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22

A "BEHAVIORAL SINK"

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Unexpected results frequently prove of more interest than anticipated ones. Such has proved to be the case in a study I have pursued during the past two years of social behavior of domesticated Norway rats. In this study rats were reared in slightly different environments. In one, the artificial "burrows" provided (Fig. 22-1) consisted of five nesting boxes connected by a system of tunnels in which alternate routes between any pair of boxes were possible. In the other, the five nesting boxes were lined up in a row along a single straight tunnel. It was my original hypothesis that these two different communication systems would alter the social organization of populations developing under their influence. Actually differences were so slight as to be of little importance.

However, certain similar characteristics of these two slightly different types of environments did produce common effects of profound influence upon the lives of the inhabitants. I shall attempt to show how certain characteristics of the environment led to the development of a pathological aggregation or a pathological togetherness of the inhabitants.

Development of such pathological aggregations led to the formulation of the concept of "behavioral sinks." A brief definition of a "behavioral sink" will facilitate the gradual unfolding of the evolution of this concept in the account presented below.

Stationary places whose characteristics are such as to lead to securing a reward by the individual who responds there may be designated as *positive response situations*

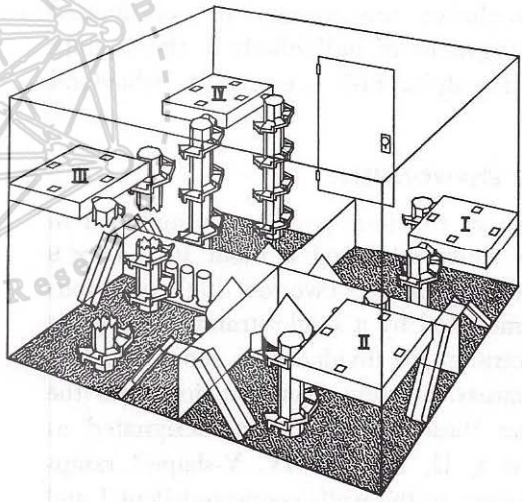

FIG. 22-1. The environment.

(PRS). One or more PRS may be distributed through the environment in such a way that when more than one is present each is sufficiently removed from the others for an animal responding to it to be unable to detect the others. If sufficient animals are present it will frequently happen that one animal will be close to another when they

simultaneously respond. Each then serves as a secondary reinforcer for the response executed by the other. In time, each animal redefines the PRS as requiring the presence of another individual. By chance, or under the influence of factors biasing the way the animals move through the environment, some one PRS will have a higher probability of animals arriving at it than will others. The animals will gradually learn that at this particular PRS they will most likely realize their developing redefinition of a PRS which requires the presence of another individual. Thus, more and more animals will gradually increase their frequency of visiting this particular PRS, which may now be designated as the alpha PRS, until very few responses are engaged in at any other PRS. These conditions and processes which culminate in a greater-than-chance reoccurrence of accentuated aggregations of individuals in the vicinity of the alpha PRS comprise a behavioral sink.

THE ENVIRONMENT

Each of the four populations included in this study inhabited a room $10 \times 14 \times 9$ feet (Fig. 22-1). Two-foot high partitions surmounted by a single-strand cattle fence electric guard divided each room into four subareas. Starting from the door into the room these subareas were designated as Pens I, II, III, and IV. V-shaped ramps adjacent to the walls connected Pens I and II, II and III, III and IV, but not Pens I and IV. Thus, insofar as locomotor communication was concerned, the environment was essentially one of four pens in a row. Mounted on the wall in the corner of each pen was an artificial "burrow" designed from a study of many burrows excavated by the author in the Norway rat's natural habitat. Each had a 9-square-foot surface through which four openings gave access to a trough or "tunnel" underneath. Along this tunnel the rats had access to five 8-inch-square nesting boxes. Two spiral ramps provided communication between the floor and each burrow. Three inches of sawdust covered the floor. A hopper containing 25 pounds of Purina Chow was located in the center corner of each pen. An 8-inch high mesh surface provided access to food around the entire circumference. In Figure 22-1 the food hopper may be identified by its cone-shaped dorsal aspect. Water was available in each pen from a series of two-quart chicken water hoppers placed in a row against one wall. During the winter months, air temperature was maintained at near 65°F. During the summer months the forced air circulating through each room made the temperature closely parallel that outside the laboratory. Each room was lighted from 1000 to 2200 o'clock by four 10-watt bulbs and from 2200 to 1000 o'clock by four additional 100-watt bulbs. A 3×5 foot window on the roof of the room enabled observation.

Strips of paper, which the rats could use for building nests, were placed periodically on the floor in the center of each pen.

Burrows in Pens I and II stood at an elevation of 3 feet from the floor while in Pens III and IV, they were at a 6-foot elevation. This introduced an "income" factor in the environment since rats living in Pens I and II had to expend only half the effort in going to the floor to secure food and water as did rats in Pens III and IV.

These environments formed two types, A and B, which differed only slightly. On one (the A type), the burrow was as shown in Figure 22-1. Its tunnel ran around the underneath side of the 3×3 foot surface. In addition, a tunnel cut across from one side to the opposite one. In the B type the surface was 1 foot wide and 9 feet long. Four

openings, equally distributed along this surface gave access to a single straight tunnel underneath, along which there was access to five nesting boxes. We shall not be concerned here with the slight differences in behavior induced by these two types of burrows.

Rooms 1A and 2A contained the A-type burrows. Rooms 1B and 2B contained the B-type burrows.

In all other details the attempt was made to make the environment ideal for the support of a population of not more than 80 rats. The criteria were based upon a three-year study of the ecology and social behavior of wild Norway rats.

SUBJECTS

Osborne-Mendel strain domesticated albino rats from the National Institutes of Health random-bred closed colony formed the original stock. In each room a pregnant female was confined to each pen by removing the ramps connecting pens. At 10 days of age litters were mixed so that in a room each female reared one male and a female progeny from each of the four litters in that room. All 32 young in each room survived to weaning. These 16 males and 16 females in each room were designated as the *1st tier* of rats. These 1st-tier rats were born February 10–20, 1958.

At 45 days of age the mothers were removed, and communication between pens was permitted by placing in the ramps as described above. From the litters born to 1st-tier parents during the latter part of May and the first of June, 1958, four males and four females born in each pen were permitted to survive. These 16 males and 16 females in each room formed the *2nd tier*.

Similarly, a *3rd tier* in each room was formed from young born during the middle of August, 1958. Their parents were either 1st-tier or 2nd-tier rats. Up to the time of weaning of 3rd-tier rats, few deaths of weaned rats had occurred other than those relating to removal of excess young by the investigator.

All rats were individually marked by either metal ear tags or by coded removal of one to three toes. In addition, each rat was marked with two colored dye markings of the pelage which permitted identification from the overhead window.

OBSERVATIONAL PROCEDURES

Each four to eight weeks, or occasionally at shorter intervals, all animals were captured. Each was weighed and measured, and additional data were recorded for each individual: pregnancy, lactation, condition of pelage, number and location of wounds, and various other signs of health. At this time, size, age, and health of litters were noted. Records were kept of complexity of nests and extent of fouling with urine or feces.

Periodically, three to six hours of observation of each room was made through the overhead window. Dictated records, later transcribed for analyses, supplemented tallied records of more frequent and easily categorized behaviors. Emphasis was placed on sexual, aggressive, feeding, drinking, and nest-building behavior as well as movements and place of activity.

A record was maintained of the total amount of water and food consumed in each pen through each consecutive two-week period.

DIFFERENTIAL RESIDENCE

Place of capture during the 12 hours of minimum activity and amount of water consumed both reflect residence. Water consumption as a residence index derives from the typical observed behavior that a

TABLE 22-1 FREQUENCY OF RESIDENCE ACCORDING TO PEN OF RESIDENCE 1ST- AND 2ND-TIER RATS, MAY–SEPTEMBER 1958

	PEN				TOTAL
	I	II	III	IV	
Observed	343	467	331	245	1386
Expected (3:4:3:2 ratio)	347	462	347	232	1388

Contingency $X^2 = 1.57$. p of X^2 between .7 and .5.

rat usually drank just after emerging from a period of inactivity and just prior to reinitiating a period of inactivity. Such drinking usually took place in the pen where the rat slept.

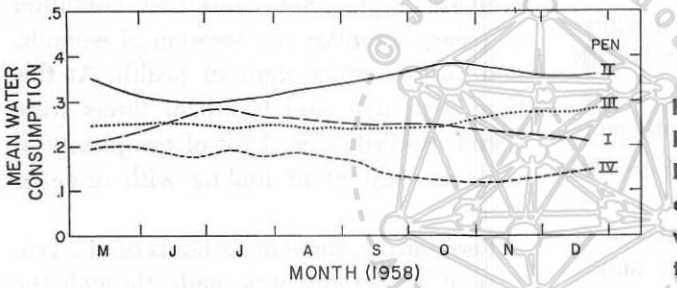

FIG. 22-2. Mean water consumption by pen across Rooms 1A, 2A, 1B, 2B. For each room, every two weeks, the consumption in each pen was converted to the proportion it formed of the total in that room.

Surveys of all rooms from May through September, 1958, provided 735 capture locations for 1st-tier rats and 651 for 2nd-tier rats (Table 22-1). Figure 22-2 shows the mean relative water consumption for a somewhat longer period.

Both sets of data reflect a greater usage of Pen II for residence-related behavior. Pens I and III exhibited nearly equal usage, while Pen IV consistently fell below all the other three pens.

I recognized from the beginning one factor which might contribute to such a differential usage. Use of burrows should be inversely proportional to their distance from the floor. Thus the operation of this factor alone would result in a 2:2:1:1 ratio of usage for Pens I:II:III:IV.

During the first few months, frequent movement between pens was the rule. In fact, from watching the activity going on as I sat at the window above the room, I developed a fairly strong impression that there was some interval of time after which if a rat continued to be active it just had to get out of the pen it was then in and go elsewhere. The operation of this process leads to a condition where in time there will be only half as many rats in the two end pens as in the two center ones. A rat in an end pen (I and IV) can only go to a center pen (II or III), whereas a rat in a center pen can go to either the adjoining end pen or the other center pen. Thus more rats will leave the end pens than will be compensated by rats entering from center pens. In time this will lead to a 1:2:2:1 ratio of usage of Pens I:II:III:IV.

Dr. Clifford Patlak has formalized this concept as follows:

1. Consider a ramp connecting two pens.
2. Consider that a rat has a constant tendency per unit time to leave a pen independent of the number of ramps.
3. Therefore, the probability of a given rat in a pen crossing per unit time a particular ramp within that pen is inversely proportional to the number of ramps (r) in that pen.
4. Also, the number of rats in a pen crossing per unit time a particular ramp within that pen is directly proportional to the number of rats (N) in that pen.

5. In the steady state, the number of rats crossing a particular ramp in either direction will be the same.

6. Items 3 and 4 imply that the number of rats in a pen crossing per unit time a particular ramp within that pen will be equal to $\frac{N}{r} \times K$ where K is a constant of proportionality independent of pen.

7. Where the pens are numbered in sequence and N_i is the number of rats in the ith pen and r_i equal the number of ramps in the ith pen, then Items 5 and 6 imply that $\frac{N_i}{r_i} \times K = \frac{N_{(i+1)}}{r_{(i+1)}} \times K$.

8. Therefore $N_i = \frac{r_i}{r_{(i+1)}} \times N_{(i+1)}$.

9. By repeating this procedure for adjacent pens (i and j) it is immediately seen that

$$N_i = \left(\frac{r_i}{r_j}\right) N_j.$$

10. Consider adjoining Pens I and II in the experimental environment. Where $N_{\mathrm{I}} = 1$, $r_{\mathrm{I}} = 1$, and $r_{\mathrm{II}} = 2$ it follows from the equation in Item 8 that $N_{\mathrm{II}} = 2$. Completing the other comparisons of adjacent pens leads to the ratio of 1:2:2:1 of number of rats expected per pen across the series I:II:III:IV.

If these two factors which might affect the probability of a rat's selecting a particular pen as a place of residence were of equal importance, their values for each pen might be summated. This produces a 3:4:3:2 ratio of expected usage of Pens I:II:III:IV. In other words the expected probabilities respectively will be: 0.250, 0.333, 0.250, and 0.167.

As may be seen from Table 22-1 the observed and expected number of rats from each place of capture closely approximate each other. Similarly, water-consumption levels for the four pens vary rather closely about the expected levels. Thus the effort required to reach the burrow from the floor and the departure from one pen to another following the lapse of some average period of time form the most logical, as well as the minimum, assumptions to account for the differential usage of pens as places of residence. For the purpose of considering the development of a behavioral sink, attention must be focused on Pen II with its higher probability of residence.

THE FOOD HOPPERS AS A POSITIVE RESPONSE SITUATION (PRS)

Three types of PRS existed in each pen of each room. They were the water hoppers, the nesting boxes, and the food hoppers. The former two may be summarily dispensed with as potentially being involved in the development of a behavioral sink on the following grounds. The act of drinking required only a few seconds to complete. Thus the chance of two rats drinking side by side was low. Furthermore, the probability of drinking in a pen being visited, but not the rat's pen of residence, was low. Whereas sleeping was a prolonged response, its major duration involved reduced perceptual awareness. Furthermore, the presence of five nesting boxes in each burrow reduced the opportunity of contact with another rat at the time of initiation of sleep.

Eating typically occurred intermittently during most phases of the rat's travels from one pen to another. Securing sufficient food to satiate the rat's hunger required a continuous effort of up to several minutes. The necessity of gnawing through the wire mesh of the hopper called for this greater effort. Thus when one rat was eating there was a fair chance that another rat might join it with an ensuing period of eating side by side.

With this background we many now turn

our attention to the detailed history of food consumption (Fig. 22-3) in Room 2B. The history of the four rooms was somewhat different, but 2B closely reflected the typical changes which occurred in all the rooms.

Initially, in marked contrast to the more uniform distribution of sleeping and drinking, eating was almost entirely concentrated in Pen II. Through the next three months, eating in Pen II declined but never quite reached the level of 0.333 anticipated on the basis of the forces governing probability of determining residence.

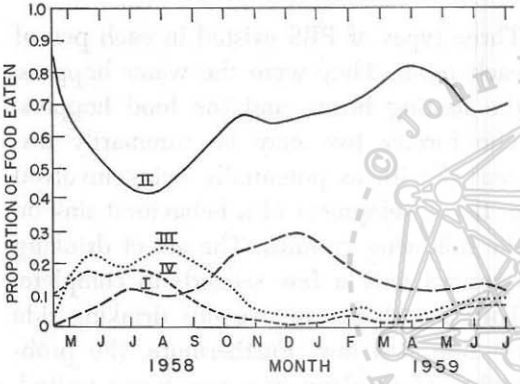

FIG. 22-3. Food consumption, Room 2B. Roman numerals refer to pens.

Initial concentration of eating in one of the four pens has been interpreted as resulting from a "litter-association factor." During nursing each rat gains contact with one or more of its litter mates. Presumably by the time of weaning each rat has defined the food acquisition behavior as requiring the presence of another individual. Behavior of recently weaned rats supports this notion. Most frequently several young rats feed simultaneously, and furthermore, they crowd their mouths together as if attempting to gnaw at the same piece of food—this despite the fact that most of the extensive feeding surface remains bare of any rats eating.

Nearly immediately following insertion of the ramps between pens the young rats concentrated all of their feeding in the one pen where, by the operation of factors previously discussed, they were most likely to find their conditioned definition of a feeding PRS. The pens thus selected were 1AIII, 2AII, 2BII and 1BII. That Pen III might occasionally be selected is not surprising in view of the indeterminancy of the system. However, the probability of Pen IV's ever becoming a major pen of feeding is rather remote. For the rats to maintain their concentrated eating in one pen each rat must experience frequent reinforcements in the form of proximity with another while eating. Obviously such frequency was not sufficient for there ensued a period of continuous decline in amount of eating in the pen originally selected by the weanling 1st-tier rats.

By the end of June, 1958, the 32 2nd-tier rats were weaned, and by mid-September the 32 3rd-tier rats joined the others in free-feeding acts. The same forces affecting residence of the 1st tier also applied to those two younger tiers. On the average, one-third of the rats lived in Pen II. However, the pen where young rats were most likely to find other rats eating was the one where their elders were still concentrating their eating. Thus, sometime between June and September sufficient numbers of rats were present to reinitiate the social definition of the feeding PRS among the older rats and retard its loss among the younger rats. Gradually more rats came to 2BII to feed and simultaneously reduced their eating elsewhere. A common observation was that a rat resident in Pen IV would go down to the floor, perhaps drink, and then cross over and through Pen III to Pen II before engaging in eating.

This latter phenomenon facilitated the development of territoriality. In each pen

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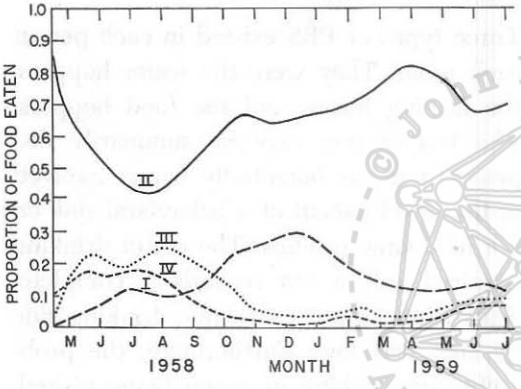

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This latter phenomenon facilitated the development of territoriality. In each pen

there were usually one or more very aggressive males who became active later than their subordinates. By the time the dominant male in Pen IV became active he would likely find himself alone. As a subordinate rat living in Pen IV started back over the ramp connecting Pens III and IV after a period of eating in Pen II, he was likely to run into the dominant Pen-IV male as he was starting on his trip to Pen II to eat. These circumstances were ideal for the subordinate rat's associating departure from Pen IV with escape from the dominant male there. Without himself being completely responsible, the dominant male in Pen IV also became territorial. In time the process extended to Pen III so that he was left with a harem of 20 females.

This forms a circular series of events in which the development of the food hopper in Pen II as an alpha PRS facilitated development of a territorial male. In turn, the territoriality of this male increased the effectiveness of the food hopper in Pen II as an alpha PRS. All this time Pen II and, in particular, the immediate environs of its food hopper had developed all the attributes of what I now term a "behavioral sink."

An important facet of this sink is the relative numbers of individuals so involved in comparison with the group size typical of the species. In an unpublished extensive study of wild Norway rats the average group size was 11 individuals. Yet here in proximity to the alpha feeding PRS the size commonly exceeded this figure. Further discussion of this topic will be presented farther on in this paper.

Before turning to consequences of the behavioral sink, a brief comment regarding the other three rooms is in order. In Rooms 1A and 2A, territorial males with associated harems developed in Pen I. As was the case for the pens dominated by the territorial males in Room 2B, these pens could also be designated as "brood pens" since here the females were markedly successful in rearing young in comparison to females residing elsewhere. Room 1B exhibited a very odd history. Following the accidental death by suffocation of seven 1st-tier male residents in Pen II in June, 1958, the major pen of feeding shifted from Pen II to Pen III. But Pen III never gained real ascendency. In fact during the last few months there developed a marked oscillation in relative amount of feeding in each of the four pens. All abnormal behaviors developing in the other rooms became even more accentuated here.

NORMAL BEHAVIOR

Abnormal behavior associated with the development of a behavioral sink must be viewed against the normal. I use the term *behavior* in the following sense. It includes both a perceptual and a motor phase. Sustained attention to one stimulus characterizes the perceptual phase. Similarly, a sustained period of repeating a specific response characterizes the motor phase. Higher levels of behavior require sustained attention toward an object or situation whose identification involves integration of several distinct cues or stimuli. In the motor phase there must be expressed an orderly sequence of discrete but different acts.

The following normal behavior characterized most 1st- and 2nd-tier rats of reproductive age through September, 1958. They exemplify my definition of normal behavior.

• NEST BUILDING

Rats of both sexes build nests, but this behavior becomes intensified by females just preceding and just following parturition. If a rat picks up a strip of paper from the floor and carries it up into a nesting

box, it will most likely make several such trips in close succession before engaging in an unrelated behavior. Completion of a nest may require several nest-building behaviors such as the one described. The end product forms a fluffy intermeshed mass of paper strips surrounding a deep cuplike depression, and frequently the mesh work extends dorsally over the cup to form a hood.

• TRANSPORT OF YOUNG

This behavior characterizes females having young under 15 days of age. When such a female, while with her young, is disturbed by either the experimentor or by an invading strange rat, she customarily transports the entire litter from one place to another. Such a transport is not interrupted by any other behavior until the entire litter has been moved to the same place.

• EATING

As described previously the behavior of eating involves quite a long series of gnawings at the surface of the hopper.

• SEXUAL BEHAVIOR

For the present discussion, emphasis will be placed upon the male's behavior. Its culmination involves mounting an appropriate receptive female. However, it includes a passive perceptual phase and an active pursuit phase. In the latter, following the withdrawal of a receptive female into a burrow, the male follows her to the burrow opening but does not pursue her into the burrow. He waits there quietly or with intermittent movements back and forth with his head protruding into the burrow opening. The full sexual dance characteristics of wild Norway rats in their natural habitat did not develop fully on the artificial burrows in the absence of the conical mound of dirt. Eventually the fully receptive female emerges and is pursued by the male until he overtakes her. The chase culminates in intromission as the male mounts the receptive female while holding her with his teeth so gently by the scruff of her neck as not to cut the skin. Simultaneously he exhibits pelvic thrusting as she exhibits lordosis.

The passive sexual behavior is perceptual, involving the integration of a graded set of cues. The male must perceive that the sexual object is an adult, that it is a female, and that it is a receptive female. This formulation of a passive perceptual sexual behavior is an inference derived from the development of inability to select appropriate sex partners as discussed below.

• AGGRESSIVE BEHAVIOR

Males more frequently than females inflict wounds on other rats, usually other adult males. I shall not attempt here to describe the full sequence of related acts which culminates in one rat's biting another. Suffice it to say that there arises a stage in the conflict when one rat turns and flees. At this moment the dominant member frequently bites the fleeing rat on its posterior dorsal aspect. Wounds rarely were noted on other parts of the body preceding development of the behavioral sink. Wounds typically do not exceed 5 mm. in length and rarely extend through the skin.

ABNORMAL BEHAVIOR

Beginning in September, 1958, and continuing to a climax by April, 1959, these behaviors markedly changed in character. The change was gradual both in terms of degree of change characterizing any one individual and with reference to the number of individuals exhibiting more marked abnormality of behavior. This period started with the weaning of the 3rd tier and con-

tinued to their full adulthood at 8 to 9 months of age. The average number of 1st- to 3rd-tier adults per room in February, 1959, was 77 (Table 22-3, Row 1).

• NEST BUILDING

Failure to organize paper strips taken into the nesting boxes formed the first indicator of disruption of this behavior. Although many strips were transported they were just left in a pile and trampled into a flat pad with little sign of cup formation. Then fewer and fewer strips reached the nesting box. Frequently a rat would take a single strip, and somewhere along the way it would drop the strip and then engage in some other behavior. In the extreme state of disruption, characterizing at least all major pens of feeding, the nesting material would remain in the center of the room for days. Even when females delivered litters in the burrow in the major pen of eating, no nest was formed; the young were merely left on the bare sawdust periodically placed in every box by the experimentor.

• TRANSPORT OF YOUNG

In the normal condition when females had litters in separate boxes, the litters were maintained intact with no mixing, As the behavioral sink developed, litters became more and more mixed. When only one litter was present in a burrow the young frequently became scattered among several boxes. This resulted from the female's interrupting the transport behavior by some other behavior. The consequence of a reinitiation of transport resulted in even greater scattering because the second terminus of transport was likely to be some nesting box other than the first. In the extreme state of disruption the terminus of transport was undirected. The mothers would take a pup out of the burrow and start toward the floor with it. Anywhere along the way or any place on the floor the mother would drop the pup. Such pups were rarely ever retrieved. They eventually died where dropped and then were eaten by other rats.

• EATING

Unfortunately, no measures of disruption of this behavior were made. I say unfortunate because, as discussed below, alteration of the duration of this behavior—that is, shortening it—should be the first behavior disrupted. See the discussion for elaboration of this point.

• SEXUAL BEHAVIOR

The first sign of disruption involved more frequent attention to and attempts at mounting females who indicated no sign of being receptive. Later, males mounted other males, and a few of these, particularly 3rd-tier males, seemed to prefer other males as sexual partners. In the final phase, young rats, even recently weaned ones of both sexes, were mounted. Such abnormality may best be termed *pansexuality*. In essence, the perceptual behavioral phase of recognition of a sexual partner became so disrupted that fewer and fewer elements of the perceptual pattern were requisite for shifting from the perceptual phase of recognition of sex partners to the active behavioral phase of pursuit, mounting, and pelvic thrusting. Pursuit also became altered. With increasing frequency males who followed a receptive female to the burrow also followed her into and through the burrow. Such intrusion produced further disturbance to lactating females and thus aggravated the already disturbed transport behavior. Another element of disruption of normal sexual behavior involved the scruff-of-the-neck biting act during mounting. As the behavioral sink

became accentuated in its influence, many females following their period of receptivity were characterized by literally dozens of nicks about the dorsal aspect of the neck. Males subjected to homosexual advances exhibited similar wounds, but fewer in number.

• AGGRESSIVE BEHAVIOR

Three abnormal aggressive acts developed as the behavioral sink became established. The first of these was tail biting. A peculiarity of this behavior was that males alone exhibited tail biting insofar as I could determine. Furthermore, the population became divided into tail biters and those who were bitten on the tail. The latter category included both sexes. At times it was impossible to enter a room without observing fresh blood splattered about the room from tail wounds. A rat exhibiting tail biting would frequently just walk up to another and clamp down on its tail. The biting rat would not loosen its grasp until the bitten rat had pulled loose. This frequently resulted in major breaks or actually severance of the tail.

The population in each room passed through this phase of tail biting of adults by other adults. Its duration varied from one to three months following the peak development of the behavioral sink. Young weaned during this period received similar treatment from adult biters, although in earlier, more normal states no tail wounds were inflicted on young rats and only rarely were body wounds received until well after sexual maturity. The population in Room 1A was allowed to survive beyond July, 1959, when rats living in the other three rooms were autopsied. A sixth tier was allowed to survive to Room 1A until many of them had reached sexual maturity. And yet from weaning to sexual maturity most of these 6th-tier young received several tail bites despite the fact that adults were rarely any longer receiving such wounds. It is difficult to escape the conclusion that the behavior of bitten rats in some way influences the probability of attack by biters. In some way the rats who are subject to being bitten on the tail alter their behavior in such a way as to avoid elicitation of attack by biters. That the biters do not alter their behavior is evinced by the fact that young rats which have not had the opportunity to learn the appropriate alteration to their behavior are attacked by the biters.

The basis of this behavior has so far eluded me. From several very incomplete lines of evidence presently available I can only say that I suspect that tail biting derives from a displacement of eating behavior rather than stemming from modification of aggressive behavior.

Inflicting small nicks about the shoulders during sexual mounts becomes an aggressive behavior insofar as the recipient is concerned. The third aberration takes the form of slashing attacks. Gashes ranging from 10 to 30 mm. may be received by either sex on any portion of the body. The depth of such wounds frequently extend down into the muscles or through the abdominal wall.

CHANGES IN REPRODUCTIVE PHENOMENA

A general survey of all the records supports the conclusion that there was a reduction in conception or at least a reduction in pregnancies continued to the age when embryos could be detected by palpation. However, as yet no detailed analysis has been prepared. Also, pregnant females exhibited difficulty in continuing pregnancy to term or in delivering full-term young. Both phenomena were noted only after the behavioral sink began developing. Several females were found near term lying on the

floor with dark bloody fluid exuding from the vagina. I never found any evidence that these females delivered. One died while I watched her from the overhead observation window. She was immediately autopsied. Extensive dark hemorrhagic areas in the uterus suggested that the fetuses died before the mother. Another apparently full-term female was autopsied shortly after death and found to contain several partially resorbed full-term embryos. Some of these had been released into the abdominal cavity following rupture of the uterus.

Upon palpation for pregnancy, more and more females were recorded as containing large hard masses in the abdomen. These sometimes reached a diameter of 90 mm. Usually death occurred before attainment of such size. A group of females with these abdominal masses were autopsied. The enlargements proved to be thick-walled dilatations of the uterus. Usually these dilatations contained a purulent mass. Partially decomposed fetuses were found in some of the rats in which these dilatations were still relatively small.

Eleven females with these masses, some from each of the three tiers, were autopsied by Dr. Katherine C. Snell of the National Cancer Institute. The general picture of the uterus was one of severe chronic suppurative endometritis, myometritis, and peritonitis with extension of the process to the fallopian tubule and ovary on one or both sides. Areas of focal inflammation of slight to moderate degree occurred in all kidneys.

The adrenal glands were normal in rats from the 3rd tier. Among 1st-tier rats all showed some degree of congestion of the adrenal glands with dilated vascular spaces in the cortex filled with red blood cells or fibrin or both. The adrenal of one 2nd-tier rat was normal. The other four 2nd-tier rats showed marked congestion of the reticular and fasicular zones of the cortex with dilated vessels filled with red blood cells, precipitated fibrin, or both.

Some of these 11 rats, as well as 4 others autopsied because of obvious mammary tumors, showed the following pathologic lesions in one or more females: (1) fibromyoma of a uterine horn; (2) fibrosarcoma of the mammary gland; (3) fibroadenoma of the mammary gland; (4) angiomatous adenoma of the adrenal cortex; (5) granulomas of the liver; (6) papillary cyst of the thyroid.

One 2nd-tier female was autopsied because a few days previously she was noted to be apparently near term, but she had considerable dark blood about the vagina. Upon autopsy the uterus was found to contain five healthy-appearing fetuses, four in the right horn and one in the left. The myometrium of the corpus and the cervix of this rat were inflamed, and the lumen of the horn near the cervix contained clotted blood that may have been associated with premature separation of the placenta.

From my own observations and the brief synopsis of Dr. Snell's findings, it appears that concomitant with the development of the behavioral sink females experienced difficulty in carrying young to term or if they carried to term they were sometimes unable to deliver. The extent to which the uterine infections preceded or followed failure to deliver is unknown.

Presence of tumors was from a highly selected sample. No conclusion is warranted concerning the influence of behavior upon incidence of the tumors. Dr. Snell pointed out another complicating factor. First-tier rats were marked with a black hair dye. Second-tier rats were marked with a red stamp-pad ink, and third-tier rats were marked with a combination of picric acid and a green oscillograph pen ink.

Known or suspected constituents of these dyes are known to be absorbed through the skin, to be toxic, and some possibly carcinogenic. That these dyes might have had some effect upon reproductive success and even upon behavior cannot be ruled out on the basis of present data. Evidence will be cited below why I suspect they were unimportant in producing abnormal behavior or in altering reproductive success.

MORTALITY OF FEMALES

By June, 1959, the populations in Rooms 1A, 2A and 2B had become predominately male in composition. Many females were known to have died following symptoms indicating complications with pregnancy or delivery. Others were too far decomposed when found dead to warrant autopsy. Comparative mortality for males and females to June, 1959, is shown in Table 22-2. Comparisons are based upon an original *N* of 48 rats in each of the six tier and sex categories.

Second-tier females despite their younger age experienced a much higher risk of death than did their older 1st-tier associates. Apparently attainment of sexual maturity under conditions of a developing behavioral sink predisposes rats to complications of pregnancy more acutely than among rats who matured in a more placid environment.

TABLE 22-2 MORTALITY

TIER	MONTHS OF AGE, JUNE, 1959	PROPORTION DEAD BY JUNE, 1959		FEMALES DYING FOR EACH MALE DYING
		MALES	FEMALES	
1st	15.5	.187	.582	3.1
2nd	12.0	.104	.562	5.4
3rd	9.5	.061	.125	2.1

The population in Room 1A was allowed to survive for several months beyond the termination of the populations in the other three rooms during July, 1959. Between June and September, 1959, only 0.140 of the 43 males alive in June died. In contrast 0.375 of the 32 females alive in June died.

POSSIBLE ROLE OF VITAMIN A

Complications with pregnancy, accentuation of frequency and severity of skin lesions, occasional abnormal appearance of eyes and surrounding membranes, blocked urethras, hemorrhagic bladders, and an occasional bladder or kidney stone suggested the possibilty of some dysfunction of Vitamin-A metabolism (Moore, 1957). Dr. Stanley R. Ames of the Distillation Products Industries consented to assay Vitamin A in the liver and sera of representative rats. This sample taken in July and August, 1959, from Rooms 1B, 2A, and 2B included both sexes, all three tiers, and brood-pen and nonbrood-pen rats. Total liver-storage levels ranged from 45,000 to 60,000 I.U. of Vitamin A. This contrasts with levels of 750 to 1,000 I.U. in year-old male rats on natural foods studied by Dr. Ames.

In December, 1959, livers from a second group of rats were sent to Dr. Ames. These included rats of several ages, from a wide range of size and complexity of social groups. Vitamin-A storage in the liver increased with age. No relationship existed between social background or size of group and Vitamin-A storage in the liver. The Purina Ralston Company informed Dr. Ames that the chow they had supplied me had a rating of 12 I.U. of Vitamin A per g. On the basis of an average intake of 15 g. of food per day and a 50 per cent storage of the Vitamin A consumed each day, Dr.

Ames concluded that the observed levels of Vitamin A with age would result.

The only rats which up to the termination of this study might have served as adequate controls for Vitamin-A assay were disposed of before I realized the necessity of a control group. Even so the history of these 18 females and 9 males does shed light on the problem. They were rats of the same age as the 3rd tier. In fact they were excess 3rd-tier rats born in Room 1A and removed before sexual maturity.

In contrast, they were housed in breeding cages containing two females and one male. All females reared several litters successfully, with no indication of complications with pregnancy. Nor were they characterized by abnormal nest building or transport behavior. They also were on a pure Purina Chow diet only supplemented by one orange per rat per week.

Complications relating to pregnancy characterizing my rats in the behavioral-sink environment resemble those observed in studies of Vitamin-A toxicity (Moore, 1957, Chapter 28). However, in most such experimental studies of Vitamin-A toxicity, liver-storage levels 10 times that seen in my rats were attained by administering very high levels in the diet. Since my rats in breeding cages failed to evince any difficulty with reproduction, even though they attained similar relatively high levels of Vitamin-A storage, Dr. Ames concluded that, if Vitamin A did play a role in the observed impairment of reproduction in my behavioral sink social colonies, it must mean that social stressors reduce the tolerance to Vitamin-A toxicity.

In conclusion, I can only say that complete uncertainty reigns as to the involvement of Vitamin A in the present study. It represents the type of previously unsuspected variables which inevitably arise when one attempts to gain insight into complex social systems. Only further studies can clarify their possible role.

FATE OF YOUNG

Detailed records were maintained for young born between December 25, 1958, and January 30, 1959. This group of young comprised the 5th tier of rats. Like all other tiers than the first three, they were removed prior to sexual maturity. These records provide insight into the relative impact of a developing behavioral sink upon survival and maturation. Relevant data are summarized in Table 22-3.

At this time each of the pens in the four rooms could be placed in one of three categories. *Brood pens* (1AI, 1BI, 2AI, 2BIII, and 2BIV) not only contained fewer resident adults, but the adults present were mostly females. Many young born here survived. Most of the residents ate elsewhere. *Major pens of feeding* (1AIII, 1BIII, 2AII, 2BII) *by adults* were those in which most of the adults, regardless of pen of residence, came and ate most frequently. The seven remaining pens, intermediate in their characteristics, formed the third group, *other pens.*

This table includes data from all four rooms (1A, 1B, 2A, and 2B). Since each category of usage of pens includes a different number of pens, means of the raw data provide a more precise insight into the developed differential usage of the available environment. In some instances the raw data pertaining to the pens in each room were first converted into proportions of the total in that room for that item. Thus, in examining Table 22-3, if the proportion under each category of pen is multiplied by the number of pens in that category, the sum of these three products equals 4.00. Had the usage of all pens been

TABLE 22-3 CHARACTERISTICS OF 5TH-TIER RATS AND THEIR SOCIAL ENVIRONMENT OF ADULTS

DATUM CATEGORY*	CATEGORY OF PEN A: 5 BROOD PENS	B: 4 MAJOR PENS OF FEEDING BY ADULTS	C: 7 OTHER PENS	D: TOTAL (OR $\bar{x}$)
		I. Adults		
1. Resident rats				
a. Observed $\bar{x}$	9.7	24.5	23.0	307.5
b. Expected $\bar{x}$	17.9	22.4	18.4	307.9
c. Observed $\bar{x}$ proportion	.126	.319	.299	3.999
2. Proportion of residents males	.258	.556	.680	.591($\bar{x}$)
3. Food consumption				
a. Expected $\bar{x}$ proportion	.233	.292	.238	4.000
b. Observed $\bar{x}$ proportion	.049	.633	.175	4.002
4. Rats seen/3 hrs. ($\bar{x}$)	16.1	49.9	36.4	535
5. Contact index ($\bar{x}$)	41.7	170.8	102.9	1612
		II. 5th-Tier Young		
6. $\bar{x}$ age in days when first seen	6.18	3.00	3.03	4.58($\bar{x}$)
7. $\bar{x}$ total observed for first time	51.30	28.20	25.60	558
8. $\bar{x}$ survived to marking	36.0	0.75	5.70	223
9. $\bar{x}$ marked which survived to March, 1959	26.2	0.25	1.60	143
10. $\bar{x}$ residents in March, 1959				
a. Male	7.00	5.25	1.86	69
b. Female	4.00	7.50	5.60	89
11. *a.* $\bar{x}$ feeding acts	5.4	158.5	31.7	883
b. $\bar{x}$ proportion of feeding acts	.025	.718	.143	
12. $\bar{x}$ size feeding groups	0.15	3.35	0.66	1.33($\bar{x}$)

* $\bar{x}$ = mean.

identical the mean proportion of usage under each category would have been 0.25.

The following comments will assist in evaluating the data in Table 22-3.

ROW 1 a and b. The observed number of residents was based upon two surveys, one conducted just prior to the weaning of 5th-tier young and a second during the first week in March, 1959, at the time the young were removed. The fewer number of adults in the brood pens comprises the most important facet of these data. Expected numbers were based upon the theoretical 3:4:3:2 ratio for Pens I:II:III:IV. This ratio did closely approximate the observed residence during the early history of these populations (Table 22-1). The pen where the rat stayed during the 12 hours of reduced activity is designated as its place of residence. The shift in residence accompanying the development of the behavioral sink entailed a decrease in what became the brood pens, with a corresponding increase elsewhere.

ROW 2. The low proportion of adult males in brood pens resulted in part from persistent antagonistic action by territorial males in excluding other males. Some of

these excluded males settled in the major pen of feeding. However, the great increase in proportion of males in the "other pens" indicates that these males excluded from the brood pens were also largely excluded from the second category of favored type of location, the major pen of feeding.

ROW 3 a and b. The expected proportion of food consumption was based upon the theoretical 3:4:3:2 ratio for usage of Pens I:II:III:IV as discussed with reference to Figure 22-2. In other words, this ratio should have held if rats had eaten where they resided and no shift of residence had taken place during the development of the behavioral sink. However, the observed eating in the four feeding pens diverged markedly from the expected. Of particular note is the fact that rats resident in the brood pens were attracted over into the feeding pens much more so than were those living in the "other" pens. Comparison of Rows 1 *c* and 3 *b* indicates that .611 (i.e., .126 — .049/.126) of the eating by rats resident in the brood pens was in the major feeding pens; while only .415 (i.e., .299 — .175/.299) of the feeding by rats in the "other pens" was in the major feeding pens. These calculations refer to net changes. This forms perhaps the strongest evidence that all adults were in fact caught in the behavioral-sink phenomenon.

ROW 4. During February, 1959, Dr. Kyle R. Barbehenn and the author each observed each room for a total of three hours. The total number of different rats visiting each pen at least once during the three hours was recorded. Obviously many rats visited pens other than their place of residence. Nevertheless the greatest increase in visitation characterized the feeding pens.

ROW 5. Each above three-hour period was divided into four 45-minute periods. During each of these shorter periods a tally was made for each rat that was seen on the floor or on the burrow in each pen. The sum of these for a three-hour period formed the contact index for each pen. At least in a rather crude way it reflects the probability of a rat's contacting another in a particular pen. Dividing the data in Row 5 by that in Row 4 produces quotients of 2.59, 3.42, and 2.83 respectively for the three columns. This means that not only do more rats visit the feeding pens but they spend longer times there.

These data in Part I of Table 22-3 reflect the profound changes which had taken place among adult rats during the development of the behavioral sink. They primarily concern the differential usage of space. In Part II of Table 22-3 is shown how this differential usage of space by the adults affected their progeny.

ROW 6. Mean age of 5th-tier litters when first seen: At intervals of less than two weeks the nest boxes in all burrows were examined for litters. At this time their age in days as judged by relative development was noted. Results are based upon 558 young observed during a five-week period. Since litters in the brood pens averaged twice as old as litters elsewhere, birth in the brood pen favored early survival. If there had been complete survival there should have been as many litters in the 1–4 day age range as in the 5–8 day range. For the 5 brood pens the number of young of these two ages was 115:91 whereas in the remaining 11 pens it was 235:51. Thus, no more than 0.217 of the young survived beyond four days if born outside the brood pens while 0.79 of the young in the brood pens survived past the first four days.

ROW 7. Mean total known to be born per pen: Approximately twice as many rats per pen survived to the survey dates in the brood pens as elsewhere.

ROW 8. Mean numbers per pen which

survived to age of marking: If the young survived to about 8–10 days of age, one or two toes were removed as a permanent identification. These few days witnessed a marked differential in mortality with the brood-pen young having by far the best chance for survival.

ROW 9. Mean numbers per pen which survived to March 2–6, 1959: At this time when all surviving marked young were removed they ranged in age from 40 to 70 days of age. Of the 142 survivors 130 were born in the five brood pens. In other words 0.51 of the 256 rats born in the five brood pens survived for at least 40 days, whereas only 0.04 of the 302 rats born outside of the brood pens survived to 40 days of age. Thus, if a rat was born in a brood pen its chances of being weaned were 12.75 times those of rats born outside of the brood pens where they were subject to the full impact of disturbances created by the behavioral sink.

ROW 10. Mean number of 5th-tier residents per pen: Residence refers to the pen of capture during the March 2–6, 1959, period when these young were removed. As may be seen by contrasting Row 9 with the sum of Rows 10 *a* and 10 *b*, 58 per cent of the surviving young which were born in the brood pens now lived elsewhere. Actually this change in residence resembled closely that exhibited by the original 1st-tier rats at about the same age during the period immediately following insertion of the ramps between pens at the start of the colonies. Of the 111 1st-tier young surviving to 11 weeks of age, 0.351 resided in the major feeding pens, whereas 0.359 of the 142 5th-tier young resided in these pens. Selection of place of residence by 5th-tier young must therefore be governed primarily by the two factors, height of burrows and endedness of the environment, in a similar manner as these factors affected selection of residence by earlier generations. This means that the existing behavioral sink, including the marked differential residence by adults (Table 22-3, Rows 1 *a*, 1 *b*, and 1 *c*) in no way affected place of residence of the 5th-tier young. However, those 5th-tier young which did select the major feeding pens as a place of residence were exposed to a heightened association with adults during periods of rest. Furthermore, the differential sex ratio of adults (Table 22-3, row 2) seemed to affect selection of place of residence by these sexually immature 5th-tier young. Of the young males, 51 per cent remained in the five brood pens with their mothers, where also their resting contact with males was low. In contrast, 77 per cent of the females changed their residence to the remaining pens where their probability of associating with males during periods of rest was high.

ROWS 11 and 12. Feeding by 5th-tier young: During the six hours of observation of each room during February, 1959, periodic recordings were made of the number of 5th-tier young feeding in each of the four pens then being observed; 187 sets of such observations were tallied. A mean of 48 such observations per pen was recorded for each of the three classes of pens. A rat eating at a hopper was defined as a "feeding act." The great preponderance of these feeding acts was in the pen where the adults were also concentrating their feeding. Furthermore, in the major pen of feeding by adults the young usually ate in association with others of their age class, but this was rarely true elsewhere. Thus, despite a greater dispersal of place of residence, the young concentrated their feeding in those pens where contact with adults was greatest and where their behavior was most likely to be interrupted by other rats of all ages. Contrasting Row 11 *b* with Row 3 *b* suggests that a greater

proportion of the eating by young 5th-tier rats took place in the major pen of eating than was true for adults.

EARLY GROWTH OF 1ST- AND 5TH-TIER MALES

Log-log graphic plots of the data in Table 22-4 reveal that at between 50 and 70 days of age the 5th-tier males averaged 35 g. less in weight than did the 1st-tier males who grew up in the absence of a behavioral sink. At all ages prior to weaning many of these 5th-tier young were characterized by various states of emaciation. Only a few were as plump as their 1st-tier predecessors at the same age. Failure of the mothers to nurse their scattered young frequently enough certainly contributed to this retardation before weaning. Even where litter size in a single nesting box continued large enough to provide adequate stimulation for a normal mother to nurse properly, such 5th-tier litters still were retarded in growth prior to weaning. In the absence of direct observation of nursing I can only suspect that both the perception of the litter as cues initiating nursing and the behavior of nursing itself were disrupted as were other behaviors under the influence of the behavioral sink. See the comments in the Discussion section with regard to the possibility of Billingham's "runt disease" having been a contributing factor to the retarded development of these 5th-tier young.

TABLE 22-4 EARLY GROWTH OF 1ST- AND 5TH-TIER MALES

1ST TIER			5TH TIER		
N	$\bar{X}$ AGE IN DAYS	$\bar{X}$ WT. GRAMS	N	$\bar{X}$ AGE IN DAYS	$\bar{X}$ WT. GRAMS
62	49.2	178.0	19	50.2	142.3
62	88.1	322.0	16	58.7	174.0
			28	70.5	221.4

$\bar{x}$ = mean.

DISCUSSION

Disruption of a sequential series of related perceptions or of a sequential series of similar or related responses formed a common characteristic in the development of all forms of abnormal behavior associated with the behavioral sink. We may then ask, "What was the origin of these disruptions?"

A relevant theoretical model of social interaction has already been presented (Calhoun, 1957, pp. 349–354). This model assumes that there are types of interaction between two individuals which lead to some satisfaction from the interaction. Such satisfaction places each individual in a refractory state during which time further interaction will fail to enhance the amount of satisfaction. By a refractory state I mean a period of inattentiveness, physiological unresponsiveness, or subthreshold motivation. At the end of the refractory period the individual again is in a responsive stage. However, if such a responsive individual interacts with another who is in the refractory state, the former individual will be thrown into a false refractory state during which time he no longer can add to a theta amount of total satiation from social interaction desired over some more extended period of time. Depending upon the intensity or duration of such social interaction there is some optimum group size assuring attainment of this theta amount of social satiation. Any reduction or increase in group size from the optimum with reference to a particular intensity or duration of interaction leads to a reduction in social satiation if the intensity of the response remains constant. As the group size increases, its members may continue to attain their desired level of social satiation provided

they continue to reduce the intensity or duration of interaction.

In the present study the over-all group size in each room did increase with time. Also due to the charactetristic of the feeding positive response situation in conjunction with certain factors biasing residence and movement between pens, the rats did develop the behavior of seeking proximity with other rats while eating. Each rat attempted to maximize the duration of total time of feeding during which it was in proximity with another rat similarly engaged in feeding. Concentration of feeding activity in a single pen increased the probability of engaging in such social interaction. However, this increase in animals in the major pen of eating has the curious consequence of requiring individuals to reduce the durations of each behavior, or otherwise the amount of eating side by side will actually become reduced. Full appreciation of this process requires examination of the mathematical model cited.

As pointed out earlier, no measurements were made of duration of feeding. However, following the above logic there should have arisen a gradual shortening of durations of feeding through the history of the colonies after June, 1958. Fewer long duration periods would be replaced by many shorter ones for each rat. Furthermore, it is most logical to assume that the changes in physiology permitting a reduction in the duration of feeding would serve as a governor reducing the duration of all other behaviors.

Feeding behavior happens to be one in which reduction of its duration and increase in its frequency can still lead to an animal's securing adequate satiation in the sense of sufficient nutrition. However, if behaviors including perception of sex partners, appropriate response to sex partners, building nests, or transport of young are shortened, they culminate in inappropriate action or failure to complete some product of the behavior which is of value to survival.

The picture developed here is one of rapid shifting from one type of behavior to another, none of which persists for long before again changing to some other type. This presents the opportunity for a component of one type of behavior to be replaced by an inappropriate component from another.

Such confusion of parts of one behavior with another may be involved in the following:

A mother rat takes a pup from a nesting box and transports it down the spiral ramp to the floor where she drops and deserts it near the food hopper or the supply of nesting material. It is as if the behavior of transporting young had been shut off while she still had the pup in her mouth, and she just carried it part way during her initiation of an unrelated behavior.

Dropping nesting material halfway up the spiral ramp before getting to a nesting box seems to be a similar type.

I also cannot help but wonder if the infliction of wounds during sexual mounts and the tail biting really are insertions of a feeding act in the midst of the sexual mount or of the behavior of investigating another.

The attempt in this discussion represents an effort to construct a logical framework which might help in understanding the origin of the abnormal behavior arising as the behavioral sink developed. None of the observations form proof for the formulation.

Dr. Snell suggested that the utilization of dyes for marking the rats may have been a factor in the observed changes. Although they may have affected the likelihood of

tumors developing, it appears to me unlikely that they were important in affecting behavior or maternal physiology. Regardless of the dye used, representatives of all three tiers exhibited similar changes. Furthermore, despite use of these dyes the alterations in behavior and physiology did not appear until the development of the behavioral sink.

Alteration of maternal reproductive physiology represents an area of phenomenology associated with the behavioral sink concerning which observed data fail to permit adequate insight into its origins. All that can be said is that some set of circumstances increased the prevalence of uterine hemorrhaging, death of fetuses before term, inability to deliver full-term fetuses, and extreme enlargement of some one segment of the uterus. No doubt social stressors contributed to an endocrine imbalance increasing the probability of these conditions. I also cannot help but wonder if the observed Vitamin-A levels of 45 to 60 thousand units per whole liver of adult rats might have been involved. If so, social stressor must have led to a lowered threshold to Vitamin-A toxicity. I am currently engaged in a series of studies in which both intensity of social stressors and Vitamin-A level of the diet form a matrix. Findings from these studies may throw light upon this puzzling set of phenomena.

In addition to behavioral disturbances among adults of both sexes and to impaired maternal reproductive physiology, fate of young born into an environment characterized by a behavioral sink forms an area of impact. Of the 558 young known to be born at the height of the behavioral sink, only one-fourth survived to weaning. Retarded growth characterized their later development. Poor maternal care undoubtedly contributed to the poor survival. Yet the recent account of experimentally induced "runt disease" described by Billingham (1959) suggests that histoincompatibility may also be a contributing factor.

Newborn mice, heterozygous for certain histocompatibility genes, if injected with leucocytes or macerated spleen from a homozygous donor develop runt disease. Their growth becomes markedly retarded, and their fur is sparse and matted. Donor lymphoid tissue invades the host's lymphoid tissue and elaborates antibodies there which destroy the host's lymphoid tissue. Through lack of adequate lymphoid tissue to battle pathogenic invaders, the runts often die young. Billingham suggests that a similar phenomenon may account for certain hemolytic diseases in newborn children provided placental hemorrhaging prior to birth has made possible invasion of maternal leucocytes into the fetal circulation.

I wish, here, merely to point out that the scrawny Osborne-Mendel rats born during the behavioral sink stage of the colonies may well have been suffering from Billingham's runt disease. Uterine hemorrhaging did characterize many females prior to parturition. Furthermore, the stem mothers from which the populations started came from a random-bred stock known to be far from homozygous. Here again we encounter a provocative set of observations which suggest an hypothesis incapable of substantiation from the recorded data.

This has been a study whose value lies not in rigorous validation of prior hypotheses but rather in its revelation of a striking phenomenon, the behavioral sink, and in the many hypotheses generated from the observations. In this connection, one cannot help but wonder concerning the impact of behavioral sinks upon the course of evolution.

Certainly many species have encountered situations leading to behavioral sinks. For example, consider a species for which several sources of water occurred within the home range of each individual. Following this phase in its evolution there arose a gradually developing xeric era. Previously members of this species had lived in small family groups or in local colonies averaging a dozen or so adults. However, as sources of water became sparser, members of adjoining families or colonies were more likely to arrive simultaneously at the same water hole. Although each family or colony might initially visit one or more water holes, one in particular would develop the character of an alpha positive response situation, since each individual's developing requirement for proximity with associates while drinking would more likely be achieved there.

Under these circumstances many young and many gravid females would die as a direct or indirect consequence of the incompatibility of maternal physiology with the abnormal aggregations accompanying a behavioral sink. Natural selection will favor survival of genotypes capable of tolerating continued association with many other individuals. By the same token, these survivors will now seek to avoid becoming isolated from their neighbors, since their physiology now no longer functions most effectively in the absence of frequent interactions with others. Such a sequence of circumstances and events forms a plausible path leading to the evolution of herd-type species. By a herd-type species I mean any species in which each individual has a fairly high probability of contacting at least 100 other individuals.

SUMMARY

Populations of domesticated albino rats were allowed to develop in rooms such that each population had access to four similar pens each 5×7 feet. Ramps over adjacent pens formed a linear communication system such that there were two end pens and two center pens. In one end pen and its adjoining center pen artificial "burrows" were placed on the wall 3 feet above the floor. In the other two pens these burrows were 6 feet above the floor.

The endedness of the row of four pens tended to make twice as many rats select the two central pens as places of living as selected the two end pens. On the other hand, the lower elevation of the burrows tended to make twice as many rats select the two pens on one end of the series as places of habitation as selected the two pens on the other end of the series. Operating together, these two biasing factors formed a theoretical biasing residence ratio of 3:4:3:2 along the series of four pens. Observed residence closely approximated the theoretical.

A large food hopper was located on the floor of each pen. Such spatially restricted structures are defined as *positive response situations*. Since more rats lived in one pen than in any of the other three, the chances were greatest there that when one rat was eating another would come and eat beside it. Once the number of rats in a room increased above a certain level, this frequency of contact while eating increased sufficiently that the rats developed a new definition of the feeding situation to include the presence of another rat. Gradually eating in the other three pens declined until 60–80 per cent of all food consumption was in this one of the four pens.

The development of this atypical aggregation under the influence of the several conditions and processes involved forms what I have termed a *behavioral sink*.

Concomitant with its development many abnormal behaviors and disturbances of

reproduction began to appear. Females experienced difficulty in carrying fetuses to term, and if they carried to term they were sometimes unable to deliver young. Death frequently occurred at this time. If they survived, one region of the uterus enlarged until it was sometimes as large as the former size of the rat. Such affected rats always died. Females developed a mortality rate 3.5 times that for males.

On the behavioral side, males developed a pansexuality in which they would mount other rats regardless of their age, sex, or receptivity. Infliction of wounds during mounting developed. An abnormal response of biting the tails of other rats also developed. Nest-building behavior became completely disrupted. Transport of young by lactating rats became so disorganized that young became so scattered that they were no longer nursed.

A theoretical model for the origin of these abnormal behaviors is proposed. Briefly it points to reasons why the duration of each feeding behavior should become shortened. This change in rhythm of eating causes other behaviors to shorten with the end result that the behavior becomes inappropriate or incomplete. Thus the development of a behavioral sink leads to a state of sustained inordinate aggregation which may be called "pathological togetherness."

REFERENCES

BILLINGHAM, R. E. 1959. Reactions of grafts against their hosts. *Science. 130:* 947–953.

CALHOUN, J. B. 1957. Social welfare as a variable in population dynamics. *Symposia Quant. Biol.* (Cold Spring Harbor, N.Y.). *22:* 339–356.

MOORE, T. A. 1957. *Vitamin A.* New York, Elsevier, 645 pp.