TRANSPORT OF YOUNG
IN
THE NORWAY RAT

By

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TRANSPORT OF YOUNG
IN
THE NORWAY RAT

TO
MY
MOTHER

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Abstract

During the first two to three weeks of their life, the altricial young of the Norway rat remain in a nest constructed by the mother. If this nest is disturbed, the mother will abandon it and transport her young individually to a new location.

When the nests of lactating rats were destroyed daily from the day of birth (day 0) through day 30 of lactation, it was found that the probability of transport of young was high until the beginning of the third week postpartum. After day 14, the probability of transport began to decrease, and 90% of mothers had ceased transporting entirely by day 20.

When the nest box of a day 4 or day 12 mother was not disturbed, or when a concealing paper nest remained after the cover of the box was removed, the probability of transport was very low. However, exposure of the mother and young, destruction of the nest, and flooding of the nest were found to be sufficient to elicit transport.

The elimination of pup distress signals by anesthetization of the litter did not decrease the probability, nor increase the latency of transport. Therefore, mothers appear to be responding directly to the characteristics of

the disturbance itself, rather than to the distress of the pups.

Although distress signals from the young are not necessary for the elicitation of transport behavior, they are sufficient to increase the probability of transport when the mother and young remain concealed by a paper nest after the nest box cover is removed. Distress cries emitted by a single pup induced the mother to transport the entire litter. No preference was shown for the pup emitting the cries.

The young also facilitate their transport to a safe nest by exhibiting a characteristic transport response in which all of their extremities are tucked in close to the body. This pup transport response is normally elicited by the tactile stimulation of the skin received from the mother's teeth. Grasping the skin of almost any area on the dorsal and lateral surfaces of the body was sufficient to elicit the transport response, and mothers were observed to carry pups by grasping the skin anywhere in these areas.

The pup transport response develops gradually over the first 10 days of life, and then can be reliably elicited until the end of the third week postpartum. After this time, the response becomes more difficult to elicit.

The ontogeny of the pup transport response suggests its function; that is, the response is seen during the time that mothers will still carry larger pups which may be unwieldy. The elimination of the pup transport response by light anesthesia does not impede the transport behavior of the mother on day 5, when pups are relatively small. On day 12, however, when pups have become relatively large, elimination of the transport response causes the pups' limbs to drag along the ground, interfering with the mother's locomotion and increasing the time necessary to transport young, either through a tunnel or in an open runway.

The rat mother and young thus interact on several levels to ensure the safety of the litter after nest site disturbance.

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INTRODUCTION

When living in the wild, rats perform a wide range of activities in connection with the care of their altricial young. One component of maternal care in the rat is the construction and maintenance of a nest (Denenberg, Taylor & Zarrow, 1969; Lee & Williams, 1974; Sturman-Hulbe and Stone, 1929) in which the young remain continuously for two to three weeks following parturition. During this period the nest is the site of all mother-litter interactions, and functions to insulate the pups during the absence of the mother (King, 1963; King & Connon, 1955).

If the nest is disturbed in any of a variety of ways, the mother finds another location, and moves her litter to the new site (Calhoun, 1962a). It has been suggested that in the wild mammals change their nest sites due to the need for sanitary quarters (*Sciurus carolinensis*, Fitzwater & Frank, 1944), following destruction of the nest (*Peromyscus leucopus noveboracensis*, Smith, 1939), or after invasion of the nest by adult conspecifics (*Rattus norvegicus*, Calhoun, 1962b). Movement of the nest site following disturbance of the nest by a human observer has been observed in mice (*Peromyscus maniculatus*, Hansen, 1957), voles (*Microtus agrestis*, Godfrey, 1953), raccoons (*Procyon lotor*, George & Stitt, 1951), pine squirrels (*Tamiasciurus fremonti fremonti*, Hatt, 1943), red squirrels (*Sciurus hudsonicus* loquax, Klugh, 1927), black bears (Ursus americanus, Erickson & Martin, 1960), red fox (Vulpes vulpes, Sheldon, 1949), flying squirrels (Glaucomys sabrinus, Kittredge, 1928), and muskrats (Ondatra zibethica zibethica, Errington, 1939).

In some rat species the young cling tightly to the nipples of the mother when she flees from a disturbed nest, and the litter is transported as a group. In fact, the incisor teeth of some young are specialized to provide a firm grip on the teat (e.g., Neotoma f. floridana, Hamilton, 1953; Neotoma floridana rubida, Svihla & Svihla, 1933). In Rattus norvegicus, however, the mother transports her young by grasping them with her teeth and carrying each pup individually to the new site (Ewer, 1968).

Transport behavior by the mother presumably increases the probability that the young will survive after nest site disturbance. However, very little is known about the responses of mother rats to nest site disturbance, nor about the responses of the young to being transported. In the first experiment, I determined the period during lactation when mothers will reestablish their nest in a new location after their original nest has been disturbed. Subsequently, I discuss the stimuli which provoke maternal transport of young, as well as the role of the pup in both the elicitation and facilitation of transport behavior in mother rats.

CHAPTER I

Experiment 1

Calhoun (1962a) found that when the nest of a lactating rat living in semi-natural conditions was disturbed by lifting the cover of her nest box, the mother would frequently build a nest at some other location and transport each litter member to it. He also reported an instance of transport behavior occurring after a burrow had been inundated during a rainstorm. In this case, the mother transported her young to a drier location in which there already was a nest present, and then transported them back to the home burrow after it had dried. Transport may also occur when the nest is invaded by a strange rat (Calhoun, 1962b).

Since I wanted to study transport behavior systematically under controlled conditions, I first had to determine whether lactating rats would exhibit the behavior that had been described in the field in the laboratory. I was also interested in determining whether the same pattern of transport behavior would be exhibited at different stages of lactation. I, therefore, disturbed the nest sites of lactating rats on each day of lactation, and recorded both the latency to begin transport of the litter to a new nest site, and the proportion of mothers which transported their entire litter during the test session.

Method

Subjects

The subjects were 10 Wistar albino female rats, purchased as virgins (225-250 g) from Canadian Breeding Farms, St. Constant, Quebec.

Procedure

The females were mated, and approximately 3 days before parturition were placed individually in large wire mesh floor cages (91 x 91 x 30 cm) which contained two wooden nest boxes (29 x 29 x 15 cm) with detachable covers, each having two entrances (8 x 8 cm) located 8 cm above the floor of the box. The lights came on at 0900 hr and went off at 1900 hr. The females had ad lib access to food (Purina Laboratory Chow) and water. Paper strips were provided for nesting material. In all cases, the female chose one of the wooden boxes as her nest site, and used the paper strips to construct a nest. On the day of parturition, litter size was standardized at six pups. This procedure was accomplished as unobtrusively as possible, and the cover of the nest box was quickly replaced.

Each female was tested daily for transport behavior at approximately 1200 hr on days 0 (the day of parturition) through 30 postpartum. At the start of testing, the cover of the nest box, and all of the nest material in the box were removed. A timer was started when the cover was lifted. The observer remained quietly seated in the room, approximately 1 m from the cage, and the behavior of the mother was observed until transport of the pups occurred. If transport had not taken place within 30 min, the test was stopped, the cover of the nest box was replaced, and a transport latency of 30 min was assigned for that day.

Results and Discussion

As can be seen in Figure 1, transport was somewhat unreliable on days 0-2 of testing, with only 50-70% of mothers transporting all six of their pups during the test session. However, beginning on day 3, and continuing to day 14, at least 80% of mothers transported all of their pups, and all mothers transported at least once during the testing. The median latency to transport the first pup (Figure 2) was also low on days 3-14. After day 14, mothers were less likely to transport following nest site disturbance. Only one mother was observed to transport any young after day 20.

After the destruction of the nest, the mother typically spent several minutes in the nest box, rearing and sniffing, and then left the disturbed nest and returned several times. In no instance did a mother take a pup with her the first time she left the disturbed nest. In all cases the mother also entered the undisturbed box one or more times before transport began.

Figure 1

Percentage of mothers (N = 10) transporting their entire litter of six pups during the 30 min testing session when nest site was disturbed daily, from the day of birth (day 0) through day 30 of lactation.

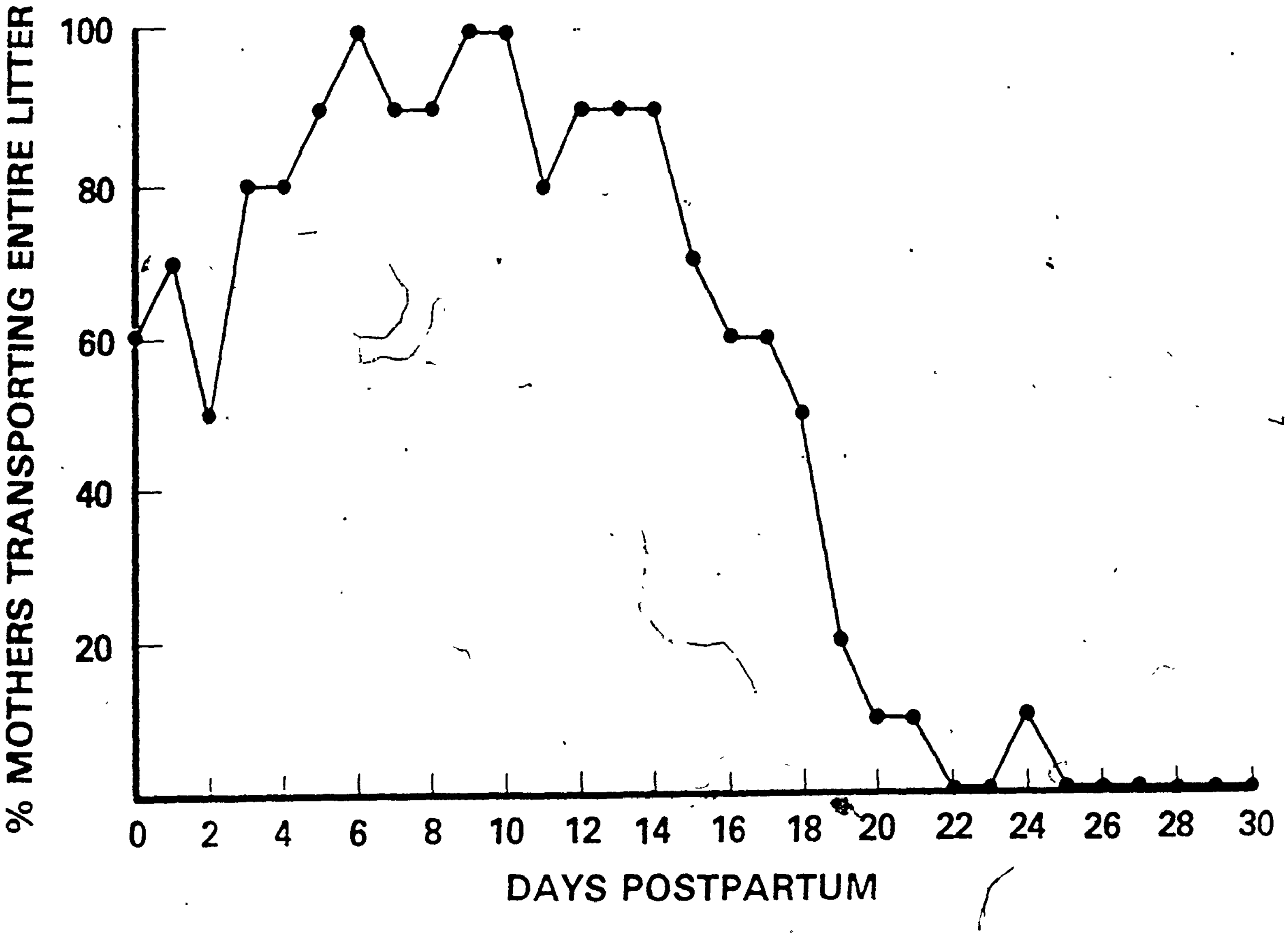
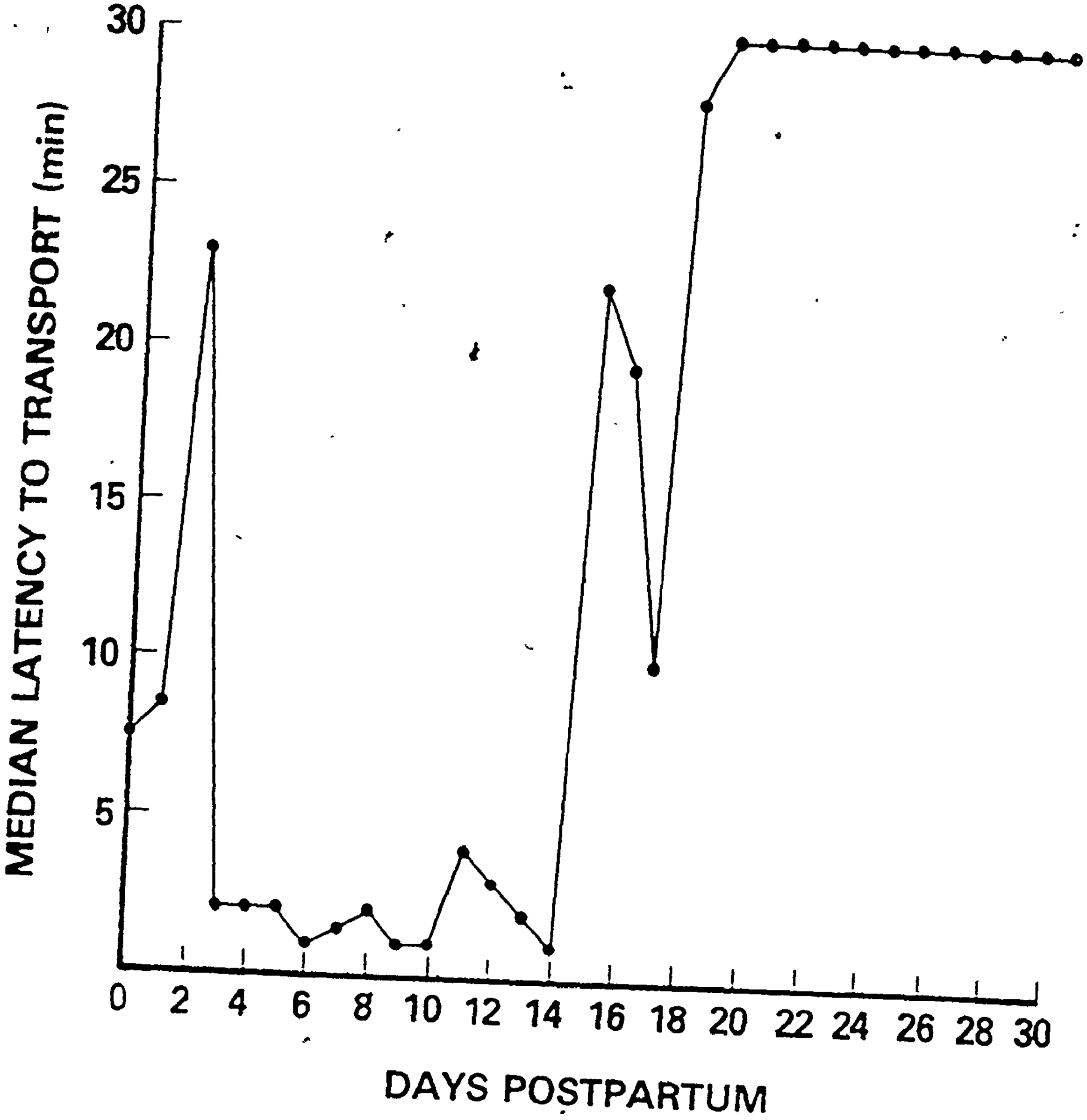

% MOTHERS TRANSPORTING ENTIRE LITTER
100
80
60
40
20
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
DAYS POSTPARTUM

Figure 2

Median latency of mothers (N = 10) to begin transport after nest site disturbance, when nests were disturbed daily, from the day of birth (day 0) through day 30 of lactation. Mothers not transporting during the testing session were assigned a latency of 30 min.


MEDIAN LATENCY TO TRANSPORT (min)
30
25
20
15
10
5
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
DAYS POSTPARTUM

Between days 0-14, the probability is .97 that, once the first pup has been transported, the rest of the litter will be immediately transported with no additional exploratory behaviors on the part of the mother. Between days 15-20, this conditional probability dropped slightly to .87. After day 20, the observed conditional probability was zero; that is, other behaviors always occurred between the initiation and the conclusion of transport.

These observations indicate that lactating rats will transport their young from a disturbed nest site in the laboratory, and the proximate causation of this behavior is thus amenable to study under controlled conditions. Moreover, transport behavior occurs during the time that the young are relatively helpless and immobile. The behavior begins to decline at approximately the beginning of the third week of lactation, as the pups are becoming capable of coordinated locomotion. This pattern of maternal responsiveness is similar to that observed for retrieval of displaced pups back to the nest (Rosenblatt, 1965, 1969; Rosenblatt & Lehrman, 1963).

Experiment 2

The results of Experiment 1 demonstrated that a disturbance of the nest site elicited transport behavior in most mothers until day 18 postpartum. The type of disturbance used consisted of the removal of the nest box cover and the actual destruction of the paper nest, resulting in the complete exposure of the young.

Mother rats have also been induced to transport their young when their nest box, located in a darkened area of the cage, was moved into an area of high illumination (Sturman-Hulbe & Stone, 1929). Sixty-six percent of the mothers moved their young back to another nest box which remained in the darkened area, while none of the control females moved their young after their nest boxes were moved from one area of high illumination to another. The behavior of these control subjects prompted Sturman-Hulbe and Stone to suggest that when no advantage is to be gained by moving the nest, as was the case when there was no darkened nest site available, the mother will remain in the original nest site. However, when a fan was placed adjacent to the nest to disturb the nest materials, or when electric heaters produced excessive heat in the vicinity of the nest, every female moved her nest at least once during the testing. These data suggest that mothers are not responding inflexibly to any nest site disturbance by transporting their young, but perhaps are in some way gauging the urgency of the situation, or the superiority of alternative nest sites before relocating their nest.

In the following experiment, nests were disturbed in several ways to determine the sorts of stimuli to which the lactating rat will respond by transporting her young, and to determine whether mothers will respond differentially to different types of disturbances. The disturbances chosen were similar to those reported by Calhoun (1962a) as eliciting transport in rats living in semi-natural conditions.

Method

Subjects

The subjects were 60 Wistar albino female rats, obtained as virgins from Canadian Breeding Farms.

Procedure

The females were mated, and, within 3 days of parturition, were placed individually in the floor cages under the same conditions as described in Experiment 1. The occurrence of parturition was determined by the appearance of a nest in one of the nest boxes, and by the squeals of the young, which could be heard when the cover of the box was slightly raised at one edge. The cover was not actually removed, to avoid disturbing the nest before the actual test, and litters were, therefore, not reduced in size.

Transport tests took place on either day 4 or day 12 postpartum, with six females being randomly assigned to each of three disturbance groups on each day, and 12 females assigned to each of two undisturbed control groups. The tests were started between 1200 and 1600 hr, at a time when the mother was in the nest box with her young.

In one disturbance group, the cover of the nest box was carefully removed, but the paper nest inside the box was left intact. The quality of the nest was noted according to the following scale:

3 Nest box full of paper, pups completely covered.
2 Walls of paper nest high, pups in small clearing in paper, partially covered with paper.
1 Walls of paper nest high, large clearing for pups, no paper covering pups.
0 Walls of paper nest low, only a padded mat.

A second disturbance corresponded to the procedure used in Experiment I. The nest box cover and all of the nest material in the box were removed, but the mother and pups were not actually touched. In a third group the nest box was slowly flooded (3.5 ml of water/sec) by inserting a Tygon tube, which was connected to an elevated reservoir of water at room temperature, into the nest box.

In the undisturbed group, the behavior of the mother was simply observed on the afternoon of the test day, commencing at a time when the mother was in the nest. In both groups in which the cover of the box was removed, a timer was started when the cover of the box was lifted. In the flooded group, the timer was started when the flow of water was started. The behavior of the mother in all groups was observed until transport had occurred, or for a maximum of 3 hr. A transport latency of 180 min was assigned if no transport occurred during the test session.

Results

Table 1 shows the observed frequencies of transport behavior on days 4 and 12 when the nest is undisturbed, or disturbed as described above. When the nest was not disturbed, not a single mother transported her young, but any disturbance of the nest site, however, increased the probability of transport.

In order to determine whether the mothers responded differentially to the different types of disturbance used, an analysis of variance was performed on the latencies to transport the first pup for all of the disturbance groups. The undisturbed group was not included in this analysis. Figure 3 shows the median latency to transport the first pup after each type of disturbance.

Because the variances of the disturbance groups were not homogeneous, the raw scores were subjected to a logarithmic transformation, and the analysis was performed using these transformed scores. The analysis of variance indicated that there was a significant main effect due to type

Table 1

Observed frequency of transport on day 4 and day 12 after various types of nest site disturbance.

Table 1

Day 4

Nest Site Disturbance

	No Disturbance	Remove Cover	Remove Cover and Paper	Flood
Transport	0	5	6	6
No Transport	12	1	0	0

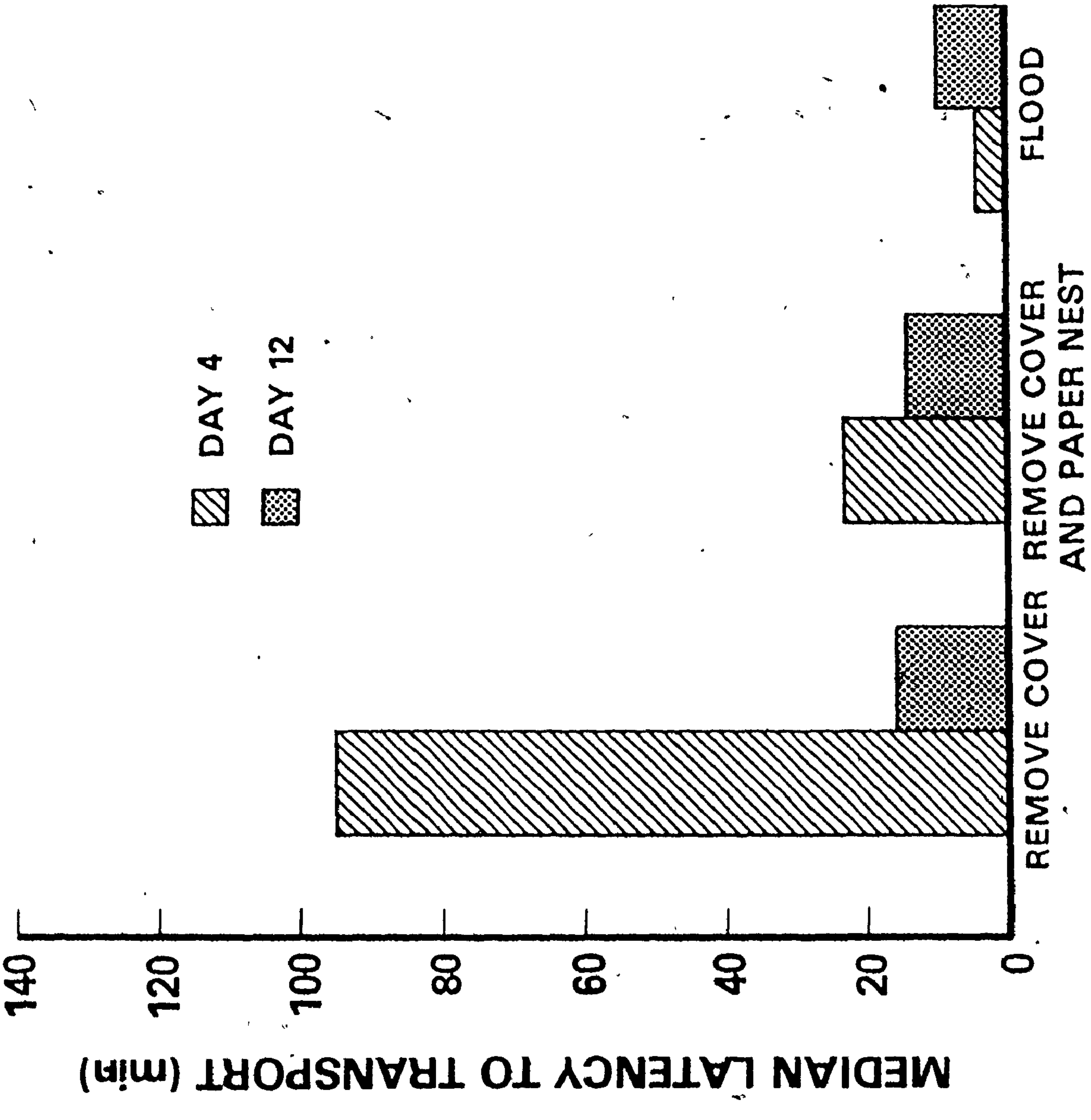
Day 12

Nest Site Disturbance

	No Disturbance	Remove Cover	Remove Cover and Paper	Flood
Transport	0	6	6	6
No Transport	12	0	0	0

Figure 3

Median latency of mothers to begin transport after various types of nest disturbance. Each mother was tested only once. Mothers not transporting during the testing session were assigned a latency of 180 min. N = 6 in each group.


MEDIAN LATENCY TO TRANSPORT (min)
0
20
40
60
80
100
120
140
▨ DAY 4
▩ DAY 12
REMOVE COVER
REMOVE COVER AND PAPER NEST
FLOOD

of disturbance ($F(2,30) = 12.68$, $p<.001$) and a significant interaction between days postpartum and type of disturbance ($F(2,30) = 5.16$, $p<.05$), but no overall effect of days postpartum ($F(1,30) = .84$, $p>.05$). Multiple comparisons of the transformed group means using the Scheffé method (Siegel, 1956) indicated only one significant comparison: day 4 mothers in the group in which only the nest box cover was removed had a significantly longer latency to transport than day 4 mothers in the group whose nest was flooded ($p<.05$). Latency to transport in the group whose nest was destroyed was intermediate, and was not different from the other two groups. The latencies to transport after the different types of disturbance were not significantly different on day 12.

As in the previous experiment, no mother took a pup with her the first time she left the disturbed nest. Typically, the mother investigated the disturbed nest box for a period of time, then left the nest and investigated the entire cage, including the undisturbed box, before transporting the first pup. Again, once the first pup had been transported, the rest of the litter was quickly transported.

The nests of the day 4 females ($\bar{X}$ rating = 2.2) were of significantly higher quality than the nests of day 12 females ($\bar{X} = 1.3$)($t = 3.1$, $p<.02$).

Discussion

Sturman-Hulbe and Stone (1929) have suggested that when no advantage is to be gained by changing nest sites, the female will remain in the original nest. The results of this experiment support that suggestion. When the nest was not disturbed, not a single mother transported her young, but each type of disturbance of the nest site, however, increased the probability that the female would reestablish her nest in a new location. Furthermore, it was also shown that day 4 mothers do respond differentially to different types of nest disturbance which could be interpreted as being of different levels of severity. The day 4 mothers took significantly longer to transport when only the nest box cover was removed than when the nest was flooded.

Day 12 females, however, did not respond differently to the three types of disturbance. This lack of a differential response may have occurred because, although the removal of the cover of the nest box exposed the paper nest on both day 4 and day 12, the effect of this treatment may have been more severe on day 12, since the nests of day 12 dams were not as well maintained as those of day 4 mothers. On day 4, nests generally contained a large quantity of paper, woven into a fairly tight mass, with high walls built around the mother and pups, often completely concealing them. By day 12, however, the quality of the paper nest had declined, and the mother and litter typically were not covered by nest material. Thus, removing the cover of the nest box was more likely to expose the day 12 mother and litter than the day 4 mother and litter. This factor may have accounted both for the tendency of day 12 mothers to initiate transport more quickly than day 4 mothers after removal of just the nest box cover, and for the fact that day 12 mothers transported as quickly after this type of disturbance as they did when their nests were flooded. The effects of flooding or complete removal of the paper nest did not depend on nest quality, and both day 4 and day 12 mothers transported relatively quickly after these disturbances. These data suggest that exposure of the mother and/or pups may be one of the factors which will induce the mother to transport her young to a more sheltered location.

Experiment 3

In the previous experiment, it was shown that lactating rats respond to several types of disturbance of their nest site by transporting their young. It is possible that the female is reacting directly to the disturbance of the nest, and is simply removing her young from a place which has become unsuitable either for the pups or for herself (Ewer, 1973). On the other hand, the disturbances chosen may have caused the pups to experience distress, and the mother may be responding to distress signals from the pups by transporting them to a new nest site.

In fact, the young of a number of rodent species, including rats, emit ultrasonic calls when they are in distress (Allin & Banks, 1971; Bell, 1974; Hart & King, 1966; Nitschke, Bell, Bell, & Zackman, 1976; Noirot, 1966; 1968; Noirot & Pye, 1969; Okon, 1970; 1971; 1972; Oswalt & Meier, 1975; Sales & Pye, 1974; Sewell, 1968), and that adult rodents can perceive these sounds (Dice & Barto, 1952; Gould & Morgan, 1941; Gourevitch & Hack, 1966; Sales & Pye, 1974) and will orient to them (Ralls, 1967; Sewell, 1970). Several authors have suggested that ultrasounds might induce the mother to search for a displaced pup and retrieve it back to the nest, (Allin & Banks, 1971; Sewell, 1968; 1970). Indeed, Allin and Banks (1972) have presented evidence that recorded pup ultrasounds induce some mothers to leave the nest and investigate the source of the sounds. However, there has not actually been a demonstration that pups emitting ultrasounds are retrieved with a higher probability or a shorter latency than pups not emitting ultrasounds. Moreover, since high frequencies are attenuated very rapidly and are only audible very close to their source (Sales & Pye, 1974), ultrasounds would seem to be an unreliable mode of communication unless the mother and pup were already in close proximity.

If the nest disturbances used in the previous experiment actually did induce ultrasonic distress calls from the pups, such calls may have increased the probability that the mother would transport the pups to a new nest. Indeed, the pups might even emit ultrasounds differentially after the different types of disturbance, which might account for the differential maternal response observed. If this were the case, then when pups are prevented from emitting ultrasounds, one would expect to find a decreased probability of transport, or perhaps an increased latency to begin transport. In the following experiment, all of the pups in each litter were anesthetized to prevent any response by them to the nest site disturbance, and the latency of the mother to begin transport was recorded.

Method

Subjects

The subjects were 72 Wistar albino female rats purchased as virgins from Canadian Breeding Farms.

Procedure

To allow the removal of pups from the nest box without handling or disturbing the mother, each female was trained to associate an auditory cue with the availability of water. The mothers would then leave their nest box and enter a small box within their cage where water was available when the auditory cue was presented. The manipulations of the pups were performed while the mother was drinking.

The virgin females were first placed with males in breeding cages, where water was available for approximately 8 hr/day. Each evening at 2300 hr the water bottles were removed, and approximately 16 hr later, the bottles were replaced while an auditory cue (keys jangling) was presented. This procedure was repeated daily during gestation, and all of the subjects learned to associate the auditory cue with the availability of water. Approximately 3 days before parturition, each female was placed in one of the large floor cages described in Experiment 1. In addition to the two nest boxes already described, there was also a small wire mesh and metal box (19 x 18 x 18 cm), having an entrance (7 x 7 cm) which could be closed by a sliding panel. The females had to enter this box to obtain water. Two days of acclimatization to the new environment were allowed before the water deprivation schedule was resumed.

Each day, upon presentation of the auditory cue, the female would leave her nest box and enter the watering box.

The sliding door of the box was then closed for 10 min, to accustom the female to confinement in the box. For the remainder of the 8 hr watering period, the female was allowed to enter and leave the water box at will. Each subject was confined in the watering box a minimum of five times before the day of testing, although two to three repetitions of this procedure were sufficient to eliminate escape attempts.

On the test day, while the female was confined in the watering box, the pups were removed from the nest box. In the experimental groups, six pups received the anesthetic (Tribromoethanol in a polyethylene glycol solution, .02 mg/gr body weight, injected intraperitoneally). In the control groups six pups received an equivalent volume of the vehicle solution. The six pups were then replaced in the nest, any paper which had been covering the pups and the cover of the box were replaced, and the mother was allowed to leave the watering box. This entire procedure took less than 10 min.

Transport tests took place approximately one hr later, after the mother had rejoined her pups. Again, subjects were tested on either day 4 or day 12, using the three disturbance procedures described in Experiment 2. The flow of water in the flooded condition was 6.5 ml/sec.

In all groups in which pups were anesthetized, the absence of ultrasonic cries was confirmed with the use of a Holgate ultrasonic receiver (Model MKV) tuned to transform ultrasounds at a frequency of 40 ± 10 kHz into audible sounds.

This is the range of ultrasounds which I found to be emitted most frequently by distressed infant rats (see also Allin & Banks, 1971). These transformed ultrasounds were monitored with earphones, to prevent the mothers from being disturbed by the noise. Presence or absence of ultrasonic calling was also monitored in the control groups. In addition, every 10 min during the testing, a wide range of frequencies was briefly monitored, in order to detect any ultrasonic cries that were not within the 30-50 kHz range.

Results

Table 2 shows the observed frequency of transport after each type of nest disturbance. Anesthetizing the pups did not decrease the probability of transport after any of the nest disturbances (*p*'s>.05, Fisher Exact Probability Test, Siegel, 1956).

Figure 4 shows the median latency to begin transport. As in the previous experiment, the variances of the latency data were not homogeneous, so the raw scores were transformed into logarithms, and an analysis of variance was performed using these log scores. There was a significant main effect on latency to transport due to type of disturbance (*F*(2,60) = 42.5, *p*<.001) and day of testing (*F*(1,60 = 17.96, *p*<.001), but there was no effect due to the anesthetization of the pups (*F*(1,60) = 0, *p*>.05). Anesthetized pups were transported as

Table 2

Observed frequency of transport on day 4 and day 12 after various types of nest site disturbance, when pups are anesthetized (Asleep) or injected with the vehicle for the anesthetic (Awake).

Table 2

Day 4

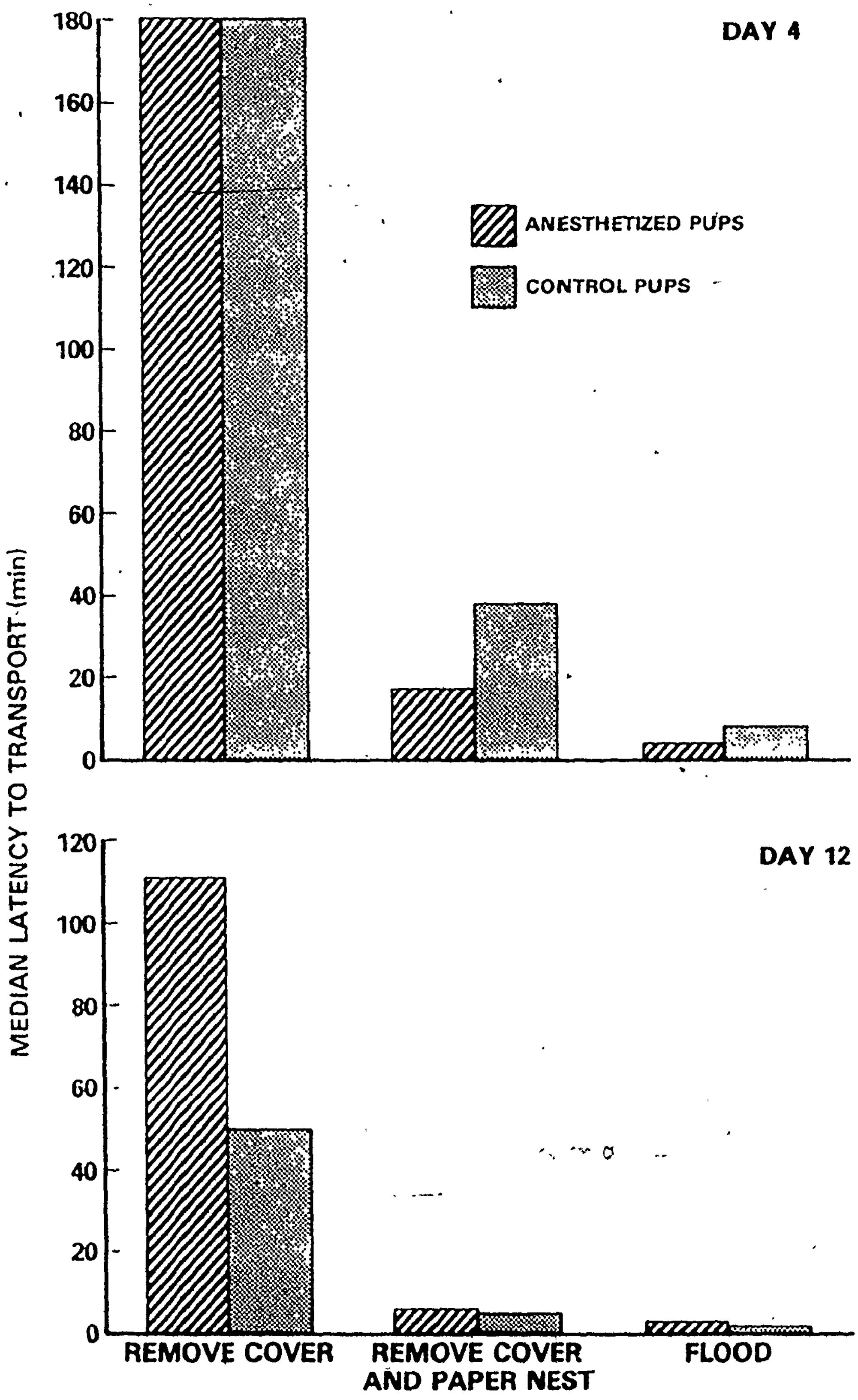
	Remove Cover		Remove Cover and Paper		Flood	
	Pups		Pups		Pups	
	Awake	Asleep	Awake	Asleep	awake	Asleep
Transport	1	2	6	6	6	6
No Transport	5	4	0	0	0	0

Day 12

	Remove Cover		Remove Cover and Paper		Flood	
	Pups		Pups		Pups	
	Awake	Asleep	Awake	Asleep	Awake	Asleep
Transport	5	3	6	6	6	6
No Transport	1	3	0	0	0	0

Figure 4

Median latency of mothers to begin transport after various types of nest disturbance when pups are anesthetized or awake (Control pups). Each mother was tested only once. Mothers not transporting during the testing session were assigned a latency of 180 min. N = 6 in each group.


180
160
140
120
100
80
60
40
20
0
DAY 4
ANESTHETIZED PUPS
CONTROL PUPS
MEDIAN LATENCY TO TRANSPORT (min)
120
100
80
60
40
20
0
DAY 12
REMOVE COVER
REMOVE COVER AND PAPER NEST
FLOOD

quickly as normal pups after each type of nest site disturbance on both day 4 and day 12. None of the interactions were significant.

Post hoc tests using the Scheffé method indicated that on both day 4 and day 12, the transport latencies of the groups in which only the nest box cover was removed were significantly longer than when the paper nest was destroyed, or when the nest was flooded, but the latter two groups were not different from each other. Although there was an overall effect due to day of testing, with day 12 mothers transporting more quickly than day 4 mothers, the latencies of day 4 and day 12 mothers in the same disturbance groups were not significantly different.

Although the results of these analyses suggest that pup distress signals play no role in the elicitation of transport, a consideration of the relationship between the probability of pup ultrasound emission and the probability of transport does suggest that ultrasonic cries play a role in the elicitation of transport behavior in the mother. Specifically, it was observed that when the nest box was flooded, all of the unanesthetized litters on both day 4 and day 12 emitted frequent ultrasonic calls. Removing the ultrasounds as a cue did not decrease the probability of transport, nor increase the mothers' latency to transport. Therefore, one can conclude that distress cries from the pups were not necessary to elicit transport behavior by the mother in this situation.

Moreover, distress signals from the young cannot account for the rapid response of the mother to the flooded nest. In the other disturbance situations, however, not all of the unanesthetized litters responded to the nest site disturbance by emitting distress cries.

When both the cover and paper were removed some ultrasonic cries were emitted by the unanesthetized pups of 67% of day 12 litters, and 33% of day 4 litters. However, those pups that did emit ultrasounds were not transported more quickly than those that did not, and every mother tested in this situation moved her pups during the test session. Therefore, after complete destruction of the nest as well pup ultrasounds seem to play no role in the elicitation of transport.

When only the cover of the nest box was removed, and the paper nest was left intact, 33% of the day 4 unanesthetized litters emitted ultrasounds (see Table 3); however, in this situation these were the only control litters to be transported. Ninety percent of all litters which did not emit ultrasounds were left in the disturbed nest for the entire 3 hr observation period. In each of these cases, the litters were completely concealed by a large paper nest. In other words, when the cover of the box is removed, and a large paper nest remains to conceal the pups, the probability of transport is significantly increased if the pups emit ultrasonic cries ($p < .05$, 1-tailed, Fisher Exact Probability Test). Only one

Table 3

Observed frequency of transport on day 4 after removal of the nest box cover, when pup ultrasounds are present or absent.

Table 3

Day 4

	Ultrasounds Present	No Ultrasounds
Transport	2	1
No Transport	0	9

day 4 mother transported young that did not emit any ultrasounds, and these pups were in a nest which did not conceal them.

On day 12, 67% of unanesthetized litters emitted ultrasounds when the cover of the nest box was removed, but this did not significantly increase the probability that they would be transported (p>.05, Fisher Exact Probability Test). Although all mothers whose litters emitted ultrasounds transported, a number of mothers whose pups did not emit ultrasounds also transported (see Table 4A). Therefore, some factor other than distress cries must be responsible for the elicitation of transport in those cases. As with the day 4 groups, those litters which did not emit ultrasounds but were transported were contained in nests which did not completely conceal them. Also, some mothers in both the experimental and control groups failed to transport, and it was noticed that all of these mothers had built very large nests that completely concealed their litters and that none of these litters had emitted ultrasounds. When only those mothers whose litters did not emit ultrasounds are considered (see Table 4B), the presence of a nest which completely conceals the litter decreases the probability of transport (p<.05, Fisher Exact Probability Test).

Discussion

The results of Experiment 3 demonstrate that in those

Table 4

Observed frequency of transport on day 12 after removal of the nest box cover, when:

A. pup ultrasounds are present or absent;

B. there are no ultrasounds emitted by the litter, and the paper nest conceals or does not conceal the mother and her young.

Table 4

A.

Day 12

	Ultrasounds Present	No Ultrasounds
Transport	4	4
No Transport	0	4

No Ultrasounds

B.

	Nest Conceals Mother and Pups (Nest = 3)	Nest Does Not Conceal Mother and Pups (Nest < 3)
Transport	0	4
No Transport	4	0

situations where the paper nest was destroyed, or the nest was flooded, distress signals from the pups were clearly not necessary for the elicitation of transport. The implication of these data is that the mother rat appears to respond directly to the nest disturbance itself, rather than relying on pup distress cries to stimulate transport behavior. However, when only the cover of the nest box was removed, while the paper nest was left intact, two factors increase the probability that the young will be transported. First, when the paper nest conceals the litter, mothers whose pups emit ultrasounds are more likely to transport than mothers whose pups do not emit ultrasounds. In fact, in no case did a mother fail to transport pups which emitted ultrasounds. Second, when their pups did not emit ultrasounds, those mothers whose nests did not completely conceal their litters were more likely to transport than mothers whose nests did conceal their litters. In other words, either the presence of pup distress cries, or the absence of a nest which conceals the young may be sufficient to increase the probability of transport of the young. These two possibilities will be specifically tested in the following two experiments.

Experiment 4

The results of Experiment 3 suggested that mother rats were more likely to transport after removal of their nest box cover when the remaining paper nest did not conceal their pups, than when the pups were completely concealed by nest material. If this is the case, then mothers that are not able to build a large concealing nest should have a higher probability of transporting their pups than mothers who are able to build such nests.

In this experiment, a group of mothers was provided with wood shavings rather than paper for nest material. Although the wood shavings could be piled around the pups, it was not possible to construct a nest which would completely conceal the young. In addition, in order to eliminate the effect of distress signals from the pups on the probability of transport, litters were anesthetized before the nest disturbance.

Method

Subjects

The subjects were 12 Wistar albino female rats obtained as virgins from Canadian Breeding Farms.

Procedure

Subjects were bred, and trained to associate an auditory cue with the presence of water, as described in

Experiment 3. Approximately 3 days before parturition, the females were placed individually in the large floor cages. Conditions were identical to those described in Experiment 3, except that the only nest material available was small pieces of wood shavings, approximately 1-2 cm square (Sanilit, Ltd.), rather than strips of paper.

As in Experiment 3, the mothers were trained to enter the watering box to drink. On the test day all of the pups were removed from the nest, and six were anesthetized or injected with the vehicle solution, while the mother was confined in the box. Approximately 1 hr after the replacement of the six treated pups and the release of the mother, the cover of the nest box was removed, completely exposing the mother and pups. The absence of ultrasonic distress cries from the anesthetized pups was confirmed with the use of the ultrasonic receiver. The unanesthetized control litters were also monitored to determine whether they responded to the disturbance by emitting ultrasounds.

Only day 4 mothers were tested, since they normally built nests which concealed their pups when provided with paper strips. The behavior of the mother was observed until transport had occurred, or for a maximum of 3 hr.

Results

As can be seen in Table 5, which shows the observed frequency of transport in each group, the mothers having

Table 5

Observed frequency of transport on day 4 after removal of the nest box cover, when the nest is constructed of paper strips or wood shavings, and when pups are anesthetized (Asleep) or injected with the vehicle for the anesthetic (Awake).

Table 5

Day 4

	Paper Nest		Wood Shaving Nest	
	Pups		Pups	
	awake	asleep	awake	asleep
Transport	2	1	6	6
No Transport	4	5	0	0

nests of wood shavings were more likely to transport than mothers having paper nests ($p < .05$, Fisher Exact Probability Test). The groups of mothers having paper nests were subjects of Experiment 3 who had undergone the same training procedure as the mothers in this experiment.

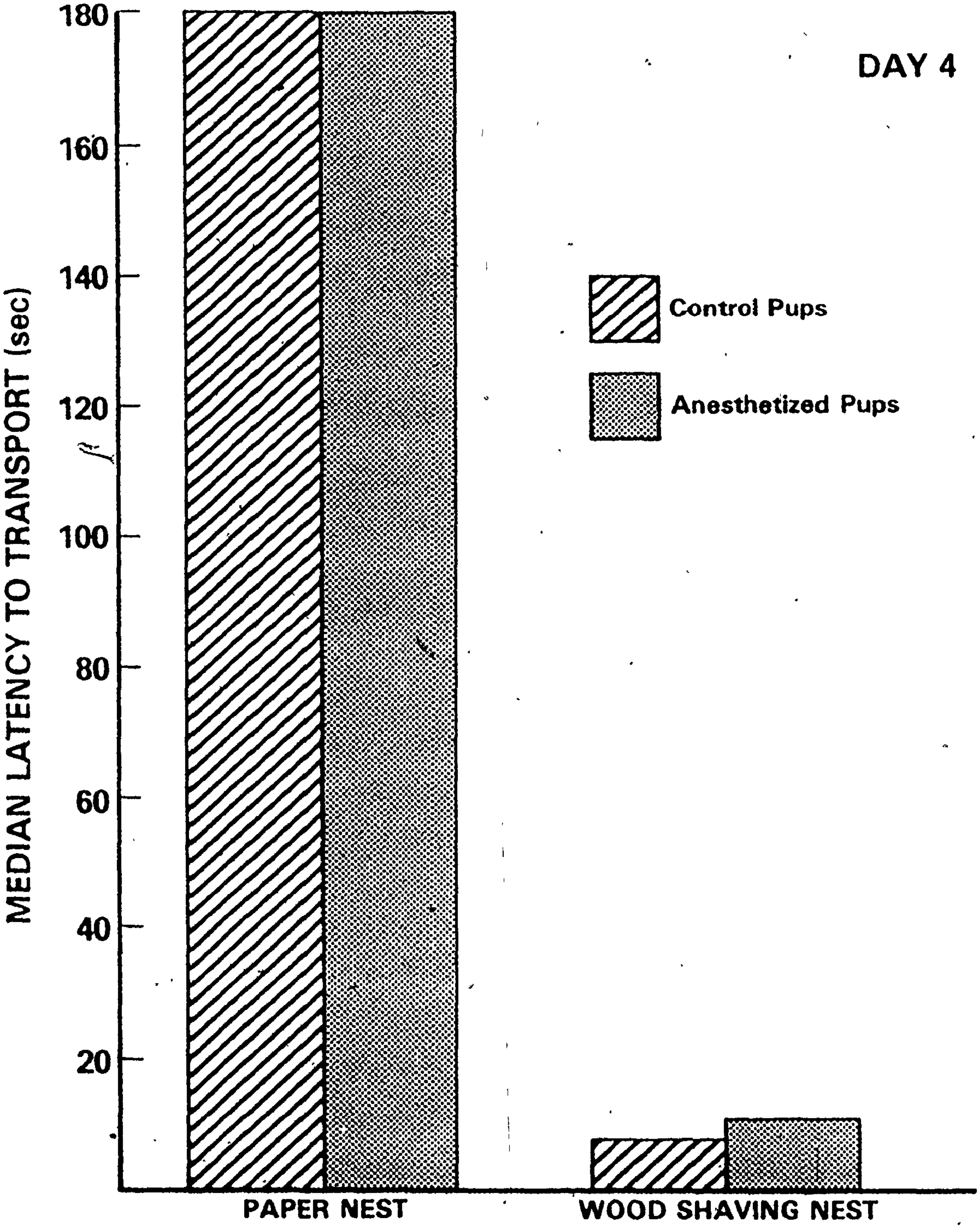
Figure 5 compares the median latency to begin transport after nest box cover removal when mothers had access to wood chips or paper strips for nest material. An analysis of variance performed on the latency data indicated that there was no main effect due to the treatment group of the pups ($F(1,20) = 2.67$, $p > .05$), nor was there an interaction between pup treatment and the type of nest material available to the mothers ($F(1,20) = 1.99$, $p > .05$); however, there was a significant main effect due to the type of nest material available ($F(1,20) = 38.1$, $p < .001$). The mothers that had wood shavings for their nest material transported significantly faster than those mothers who had access to paper strips, regardless of whether their pups were able to respond to the nest disturbance. In fact, all of the unanesthetized pups in the wood shaving nests did emit ultrasounds when the cover of the nest box was removed.

Discussion

As predicted from the results of Experiment 3, when pups are exposed by the nest disturbance, mothers are more likely to transport than when the same disturbance leaves

Figure 5

Median latency of mothers to begin transport after nest box cover had been removed when nest was built of either paper strips or wood shavings, and when pups were anesthetized or awake (Control pups). Each mother was tested only once. Mothers not transporting during the testing session were assigned a latency of 180 min. N = 6 in each group.


DAY 4
Control Pups
Anesthetized Pups
MEDIAN LATENCY TO TRANSPORT (sec)
180
160
140
120
100
80
60
40
20
PAPER NEST
WOOD SHAVING NEST

them concealed by a large paper nest. One can also conclude that distress signals from the pups are not necessary for the elicitation of transport when pups have been completely exposed by the nest disturbance. Although all of the unanesthetized litters in wood shaving nests emitted ultrasounds, eliminating those signals did not decrease the probability of transport, nor did it increase the latency to begin transport. These data suggest that one of the functions of the nest is to conceal the pups and/or the mother.

Experiment 5

In Experiments 3 and 4 it was found that distress cries from the pups were not necessary for the elicitation of transport by the mother, but the data suggested that ultrasonic distress cries from pups are sufficient to increase the probability of transport when the mother and litter are still concealed. If pup ultrasounds are sufficient to elicit transport, then adding ultrasounds in a situation where transport does not usually take place, or takes place after a long latency, should increase the probability of transport or decrease the latency to begin transport. In this experiment ultrasonic distress cries were experimentally introduced to the nest area after nest disturbance. Testing was done on day 4, when mothers build large, concealing nests, and pups in these nests do not typically emit distress cries when only the nest box cover is removed.

Method

Subjects

The subjects were 20 virgin Wistar albino rats obtained from Canadian Breeding Farms.

Procedure

As in Experiment 3, the females were mated, and then trained to associate an auditory cue with the availability of water, and to enter the watering box in the floor cage upon presentation of the auditory cue. On day 4 postpartum, while the mother was in the watering box, her pups were removed, six were anesthetized and replaced in the nest, and the mother was released. Transport tests were started approximately 1 hr later, after the mother had rejoined her pups. Only mothers with nests which completely concealed their young were tested.

After removal of the nest box cover, in the experimental group (N = 10) a day 4 pup culled from the female's own litter was handled for 3 min, directly behind the open nest box. Handling consisted of gently rolling the pup between the fingers, which caused the pup to emit frequent ultrasonic cries as detected with the ultrasound receiver tuned to 40 ± 10 kHz. Few, if any, audible cries were emitted by the handled pup. An anesthetized day 4 pup was presented in the same manner to the 10 mothers in the control group to equate olfactory and visual cues emitted by the stimulus pup. The mothers' own anesthetized litters were monitored with the ultrasound receiver to ensure that they did not emit ultrasounds. Only mothers with nests which completely concealed their young were tested.

The behavior of the mother was observed until all of the pups were transported, or for a maximum of 3 hr. Mothers not beginning transport within 3 hr were assigned a latency of 180 min.

Results

All of the mothers that had ultrasounds added at their nesting site after nest disturbance oriented toward the pup emitting the ultrasounds for the entire time it was presented. The control mothers did not orient toward the anesthetized stimulus pup.

Table 6 shows the observed frequency of transport in both groups. Ninety percent of mothers exposed to pup ultrasounds transported their young, while only 20% of mothers not exposed to ultrasounds moved their young ($p < .005$, Fisher Exact Probability Test).

Discussion

Experiments 3 and 4 have shown that pup distress signals are not necessary for the elicitation of transport behavior when the pups are exposed by the nest disturbance, or when the nest is flooded, but the results of the present experiment indicate that they are sufficient to increase the probability of transport when the mother and young remain concealed after nest site disturbance. The pups can thus play an active role in inducing their mother to transport them from a disturbed nest. These data establish for the first time a function of ultrasonic distress calls in infant rats.

Table 6

Observed frequency of transport on day 4 after removal of the nest box cover, when pup ultrasounds are added or when there are no ultrasound~~s~~ emitted by the litter.

Table 6

	Day 4	
	Ultrasounds Added	No Ultrasounds
Transport	9	2
No Transport	1	8

Experiment 6

In the previous experiment, a single pup emitting ultrasounds induced the mother to transport the entire litter. These distress calls may serve as a general alarm which stimulates the mother to transport without preference, or they may aid the mother in locating the individual pup emitting the call. If the latter were the case, those pups that emit ultrasonic cries in response to the nest disturbance might be the first to be removed from the disturbed nest to a place of safety. It was not possible to ascertain from the previous experiment whether mothers prefer to transport vocalizing pups first, since the pup emitting the ultrasonic cries was not actually present in the nest, and could not be chosen first for transport.

Although we know from Experiments 3 and 4 that silent pups will be transported, in this experiment I investigated the possibility that, when given a choice, the mother may transport pups that are emitting ultrasounds in preference to those that are not. I allowed only one pup in each litter to emit ultrasonic calls after a nest disturbance, and observed whether this pup was transported preferentially by the mother. If mothers do transport the vocalizing pup first, then those pups which emitted distress cries with the shortest latency, or cried loudest, might have a higher probability of surviving than their slower or quieter littermates.

Method

Subjects

The subjects were 12 Wistar albino female rats obtained as virgins from Canadian Breeding Farms.

Procedure

Six females were assigned to each of two groups, one group tested on day 4 postpartum and one group on day 12. The females were bred and subjected to the water-deprivation schedule that was described in Experiment 3. Approximately 3 days before parturition the females were placed in the floor cages under the same conditions as in Experiment 3. On the test day, the litter was reduced in number to six pups while the mother was drinking. Five of the pups were anesthetized, and the sixth pup was left untreated.

To facilitate identification of the normal pup, its tail was colored red with an indelible felt-tipped marker. The tails of the anesthetized pups were colored black with a similar pen. These six pups were replaced in a group in the nest box, and the mother was released. Approximately 1 hr later the nest was disturbed by flooding (3.5 ml/sec). The behavior of the mother was observed until transport of the young had occurred. Particular attention was paid to the order in which the young were removed from the flooded nest box. It was expected that, if pup ultrasounds do facilitate the location of distressed pups, then the awake, vocalizing pup would be transported before the anesthetized pups. I realized, however, that the awake pup might emit cues other than ultrasonic cries which could contribute to any observed maternal preference for transporting it. If the awake pup were transported preferentially, I would not be able to conclude that ultrasonic cries were specifically responsible for this maternal preference. However, if no preference was observed, then it would indicate that distress cries from the pups are a stimulus for litter transport, and are not used to locate the pup emitting the cries.

The emission of ultrasonic calls by the awake pup was confirmed by monitoring the litter with the ultrasound receiver. Lack of ultrasonic calling was individually confirmed in the anesthetized pups immediately before replacing them in the nest, and immediately after the transport test had ended, while the pups were still wet.

Results

The observed order in which the vocalizing pup was transported from the disturbed nest was compared with the theoretical order if pups were selected for transport at random, by use of the Kolmogorov-Smirnov One-Sample Test (Siegel, 1956). This test indicated that on both day 4 and day 12 the mother transported pups in random order. The awake, vocalizing pup was not transported in preference to the anesthetized pups (D = .17 and .33, on days 4 and 12, respectively, p's>.05).

Discussion

Although the mother responds to pup distress signals after nest site disturbance with an increased probability of transport, she responds to the entire litter, rather than to the individual distressed pup. While it is undoubtedly to the mother's advantage to transport all of her young to a new nest site after nest disturbance, it is perhaps surprising that she does not prefer to transport first those young that indicate that they are in distress. However, the mother's failure to have a differential response to individual pups emitting ultrasounds has the effect of precluding the possibility that littermates can compete with each other for the mother's attention in this situation.

For example, after some types of nest disturbance, such as flooding, the mother may not be able to remove all of the pups from the nest safely, and a pup might be able to ensure, by crying first or loudest, that it was the first to be removed from the nest. This situation would encourage pups to emit distress calls at the slightest disturbance, or cry more loudly than their distress warrants, in order to ensure that they were among the first transported to safety in the event that the disturbance proved serious. As long as the mother preferred to transport pups that made distress signals, any pup which did not join in the competition would be left until last and would probably fare worse than its noisier siblings. However, if this pup strategy caused instances of unneccessary transport, or attracted the attention of predators, it would be maladaptive for both the mother and the pups.

The mother could avoid being deceived by her pups by totally disregarding their distress cries, and transporting only when she determined that the situation warranted it, but by using this strategy she may fail to respond appropriately to their distress cries when they are truly in distress. However, if the mother responds to pup distress signals by transporting all of the litter in apparantly random order, a pup would have little to gain by unnecessarily being the first to emit distress cries after a nest disturbance, or crying louder than his siblings. Pups should cry only if truly distressed. Moreover, any benefits gained by emitting distress cries after nest site disturbance are gained for the entire litter.

SUMMARY

In the preceding series of experiments, lactating rats were observed to respond to nest site disturbance by transporting their young to a new nest site, until about the middle of the third week postpartum. The data suggest that the mother may be employing two strategies to ensure that her young continue to be nurtured in a safe place. First, mothers transport when they are disturbed at their nest site, regardless of whether the pups appear to be in distress. Exposure of the concealed pups, destruction of the nest, and flooding of the nest were sufficient to elicit transport of the young, even in the absence of distress signals from the young. While the mothers' behavior may not be in direct response to stimuli emitted by the pups, it may increase the probability that both mother and young will survive the disturbance.

Second, mothers respond to distress signals from the pups by moving them to a new nest site after nest disturbance, even under circumstances which did not ordinarily elicit transport of young in the absence of distress signals. The pups can thus play an active role in promoting their own well-being by emitting distress signals.

The present work has also shown that distress cries from a single pup are sufficient to elicit transport of the entire litter. The mother also does not discriminate among the pups, thereby minimizing competition between siblings to be transported first from the disturbed nest.

CHAPTER II

In Chapter I, I presented data indicating that the infant rat could play a part in inducing the mother to reestablish her nest site after nest disturbance. It seems possible that the young might also behave in such a way as to facilitate their transport to a new nest site while they are being carried. Indeed, the offspring of some mammals assume a limp posture and do not struggle while being carried by their parent. Typically, the fore and hind feet simply hang limply, with the digits widely splayed, and the young remain relative motionless. The young of ring-tailed cats (Bassariscus astutus, Richardson, 1942), domestic cats (Felix cattus) and dogs (Canis familiaris)(Snyder, 1923; Kleiman, 1974), and acouchi (Myoprocta pratti pocock, Kleiman, 1972) have been reported to exhibit this response.

In many species of mice the young are pictured or described as curling their bodies in a semicircle, or curling around the neck of the mother when the infant is carried by the belly (Peromyscus leucopus noveboracensis, Hall, 1928; Svihla, 1932; Peromyscus maniculatus, Huestis, 1933). Similar curled postures are also described in infant squirrels (Sciurus carolinensis, Hatt, 1927; Nichols, 1958;

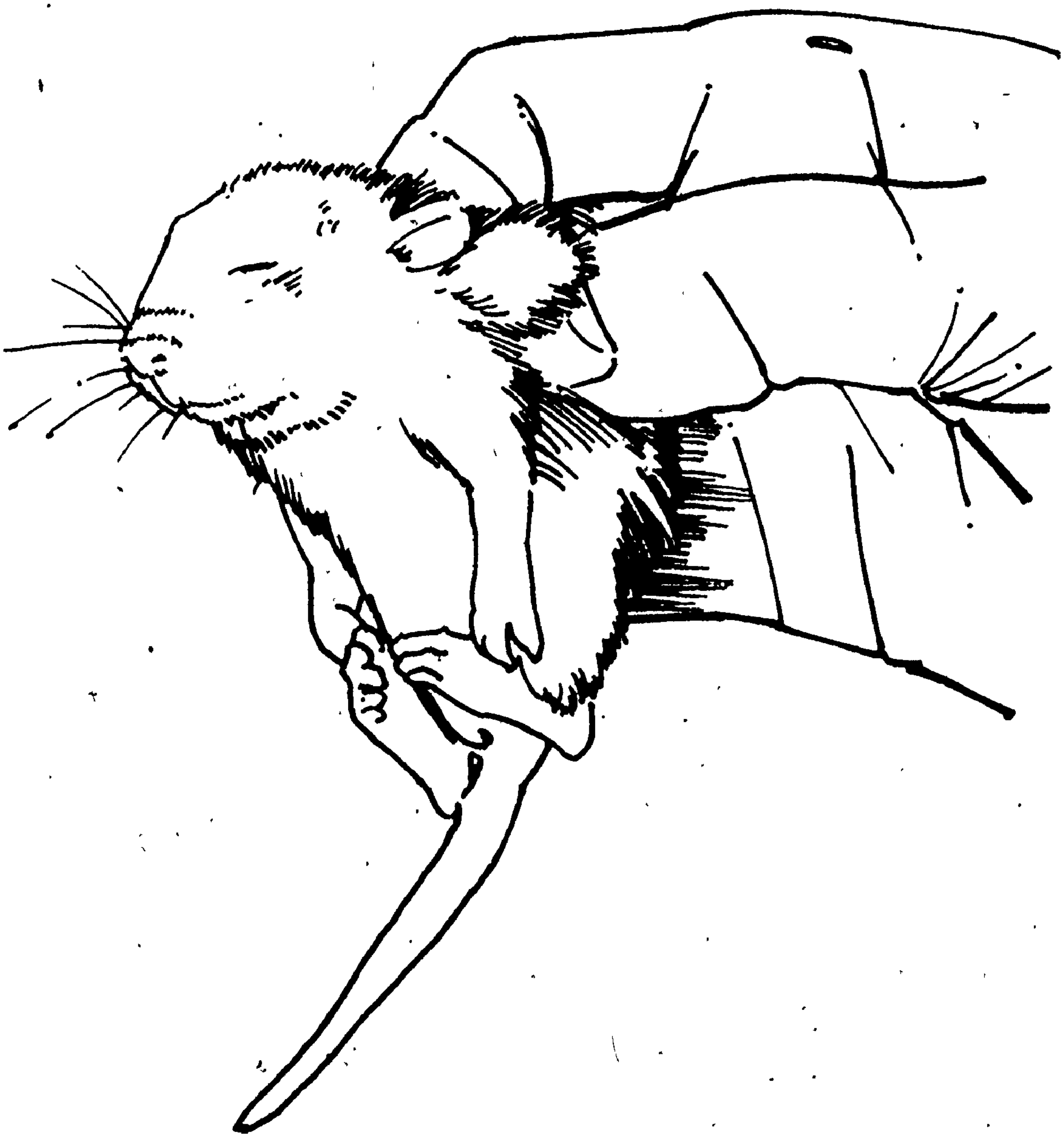
1923); Glaucomys volans saturatus, Svihla, 1930), as well as chipmunks (Eutamias dorsalis dorsalis, Svihla & Svihla, 1930), woodchucks (Marmota monax, Burtt, Maiorana, & Hailman, 1975), bushbabies (Galago senegalensis moholi, Doyle, Anderson, & Bearder, 1969), woodrats (Neotoma albigula, Richardson, 1943), and the red mongoose (Herpestes sanguineus, Ewer, 1973).

Observations of the rat pups being transported in the preceding set of experiments revealed that even the mobile pups of day 12 or older did not normally struggle or resist the attempts of the mother to pick them up. Nor did they hang passively limp, but instead adopted a characteristic posture in which all of the extremities were tucked in close to the body. Figure 6 shows a pup of 15 days of age exhibiting what will be referred to as the transport response. Both the forelegs are adducted against the body, both hind legs are flexed and held close to the body, and the tail is curled toward the belly.

In the following experiments, I investigated the proximate causation, the development, and the functional significance of this transport response of the infant rat.

Figure 6

Drawing from photograph of infant albino rat aged 15 days exhibiting the transport response.



Experiment 7

I first determined the sort of stimulation that is required to elicit the transport response. Observations of mother rats transporting their young suggested several types of stimuli which might be involved in the elicitation of the transport response. For example, activation of stretch receptors in the limbs or mechanoreceptors in the foot pads may indicate to the pup that it has been lifted off the ground. Similarly, the activation of the vestibular apparatus by the slight shaking to which the pup is subjected as the mother carries it may elicit the transport response. It is also possible that the olfactory, auditory, or visual stimuli associated with the mother elicit the transport response in the pups. The most obvious possibility, however, is that stimulation of the mechanoreceptors of the pup's skin by the mother's teeth elicits the transport response. The following experiment was an attempt to discover whether the tactile stimulation of the skin normally received from the mother's teeth is necessary to release the transport response in infant rats.

Method

Subjects

The subjects were 36 albino Wistar rat pups, 16 to 20 days of age, born in the laboratory colony to multiparous females.

Procedure

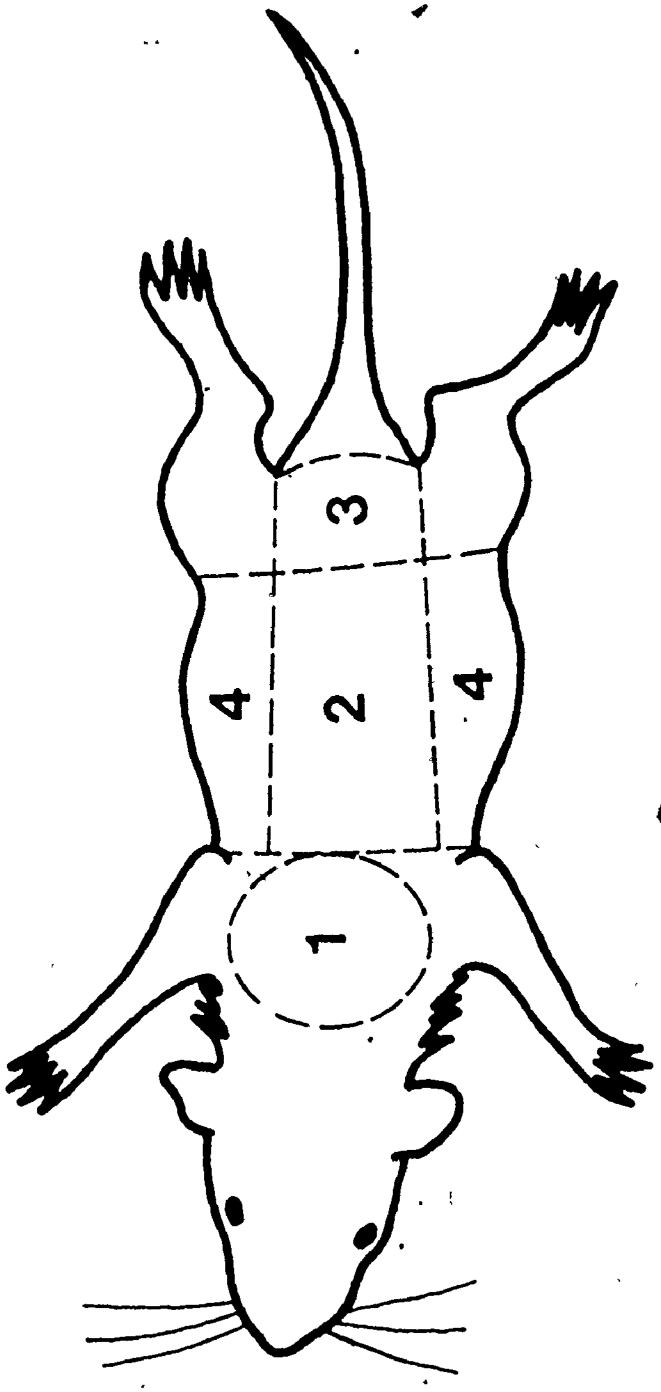
Six pups were randomly assigned to each of the experimental and control groups. In order to investigate the response systematically, but without the necessity of inducing mothers to transport young, the transport response was elicited by the experimenter by grasping the skin of the pup with the forefinger and thumb. The dorsal surface and flanks of each pup were shaved, and test areas were then outlined on the pups' backs with a felt-tipped marker. I elicited the transport response from three areas on the pups' bodies: the nape of the neck, the mid dorsal region, and the flank (corresponding to areas 1, 2, and 4, respectively, in Figure 7).

The characteristics of the postural response were coded by allowing 5 possible points for the response: 1 point for each forearm adducted against the body, 1 for each hind limb flexed against the body, and 1 for the tail being curled between the legs and toward the belly.

The score for the transport response elicited by grasping each of the three test areas was then recorded for each pup before any experimental manipulation took place (Pre Test). The order in which the different areas were tested was randomly varied for each pup. Care was taken that only the skin outlined for each area was stimulated. After the Pre Test responses had been recorded, either 1 mg

Figure 7

Skin areas of infant rats which were grasped to elicit the transport response.


1
2
3
4
4

of 2% Xylocaine (Lidocaine hydrochloride, a local anesthetic) or the same volume of isotonic saline was injected subcutaneously into one of the outlined areas of the body. The extent of the anesthetized skin was mapped on the pup's back in a contrasting color of marker, by pricking the skin with a needle and recording whether the pup responded by squealing or by reflexive contraction of the area. This ensured that anesthetized skin was not grasped unintentionally when testing unanesthetized areas, as the area of anesthesia sometimes entered the boundaries of an unintended area.

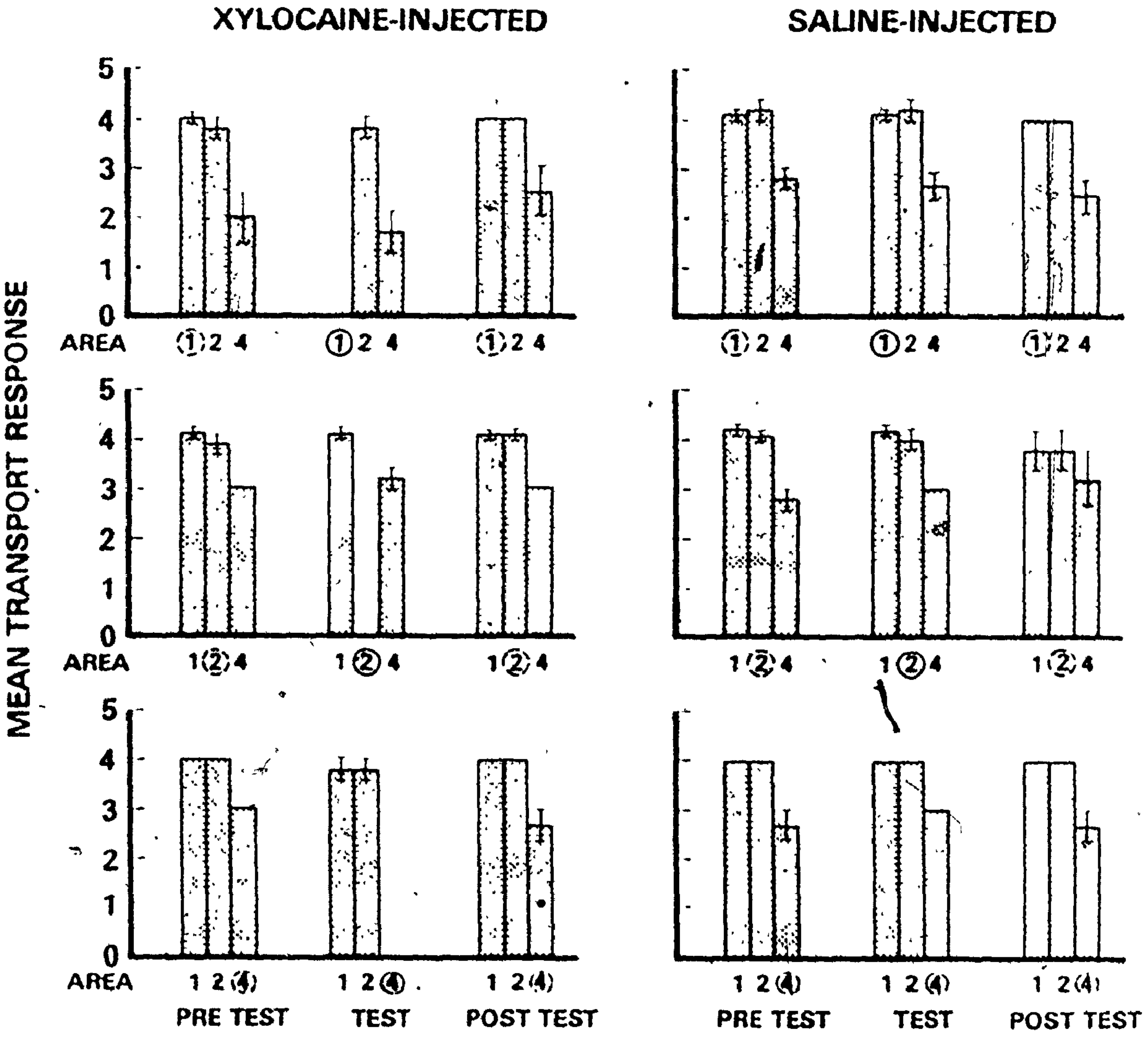
If the pup exhibited no response to the noxious stimulation, it was assumed that sensory information from that area of skin was eliminated. Then the pup was picked up again by each of the marked areas, including the injected area, in order to elicit the transport response, and the score for the response was recorded. In addition, all the pups were retested 24 hr later.

Results

Figure 8 shows the score for the posture elicited by stimulation of each area during each phase of the testing. The area which received the injection is circled. As can be seen in the figure, during the pre-injection test (Pre Test) the elicitation of the transport response was readily accomplished by stimulation of any of the areas tested. After

Figure 8

Mean transport response (maximum = 5) after injection of local anesthetic or saline in specified skin area. Pups (N = 6 in each group) were tested before injection (Pre Test), immediately after injection (Test), and 24 hours after injection (Post Test). Area of injection is circled. Vertical bars indicate ± 1 S.E.M.


XYLOCAINE-INJECTED
SALINE-INJECTED
MEAN TRANSPORT RESPONSE
5
4
3
2
1
0
AREA
①2 4
①2 4
①2 4
①2 4
①2 4
①2 4
1②4
1②4
1②4
1②4
1②4
1②4
1 2④
1 2④
1 2④
1 2④
1 2④
1 2④
PRE TEST
TEST
POST TEST
PRE TEST
TEST
POST TEST

the Xylocaine injection (Test) stimulation of all areas except the anesthetized area still elicits the normal response. Each pup thus serves as its own control against some general central effect of the drug. When the anesthetized area was grasped, no components of the transport response were seen in any of the pups. Typically, all of the limbs were extended, and often the pups struggled while being held.

Pups which had received saline injections showed the normal transport response when grasped by the injected area. The simple injection of fluid had no effect on the elicitation of the transport response. When the local anesthetic had worn off after 24 hr, the test was repeated (Post Test), and the transport response was again easily elicited from all areas.

Discussion

These data indicate that cutaneous stimulation is sufficient to elicit the transport response, although they do not rule out the possibility that other stimuli are also involved.

Experiment 8

Having established that the sensory stimulation of the skin (normally provided by the mother's teeth) is sufficient for the elicitation of the transport response, I then wanted to determine at what age the infant rat exhibits the transport response, whether the mother picks the pup up by a specific area of the body in order to elicit the response, and if stimulation of all body areas is equally effective in eliciting the response.

Method

Subjects

The subjects were 930 Wistar albino rat pups, born to primiparous and multiparous females living in the laboratory colony.

Procedure

Each female gave birth and raised her litter, culled to six pups on the day of birth, in a clear plexiglass cage (28 x 30 x 15 cm). Purina rat pellets and water were available ad lib, and paper strips were provided for nest material.

Pups were tested for the presence of the transport response on the day of birth (day 0) through day 30 postpartum. Each pup was tested on only one day, and 30 pups (5 litters of 6 pups) were tested at each age.

On the test day, the pups were removed from the nest and placed together in a small bowl. Each pup was tested for its response when grasped in various areas of the body. The scoring method described in Experiment 7 was used to quantify the response.

The body of the infant was divided into the four general areas shown in Figure 7, chosen because it has been reported that the mother usually grasps the pup on the dorsal surface of the body (Ewer, 1968; Causey & Waters, 1936). Areas 1, 2, and 4 correspond to those tested in Experiment 7.

The transport response elicited when the pup was grasped by each of these areas was recorded. The order in which each area was grasped was random for each pup, and at least a minute passed between the testing of each area in a single pup, in order to prevent adaptation of the response. After all the pups had been tested in this way by the experimenter, they were placed outside the nest area in the home cage. When the mother retrieved each one back to the nest area, both the transport response of the pup and the area of the pup's body which the mother grasped in her teeth was recorded.

Results

In order to calculate the proportion of pups which exhibited the behavior at each age, a transport response was defined as at least three extremities held against the body. Figure 9 shows the proportion of pups (N = 30 observations for each point) exhibiting the transport response when picked up by the experimenter and when carried by the mother. The response of pups which are carried by the mother is virtually identical to that elicited by the stimulation applied by the experimenter.

The figure also shows that there is a gradual development of the transport response. During the first 5 days after birth, less than 50% of the infants exhibited the transport response. When the very young pup was carried, it typically squealed and struggled. By day 10, the response was present in approximately 80% of pups.

Although virtually all mothers stop transporting by day 20, the pup transport response could still be easily elicited by the experimenter in a large proportion of pups until the end of the fourth week postpartum, after which time pups did not exhibit the response as readily, and would try to escape when grasped. (However, see Appendix.)

Figure 10 shows the probability of each pup body area being grasped by the mother, on days 0 through 20 postpartum, based on 30 observations of mothers carrying pups on each day. The mother rat grasps the pup anywhere on the dorsal or lateral surface of the body. Other areas (ventrum, head, legs) are rarely grasped.

The data on the effectiveness of grasping the

Figure 9

Percentage of pups (N = 30 on each day) exhibiting a transport response (three or more limbs held against the body), when carried by the mother, and when grasped by the experimenter.

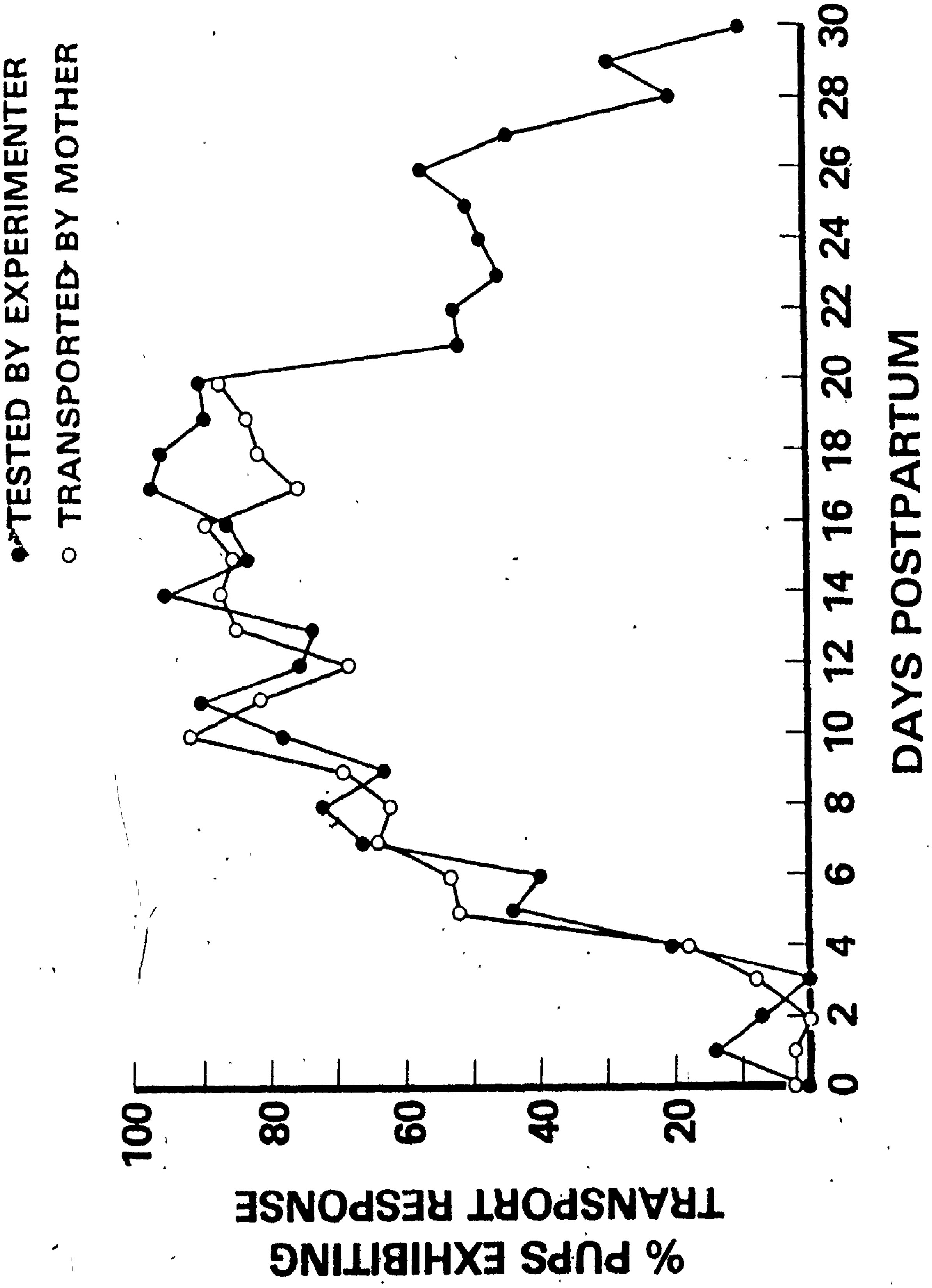
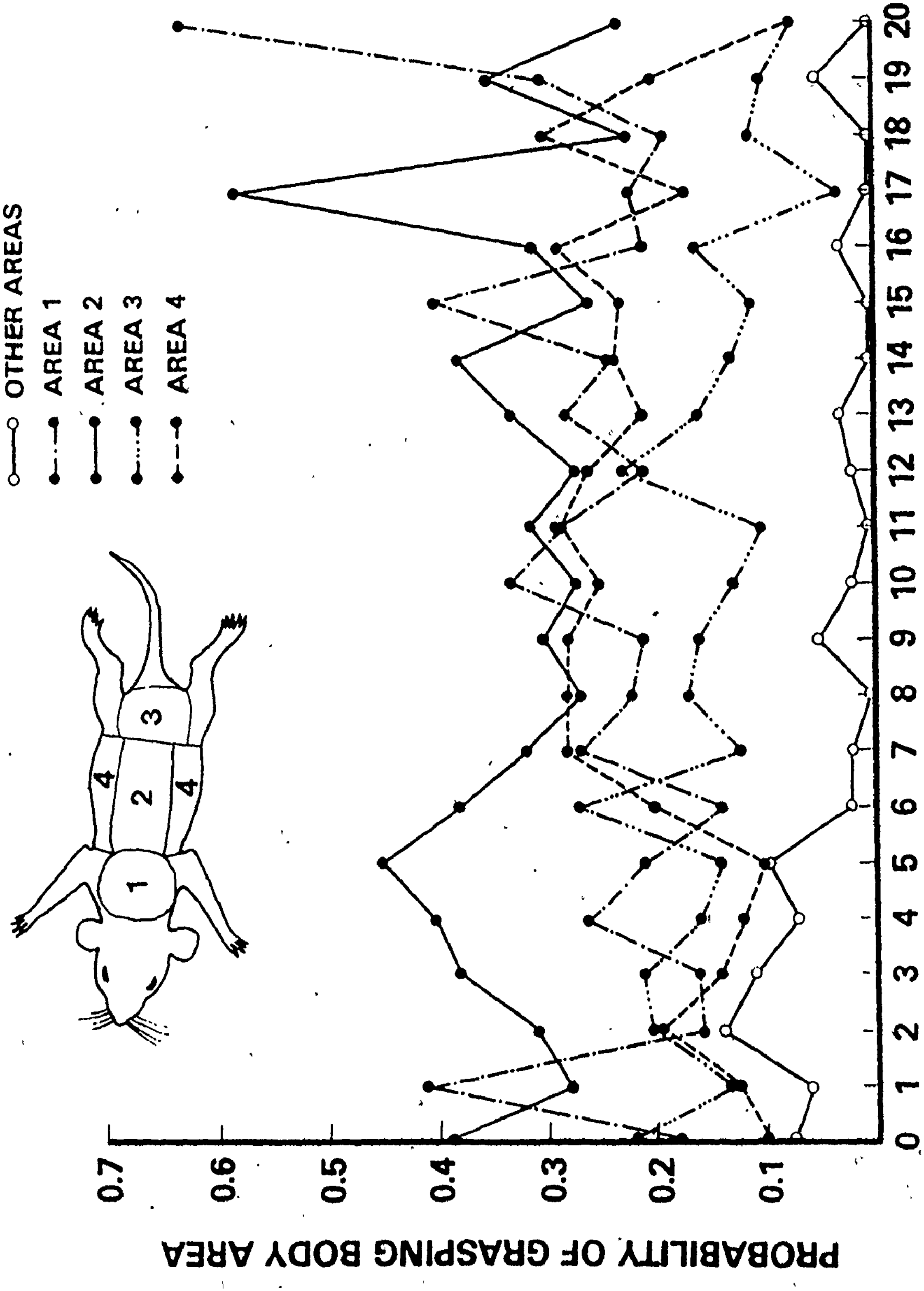

● TESTED BY EXPERIMENTER
○ TRANSPORTED BY MOTHER
% PUPS EXHIBITING TRANSPORT RESPONSE
100
80
60
40
20
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
DAYS POSTPARTUM

Figure 10

Probability of mother grasping each of the specified pup body areas during transport, based on 30 observations on each day.


OTHER AREAS
AREA 1
AREA 2
AREA 3
AREA 4
1
2
3
4
4
PROBABILITY OF GRASPING BODY AREA
0.7
0.6
0.5
0.4
0.3
0.2
0.1
DAYS POSTPARTUM
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

various areas of the body are contained in Figure 11, which shows the mean transport response elicited by the experimenter from each of the four areas tested. This figure also shows the gradual development of the transport response. The first components of the response to appear are the hind leg and tail flexion, occurring in a small percentage of pups as early as the day after birth, but usually later in the first week. The mean response does not approach the maximum score of 5 until approximately day 10.

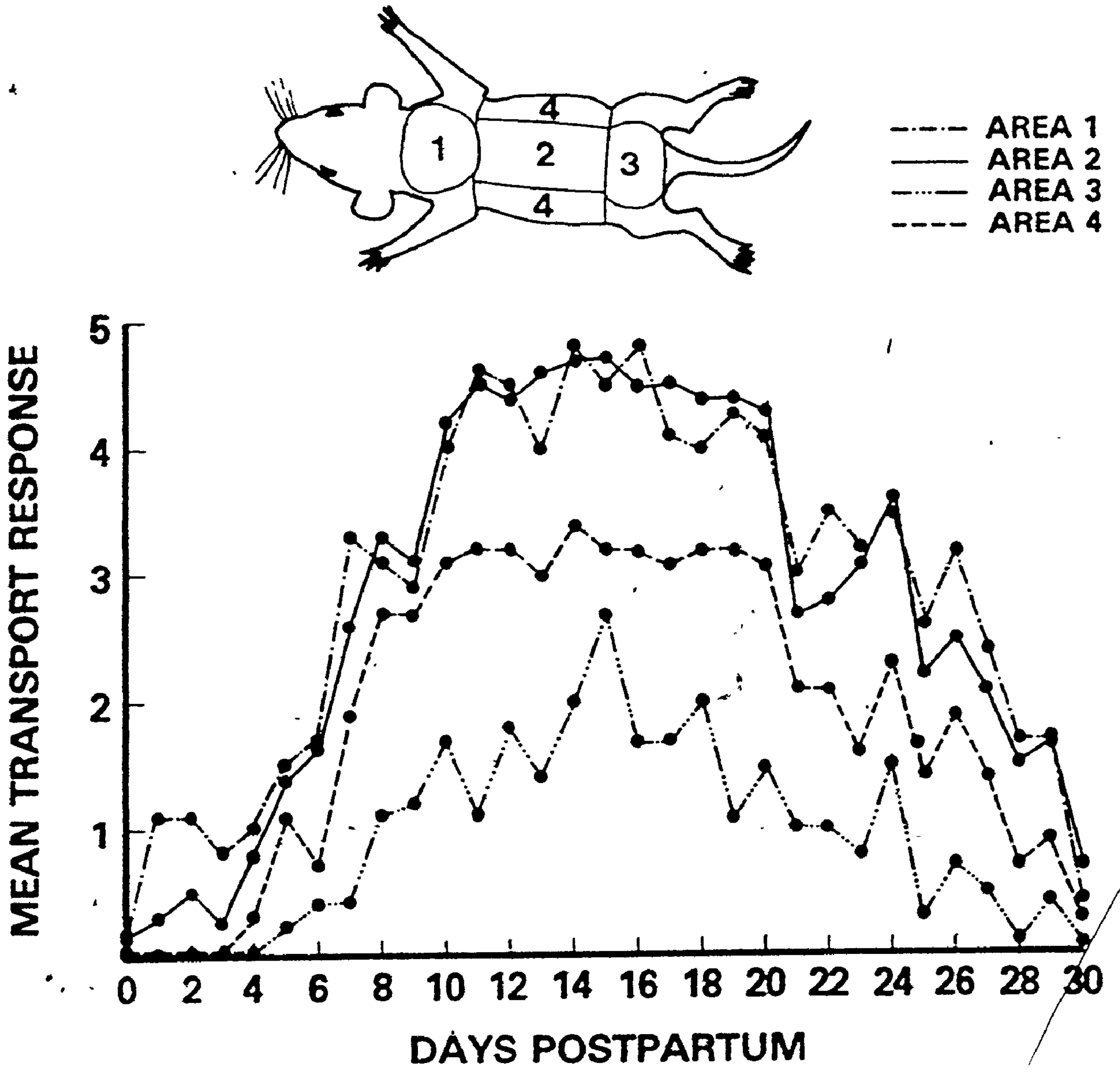
The most complete response was elicited from the nape of the neck (area 1) and the middle of the back (area 2), with the flanks (area 4) being only slightly less effective. The score for this area was lowered because when the area of skin grasped is not at the midline of the body, the contralateral forelimb is flexed and held against the body, rather than being held straight, and no point was scored for that limb. This distinction may be functionally irrelevant.

Grasping the skin at the base of the tail (area 3) rarely produced more than flexion of the hindlimbs, and sometimes curling of the tail. The forelimbs were typically extended straight out from the body.

Figure 11 also shows the gradual decline in the transport response during the fourth week postpartum. Typically, the 28-day-old rat shows defensive behavior (i.e., struggling, biting, squealing) when it is grasped. The

Figure 11

Mean transport response (maximum = 5) elicited from each specified pup body area. N = 30 observations for each body area on each test day.


1
2
3
4
4
AREA 1
AREA 2
AREA 3
AREA 4
MEAN TRANSPORT RESPONSE
5
4
3
2
1
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
DAYS POSTPARTUM

stimulation that normally elicits the transport response is ineffective at this point.

Discussion

The transport response is easily elicited by grasping the skin of virtually any area on the dorsal surface of the pup. Indeed, the mother was observed to pick up the pup by any part of the dorsal surface, but rarely by any other body area. This transport response has all of the characteristics of a reflexive response--it is a stereotyped movement or postural adjustment, and occurs in all members of the species of the proper age when the appropriate stimuli are applied (Marcus, 1972). The response develops gradually over the first 10 days of life, is reliably present throughout the third week, and begins to decline during the fourth week.

The transport behavior of the mother, on the other hand, is present from the day of parturition, and begins to decline by about day 14, ceasing entirely at approximately the end of the third week. So the transport response of the pup can be readily elicited during the time that mothers will still transport young which may have grown to be relatively unwieldy. The response becomes much more difficult to elicit only a few days after the mother will no longer carry her young.

A gradual increase in difficulty in eliciting a transport response has been described in several other species, including bushbabies (Galago senegalensis bradfieldi, Sauer, 1967; Sauer & Sauer, 1963; Galago senegalensis moholi, Doyle, Anderson, & Bearder, 1969), acouchi (Myoprocta pratti pocock, Kleiman, 1974), and mice (Peromyscus maniculatus, King, 1958; Reithrodontomys megalotis longicaudus, Smith, 1936), although none of these authors mention the circumstances under which a mother would attempt to carry infants which were old enough to successfully resist transport. In the daily transport tests conducted in Experiment 1 of this thesis, only one mother was observed to attempt to transport pups after day 20, and her pups were occasionally observed to vigorously resist while being carried.

Experiment 9

In some species that carry their young by grasping a fold of skin in their teeth, the young hang limply in a suspended position (Kleiman, 1972; Sauer, 1967; Snyder, 1923). The value of this slack carrying posture would appear to lie in the elimination of any struggling on the part of the infant which would interfere with the mother's attempts to carry it. However, the transport response of the infant rat is somewhat more complicated. Not only does the infant not struggle, but the limbs and tail are tucked close to the body, thus making a more compact bundle.

This type of transport response may exist because it increases the probability that the infant will be successfully carried to the nest site. It may help to prevent injury to the pup, which might otherwise strike its limbs against the walls of a burrow or other objects in the environment (Sauer, 1967). On the other hand, the value of the response may lie in simply making it physically easier for the mother to carry the pup, particularly if she has to pass through thick brush, a narrow tunnel, or along tree branches (Doyle et al., 1969). For example, Snyder (1923) has observed that it would be very difficult for a mother squirrel to carry its young if the infant hung limply suspended from her teeth, because she has comparatively short legs. He suggests that if the limbs of the infant were not tucked out of the way, they would drag along the ground, or scrape against the tree trunks, and greatly interfere with the mother's locomotion. This adaptation may be very important in arboreal species, where the accidental dropping of the infant might prove fatal to it. The ventral grasp typical of squirrel mothers also assures that the limbs of the infant will not drag, because the pup's limbs curl around the mother's neck.

The mother rat, too, has relatively short legs, and a limply hanging infant might be expected to interfere with her locomotion as well, particularly during the second and third week postpartum, when the pups have become relatively large compared with the size of the mother. In fact, the percentage of pups exhibiting the transport response is not high until the middle of the second week postpartum. This suggests that the ontogeny of the transport response is such that the response appears reliably at a time when the expression of such behavior will facilitate the transport of the young; that is, when the pups have become relatively large.

Accordingly, if the pup transport response were prevented, one would expect mothers to have difficulty when carrying large pups, while small pups should be transported easily whether or not they exhibit the transport response. Therefore, in the following experiment mothers were allowed to carry both pups that exhibited the normal transport response, and pups that hung limply due to light central anesthesia, either on day 5 postpartum, when their pups were small, or on day 12, when pups had become relatively large.

Mothers were induced to carry pups by presenting them with a standard retrieval situation in which the pups are placed outside of the nest box.

Method

Subjects

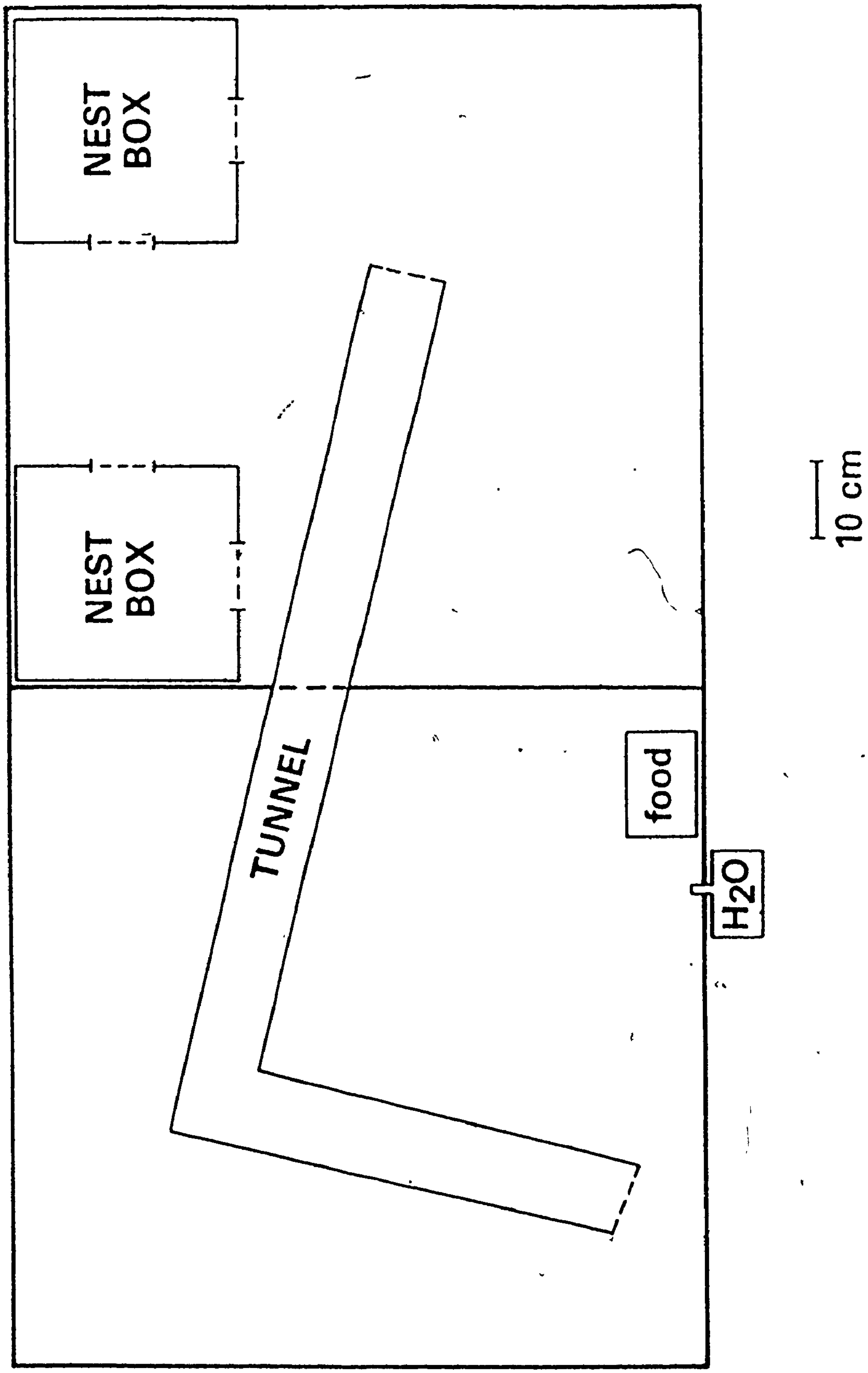
The subjects were 10 Wistar albino virgin females obtained from Canadian Breeding Farms, the members of their first litter, and foster infants taken as needed from the laboratory colony of multiparous females and their litters.

Procedure

The females were bred, and approximately 3 days before parturition, were placed individually in large metal floor cages similar to those described in Experiment 1, but twice as long (82 x 91 x 30 cm). The cage was divided into two sections by a hardware cloth partition. A tunnel (9 cm in diameter) constructed of chicken wire passed through a hole (12 cm in diameter) at floor level in the center of the partition, allowing the rat access to both sides of the cage (see Figure 12). This tunnel is comparable to or slightly larger than the dimensions of tunnels dug by domesticated rats in a semi-natural environment (Boice, 1977; Flannelly & Lore, 1977; Pisano & Storer, 1948). There was one right angle bend in the tunnel 61 cm from its entrance, and then a straight segment of 122 cm which terminated on the side of

Figure 12

Top view of cage set-up used in Experiment 9.


NEST BOX
NEST BOX
TUNNEL
food
H_2O
10 cm

the cage containing the two nest boxes.

The wooden nest boxes and a large quantity of paper nesting material were placed on one side of the divider, and food and water were placed on the opposite side. The female was initially placed in the cage on the side which contained the nest boxes. Within 12 hr, all of the females had used the tunnel to enter the other side of the cage, as indicated by food and water consumption and the presence of fecal material.

The nest boxes were checked daily for the birth of litters, and the day of parturition was recorded, but litters were not reduced in size. The testing was conducted either 5 or 12 days after parturition, with separate groups of 5 females being tested on each day.

On the day of testing, during the light portion of the day-night cycle, the litter was removed from the nest box. Each pup was weighed and marked with a felt-tipped marker for identification. Only pups with no obvious signs of injury (no cuts or bruises) were used.

To equate the weight of the pups in each group, each pup was matched with a pup in <u>each</u> of the other groups which differed in weight from it by no more than 1 g. It was, therefore, usually necessary to fill the groups with foster pups of the same age if the mother's own litter did not contain enough pups of similar weight. As far as possible, the foster pups were distributed equally between the three treatment groups. Each mother carried a total of 18 pups--six pups in each of three conditions.

Each pup was assigned to one of three groups: normal (no treatment), lightly anesthetized (injected subcutaneously with lidocaine hydrochloride, 20 mg/cc, .05 cc on day 5, .1 cc on day 12), or saline-injected (injected subcutaneously with the appropriate volume of isotonic saline). The normal and saline-injected groups continued to exhibit the transport response when grasped by the experimenter or by the mother. The lightly anesthetized pups hung limply rather than exhibiting the normal transport response.

After the pups were given the appropriate injections they were then placed in a holding cage while the mother was given three preliminary retrieving trials in order to habituate her to the test situation. Three untreated pups of the appropriate age were placed on the side of the cage opposite to the nest boxes, ensuring that the mother could only reach them by way of the tunnel and could only return them to the nest by carrying them back through the tunnel. In this way, the tunnel both simulated the burrow system inhabited by the rat in its natural environment, and also standardized the path taken by the female when carrying young so that the time taken to carry a pup a designated distance could be accurately recorded.

After the mother had located and retrieved the three practice pups, the experimental and control pups were placed individually in random order in the cage. As measures of the efficiency of pup transport, both the time necessary to transport each pup through the tunnel, and the number of times the mother dropped each pup were recorded. In addition, at the conclusion of the testing, all of the pups were examined for any obvious signs of injury resulting from the mother's teeth, or from their limbs being scraped against the floor or walls of the tunnel.

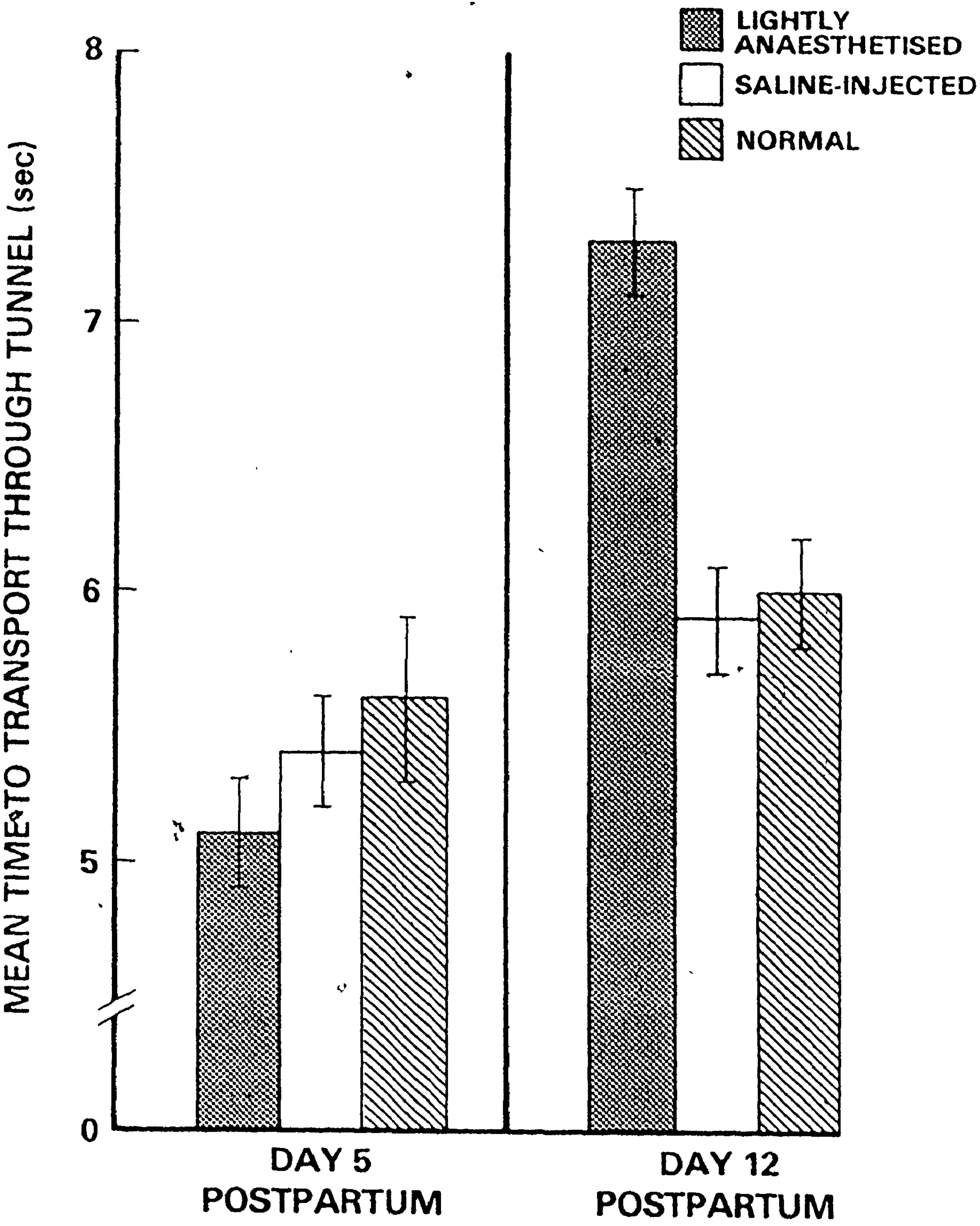
Results

Figure 13 shows the mean time required to carry the pups in each group through the tunnel on day 5 and day 12. Mean times to carry the pups in each group were computed for each mother using 6 scores for each group of pups on day 12, but only 3 scores in each group on day 5. Fewer scores were available on day 5 because it was necessary to use only those matched sets of times in which both the normal and saline-injected pups had exhibited the transport response. Thus, the number of observations on day 5 was reduced because only 50% of the control pups exhibited the transport response.

A two-way analysis of variance, with one repeated measure, was performed using the mean pup transport times for each group for each of the five mothers on day 5 and day 12. There was no main effect due to the day of testing, or the treatment group of the pup, on the time it took the mothers

Figure 13

Mean time taken to transport anesthetized or control pups through tunnel. N's = 15 and 30 pups in each group on days 5 and 12, respectively. Vertical bars indicate ± 1 S.E.M.


LIGHTLY ANAESTHETISED
SALINE-INJECTED
NORMAL
MEAN TIME TO TRANSPORT THROUGH TUNNEL (sec)
8
7
6
5
0
DAY 5 POSTPARTUM
DAY 12 POSTPARTUM

to carry the pups through the tunnel ($F(1,8) = 5.21$ and $F(2,16) = 3.21$, respectively, p's$>.05$), but the interaction of the two factors was significant ($F(2,16) = 10.79$, $p<.01$). Post-hoc comparisons using the Scheffe method indicated that on day 5 there were no differences between any of the groups in the time taken to carry pups through the tunnel. On day 12, however, it took mothers significantly longer to carry the anesthetized pups which did not exhibit the transport response, than normal or saline-injected pups. The time taken to transport the latter two groups did not differ. The lack of effect on day 5 suggests that the observed differences on day 12 were not due to non-specific effects of anesthetization of pups on maternal responses.

In addition, there were no differences in any of the groups in the number of times a pup was dropped ($F(2,16) = .004$, $p>.05$), nor were any pups injured during the testing.

Discussion

The transport response of the infant rat is seen during the time that the pups are large and may be difficult to carry, but are still being transported by the mother. On day 5 postpartum, only 50% of pups exhibit the transport response, but these pups are still relatively small, and the day 5 mother was not hampered when carrying a limply hanging pup when compared with the time it took her to carry a normal or saline-injected pup that *did* exhibit the transport response. However, on day 12, when pups are much larger, eliminating that response significantly increased the time it took the mother to carry those pups.

Observation of the mothers' progress through the tunnel revealed that the limbs of the limp day 12 pups dragged along the ground while they were being carried, often causing the mother to stumble over them. When the mothers were carrying these same pups outside of the tunnel, they awkwardly elevated their heads, which had the effect of preventing the pup from dragging on the ground. When the mother entered the tunnel, however, she had to lower her head to its usual level. The limbs of control pups did not drag, but were held close to their bodies, and mothers did not elevate their heads when carrying these pups. The transport response of infant rats thus facilitates the transport of young when they are large enough to be relatively unwieldy.

Experiment 10

The results of the previous experiment suggested that the transport response of the infant rat can facilitate its transport by the mother when it is large enough to impede her locomotion. The pup response may be important because the rat normally lives in a burrow system, which prevents the mother from lifting her head high enough to keep the pup from dragging on the ground. However, rats living in a semi-natural environment have been observed to transport above ground as well as through burrows (Calhoun, 1962a). It, therefore, is possible that the pup transport response facilitates the performance of this maternal behavior both above ground and within a tunnel.

In the following experiment I determined whether the transport response of the infant rat is functionally significant both outside of and within the confines of a tunnel. If so, the elimination of the transport response should decrease the mother's efficiency in an unenclosed runway as it did in the tunnel.

Method

Subjects

The subjects were five Wistar albino female rats obtained from Canadian Breeding Farms.

Procedure

The virgin females were bred on arrival, and placed in floor cages exactly as described in the preceding experiment. There was only one difference in their living conditions--the tunnel which ran from one side of the cage to the other had been cut open, and was now simply a runway 10 cm wide, with walls 10 cm high. This runway still passed through the opening in the center divider, and at this point the runway was covered (9 cm high) for 3 cm.

All procedures were exactly as described in the previous experiment, with two expections. Only day 12 mothers and pups were tested, since the elimination of the pup transport response on day 5 did not affect maternal transport behavior. In addition, the saline-injected control group of Experiment 9 was not included, since the time taken to carry those pups did not differ from the time taken to carry untreated pups.

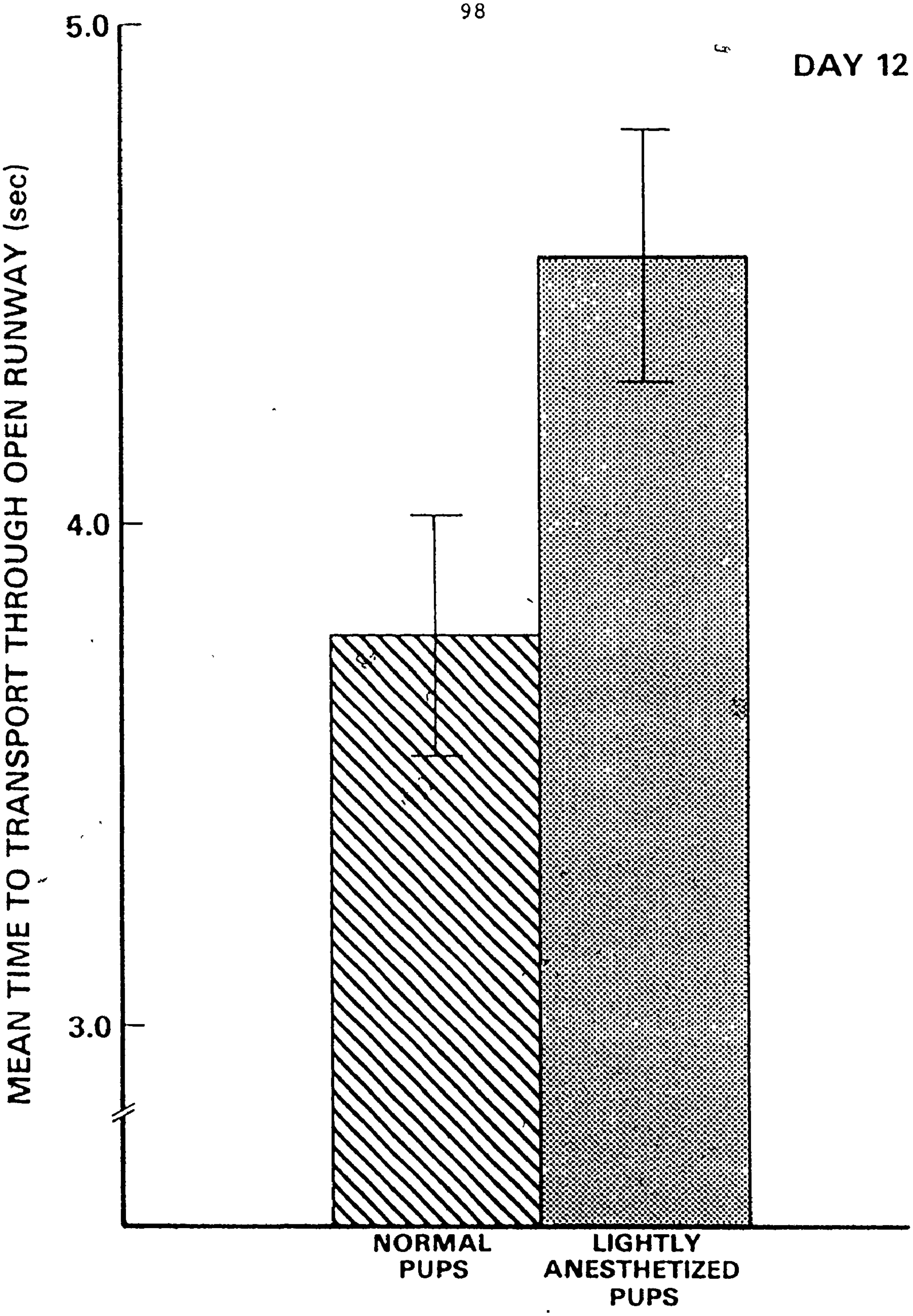
Results

Figure 14 shows the mean time taken by the mothers to carry untreated pups that exhibited the transport response, and anesthetized pups which hung limply. Again, the mean times for each mother to carry the pups in each group, based on three observations in each pup group, were calculated.

A treatments-by-subjects analysis of variance indicated a significant effect due to pup treatment group

Figure 14

Mean time taken to transport anesthetized or control pups through open runway. N = 15 pups in each group. Vertical bars indicate ± 1 S.E.M.


DAY 12
MEAN TIME TO TRANSPORT THROUGH OPEN RUNWAY (sec)
5.0
4.0
3.0
NORMAL PUPS
LIGHTLY ANESTHETIZED PUPS

($\underline{F}(1,4) = 72$, $\underline{p} < .005$). Again, it took the mothers longer to carry pups which did not exhibit the transport response than those which did exhibit the normal response.

Discussion

Even when the mother transports young outside of a tunnel, elimination of the transport response of the infant significantly increases the amount of time taken to carry the pup a standard distance. These data indicate that the transport response of the infant rat is an adaptation which facilitates transport both outside and within an enclosed tunnel. The pup transport response, therefore, appears to be a specific adaptation to deal with the anatomical characteristics of the mother rat.

GENERAL SUMMARY

The data that I have presented suggest that the mother and young interact on several levels to deal effectively with emergency conditions in the nest. The mother responds to nest site disturbance by reestablishing her nest in a new location and transporting each pup to the new nest.

In most cases, the mother rat appears to initiate transport in response to environmental stimuli which are disturbing to her. Moreover, it may be the general case that mother rats do not only provide maternal care in direct response to stimuli emitted by their pups, but, rather, respond to acute changes in their own maternal state. For example, Leon, Croskerry, and Smith (in press) have suggested that mothers respond to changes in their own temperature, as opposed to monitoring pup temperature, to regulate the duration of mother-young contact. However, as a result of the mother's concern with her own thermal homeostasis, the temperature of the litter is maintained within an optimal range for growth. Similarly, the mother may not be responding directly to distress signals from her young when she transports them from a disturbed nest, but as a consequence of her behavior, the young are kept in a safe nest site.

The mother is also capable of responding to distress signals from the young with an increased probability of transport in the absence of other cues indicating a severe nest disturbance. Typically, however, a disturbance which induced distress calls in the young was also sufficient to elicit transport in the absence of the distress signals. The redundancy which seems to be built into this system increases the probability that the pups will be transported from a disturbed nest to a safe place.

Pups contribute to their own well-being indirectly by emitting distress signals after nest site disturbance which, although possibly redundant in many situations, do elicit maternal response to their distress. The young also affect their own survival directly, by engaging in reflexive behaviors such as the postural transport response, which facilitates their removal to a safe nest site. This response appears gradually over the first week of life. When the pups are small, the elimination of the pup transport response has no apparent effect on the mother's behavior. By day 12, however, when pups are larger, the elimination of the transport response impedes the transport behavior of the mother. It seems, therefore, that the pup transport response appears shortly before it facilitates the transport of the young. The decline of the transport response lags slightly behind the time that mothers cease transporting their young. In this way, the pup response is present during the entire time that mothers will transport pups which are large enough to be unwieldy.

These adaptations by both the mother and young contribute to the immediate survival of the young after disturbance of the nest, and thus to the success of the reproductive attempt.

Appendix

At approximately the end of the fourth week postpartum, the transport response of the infant rat became more difficult to elicit when the experimenter grasped the skin of the pup. Instead, the pup would try to avoid being picked up, or would squeal, struggle violently, or try to bite while being held by the experimenter. However, it is a common laboratory observation that adult rats will respond to being picked up by their dorsal skin with a behavior analagous to the transport response of the infant. One possible explanation is that the handling that laboratory rats normally receive eliminates the defensive behaviors described above, thereby allowing the elicitation of the transport response even in adulthood. The pups used in Experiment 8 were tested only once, and were unhandled up to the point of testing.

If the development of competing defensive behaviors does interfere with the elicitation of the transport response in weanling rats, then extensive handling should eliminate the defensive reaction and should also reinstate the easy elicitation of the transport response. In the following experiment weaned rats were handled for several days before testing. The transport response elicited from them was compared with the response of unhandled rats of the same age.

Method

Subjects

The subjects were 36 40-day-old rat pups which had been born in our laboratory colony to multiparous Wistar albino females.

Procedure

Six litters were culled to six pups on the day of birth, and were housed with their mothers in a clear Plexiglass cage (28 x 30 x 15 cm). At 21 days of age the pups were weaned, and each litter was divided into two groups of three pups.

One group of pups from each litter was handled daily from days 20 to 40. Handling consisted of removing the pup from the cage, stroking it for 20 seconds, and returning it to the home cage. The other half of the pups were not handled at any time after weaning, other than being transferred by the tail to a clean cage once a week.

On day 40, each pup was tested for the transport response by grasping the skin of the mid dorsal region (area 2). The response of the pup was scored as described in Experiment 7. If the pup did not exhibit any component of the transport response after 5 sec, a zero was scored for the immediate response, and stimulation was continued for a maximum of an additional 15 sec. Any component of the transport response which could be elicited during that time was recorded as a response to persistent stimulation. In addition, any defensive behaviors emitted by the pup were scored as follows: one point was scored if the pup squealed, struggled, or tried to bite the experimenter after a grasp had been achieved, or if the pup exhibited a startle response (jumping or turning quickly) when first grasped, with the effect that the first attempt to grasp the pup was unsuccessful.

Results

Figure 15A shows the mean score for defensive behaviors in the handled and unhandled groups (N = 18 in each group). The unhandled rats exhibited significantly more defensive behavior than the handled rats (*t* = 4.99, *p*<.001). They typically struggled and tried to bite, whereas the only defensive behavior exhibited by the handled rats was infrequent squealing while being held.

Figure 15B shows the mean transport response exhibited by the handled and unhandled rats, and by the unhandled rats after persistent stimulation. All of the handled rats exhibited the transport response immediately, and persistent stimulation was not necessary.

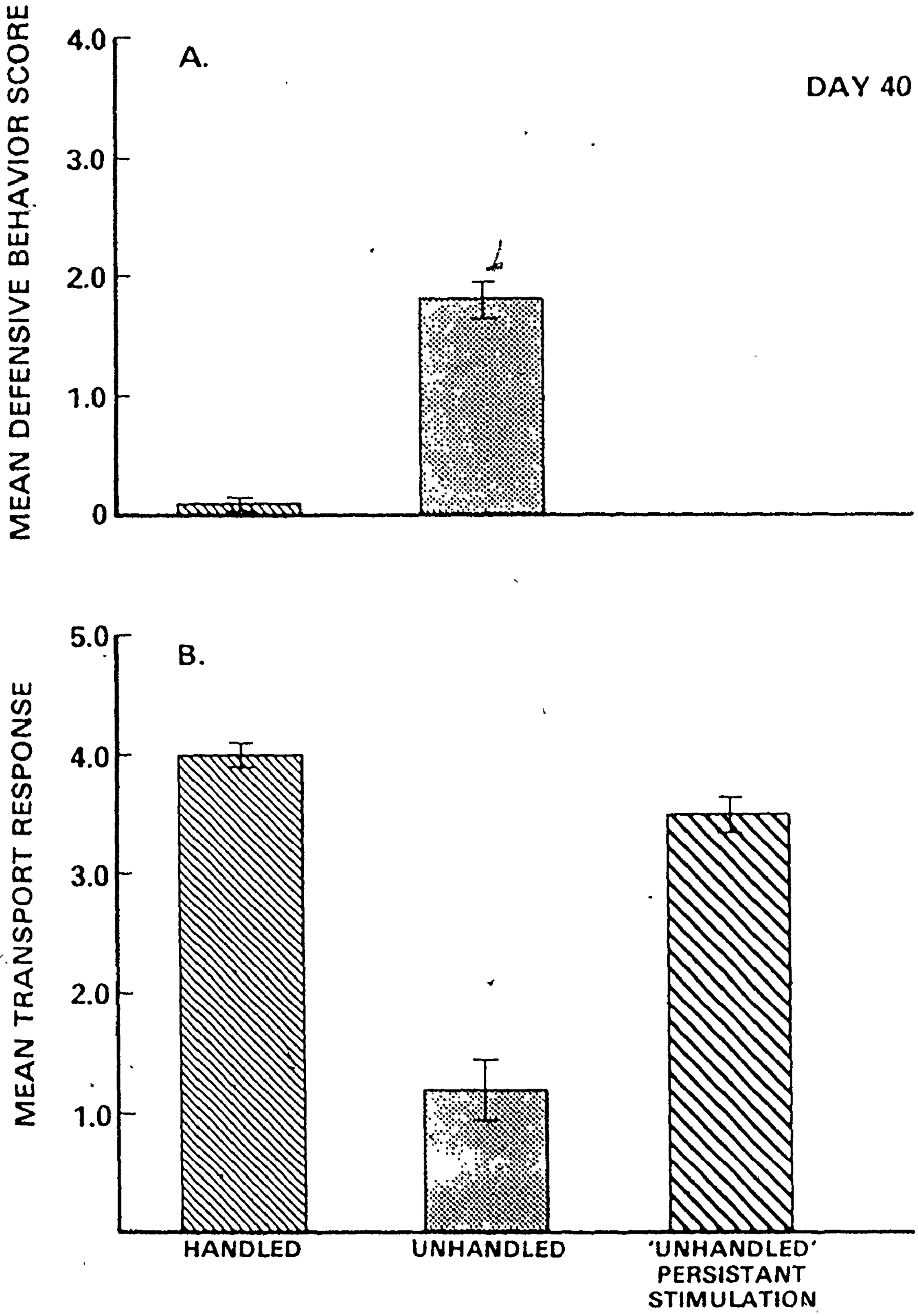
During the first 5 sec of stimulation, the mean

Figure 15

Effect of daily handling of pup on transport response in 40-day-old rats.

A. Mean score for defensive behavior (maximum = 5) when transport response is elicited from handled and unhandled pups. N = 18 in each group. Vertical bars indicate ± 1 S.E.M.

B. Mean transport response (maximum = 5) elicited from handled and unhandled pups, and after persistent stimulation in those unhandled pups which did not exhibit an immediate transport response. N = 18 in each group. Vertical bars indicate ± 1 S.E.M.


A.
DAY 40
MEAN DEFENSIVE BEHAVIOR SCORE
4.0
3.0
2.0
1.0
0
B.
MEAN TRANSPORT RESPONSE
5.0
4.0
3.0
2.0
1.0
HANDLED
UNHANDLED
'UNHANDLED' PERSISTANT STIMULATION

transport response of the handled rats was significantly higher than that of the unhandled rats ($t = 6.1$, $p < .001$), which typically struggled during the first few seconds of testing. After persistent stimulation most of the unhandled rats were induced to exhibit the transport response. Their mean score for the response was then no different from the immediate response of the handled rats ($t = 1.78$, $p > .05$).

Discussion

When weaned unhandled rats are grasped in an attempt to elicit the transport response, their first response is typically a defensive reaction, such as struggling or biting. However, if stimulated persistently, the transport response can usually be elicited. Well-handled rats of the same age do not typically exhibit defensive behaviors when picked up by the skin of the back, and the transport response can be readily elicited from them. Doyle, Anderson, and Bearder (1969) have similarly observed that as the infant bushbaby (*Galago senegalensis moholi*) grew older, it would try to prevent the mother from achieving a grip on it. However, once the grip had been achieved, it would immediately exhibit the transport response. Adult animals were also observed to exhibit the response if a proper grip could be effected.

Thus, the apparent disappearance of the transport response in the maturing rat pup can be reinterpreted as being the result of the development of competing responses to the same stimulation that are higher on a response hierarchy. The development of these competing responses can be blocked by handling of the pups.

BIBLIOGRAPHY

Allin, J. T., & Banks, E. M. Effects of temperature on ultrasound production by infant albino rats. Developmental Psychobiology, 1971, 4, 149-156.

Allin, J. T., & Banks, E. M. Functional aspects of ultrasound production by infant albino rats (Rattus norvegicus). Animal Behavior, 1972, 20, 175-185.

Bell, R. W. Ultrasounds in small rodents: arousal-produced and arousal-producing. Developmental Psychobiology, 1974, 7, 39-42.

Boice, R. Burrows of wild and albino rats: effects of domestication, outdoor raising, age, experience, and maternal state. Journal of Comparative and Physiological Psychology, 1977, 91, 649-661.

Burtt, E. H., Jr., Maiorana, V. A., & Hailman, J. P. Mother woodchuck transports her seven young to new nest. Mammalia, 1975, 39, 714-716.

Calhoun, J. The Ecology and Sociology of the Norway Rat. Public Health Service Publication No. 1008: 288. Bethesda: U.S. Department of Health, Education & Welfare. 1962a.

Calhoun, J. A Behavioral Sink. In E. L. Bliss (Ed.), Roots of Behavior. New York: Harper, 1962b.

Causey, D., & Waters, R. H. Parental care in mammals with especial reference to the carrying of young by the albino rat. Journal of Comparative Psychology, 1936, 22, 241-254.

Denenberg, V. H., Taylor, R. E., & Zarrow, M. X. Maternal behavior in the rat: an investigation and quantification of nest building. Behaviour, 1969, 34, 1-16.

Dice, L. R., & Barto, E. Ability of mice of the genus Peromyscus to hear ultrasonic sounds. Science, 1952, 116, 110-111.

Doyle, G. A., Anderson, A., & Bearder, S. K. Maternal behavior in the lesser bushbaby _Galago senegalensis moholi_ under semi-natural conditions. _Folia Primatologica_, 1969, _11_, 215-238.

Erickson, A. W., & Martin, P. Black bear carries cubs from den. _Journal of Mammalogy_, 1960, _41_, 408.

Errington, P. L. Observations on young muskrats in Iowa. _Journal of Mammalogy_, 1939, _20_, 465-467.

Ewer, R. F. _Ethology of Mammals_. London: Logos Press Limited, 1968.

Ewer, R. F. _The Carnivores_. Ithaca: Cornell University Press, 1973.

Fitzwater, W. D., & Frank, W. J. Leaf nests of gray squirrel in Connecticut. _Journal of Mammalogy_, 1944, _25_, 160-170.

Flannelly, K., & Lore, R. Observations of the subterranean activity of domesticated and wild rats (_Rattus norvegicus_): a descriptive study. _Psychological Record_, 1977, _27_, 315-329.

George, J. L., & Stitt, M. March litters of racooons (_Procyon lotor_) in Michigan. _Journal of Mammalogy_, 1951, _32_, 218.

Godfrey, G. K. A technique for finding _Microtus_ nests. _Journal of Mammalogy_, 1953, _34_, 503-505.

Gould, J., & Morgan, C. Hearing in the rat at high frequencies. _Science_, 1941, _94_, 168.

Gourevitch, G., & Hack, M. H. Audibility in the rat. _Journal of Comparative and Physiological Psychology_, 1966, _62_, 289-291.

Hall, E. R. Notes on the life history of the woodland deer mouse. _Journal of Mammalogy_, 1928, _9_, 255-256.

Hamilton, W. J., Jr. Reproduction and young of the Florida Wood Rat, _Neotoma f. floridana (Ord)_. _Journal of Mammalogy_, 1953, _34_, 180-189.

Hansen, R. M. Communal litters of _Peromyscus maniculatus_. _Journal of Mammalogy_, 1957, _38_, 523.

Hart, F. M., & King, J. A. Distress vocalizations of young in two subspecies of Peromyscus maniculatus. Journal of Mammalogy, 1966, 47, 287-293.

Hatt, R. T. A gray squirrel carries its young. Journal of Mammalogy, 1927, 8, 244-245.

Hatt, R. T. The pine squirrel in Colorado. Journal of Mammalogy, 1943, 24, 311-345.

Huestis, R. R. Maternal behavior in the deer mouse. Journal of Mammalogy, 1933, 14, 47-49.

King, J. A. Maternal behavior and behavioral development in two subspecies of Peromyscus maniculatus. Journal of Mammalogy, 1958, 39, 177-190.

King, J. A. Maternal behavior in Peromyscus (mice). In H. L. Rheingold (Ed.), Maternal Behavior in Mammals. New York: John Wiley & Sons, Inc., 1963.

King, J. A., & Connon, H. Effects of social relationships upon mortality in C57BL/10 mice. Physiological Zoology, 1955, 28, 233-239.

Kittredge, J., Jr. Can the flying squirrel count? Journal of Mammalogy, 1928, 9, 251-252.

Kleiman, D. G. Maternal behaviour of the green acouchi (Myoprocta pratti pocock), a South American caviomorph rodent. Behaviour, 1972, 43, 48-84.

Kleiman, D. G. Personal communication to Dr. M. Leon. 1974.

Klugh, A. B. Ecology of the red squirrel. Journal of Mammalogy, 1927, 8, 1-32.

Lee, M. H. S., & Williams, D. I. Long term changes in nest condition and pup grouping following handling of rat litters. Developmental Psychobiology, 1974, 8, 91-95.

Leon, M., Croskerry, P. G., & Smith, G. K. Thermal control of mother-young contact in rats. Physiology and Behavior, in press.

Marcus, E. M. The motor system and the integration of reflex activity. In B. A. Curtis, S. Jacobson, & E. M. Marcus (Eds.), An Introduction to the Neurosciences. Philadelphia: W. B. Saunders Co., 1972.

Nichols, J. T. Food habits and behavior of the gray squirrel. *Journal of Mammalogy*, 1958, *39*, 376-380.

Nitschke, W., Bell, R. W., Bell, N. J., & Zachman, T. The ontogeny of ultrasounds in two strains of *Rattus norvegicus*. *Experimental Aging Research*, 1976, *1*, 229-242.

Noirot, E. Ultrasounds in young rodents. I. Changes with age in albino mice. *Animal Behavior*, 1966, *14*, 459-462.

Noirot, E. Ultrasounds in young rodents. II. Changes with age in albino rats. *Animal Behavior*, 1968, *16*, 129-134.

Noirot, E., & Pye, D. Sound analysis of ultrasonic distress calls of mouse pups as a function of their age. *Animal Behavior*, 1969, *17*, 340-349.

Okon, E. E. The temperature relations of vocalization in infant golden hamsters and Wistar rats. *Journal of Zoology (London)*, 1971, *164*, 227-237.

Okon, E. E. Factors affecting ultrasound production in infant rodents. *Journal of Zoology (London)*, 1972, *168*, 39-148.

Oswalt, G. L., & Meier, G. W. Olfactory, thermal, and tactual influences on infantile ultrasonic vocalizations in rats. *Developmental Psychobiology*, 1975, *8*, 129-135.

Pisano, R. G., & Storer, T. I. Burrows and feeding of the Norway rat. *Journal of Mammalogy*, 1948, *29*, 374-383.

Ralls, K. Auditory sensitivity in mice: *Peromyscus* and *Mus musculus*. *Animal Behavior*, 1967, *15*, 123-128.

Richardson, W. B. Ring-tailed cats (*Bassariscus astutus*): their growth and development. *Journal of Mammalogy*, 1942, *23*, 17-26.

Richardson, W. B. Wood rats (*Neotoma albigula*): their growth and development. *Journal of Mammalogy*, 1943, *24*, 130-143.

Rosenblatt, J. S. The basis of synchrony in the behavioral interaction between the mother and her offspring in the laboratory rat. In B. M. Foss (Ed.), *Determinants of Infant Behavior III*. London: Methuen & Co., Ltd., 1965.

Rosenblatt, J. S. The development of maternal responsiveness in the rat. *American Journal of Orthopsychiatry*, 1969, *39*, 36-56.

Rosenblatt, J. S., & Lehrman, D. S. Maternal behavior of the laboratory rat. In H. L. Rheingold (Ed.), *Maternal Behavior in Mammals*. New York: John Wiley & Sons, Inc., 1963.

Sales, G., & Pye, D. *Ultrasonic Communication by Animals*. London: Chapman & Hall. 1974.

Sauer, E. G. F. Mother-infant relationship in galagos and the oral child-transport among primates. *Folia Primatologica*, 1967, *7*, 127-149.

Sauer, E. G. F., & Sauer, E. M. The South West African bush-baby of the *Galago senegalensis* group. *Journal of South West Africa Scientific Society Windhook*, 1963, *16*, 5-36.

Sewell, G. D. Ultrasound in rodents. *Nature (London)*, 1968, *217*, 682-683.

Sewell, G. D. Ultrasonic communication in rodents. *Nature (London)*, 1970, *227*, 410.

Sheldon, W. G. Reproductive behavior of foxes in New York State. *Journal of Mammalogy*, 1949, *30*, 236-246.

Siegel, S. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill Book Company, Inc., 1956.

Smith, C. F. Notes on the habits of the long-tailed harvest mouse. *Journal of Mammalogy*, 1936, *17*, 274-278.

Smith, W. P. The transfer of a *Peromyscus* family. *Journal of Mammalogy*, 1939, *20*, 108.

Snyder, L. L. A method employed by the black squirrel in carrying its young. *Journal of Mammalogy*, 1923, *4*, 59.

Sturman-Hulbe, M., & Stone, C. P. Maternal behavior in the albino rat. _Journal of Comparative Psychology_, 1929, _9_, 203-237.

Svihla, A. A comparative life history study of the mice of the genus _Peromyscus_. Miscellaneous Publication 24, University of Michigan Museum of Zoology, 1932.

Svihla, A., & Svihla, R. D. How a chipmunk carried her young. _Journal of Mammalogy_, 1930, _11_, 314-315.

Svihla, A., & Svihla, R. D. Notes on the life history of the woodrat, _Neotoma floridana rubida Bangs_. _Journal of Mammalogy_, 1933, _14_, 73-75.

Svihla, R. D. A family of flying squirrels. _Journal of Mammalogy_, 1930, _11_, 211-213.