, 1974	NW (330°)
8	August 4, 1975	SW (200°)
9	August 16, 1975	SW (230°)
10	September 18, 1975	NE (80°)

Table 17. Homing success from release points B-2 and K-11 related to wind direction (inexperienced mice).

<u>Released at B-2</u>			<u>Released at K-11</u>		
Number Released	Number Homed	Percentage Homing	Number Released	Number Homed	Percentage Homing
<u>Wind Direction From the Northwest, West and Southwest:</u>					
Intact, Blinded and Saline-Injected					
26	14	53.8	31	9	29.0
Zinc Sulfate-Injected					
5	0	0.0	8	4	50.0
<u>Wind Direction From the Northeast and Southeast:</u>					
Intact, Blinded and Saline-Injected					
15	10	66.7	16	5	31.3
Zinc Sulfate Injection					
0	--	----	1	1	100.0

Table 18. Homing success of inexperienced mice homing
with the wind and against the wind.

Number Released	Number Homed	Percentage Homing
<u>Homing With the Wind:</u>		
Intact, Blinded and Saline-Injected:		
46	19	41.3
Zinc Sulfate-Injected:		
8	4	50.0
<u>Homing Against the Wind:</u>		
Intact, Blinded and Saline-Injected:		
42	19	45.2
Zinc Sulfate-Injected:		
6	1	16.7

of returns was higher from east to west irregardless of wind direction (Table 18). Anosmic mice, however, had higher homing frequencies, although not significantly, when traveling with the wind. Homing in an east to west direction and with the wind could not be tested in inexperienced, anosmic mice because none were released at B-2. From this study, then, there is no evidence to show orientation by wind borne odors.

Saint-Girons and Durup (1974) suggested that bank voles (Clethrionomys glareolus) and field mice (Apodemus sylvaticus) were aided in homing a distance of 100 to 130 meters by olfactory cues coming from the center of activity, since the wind direction was constant during the entire homing study. Saint-Girons and Durup (1974) also found that bank voles (C. glareolus) homed better from a north to south and from a south to north direction than either east to west or west to east. Therefore, because homing directions were different in Saint-Girons and Durup's study and the present study, homing was not related to the compass bearing. In Cooke and Terman's study (1975) homing directions were north to south and south to north, and P. l. noveboracensis showed no significant homing differences due to direction, but wind direction was not examined.

Other means of orientation have been suggested, such as by acoustical cues, which was possible in this study since a highway lies to the east of release point B-2 (Figure 1, Figure 2). Saint-Girons and Durup (1974)

suggested the possibility of homing by acoustical cues because of the existence of a highway near their study area. Dole (1972b), however, found that deaf leopard frogs (Rana pipiens) were still able to orient homeward.

Topographical features have been known to act as barriers to homing, such as a small stream (3 to 4 meters wide) (Savidge 1973) and a canal (Furrer 1973) in P. leucopus and P. maniculatus, respectively. These studies suggest that a highway to the east of release point B-2 (Figure 1) might have acted to channel the mice in a westerly direction or might have been an auditory cue to the mice homing from either direction. However, the homing of anosmic mice only was reduced suggesting that the variables of topography and sound were not differentially effective. Further investigation needs to be done to discover the reasons for the directional differences in homing.

In this study, mice homed better from distances of 194 meters or less (the median homing distance) than from distances greater than 194 meters. Results previously obtained by other workers such as Bovet (1972), Furrer (1973) and Debusk and Kennerly (1975) also showed that over distances of approximately 70 to 1970 meters a decreased frequency of returns occurred with increasing distance.

Previous studies have shown a rapid rate of homing in intact small mammals. The exact rate of homing in

this study is not known to the exact hour, although some mice of each treatment homed over 200 meters (some over 275 meters) between the time of release and the time of the inspection the next morning (approximately 14 hours). Among Peromyscus the following rates have previously been shown: 3200 meters in 48 hours (Murie and Murie 1931), 730 meters in eight hours (Murie 1963) and 300 meters in two hours (Griffo 1961).

The results of the present study showed that survival was significantly higher in intact mice than blinded mice, while anosmia did not adversely affect survival. Webster and Webster (1971) found that both vision and audition played significant roles in the survival of the kangaroo rat (Dipodomys merriami); however, Cooke and Terman (1975) working with P. l. noveboracensis showed no significant survival difference between intact and blinded animals for the seven days studied.

Adults and subadults showed no significant differences in homing, although since mostly adults were tested, comparisons were limited. Other studies have shown that older mice homed better than younger ones (Griffo 1961, Murie 1963 and Robinson and Falls 1965).

No differences in homing were found between males and females in the present study. Furrer (1973) found that females tended to home better than males over distances greater than in the present study, but at shorter distances no clearcut difference between the sexes was found. Murie

(1963) found that males tended to be more frequent homers than females, while Robinson and Falls (1965) working with Microtus showed no differences between the homing of males and females.

The procedure and proof of anosmia in P. l. noveboracensis were important aspects of this study. Olfactometer results showed that intact mice before injection and saline-injected mice after homing discriminated between the negative and neutral odors, but mice injected with zinc sulfate did not discriminate after having homed.

The peripheral anosmia procedure seems to have a very traumatic effect on the mice. Besides a high mortality (10 to 20%) at the time of injection, the olfactometer results of both anosmic and saline-injected mice one day after injection did not demonstrate odor discrimination. Their activity levels were also significantly lower than before injection, which also occurred in male hooded rats after an injection with zinc sulfate (Sieck and Baumach 1974).

Despite the decreased activity of saline-injected mice, their frequency of homing was higher than that of intact mice, so the injection per se did not hinder homing compared to other treatments. Further, 57% of the saline-injected mice and 76.7% of the anosmic mice had at least two days to recover from the injection prior to release on the field.

When tested after homing, the saline-injected mice

had regained their previous activity level, but anosmic mice still had maintained the lower activity. Since homing of anosmic mice was not significantly different from either saline-injected or intact mice, this decreased activity appeared not to hinder their homing.

It is bewildering that the homing percentages of saline-injected mice were higher than those of intact mice, not only the first few days, but throughout the whole recapture period. Since the visual acuity of both intact and saline-injected mice should be the same, perhaps the saline-injection increased the sensitivity of the olfactory cells.

An alternate explanation may be that intact mice from trapping periods eight, nine and ten had less knowledge of the study area than the saline-injected mice. Intact mice in these periods tended not to be captured a second time before collection until the last two days of the collection period and, therefore, perhaps had not become established on the area yet. Saline-injected mice may have been in residence longer. Strong evidence for this possibility is the fact that the proportion of saline-injected mice which homed was almost identical to that of the intact mice during trapping periods two and three (Table 2).

In this experiment the activity levels of blinded mice were not tested; however, O'Hara and Dyer (1974) found that blind guinea pigs in a closed field were more

active than normal guinea pigs. Like the other treatments 78% of the blinded mice had at least two days to recover from surgery before they were released in the field.

Olfactometer results showed that anosmia lasted for at least nine days after treatment; however, the exact duration cannot be determined from the present data. Using a 5% solution of zinc sulfate, anosmia has been shown to last from two to at least 14 days in hooded rats (Alberts and Galef 1971), four to five days in female rats (Mayer et al. 1975) and at least seven weeks in albino mice (Vandenbergh 1973). Edwards et al. (1972) using a 4% solution found that anosmia lasted four to six days in hamsters.

Five anosmic mice that were used in more than one replication in this study showed that the activity levels after homing were not different than when tested 25 to 28 days later at the beginning of the next consecutive trapping period. By this time, however, the sense of smell may have returned because mice spent less time in the paradichlorobenzene tunnel of the olfactometer. Two zinc sulfate-injected mice when tested 32 days after injection, however, did not discriminate between the odors. More studies need to be conducted and better tests need to be devised to accurately indicate the actual duration of anosmia in Peromyscus.

Histological studies have given additional evidence for the duration and the effectiveness of the peripheral anosmia procedure. The normal olfactory epithelium is a

pseudostratified arrangement of three cell types: olfactory or sensory cells, supporting or sustentacular cells and basal cells (Matulionis 1975, Schultz 1941, 1960 and Smith 1938). Irrigation with physiological saline (Smith 1938) and distilled water (Matulionis 1975, Schultz 1960) had no histological effect on the epithelium; however, different degrees of destruction of the olfactory epithelium occurred following irrigation with zinc sulfate, ranging from: 1) a surface alteration affecting the apical parts of the olfactory cells and supporting cells, 2) necrosis and sloughing of only the olfactory cells or 3) extreme degeneration leading to sloughing of the entire epithelium (Matulionis 1975, Smith 1938, Schultz 1960). The rate of regeneration and degree of necrosis of the cells varied with different strains of mice, so the surface alteration of the epithelium lasted for four days in one strain and 12 to 14 days in the other. However, it took 42 days in the former and 72 days in the latter strain for completely normal epithelium to be restored.

Matulionis (1975) found that when zinc sulfate did not make contact with areas of the nasal cavity, the olfactory epithelium remained relatively undamaged in isolated areas, or if contact time was too short then little or no effect was produced. However, his method of producing anosmia could explain the variation in effectiveness he obtained. On three consecutive days he applied a drop of 1% zinc sulfate solution at the orifice of both

external nares, which was inhaled by the mouse.

I suggest that with the more intense procedure and the greater concentration of zinc sulfate used in the present study that the effect of anosmia would be more reliable than that which Matulionis (1975) found.

Matulionis suggested (1975) that the reasons for variability in regeneration time and differences in the reactivity to the zinc sulfate between different strains of mice was due to genetic determination. This possibility, as well as the different methods of peripheral anosmia used by different workers might explain the differences in the duration of anosmia seen in the literature. More extensive work must be done to determine the actual duration of anosmia, to improve the anosmic technique and to improve the test for the proof of anosmia. These improvements then could be applied to further studies on the role of both vision and olfaction in the homing behavior of small mammals.

APPENDIX

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APPENDIX A

Experience related to homing differences of mice from release point B-2 and K-11 (A=never released previously on the study area, B=a previous release at the same release point, C=a previous release from the opposite release point and D=a previous release at both release points).

<u>Release at B-2</u>				<u>Release at K-11</u>			
Treat- ment	Number Released	Number Homed	% Homed	Treat- ment	Number Released	Number Homed	% Homed
<u>Intact:</u>							
A	25	14	56.0	A	34	10	29.4
B	8	7	87.5	B	6	5	83.3
C	2	2	100.0	C	1	0	0.0
D	0	--	----	D	0	--	----
<u>Blind:</u>							
A	10	5	50.0	A	5	0	0.0
B	11	7	60.8	B	7	5	71.4
C	2	1	50.0	C	1	0	0.0
D	2	2	100.0	D	2	1	50.0
<u>Zinc Sulfate-Injected:</u>							
A	5	0	0.0	A	9	5	55.6
B	2	1	50.0	B	8	5	62.5
C	3	3	100.0	C	1	0	0.0
D	1	0	0.0	D	1	1	100.0

<u>Release at B-2</u>				<u>Release at K-11</u>			
<u>Treat-</u>	<u>Number</u>	<u>Number</u>	<u>%</u>	<u>Treat-</u>	<u>Number</u>	<u>Number</u>	<u>%</u>
<u>ment</u>	<u>Released</u>	<u>Homed</u>	<u>Homed</u>	<u>ment</u>	<u>Released</u>	<u>Homed</u>	<u>Homed</u>
<u>Saline-Injected:</u>							
A	9	6	66.7	A	10	4	40.0
B	2	1	50.0	B	3	3	100.0
C	1	1	100.0	C	1	0	0.0
D	1	1	100.0	D	1	1	100.0
<u>Sum of Intact, Blind and Saline-Injected:</u>							
A	44	25	56.8	A	49	14	28.6
B	21	15	71.4	B	16	13	81.3
C	5	4	80.0	C	3	0	0.0
D	3	3	100.0	D	3	2	66.7

APPENDIX B

Daily homing percentages for the six day recapture period.

Treatment and Experience	1	2	3	4	5	6
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Total Mice (Irrespective of Experience):

Intact N=76

# Homed	16	10	4	3	3	2
Cumul. #	16	26	30	33	36	38
Percent	21.1	34.2	39.5	43.4	47.4	50.0

Blind N=40

# Homed	12	4	1	1	0	3
Cumul. #	12	16	17	18	18	21
Percent	30.0	40.0	42.5	45.0	45.0	52.5

Zinc Sulfate-Injected N=30

# Homed	8	4	3	0	0	0
Cumul. #	8	12	15	15	15	15
Percent	26.7	40.0	50.0	50.0	50.0	50.0

Saline-Injected N=28

# Homed	10	6	1	0	0	0
Cumul. #	10	16	17	17	17	17
Percent	35.7	57.1	60.7	60.7	60.7	60.7

Never Released Previously on the Study Area:

Intact N=59

# Homed	8	8	3	2	2	1
Cumul. #	8	16	19	21	23	24
Percent	13.6	27.1	32.2	35.6	39.0	40.7

Blind N=15

# Homed	3	0	0	1	0	1
Cumul. #	3	3	3	4	4	5
Percent	20.0	20.0	20.0	26.7	26.7	33.3

Zinc Sulfate-Injected N=14

# Homed	3	1	1	0	0	0
Cumul. #	3	4	5	5	5	5
Percent	23.1	30.8	35.7	35.7	35.7	35.7

Saline-Injected N=19

# Homed	5	4	1	0	0	0
Cumul. #	5	9	10	10	10	10
Percent	26.3	47.4	52.6	52.6	52.6	52.6

Treatment and Experience	Days					
	1	2	3	4	5	6

Previous Release at the Same Release Point:

<u>Intact N=14</u>						
# Homed	7	2	1	1	1	0
Cumul. #	7	9	10	11	12	12
Percent	50.0	64.3	71.4	78.6	85.7	85.7
<u>Blind N=18</u>						
# Homed	8	1	1	0	0	2
Cumul. #	8	9	10	10	10	12
Percent	44.4	50.0	55.6	55.6	55.6	66.7
<u>Zinc Sulfate-Injected N=10</u>						
# Homed	4	0	2	0	0	0
Cumul. #	4	4	6	6	6	6
Percent	40.0	40.0	60.0	60.0	60.0	60.0
<u>Saline-Injected N=5</u>						
# Homed	3	1	0	0	0	0
Cumul. #	3	4	4	4	4	4
Percent	60.0	80.0	80.0	80.0	80.0	80.0

Previous Release at the Opposite Release Point:

<u>Intact N=3</u>						
# Homed	1	0	0	0	0	0
Cumul. #	1	1	1	1	1	1
Percent	33.3	33.3	33.3	33.3	33.3	33.3
<u>Blind N=3</u>						
# Homed	0	1	0	0	0	0
Cumul. #	0	1	1	1	1	1
Percent	0.0	33.3	33.3	33.3	33.3	33.3
<u>Zinc Sulfate-Injected N=4</u>						
# Homed	1	2	0	0	0	0
Cumul. #	1	3	3	3	3	3
Percent	25.0	75.0	75.0	75.0	75.0	75.0
<u>Saline-Injected N=2</u>						
# Homed	1	0	0	0	0	0
Cumul. #	1	1	1	1	1	1
Percent	50.0	50.0	50.0	50.0	50.0	50.0

Treatment and Experience	1	2	3	Days 4	5	6
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Previous Release at Both Release Points:

Intact N=0

Blind N=4

# Homed	1	2	0	0	0	0
Cumul. #	1	3	3	3	3	3
Percent	25.0	75.0	75.0	75.0	75.0	75.0

Zinc Sulfate-Injected N=2

# Homed	0	1	0	0	0	0
Cumul. #	0	1	1	1	1	1
Percent	0.0	50.0	50.0	50.0	50.0	50.0

Saline-Injected N=2

# Homed	1	1	0	0	0	0
Cumul. #	1	2	2	2	2	2
Percent	50.0	100.0	100.0	100.0	100.0	100.0

APPENDIX C

Homing percentage for each distance class of intact mice
never released previously.

Distance (meters)	Number Released	Number Homed	Percentage Homed
15-34	1	0	0.0
35-54	1	0	0.0
95-114	1	1	100.0
115-134	4	1	25.0
135-154	2	2	100.0
155-174	4	3	75.0
175-194	9	5	55.6
195-214	13	4	30.8
215-234	10	3	30.0
235-254	9	3	33.3
255-274	5	2	40.0

APPENDIX D

Homing percentage for each distance class of blinded
mice never released previously

Distance (meters)	Number Released	Number Homed	Percentage Homed
155-174	4	1	25.0
175-194	4	2	50.0
195-214	2	1	50.0
215-234	1	0	0.0
235-254	3	0	0.0
255-274	1	1	100.0

APPENDIX E

Homing percentage for each distance class of zinc sulfate-injected mice never released previously.

Distance (meters)	Number Released	Number Homed	Percentage Homed
155-174	2	0	0.0
175-194	4	3	75.0
195-214	4	1	25.0
215-234	3	1	33.3
235-254	1	0	0.0

APPENDIX F

Homing percentage for each distance class of saline-injected mice never released previously.

Distance (meters)	Number Released	Number Homed	Percentage Homed
155-174	2	0	0.0
175-194	11	7	63.3
195-214	3	2	66.7
215-234	0	-	----
235-254	2	0	0.0
255-274	1	1	100.0

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