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AGGREGATIVE BEHAVIOR AND HABITAT CONDITIONING BY THE PRAIRIE RINGNECK SNAKE, *DIADOPHIS PUNCTATUS ARNYI*

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Abstract

When ringneck snakes were released in laboratory arenas in which all cover objects presented equalized physico-chemical conditions the snakes were found to follow a multinomial distribution with unequal probabilities of occupancy of each cover object. The resultant clumped distributions are the result of intrinsic aggregative drives which are not based on sexual attraction, as was evident from repeated aggregation formation among either males or females in experiments involving only one sex. Preliminary findings on effects of environmental variations in the experimental arenas indicate that aggregative behavior can be modified, at least by increasing or decreasing the dampness of the substrate.

Persistent use of the same cover object by groups of ringneck snakes indicated that there might be a bias for particular locations in the arenas. Various experimental tests demonstrated that the bias was due to presence of an attractant substance, possibly integumentary, cloacal gland, or excretory in origin, which is deposited by snakes that first frequent the particular cover site. Such sites are herein described as "conditioned habitat." Snakes will seek and return to conditioned substrate even when it is translocated in the experimental arena. Snakes apparently use visual and olfactory and/or vomeronasal sensory perception to locate the conditioned sites and to trail other snakes or locate trails left by the travels of other ringneck snakes.

The advantages of aggregative behavior and habitat conditioning are discussed and compared to denning habits of large snake species.

Introduction

Social behavior in snakes, at least in the form of epideictic display, is very limited. Passive social behavior such as aggregation is a common phenomenon, but studies on factors initiating and affecting aggregative behavior are few and are limited in scope. Reports of snake dens are common in literature, the most exhaustive discussion of the topic being that by Klauber (1956). Denning, of course, is a seasonal phenomenon principally characteristic of large snake species. Aggregation is also common among small secretive species. It may occur in hibernacula during the winter, but is also observed at other times of the year. A comprehensive study of aggregative phenomena in the northern brown snake (*Storeria dekayi*) was reported by Noble and Clausen (1936). Otherwise the reports on aggregation in small snakes have been casual statements about the number of snakes found under a single object, or descriptions of the responses of animals to extremes of temperature, humidity, light, and so forth.

The interpretation of aggregative phenomena must take into account extrinsic and intrinsic factors. The extrinsic factors relate to habitat selection in a varied environment; the intrinsic factors involve instinctive social drive in the absence of alternative physical environments. A seasoned snake collector working in a familiar area develops considerable ability to find his quarry. What he is recognizing is habitats and microhabitats and, crudely, the physiological needs of a snake. He also becomes aware that the environment is not uniform and that he is unable to satisfactorily evaluate the distinction between intrinsic and extrinsic factors bringing the snakes into the sites that he searches most exhaustively. The excellent study by Noble and Clausen (*op. cit.*) has provided many instructive clues for recognition of these conditions, but for reasons given below other approaches to the understanding of aggregative phenomena are required.

In the south central United States there are several species of small secretive snakes, generally averaging under 12 inches long and usually found under sheltering objects in the mild, moist spring months. Some species are largely solitary (*e.g., Tantilla gracilis*), others tend to occur singly or in groups of two or three under individual sheltering objects (*e.g., Tropidoclonion lineatum, Carphophis amoenus, Leptotyphlops dulcis, Sonora episcopa*), and one species (*Diadophis punctatus arnyi*) is very gregarious, often occurring in numbers of half-a-dozen or more under a relatively small piece of cover. Additionally, certain stones regularly have small snakes under them, suggesting that optimal conditions must prevail in these microhabitats. Published studies by various authors on the above mentioned species have largely confirmed these impressions.

The distribution of small secretive snakes can, of course, be assumed to be non-random in the field. Since the natural environment is variable the snakes will ordinarily be found under naturally occurring suitable cover items; hence their distribution will not be random with respect to all cover. If all cover objects had equal probability of selection as a cover object by each snake the snakes would be unable, therefore, to select cover objects on the basis of physico-chemical attraction. Under such equalized conditions, three alternative distributions of the snakes appeared possible, given sufficient but not excessive time. The snakes could be distributed as:

1) a multinomial distribution with equal probability of occupancy of each cover site or
2) a uniform distribution or
3) a multinomial distribution with unequal probabilities of occupancy of each cover site.

If the first distribution were observed no social relationships would be likely and distribution could be termed as random. If the distribution were found to be uniform, territorial behavior would be suspected, particularly if only one animal utilized an individual cover item. Finally, if a multinomial distribution with unequal probabilities of occupancy for each disc were observed, there would be evidence of social relationships. The first and third distributions would of course result in aggregations or clumps of the ringneck snakes, but the expectancy of clumps would be greatest in the third type of distribution.

The ringneck snake, *Diadophis punctatus arnyi,* was selected for the present study because of its abundance and its obvious gregariousness. Various reports call the species common, apparently assigning this category to finds of a dozen or so in an hour. Hurter (1911) reported finding 17 specimens under a rock about 24 × 18 inches. Brennan (1936) reported 14 under a flat rock. Richard B. Loomis (personal communication) knew of one case where 44 were found under a single stone. Loomis and Dundee collected 300 ringnecks, as well as many other reptiles, in one hour on April 30, 1950 in Douglas County, Kansas. On April 11, 1967 Dundee alone collected 238 ringnecks in 50 minutes in Douglas County, Kansas, from an area about 10 feet wide and 400 feet long. This latter collection included all sizes of ringnecks and counts of 15, 12, 11, 9, 9 were recorded from individual stones.

The obvious questions arising from these observations on abundance are (1) were the sites optimum habitat; (2) were individual stones particularly desirable, thus attracting more ringnecks during their wanderings; (3) were the snakes gregarious because there were so few cover objects in relation to the population size; (4) were the aggregations a result of intrinsic drive?

Not all of these questions are immediately answerable, but certain generalizations might be made providing partial answers to some of these questions. First, we can assume that the Douglas County physical setting is an optimum habitat because it regularly har-

Figure 1. Circular sand-filled arena used for experiments. Snakes seen are ringnecks to show relative size in comparison to the seven-foot diameter of tank and 12-inch diameter discs.

bors large numbers of ringnecks. Second, snakes were found beneath various sizes of stones under which the soil ranged from dry to moist. And third, the stones were loose on the ground or partially embedded. These observations indicate that the microhabitats selected were not markedly restricted. There were many flat limestone slabs that harbored various reptiles or none, but which could have served as cover for ringnecks. Hence we judge that population pressure was not severe. Only laboratory experiments can provide data for an adequate answer to the fourth question and hence the basis for the initial studies of our investigation.

Materials and Methods

The basic design of our experiments derives from the hypothesis that ringneck snakes have intrinsic aggregative drives which may or may not be modified by environmental factors.

Artificial habitats were established in the laboratory by using circular livestock watering tanks seven feet in diameter. The tanks were mounted on platforms equipped with rollers so that they could be rotated at will.

Thirty mm of mason's sand was placed on the bottom to provide a non-packing substrate. The sand could be smoothed to uniform depth.

Circular discs, 12″ in diameter, made of 1/4″ plywood and painted gray to simulate limestone were arranged radially concentric to the edge of the tank (Fig. 1). These discs could be rotated by hand, and pressed down to make them lie flush upon the substrate. Loose sand was brushed up around the perimeters of the discs to insure sealing of any irregularity that might offer easy access to the underside of the discs. The circular tank and circular discs eliminated angles that could provide biased thigmotactic satisfaction. Each disc offered equal conditions for selection as a cover site.

Most experiments were conducted using dry sand. In certain experiments with moist sand as a substrate, Bouyoucos soil moisture blocks from Industrial Instruments, Inc. were buried in the sand at strategic locations. Conductivity in the blocks was measured by a Bouyoucos Moisture Meter, also from Industrial Instruments, Inc. The experimental arenas were kept in a room usually maintained at $75 \pm 2°F$ and humidity of $57 \pm 5\%$.

Only a diffused outside light entered the room by day. Artificial light provided from the ceiling was regulated by an automatic timer to approximate normal day length, but was set to come on after dawn so that no sudden brightening would frighten the snakes.

Experiments were run with adult animals only and almost exclusively with males. The use of males was almost mandatory because of the paucity of females in field collections. Snakes used in experiments were sorted according to sex (double checked by determining presence of anal ridges and hemipenial sheaths in males).

For certain experiments the animals were marked with either brightly colored lacquer or butyrate dope for convenient recognition, thus eliminating the need for handling the snakes. Markings used were yellow, orange, and white neck rings or short dorsal stripes.

Animals were reused for experiments but were fed earthworms between experiments and were permitted to rest for about a week before being placed into arenas again. In certain experiments, particularly those involving dry sand, when snakes were gathered for re-release, water was provided *ad libitum* before release to offset dehydration.

Snakes were released from the center from under an inverted can after they had become quiescent. All releases were made during daylight hours.

Dispersal and distribution of the snakes were determined by daily daytime inspections of the arenas. Procedures included, (1) initial release of snakes and the notation of their locations without handling or displacing them, (2) daily pickup and re-release from the center, (3) daily pickup and re-release after the sand had been gathered, thoroughly mixed, redistributed, and discs washed in detergent and reset, (4) translocation of specific discs and their underlying substrate to other positions in the arena, (5) rotation of tanks to test for possible compass or light orientations.

Results

General Behavior of Snakes After Release

When the inverted can was lifted to release snakes there was little reaction and the animals usually lay quiescent for up to 10 minutes. Eventually one or more animals would begin to glide out from the center. When this movement began it was not unusual for the moving animals to be joined by others so that they appeared to stream out in pairs or triplets. Movement away from the center seemingly was cautious and exploratory but within 15 minutes most snakes were active and gradually edging from the center, though some tended to remain for periods of an hour or more. The snakes often pressed their snouts to the substrate, suggesting the use of olfaction. Their actions suggested that vision, olfaction, and vomeronasal sensing were being employed to enable the snakes to determine where they wished to move. Both vision and olfaction were stated by Noble and Clausen (1936) to be the primary senses used by *Storeria dekayi* to locate their own kind, but a later study by Wilde (1938) suggested that the vomeronasal organ (= Jacobson's organ) rather than olfaction was the effective sensory device. We are conducting experiments to determine if these senses are the major ones used by individual *Diadophis* during their dispersal and search for cover and other *Diadophis*. Eventually the radial dispersal became a concentric one because of the limiting wall of the arena, and snakes ceased to stream in pairs and triplets. Generally most snakes were hidden by day, but when the substrate was smoothed at night numerous tracks could be found the following morning, showing that considerable nocturnal movement had taken place. Snakes that might be abroad in the early morning frequently were under cover when disc checks were made in the early afternoon.

TABLE 1

Dispersal of ringneck snakes in an arena containing dry sand, 10 twelve-inch discs, 40 male snakes. Ambient temperature 75–76° F. Relative humidity 54–64%. May.

Days after release	Disc											
	1	2	3	4	5	6	7	8	9	10	open	hidden
2	1	1	1	5	6	4	0	5	1	2	14	0
3	0	2	1	2	4	7	0	6	0	2	16	0
4	1	2	0	1	4	14	0	6	0	4	8	0
5	1	2	2	0	4	17	0	4	0	2	8	0
6	1	1	1	2	4	12	0	6	1	2	10	0
7	0	2	0	0	3	24	1	6	0	0	4	0

Access to the underside of discs was accomplished by pressing the snout repeatedly against the perimeter of the disc until the head was pushed under. Only rarely did any snake burrow into the open sand.

Snakes and Substrate Left Undisturbed After Location of Snakes Noted

1. *General statement of hypothesis.*

In our first experiments we assumed that if snakes were released from a central point they would distribute randomly, and that if no aggregative drive existed, snakes would show a random distribution from day to day. A series of experiments was designed to test this hypothesis of random distribution following release. Noble and Clausen (1936) found that aggregations of *Storeria dekayi* could be forced by jostling the cages. They also found that snakes clustered in areas of presumed optimum temperature and humidity when left undisturbed, but if the clusters were disturbed the snakes would break into smaller groups. Thus it was decided that experimental animals should be left undisturbed after release. Initial experiments showed that if discs were lifted gently and the snakes counted quickly there was little evidence of excitement of the animals. After the discs were replaced the snakes were free to move at random.

2. *Results.*

In the first experiment 40 male snakes were collected and released in an arena containing dry sand and 10 twelve-inch discs. The distribution of the snakes was recorded daily. The results of this experiment are given in Table 1.

The chi-square test of the null hypothesis that the distribution was the same for each day was not significant [chi-square, 45 d.f. = 47.34 (p = .35) (Cramér, 1946, p. 443)]. We concluded that there was no difference in the distributions for the various days. Therefore we decided to pool the snake counts across days to determine an overall distribution of the snakes under the discs. A chi-square of the null hypothesis of equal probabilities of occupancy for each disc by each snake was rejected by the chi-square test (chi-square 9 d.f. = 274.89) with probability $< .01$. It was concluded that the male ringneck snakes did not follow a multinomial distribution based upon equal probabilities of disc occupancy in their dispersion in the arena.

The second experiment consisted of releasing twelve female ringneck snakes in an arena containing dry sand and 10 twelve-inch discs. Daily observations were again made. The results of that experiment are presented in Table 2. A chi-square test of the null hypothesis of homogeneous distributions for each of the 6 days was not significant [chi-square 45 d.f. = 41.16 (p = .65), non-significant]. Therefore, it was concluded that there was no difference in the distributions among the days. Tests of the equality of the probabilities of occupancy for each disc by each snake were then undertaken. Chi-square tests for days 2, 3, 4, 5, 6 and 7 were 44.41, 35.45, 45.16, 90.00, 52.50, and 92.00 respectively. Each of these chi-squares is significant. Therefore we concluded that the probabilities of occupancy for the discs were not the same for each of the 10 discs tested.

The next experiment in this series consisted of releasing 9 female ringneck snakes in an arena containing dry sand with 10 twelve-inch discs (Table 3). The initial

TABLE 2

Dispersal of ringneck snakes in an arena containing dry sand, 10 twelve-inch discs, 12 female snakes. Ambient temperature 75–76° F. Relative humidity 54–64%. May.

Days after release	Disc 1	2	3	4	5	6	7	8	9	10	open	hidden	dead
2	0	0	0	0	0	0	0	6	0	5	1	0	0
3	0	0	0	0	0	0	1	7	1	2	0	0	1
4	0	1	0	0	0	0	1	0	5	0	2	0	2
5	0	0	0	0	0	0	0	5	0	0	1	0	3
6	0	0	0	0	0	0	1	3	0	0	0	0	2
7	0	0	0	0	0	0	0	2	0	0	1	1	0

Many tracks under discs 3, 4, 7 on day 2; snakes appear to travel in groups. Never any tracks under 5 or 6 during entire run.

phase of this experiment was a duplication of the previous experiment. The findings were similar. A chi-square test of the null hypothesis of similar multinomial distributions for the various days was not significant (chi-square 30 d.f. = 11.74). Similarly, chi-square tests for days 2, 3, 4 and 5 were 24.00, 24.00, 33.13, and 60.75 respectively. Each of these chi-squares is highly significant (probability < .01). Therefore it was concluded as above that the probabilities of occupancy for each of the discs by each snake were not the same.

Additional experiments, while not designed primarily for testing the above hypothesis, did however reveal similar findings. For example, one experiment consisting of the release of 34 male snakes, 20 female snakes, and 2 of undetermined sex in an arena containing moist sand and 14 twelve-inch discs, demonstrated the following results (Table 4). The distributions

TABLE 3

Dispersal of ringneck snakes in an arena containing dry sand, 10 twelve-inch discs, 9 female snakes. Ambient temperature 76.5 ± 1.5° F. Relative humidity 48–58%. June.

Days after release	Disc 1	2	3	4	5	6	7	8	9	10	open	hidden	dead
Animals left where found.													
2	0	0	0	0	0	0	1	3	0	4	1	0	0
3	0	0	0	0	0	0	0	3	1	4	1	0	0
4	0	0	0	0	0	0	1	5	0	2	0	0	1*
5	0	0	0	0	0	0	0	7	0	1	0	0	0
Day 5 animals picked up and released from center.													
6	0	0	0	0	0	0	2	2	1	3	0	0	0
7	2	0	0	0	0	0	0	4	2	0	0	0	0
After animals picked up on day 7 arena rotated 180°; animals then released from center.													
8	1	0	0	0	0	0	2	3	0	1	1	0	0
9	0	0	0	0	0	0	0	7	0	0	1	0	0
Discs 3 and 8 and their underlying sand interchanged after pickup.													
10	0	1	0	0	0	0	0	0	5	1	1	0	1#
Discs 9 and 5 and their underlying sand interchanged after pickup.													
11	0	0	3	0	0	0	0	1	0	2	1	0	0
All snakes picked up and replaced with 18 males.													
12	0	3	0	0	0	0	0	0	1	0	14	0	0
13	0	4	1	0	0	0	0	0	1	1	11	0	0

*from disc 7 # from open

TABLE 4

Dispersal of ringneck snakes in an arena containing moist sand, 14 twelve-inch discs, 34 male snakes, 20 female snakes, and 2 of undetermined sex. Temperature 75 ± 3° F. Relative humidity 70–79%. June.

Days after release	Disc 1	2	3	4	5	6	7	8	9	10	11	12	13	14	open	hidden	dead
	Snakes left undisturbed in locations where found.																
1	1	0	0	4	1	20	5	0	2	2	0	0	3	0	19	0	0
2	1	0	0	3	1	21	5	0	9	0	0	2	1	1	12	0	0
3	1	0	3	3	0	20	1	0	17	1	0	5	0	0	5	0	0
4	0	0	3	11	7	15	5	0	11	2	0	0	0	0	2	0	0
5	0	0	1	10	12	12	6	0	13	0	0	0	0	1	0	0	0
6	0	0	0	16	7	14	6	0	10	0	0	1	0	0	2	0	0
7	0	1	1	13	5	15	6	0	9	1	0	1	0	0	2	0	1
8	0	1	3	11	9	15	5	0	9	1	0	1	0	0	0	0	0
	At termination of experiment sand under discs remained slightly moist.																

from one day to another were heterogeneous (chi-square = 131.61, significant at .05). An examination of the data revealed that only 5 of the discs were persistently occupied and the significance of the test is due to the mobility of the snakes among these discs. The chi-square test for the equality of the probability of occupancy for each of the 14 discs by each snake tested to be highly significant for each day.

In another experiment, designed primarily to test the effects of crowding, the same 56 snakes referred to in Table 4 were released in an arena with dry sand with only 7 twelve-inch discs (Table 5). Again the distributions observed (see days 3 and 4) were not significantly different, chi-square = 2.48. The probabilities of occupancy for each of the discs by each snake were not the same. Chi-square 6 d.f. = 63.07, significant at .01.

In a final experiment (See Table 6), 20 male ringneck snakes were released in an arena containing dry sand and 10 twelve-inch discs. Again strong aggregative tendencies were observed when the snakes were left undisturbed. The distributions of day 2, 3, 4, and 5 did not test significantly different. Chi-square 27 d.f. = 28.33 and again the probabilities of occupancy for the 10 discs tested to be heterogeneous [chi-square 9 d.f. = 286.94, significant at .01].

A random distribution of the snakes was not occurring. Snakes tended to occur in several exceptionally large groups as well as a number of small groups, with a continuous range of cluster sizes being the exception.

Daily Re-Release From Center

1. *General statement of hypothesis.*

As earlier noted we assumed that in the absence of intrinsic aggregative drive snakes released from the center of the arena would disperse randomly. Hence, by gathering snakes each day and re-releasing them after resetting the discs, a new set of independent distributions should be obtained if the snakes were not excited by the daily capture and release. To test this hypothesis a series of experiments was conducted.

2. *Results.*

In the first of these experiments, (See Table 7), 10 male ringneck snakes were released in an arena containing dry sand

TABLE 5

Dispersal of ringneck snakes in arena with moist sand, 7 twelve-inch discs, 34 male snakes, 20 females, and 2 of undetermined sex. Temperature 72.5 ± 1° F. Relative humidity 60–72%. June.

Days after release	Disc 1	2	3	4	5	6	7	open	hidden	dead
	Snakes left undisturbed in locations where found.									
3	7	2	17	12	4	2	2	10	0	0
4	4	1	17	12	8	2	2	10	0	0
	End of day 4 all females and undetermined sex removed; continue with 34 males only, with these being released from center day 4 but left undisturbed where found on subsequent days.									
5	2	1	14	5	2	5	2	0	0	0
6	5	0	7	5	6	4	4	1	2	0
7	4	1	9	5	3	3	5	3	0	0
8	7	0	9	4	3	3	4	4	0	0
	Soil under discs still moist at termination of experiment.									

and 10 twelve-inch discs. The snakes were collected and re-released from the center each day. All of the snakes collected were under disc 3 on the first day and continued to return to this disc after release for 3 successive days.

The results of another experiment, given in Table 8, in which 10 male ringneck snakes were re-released in an arena containing dry sand and 10 twelve-inch discs show that on days 1 through 4, disc 8 was repeatedly sought as cover.

A third experiment (see Table 6, days 6 and 7) in which 20 male ringneck snakes were released in an arena containing dry sand and 10 twelve-inch discs showed simi-

TABLE 6

Dispersal of ringneck snakes in an arena containining dry sand, 10 twelve-inch discs, 20 male snakes. Temperature 76.5 ± 1.5° F. Relative humidity 48–58%. June.

Days after release	Disc 1	2	3	4	5	6	7	8	9	10	open	hidden	dead	
	Snakes left undisturbed in locations where found.													
2	0	0	0	0	7	0	1	0	1	9	2	0	0	
3	0	0	0	0	0	0	0	0	2	15	3	0	0	
4	0	0	0	0	0	0	0	0	3	12	5	0	0	
5	0	0	0	0	1	1	0	0	2	10	6	0	2	(from open)
	After recording day 5 snakes picked up daily and released from center.													
6	2	0	0	0	4	0	1	1	5	4	1	0	0	
7	0	0	0	0	5	0	0	0	2	11	0	0	0	
	After picking up snakes on day 7 tank rotated 180° before release.													
8	2	0	0	0	2	2	0	0	0	10	2	0	0	
9	0	0	0	0	0	0	0	0	3	11	4	0	0	
	Discs 4 and 10 translocated, sand and all, to each others position.													
10	0	0	0	0	0	0	0	0	12	2	4	0	0	
	Discs 3 and 9 translocated, sand and all, to each others position.													
11	0	0	0	0	0	0	0	0	6	4	8	0	0	
	Snakes removed and replaced by 7 females.													
12	2	0	0	0	0	2	0	1	0	1	1	0	0	
13	2	0	0	0	2	2	0	1	0	0	0	0	0	

TABLE 7

Dispersal of ringneck snakes in an arena containing dry sand, 10 twelve-inch discs, 10 male snakes. Release of snakes from center each day. Ambient temperature 74 ± 1° F. Relative humidity 49–55%. July.

Days after release	Disc 1	2	3	4	5	6	7	8	9	10	open	hidden
1	0	0	10	0	0	0	0	0	0	0	0	0
2	0	0	10	0	0	0	0	0	0	0	0	0
3	0	0	10	0	0	0	0	0	0	0	0	0
4	0	0	10	0	0	0	0	0	0	0	0	0
	Ten males from another experiment released here in place of the original ten.											
5	0	0	9	0	0	0	0	0	0	0	1	0
	After pickup of snakes sand from under discs 3 & 8 interchanged; disc 6 placed on old disc 3 site (now sand of 8); disc 3 placed on old disc 6 site (still disc 6 sand).											
6	0	0	0	3	0	0	0	3	0	0	4	0
	After pickup sand scrambled and discs returned to original compass positions of 1–10.											
7	0	0	0	1	0	0	0	0	0	0	9	0
	After pickup sand scrambled again.											
8	0	0	0	4	0	0	2	0	0	0	4	0

lar results. Discs 5 and 10 were preferred over any of the other discs. A test of the homogeneity of the occupancy distributions was not significant. Chi-square 9 d.f. = 9.66 (p = 0.35).

Obviously, the null hypothesis of day to day independence of the distributions was incorrect. The distributions obtained by releasing the snakes from a central point each day were not independent from one day to another. In fact, the snakes congregated under very few discs or all snakes congregated under a single disc. We also observed that on successive days the dispersion time from the center appeared to be more abbreviated and wanderings fewer. A snake arriving near a disc that had been regularly used would tarry near that disc and attempt to burrow under it. Occasionally the snake might move off a short distance, but would soon return to the disc. In these cases olfaction or vomeronasal testing appeared to be the primary sense employed. There did not have to be another snake present under the disc, nor did another snake have to be seen to prompt the return to the disc. These observations along with the previous analysis prompted us to conclude that these data could be interpreted as the result of the trailing phenomenon that was noted by Noble and Clausen (1936). A trail used heavily the first day seemed to be providing a strong sensory stimulus so that on subsequent days snakes followed this trail and came to a particular disc at the terminus of the trail. Once the disc had been used by a number of snakes the sand under it was presumably becoming saturated with some dermal or cloacal secretion or some other "conditioner." We decided that a series of experiments should be designed to determine if the substrate was being "conditioned" so that snakes found that particular portion of substrate particularly attractive.

Habitat Conditioning

"Habitat conditioning" was first examined by introducing a different set of snakes into an arena containing "conditioned" sand. One would hypothesize that if the sand was being "conditioned" the distribution of these snakes would follow the distribution of the snakes that previously occupied the arena. The results of such an experiment are given in Table 7. A chi-square test of the null hypothesis was not significant. Therefore, it was concluded that ringneck snakes are capable of "conditioning" sand.

Next, a group of snakes that had previously been allowed to disperse on an undisturbed basis was tested by daily release from the center. These snakes had demon-

TABLE 8

Dispersal of ringneck snakes in an arena containing dry sand, 10 twelve-inch discs, 10 male snakes. Ambient temperature 74 ± 1° F. Relative humidity 50–56%. July.

Days after release	Disc													
	1	2	3	4	5	6	7	8	9	10	open	hidden	dead	
Released from center daily.														
1	0	0	0	0	0	0	0	4	0	0	6	0	0	
2	0	0	0	0	0	0	0	5	0	0	3	0	0	
3	0	0	0	0	0	0	0	9	0	0	1(d)	0	1	(from open)
4	0	0	0	0	0	0	0	7	0	0	2	0	0	
Scrambled sand after pickup; added a new 10th snake.														
5	0	0	0	1	0	0	0	0	0	7	2(1d)	0	1	(from open)
Scrambled sand after pickup; added a new 10th snake.														
6	0	0	4	0	0	0	0	0	4	0	2	0	0	
Left sand intact, no scramble, but snakes released from center.														
7	0	0	0	0	0	0	0	0	7	0	2	0	0	
Accidentally omitted data on one snake. After recording left snakes where found and sand intact but sprinkled sand around disc 9 heavily with water.														
8	0	0	0	0	0	0	0	0	8	0	1	0	0	
After recording left snakes where found and gave area around disc 9 a fresh sprinkling.														
9	0	0	0	0	0	0	0	0	8	0	1	0	0	

strated strong aggregative tendencies (see days 1-5, Table 6). The results of this experiment are reported in Table 6 (see days 6 and 7). Although there was some disorientation and scattering by the snakes following the center releases, the distribution did not test significantly different from that of the previous day [chi-square 9 d.f. $= 9.66$ ($p = 0.35$)].

Substrate and disc translocations.

Further experiments were conducted based upon the hypothesis that if habitat conditioning existed the conditioning substance was a material that could be sensed by olfaction, taste, or vomeronasal receptors. Accordingly we attempted to translocate conditioned substrate by scooping it up and placing it where a similar quantity of substrate had been removed, or by interchanging the substrate from beneath two discs.

The results of the first of these experiments is reported in Table 3 (day 10). Discs 3 and 8 and their underlying sand had been interchanged the previous day. The snakes which had been showing up mostly at disc 8 were now at the immediately adjacent position: apparently they "trailed" to favored site 8, found no conditioned substrate there, and stayed in that vicinity where perhaps some attractant still remained. The next day (day 11) three snakes appeared at position 3. This position had not been occupied in the 10 previous days. On day 10, sand from discs 5 and 9 was interchanged. On day 11 disc 9 was heavily tracked as if the snakes were investigating it. Disc 9 had probably been located via trails leading to it, but in the absence of conditioned sand the snakes did not remain there. Snakes appeared under adjacent discs 8 and 10, probably because some conditioning had developed in that area from previous days.

Table 6 gives more compelling evidence that ringneck snakes respond to conditioned substrate. On day 9, discs 4 and 10 were translocated (sand and discs included). After the release many snakes appeared to start toward the old number 10 position, apparently following old trails. But by the next day no snakes were found under disc 4, even though it occupied the formerly popular site of disc 10. Disc 10, occupying the old disc 4 site, again had snakes, apparently having been found by some wanderers. Numerous snakes occupied position 9, possibly because it had some con-

TABLE 9

Dispersal of ringneck snakes in an arena containing 10 twelve-inch discs, ten male snakes, dry sand. Ambient temperature 74 ± 2° F. Relative humidity 50–57%. Snakes released daily from center and sand scrambled daily after pickup of snakes. August.

Days after release	Disc 1	2	3	4	5	6	7	8	9	10	open
1	0	5	0	0	0	0	0	0	0	2	3
2	7	0	0	0	0	0	0	0	2	0	1
3	3	0	0	1	1	0	0	1	3	0	1
4	0	1	3	0	0	1	0	0	4	1	0
5	2	0	0	0	0	0	0	4	1	3	0
6	0	2	0	0	0	1	0	6	0	0	1

ditioning and was next to the original disc 10 location. On day 10, discs 3 and 9 were interchanged (disc and sand included). On day 11, disc 9 was popular, even though it occupied the original site of 3 which had never been used. The results of these translocations present clear evidence that the substrate must retain attractant material.

Therefore, an additional experiment was conducted to identify the respective roles of the sand and disc in the retention of the "conditioner." The results are given in Table 7. On day 5, the sands from beneath discs 3 and 8 were interchanged. Disc 3, from the popular area, was placed on the original site of disc 6, disc 6 was placed on top of the sand from number 8, and disc 8 was placed atop the translocated disc 3 sand. On day 6, conditioned sand from 3 was occupied. Disc 3 (the conditioned disc) was unoccupied and disc 4 next to the old conditioned sand site, was now occupied.

From the foregoing results we concluded that sand is a strong retainer of the conditioning material, whereas painted wooden discs are essentially non-absorbent. Also, snakes are not likely to go to a disc merely because it once covered conditioned sand.

Scrambling of substrate.

The previously described results showed that an undisturbed substrate would produce aggregations of snakes and that snakes seemed to find sites via olfactory, vomeronasal, and visual stimuli. Final evidence that an attractant was present in the preferred sites was provided by picking up all snakes and discs and scrambling the sand thoroughly before smoothing the sand and replacing the discs. The attractant would no longer occur in concentrated form, and a random distribution of the snakes would be expected. Snakes would presumably aggregate due to the aggregative forces discussed previously, but the site of the aggregations would no longer be fixed.

Table 9 shows the results of an experiment in which sand was scrambled daily from the first. No conspicuous aggregations showed up at any specific site but complete randomness did not occur. Aggregations of 3-7 snakes were frequent, reflecting the intrinsic aggregative drive.

Table 7 (days 7 and 8) shows the results of another experiment. After a conditioned substrate was scrambled disorientation of snakes was conspicuous, and numerous individuals were in the open. Similarly in another experiment (see Table 8), an aggregation established under disc 8 for four days was disorganized on days 5 and 6 after the substrate was scrambled on days 4 and 5.

Although these experiments were generally consistent, contradictory results occurred when despite daily scramblings at the ends of each of the first three days, disc 10 remained popular (Table 10). The introduction of a new group of snakes at the end of day four, along with scrambling, did not break this pattern. Strangely enough the aggregation broke up on day 6 though no scrambling had occurred. The significance of this is unclear to the investigators, but it should be noted that these snakes were huddled in the open.

Checks on Extraneous Bias in Arenas

The snakes involved in different experiments did not necessarily select discs at the same compass position for their favored cover. However, there remained the possibility that, during a given experiment, drafts, light variations, etc., could be lo-

TABLE 10

Dispersal of ringneck snakes in an arena containing dry sand, 10 twelve-inch discs, 10 male snakes. Ambient temperature 74 ± 1° F. Relative humidity 49–55%. Snakes released from center each day. July.

Days after release	Disc 1	2	3	4	5	6	7	8	9	10	open	hidden
1	0	0	1	0	0	0	0	2	1	5	1	0
After pickup sand scrambled.												
2	0	0	0	0	0	0	0	4	0	5	1	0
After pickup sand scrambled.												
3	0	0	0	0	0	0	0	0	0	8	2	0
After pickup sand scrambled.												
4	0	0	0	0	0	0	2	0	0	7	1	0
After pickup snakes replaced with 10 males from another experiment. Sand scrambled.												
5	0	0	0	0	0	0	2	0	0	4	4	0
Sand left intact after pickup.												
6	0	0	0	0	0	0	0	3	1	0	6*	0
Sand left intact after pickup. Tank rotated 180° before snakes released.												
7	0	0	0	0	0	0	0	1	0	0	7	1
8	0	0	8	0	0	0	0	1	0	0	1	0

* Five snakes huddled near disc 10, the "favored disc."

calized, or that snakes might have some intrinsic tendency for compass orientation. Such effects were checked by simple 180° rotation of the arenas.

Table 3 (days 8 and 9) shows that snakes continued to return to their usual discs, even though the discs were 180° from their old compass positions. Table 6 (day 8) shows a similar return to usual haunts. The day after a 180° rotation (Table 10, day 7), a possible compass orientation appeared. Some snakes were huddled near disc 3, the position of the previously popular disc 8. However, most snakes stayed near disc 10, a disc popular for several days previous. On day 8, a large concentration of snakes at disc 3 represents a return to the compass area closer to the area popular through the days prior to rotation.

Effects of Environmental Modifications

Field observations have indicated that ringneck snakes are usually found at times when the upper strata of soil are moist, or if the immediate surface layers are dry the soil under stones is moist. Therefore, our early experiments were conducted with the arena substrate moist. The substrate was moistened with a sprinkler before setting the discs into position. After several days the exposed soil became dry, whereas soil under the discs retained the "pleasantly moist" feel for a week or more. The term "pleasantly moist" conveys our impression that the soil felt cool to the touch and had a texture associated with dampness. Bouyoucos moisture blocks used in later experiments provided quantitative indices of soil moisture without disturbance of the substrate.

In experiments where the arena was premoistened (see Tables 4 and 5), relatively high percentages of animals were in the open for the first few days of observations. But with the passage of time and the drying of the substrate more animals retreated beneath the discs. This behavior suggested that moist soil provided an optimal habitat, and that as exposed soil dried it became less attractive than the soil beneath the discs. Obviously, another interpretation for this behavior is that snakes find excessive moisture undesirable and thus tend to avoid the high moisture level under the discs.

Field observations have consistently indicated that small snakes are not common under cover objects during very wet and rainy periods. This suggests that there may

TABLE 11

Dispersal of ringneck snakes in an arena containing premoistened sand, 10 twelve-inch discs, 67 snakes of both sexes. Temperature 21 ± 1° C. Relative humidity not noted. Initial release from center, then left where found on subsequent days. Discrepancies in counts due to difficulty of accurate counting of large groups without handling snakes. May–June.

Days after release	Disc 1	2	3	4	5	6	7	8	9	10	open	hidden	dead	soil under disc	open soil
2	8	0	0	10	4	0	4	2	7	12	5	15	0	moist	moist
4	13	2	0	9	7	5	9	1	1	17	0	2	1	moist	moist
6	7	1	8	6	7	4	10	1	8	16	0	0	0	moist	dry
8	5	3	8	12	5	2	12	1	6	13	0	0	0	moist	dry
	After recording locations and numbers of snakes sprinkled half with discs 1–5, lifting discs to sprinkle under them.														
10	2	1	1	2	3	8	15	1	11	24	0	0	0	moist	moist 1–5 dry 6–10
11	6	3	0	5	10	8	13	1	7	17	0	0	0	moist	moist 1–5 dry 6–10
12	5	1	6	9	17	6	7	1	6	10	0	0	1	moist	moist 1–5 dry 6–10
13	5	4	12	6	14	3	2	4	3	13	0	0	1	moist 1–5 dry 6–10	moist 1–5 dry 6–10
	After recording locations and numbers of snakes sprinkled side 1–5 but did not sprinkle under discs.														
14	1	0	2	0	4	16	9	5	18	9	1	0	0	moist 1–5 dry 6–10	moist 1–5 dry 6–10
15	3	0	0	3	3	13	8	3	14	19	0	0	0	moist 1–5 dry 6–10	moist 1–5 dry 6–10

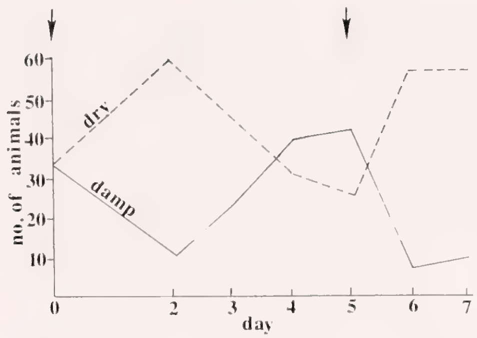

Figure 2. Response of snakes to excessive moisture conditions. On day 0 approximately same number of snakes on both halves of tank. At that time side with discs 1-5 (damp) was sprinkled with water, both around and under discs. On day 5 when both halves of tank had reasonably similar numbers of snakes the area around the discs on side with 1-5 was sprinkled. Side with discs 6-10, labeled dry, had slight moistness under discs until day 5.

Table 12

Dispersal of ringneck snakes in an arena containing moist sand, 5 twelve-inch discs, 20 female snakes. Ambient temperature 25 ± 0.5° C. Room non-air conditioned, humidity high but not measured. June.

Days after release	Disc 1	2	3	4	5	open	hidden
1	0	0	1	5	0	8	6
2	0	0	0	2	1	2	15
3	0	2	1	0	0	5	12
4	0	0	2	0	0	6	12

Animals removed from burrows at end of experiment. Six animals clustered in one group, three in another group, and three in a third group. Soil in burrows "pleasantly moist." All groups between discs 2 and 3.

on occasion be too much moisture. In nature, of course, recourse to drier subterranean haunts is possible. In our arenas snakes may have selected the surface as an avoidance reaction to excess moisture despite the exposure to daylight because there were no dry deeper strata.

In an experiment involving a large number of snakes in a pre-moistened arena, the animals were well dispersed over the first few days. Only at the start were animals observed in the open or burrowed (Table 11). At the end of day 8 thirty-three snakes were on one side of the tank under discs 1-5 and 34 snakes were on the other side under discs 6-10. At this time the side containing discs 1-5 was re-sprinkled, both around and under the discs. This moistening was followed by a rapid exodus of snakes from the freshly moistened side to the drier side. After four days conditions became similar and both sides of the tank harbored approximately equal numbers of snakes. A second sprinkling of the side with discs 1-5 on day 5 again produced the exodus. Figure 2 graphically depicts the changes of numbers in relation to sprinkling time.

Our data on actual soil moisture levels are limited at this time but they suggest that moisture content of soil is a habitat variable that can lead to modified aggregative behavior.

In experiments conducted in a room without air-conditioning evaporation from exposed soil was almost nil. Table 12 shows results from one such experiment. Numerous animals remained in the open but many others burrowed into the soil. Burrowing might provide a desired level of darkness as well as moisture. Even while burrowing the snakes tended to form groups, showing that aggregative drive occurs even under these circumstances. Thus we see that under high moisture levels the discs are not essential for cover. No alternative situations to high moisture levels were provided so a plausible explanation for the occurrence of exposed snakes as well as burrowing snakes is not available.

Studies on terrarium-confined *Diadophis* by Clark (1968) showed that the snakes would burrow. They selected, in fact, a soil more moist than a supposedly more fossorial species, *Carphophis amoenus*. Clark noted, however, that the more moist soil tended to clump, and facilitated penetration by *Diadophis*. Clark's substrates were sand and clay loam mixtures; we had no soil clumping problem with our sand substrate.

In another trial we tried "seeding" certain discs with marked snakes to determine whether sexual attraction occurred or if snakes simply went to a disc that had been seeded. This trial was run in September, at which time sexual drive probably was minimal. On the first two days of the pickups, before the seeding began, we found that

TABLE 13

Dispersal of ringneck snakes in an arena containing dry sand, 10 twelve-inch discs, 9 male and one female snakes. Maintained at 73 ± 2° C. Relative humidity 73% first day, thereafter 55–60%. Snakes released from center daily except where otherwise noted. Sand under discs smoothed at time of daily pickup. September.

Days after release	Disc 1	2	3	4	5	6	7	8	9	10	open
1	0	0	3♂♀	0	0	0	0	3	0	0	3
2	0	0	5♂♀	0	0	0	0	0	0	1	3
	Only males released from center; female placed under disc 6.										
3	0	0	0	0	0	3	0	0	0	0	6♂; ♀*
	Only males released from center; female placed under disc 1.										
4	6♂♀	0	0	0	0	0	0	0	0	0	3
	Only males released from center; female placed under disc 4. Males not released until day 6.										
8	0	0	0	7♂♀	0	0	0	0	0	0	2
9	No records taken; only 8 males released from center, along with the female. One male placed under disc 5.										
10	0	0	0	3	2	0	0	0	♀	2	2
	Released 8 males from center, placed one male under disc 2 and the female under disc 7.										
11	0	1	0	0	0	0	1♀♂	0	0	2	5

* Only one male near ♀

males aggregated with the female (Table 13). Subsequent observations after the seeding began showed no consistent patterns, regardless of whether the disc was seeded with a male or female, or both were employed (though under separate discs). Aggregations seen on days 4 and 8, involving the female, could have been sexual or could have been reflections of the tendency to come to a regularly used shelter. However, no one disc ever became popular in this experiment. On day 9 the female was released from the center with several males, and a single male was "seeded" under disc 5. By day 10 one male had joined the "seed" male under disc 5, but the female was isolated. Day 3 results also show her essentially isolated. Whether the same results might be obtained during the spring breeding season remains for subsequent experimentation.

Discussion

The formation of aggregations presumably confers some benefit to ringneck snakes. The advantages might include ease of finding sexual partners, reduction of exposed body surface, with reduced moisture loss and perhaps moderation of temperature change due to weather changes, and perhaps sensual satisfaction. Sensual satisfaction actually includes a host of taxes which are more likely the mechanisms responsible for initiating aggregation rather than a result of the grouping. Clausen (1937) showed reduced oxygen consumption in aggregated *Storeria dekayi* but the advantages of this are not clear. Reduced O_2 consumption could reflect lowered metabolism, hence lower energy requirements. Certainly if the snakes were crowded under a stone or buried in the ground, O_2 would be limited. However, the animals seemingly are not forced to aggregate in nature to conserve O_2 since numerous cover stones are available.

From our experiments some factors can be discounted as the primary cause of aggregative behavior. For example, in our experiments no need for oxygen was evident because in most situations the snakes had ample cover of equal quality available but not utilized. In addition, extremely skewed sex ratios occurred in our field collections (six males to one female) suggesting that sex drive may play a fundamental role in aggregation. In our experiments sexual drive was ruled out as an advantage of aggregation to ringneck snakes because it occurred among males in the absence of females. Henry Fitch (personal communication) confirms this sex ratio from his field studies in northeastern Kansas. He has observed that there may be a slight increase in the relative abundance of females in the summer, however the number of female snakes found then is far too low to indicate an actual sex ratio of 1:1. In future collecting, a summary of actual sex ratios for each aggregation found in the field would be instructive. Tentative observations in the field (April 1968) indicate that many groups of five aggregated adult snakes are wholly male and a group of 10 was 9 male and one female. The lack of females in many of the aggregations tends to further confirm our interpretation that sexual attraction is not a factor in aggregation. It should be noted here that sex ratios in the populations of various races of *Diadophis punctatus* reported by Blanchard (1942) range from 0.7:1 male to female to 3:1 (our interpolation). The extremes were based on small samples (under 17 animals); larger samples generally ran 1:1 to 2.4:1 (north-central Kansas) and 1.1:1 (northeastern Kansas).

A possible basis for aggregative drive is moisture conservation. Noble and Clausen (1936), Carpenter (1952), and others have observed that snakes tend to gather when humidities are low, possibly congregating in those places offering adequate or partial shelter from dehydration. Noble and Clausen also found that *Storeria dekayi* selected relatively high humidities when offered a choice and formed aggregations more readily under drier conditions. Bogert and Cowles (1947) have shown that the resistance to desiccation of reptiles may be correlated with habitats occupied. We have limited evidence that ringnecks become more gregarious when pre-moistened arenas begin to dry, but also have noted that aggregations form even when snakes are provided with drinking water and when ample soil moisture and high humidities prevail in the arenas.

Increased temperature can also produce higher metabolic rates and therefore increased water loss. Noble and Clausen (*op. cit.*) found that increased temperatures were accompanied by increased breathing rates and more moisture loss, and that under the elevated temperature conditions aggregations were more likely to form.

The possibility that reduced oxygen consumption might be advantageous should be mentioned again here. The use of more oxygen can be an indication of elevated metabolic rates, hence more loss of metabolic water. When Noble and Clausen did their studies it was believed that reptile integuments were essentially impermeable. The recent finding by Bentley and Schmidt-Nielsen (1966) that substantial loss of moisture may occur through the integument points up a need for careful analysis of moisture loss in relation to environmental conditions. Integumentary *vs.* respiratory loss notwithstanding, total moisture loss still remains the significant criterion.

Fitch (1956) reported numerous body temperature records for ringneck snakes found in the field. The most favored temperature seemed to be around 27-29° C, several degrees higher than our laboratory arenas. A laboratory temperature gradient response study by Clark (1968) closely agrees with Fitch's values. Fitch's records appear to be daytime readings (hour not stated) and body temperatures were generally 6-7° higher than optimum air temperatures. The values were not correlated. Since the other environmental variables were not quantified we cannot at this time know if temperature plays the more prominent role in stimulating aggregative drive, but aggregation seems to characterize ringnecks in the field whether the day be warm or cool. Seibert and Hagen (1947) found that *Thamnophis radix* and *Opheodrys vernalis* selected cover on an availability basis, but in hot weather they would avoid metal and go under cover that offered more effective insulation.

The observed aggregational phenomena in our arena were most pronounced during the daylight hours; tracks on the substrate and the different locations at which marked individuals were noted prove that wandering was prevalent at night. In nature nocturnal movements permit activity at times when the humidity is highest. However, in spring, when snakes are at the surface nocturnal temperatures tend to be rather low for efficient snake activity. In our laboratory neither temperature nor humidity changed noticeably during the night, only the absence of negative phototaxis was a conferred advantage.

The aggregative behavior exhibited has been identified as an intrinsic drive since the animals not only selected each other's company but also tolerated considerable population pressure (up to 24 snakes under a single disc one foot in diameter). The strength of the drive is emphasized by the formation of groups during the first day after release. In addition, snakes consistently seemed to follow each other or the trails left on the substrate.

A more dispersed distribution is illustrated by the results given in Table 11. This experiment presented the greatest population density of any experiment (6.7 snakes/disc compared to a maximum of 4 snakes/disc in other experiments). We cannot therefore dismiss the possibility of crowding as a modifying factor in aggregation.

The aggregative denning behavior of large snakes obviously insures adequate winter shelter and facilitates mating after the spring emergence. Rising temperatures as the season progresses are accompanied by departure from the den. This is adaptive because increased temperatures mean higher metabolic needs, and necessitates more food than is ordinarily available in the vicinity of dens. Large snakes do not as a rule "clump" at the den site, usually they are separated while exposed to the sun.

The aggregation of ringnecks occurs during the springtime at the same time that large snakes are still at the den. However, the ringnecks do not disperse appreciably to receive warmth. The paucity of surface activity records prevents us from knowing if ringnecks disperse during the warmer parts of the year. Thorough explanation of distributional phenomena will not be possible until adequate data on responses to environmental variables and quantification of the physiological requirements of ringnecks are available.

Regardless of what stimuli foster or hasten aggregation of ringneck snakes, and the advantages of such aggregations, our experiments have demonstrated that these snakes show a definite preference for substrates that have been traversed and occupied by other ringnecks. Ringneck snakes have shown an ability to locate other ringneck snakes, apparently by means of visual, olfactory, or vomeronasal sensing. These snakes can apparently follow trails on the substrate and recognize soil that has regularly harbored other ringnecks. The ability of ringnecks to detect each other probably is an inherited trait, not unlike the chemical cue perception for food organisms reported for newborn snakes by Burghardt (1967). Noble and Clausen (1936) found that *Storeria dekayi* can detect areas where skin alone from other *Storeria* snakes has been rubbed over clean glass. This is a truly remarkable chemical perception since the skin of snakes is said to be non-glandular and any secretions left as a snake crawls along must be miniscule.

The habitat conditioning that results from occupancy of a substrate by ringneck snakes appears to serve purposes other than those previously assigned to various animals. In a discussion of environmental conditioning presented by Allee, *et al.* (1949), the major functions of conditioning were given as: detoxification, alteration of fecundity, production of growth promoting substances, and physical alteration rendering the substrate more porous or penetrable. In ringnecks it appears that conditioning may provide cues to other ringnecks that the conditioned site is, or was, a desirable site to occupy, at least in the field.

Our experiments attempted to nullify habitat selection but the experiments may have inadvertently been conducted within the environmental range evoking aggregative drive. Nevertheless, snakes re-released daily could have gone elsewhere to form their aggregations, and had every opportunity to use visual or other means to follow their kind. In natural settings ringnecks may use the same cover object year after year because it offers optimal microhabitat conditions. There is little reason to doubt, however, that the site may be conditioned habitat whose use is perpetuated on a continuing basis.

Little is known of the homing instinct in snakes but their ability to return year after year to a den site from great distances suggests that den sites may be conditioned habitat. Regular routes are evident (Klauber, 1956). Whether the use of such routes involves a homing instinct or the trailing phenomena as exhibited by *Storeria dekayi* and ringneck snakes is not clear. The parallels between denning and aggregation are striking and are perhaps manifestations of comparable instinctive drives.

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