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The Social Use of Space

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I. Introduction

During recent years many investigators have considered the physiological consequences to the individual of altering the size of the group of which it is a member. Inherent in such studies is the assumption that for a particular species there is some optimum group size, above or below which the altered frequency or type of interactions are either stressful or fail to elicit optimum physiological states. My purpose will be to develop formulations concerning the social use of space to determine whether there might be certain optimum group sizes.

I shall consider only indirectly the physiology of individuals. Instead, emphasis will be upon relationships which determine the "physiology" of the community. The basic particle is the individual mammal. In any total assembly of such particles inhabiting a particular environment, taxonomic categories, such as species and genera, represent general classes of particles. Although several classes may share certain characteristics, each possesses characteristics peculiar to itself, which on the average differentiate it from all other classes. Furthermore, the properties of any particular particle may change through time as a function of maturation and experience. Such changes are reflected in the individual's internal milieu. Only at this level are we concerned with physiology in its classical sense.

A social system consists of particles moving through space and time. In the course of evolution and maturation, such particles may develop enhanced capacities for affecting others and, in turn, for being more affected by them. This inquiry seeks that essential nature of these particles which influences the course of social evolution. It concludes that each category of particles which we designate as a species must develop a basic group size, designated as its basic number, N_b. Then, assuming the validity of the concept of an N_b, the inquiry is extended to encompass the following questions:

1. How do changes in N from N_b alter the social system?
2. Given a species, whose groups are of the optimum N_b type, how do changes in the environment or in the nature of the particles affect the social system?
3. What are the basic organizational and interactional properties of the group?

I found very few prior studies in the literature suitable for guiding me in developing formulations adequate to satisfy these objectives. Therefore, this discourse will be neither a review of the literature nor even an adequate presentation of empirical data. Instead, the major theme concerns development of a logically sound, theoretical framework of processes underlying social phenomena.

In the course of this development some empirical data will be presented. These data are not meant to prove the correctness of the formulations. They are presented simply as background for the origin of ideas or to show that there at least exist some data which are harmonious with the developed concepts. Much of such data is presented here for the first time. I am indebted to many persons for their permission to cite such original data.

I have attempted to place many of the concepts in sufficiently precise mathematical form to permit a better understanding of the dynamics involved. My inadequacy in the field of mathematics has been buffered by the advice of several competent mathematicians: James U. Casby, Murray Eden, Samuel W. Greenhouse, Seymour Geisser, Clifford Patlak, and

John Gilbert. However, I assume full responsibility for any errors, inadequate presentation, or overextension from their initial guidance.

I have found this effort a rewarding one for the development of insight into complex social systems, and I can only hope that in some small measure it may serve as a bridge for others in their design of experiments or in their further theorizing.

II. The Bivariate Normal Type of Home Range

Home range denotes the area covered by an individual in its day-to-day activities. Field studies of many species of mammals have revealed that each individual customarily stays within a restricted area for long periods. The individual utilizes the center of such an area most intensively. With increasing radial distance from this home range center (HRC) the relative frequency of visitation per unit of area decreases. Calhoun and Casby (1958) found that the bivariate normal distribution function adequately describes home range. The following is a summary of their analyses.

In home range studies, "density function" is a mathematical expression representing the probability of an animal being present in some arbitrarily small area. Three assumptions are made:

The home range is fixed. In other words, the statistics of the home range are stationary or time independent.

There is a true center of activity although the apparent center, the mean coordinate point of capture, of activity may deviate from it.

The probability of an animal being in a unit of area decreases with increasing distances from the true center of activity. This and the second assumption suggest a bivariate normal distribution of the density function:

$$f(x, y)\, dxdy = \frac{1}{2\sigma^2\pi} \exp\left[-(x^2 + y^2)/2\sigma^2\right] dxdy \qquad (1)$$

where σ is the standard deviation of the distances in the x and y direction and is assumed to be equal for both, and x and y are measured from their respective means. This density function may be used to represent the percentage of time spent in the area $dxdy$ located at the Cartesian coordinates x, y, or in polar coordinates:

$$f(r, \theta)\, rd\theta dr = \frac{1}{2\sigma^2\pi} \exp\left(-r^2/2\sigma^2\right) rd\theta dr \qquad (2)$$

Here, the area $rd\theta dr$ is determined by r.

The density function in terms of the Cartesian coordinates is more meaningful from an ecological standpoint because it states in comparative terms the amount of time spent by an animal in a small standard area at any position in the home range. However, for the initial mathematical manipulation, it was found more convenient to express the density function in terms of polar coordinates. Then the probability of finding the animal between the radii r and $r + dr$ about the true center of the home range is:

$$f(r)dr = \frac{2}{2\sigma^2} \exp\,(-r^2/2\sigma^2)\; rdr \tag{3}$$

If Eq. (3) is integrated over the range 0 to σ we have

$$\int_0^\sigma \frac{2r}{2\sigma^2} \exp\,(-r^2/2\sigma^2)\; dr = 1 - e^{-1/2} = 0.3940 \tag{4}$$

In the above equations σ, the standard deviation of the normal distribution function, is the value of a radius within which the probability of the animal being present is 39.4%, if its movements can be described by a bivariate normal density function.

Similarly, integrating Eq. (3) over the range 0 to 2σ gives

$$1 - e^{-4/2} = 0.8645 \tag{5}$$

Similarly, integrating Eq. (3) over the range 0 to 3σ gives

$$1 - e^{-9/2} = 0.9888 \tag{6}$$

The above sigma thus delineates a single distance term by which home range may be described. The term "home range sigma" will be so utilized in following sections.

Although this sigma may be calculated from a series of coordinate points of capture by equations presented in the original paper, use of recapture radii provide a more direct means, adequate for most purposes. Calculate the mean coordinate point of capture, the approximate home range center. Then on a large scale grid map of the study area measure recapture radii, r, from this mean coordinate point of capture. Unbiased estimates of sigma, s and s_i may be calculated by the following equations:

$$s = \left[\frac{\sum_{i=1}^{n}\sum_{j=1}^{K_i} r_{ij}^2}{2(N - n)}\right]^{\frac{1}{2}} \tag{7}$$

$$s_i = \left[\frac{\sum_{j=1}^{K_i} r_j^2}{2(K_i - 1)}\right]^{\frac{1}{2}} \tag{8}$$

where:

s = unbiased estimate of the home range sigma for all the animals in a sample

s_i = unbiased estimate of the home range sigma for any particular animal

K_i = number of captures of ith animal

n = number of animals

N = total captures = $\sum_{i=1}^{n} K_i$

ij = jth observation of the ith animal

A detailed analysis of the home range for 25 male harvest mice (*Reithrodontomys*) on which there were 10 to 24 captures each indicated that there was a significant variation of sigma among animals. In other words, some animals had significantly larger home ranges than others. Therefore, in order to compare the observed recapture radii with the theoretical (Table II in Calhoun and Casby, 1958), each recapture radius was normalized into a standard measure denoted by Z in which the home range sigma for each animal was assigned a value of 1.0 and all recapture radii expressed as a proportion of this.

As may be seen from Fig. 1, the theoretical closely approximated the observed. Although this detailed analysis has been applied only to this one species, it shall be assumed for the purpose of developing further formulation that the bivariate normal distribution function adequately describes fixed home ranges of other species.

Comparison of observed and theoretical distribution of home range radii required viewing home range as a probability of capture which changes with radial distance from the home range center. Bands of equal width increase in area with radial distance from the home range center, while probability of capture per unit area decreases with increase in radial distance. Interaction of these two factors results in more captures at about one sigma from the home range center than at any other distance (Fig. 1).

However, the ecologically important aspect of the bivariate normal distribution as an expression of home range is the relative probability that an animal will be in a unit of area with respect to the radial distance of that unit area from the home range center (Fig. 2). For any given sigma characterizing a particular species, its density function in terms of area curve may be obtained by multiplying the relative sigma value on the abscissa by the observed sigma and dividing the density function values on the ordinate by the square of the observed sigma.

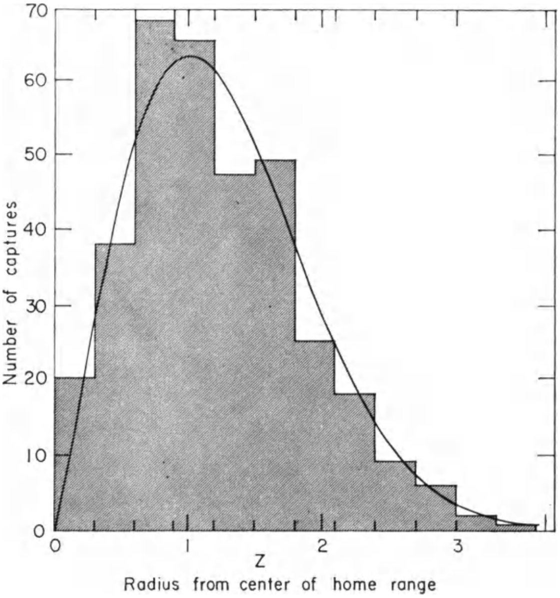

FIG. 1. Observed (histogram) and theoretical distribution of 348 recapture radii (Z) of 25 male harvest mice from the center of their home range. Z here represents a normalized measure of the bivariate normal home range sigma.

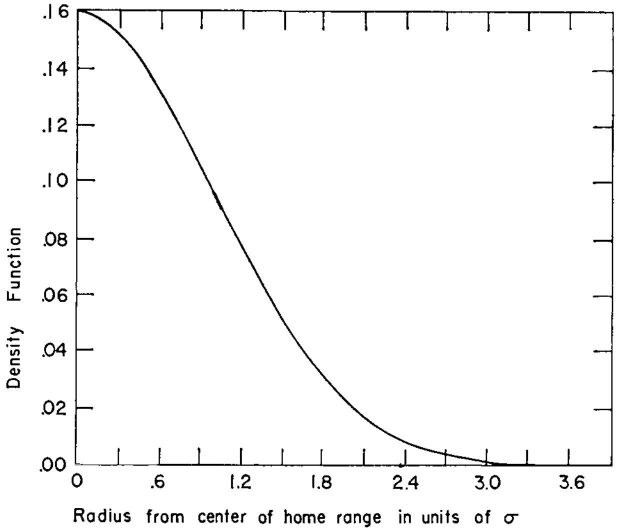

FIG. 2. Cross section of the density function of home range in terms of area. Rotation of this curve about its axis reveals the mountain-shaped topography of home range.

III. Behavioral Origins of the Bivariate Normal Type of Home Range

The fact that a particular equation happens to describe home range enables derivation of several principles regarding the use of space by an entire community. Discussion of these principles follows in Section VII. However, as a background to this discussion it will be advantageous to seek an understanding of the biological basis for the bivariate normal type of home range.

A. Activity in a One-Dimensional Habitat

Admittedly, animals rarely live in essentially one-dimensional environments. However, I suspected that if animals were placed in such environments certain regularities of behavior might be revealed which would provide insight into their use of two-dimensional environments. To this end, four 14-foot long alleys were constructed. Each had a channel 8 inches wide. Each 8 × 12-inch segment of the floor was so suspended that when a domesticated Norway rat, used as a subject, stood on such a segment a microswitch closed. This closure initiated a signal such that the exact position at every point in time was recorded on a recording oscillograph. A partition between the first and second treadles formed a home compartment. A 3 × 3-inch opening through this partition provided access to the rest of the alley. Food and water placed in this compartment further enhanced the role of this compartment as a "home." A ground glass plate, through which shone the light from a 100-watt lamp, formed the opposite end of the alley. This light served to concentrate the activities of the rats emanating from the home compartment. It was as if every foot of the alley were several feet long. Details of the effect of varying light intensity at the end of the alley on explorations will be presented elsewhere. This apparatus is referred to as the Ferguson Activity Alley.

Suffice it to consider the results from 73 rats, each run for 72 hours in the alley. Each rat made from 10 to 30 excursions out into the alley each night. Despite the presence of the bright light at the end of the alley, one-fourth of the trips terminated at the end of the alley. In other words, the end of the alley formed a barrier. Most of the trips thus terminated at the end of the alley presumably would have represented trips of greater length had the alley only been longer. Most of the time a rat would go out to some intermediate distance, stop momentarily, and then turn around and go directly back home. Occasionally, a rat would wander back and forth from the point of initial termination. All trips with such vacillations and those ending at the barrier were excluded from the initial analysis.

1. Trip-Terminations in an Unstructured One-Dimensional Habitat

The initial investigation focused upon examination of the distances from the home compartment at which nonvacillating trips terminated in the unstructured alley. "Unstructured" denotes the absence along the alley of any stimuli likely to elicit responses and so induce a rat to stop. Rats were placed in the alley during the middle of the afternoon, a time of minimal activity within their normal 24-hour rhythm of activity. And yet when placed in the alley every rat exhibited a 2- to 3-hour period of hyperactivity. Further details of the decay curve of this hyperactivity are discussed in Section III, A, 3.

For 73 rats complete records (Table Ia) were available for all trip-

Table Ia

Number of Trips Terminated with Reference to Distance from Home

Distance in feet of termination	Unstructured alley		Structured alley	
	During first 2.5 hours	During next 3 6 A.M.–6 P.M. periods	Strips of paper	Pellets of food
1	274	558	1053	955
2	204	407	839	643
3	150	315	723	509
4	104	277	302	375
5	99	294	194	288
6	81	219	230	258
7	56	139	151	163
8	58	115	149	137
9	47	98	112	119
10	39	113	57	104
Σ	1112[a]	2535[a]	3810	3551
Barrier and vacillating trips	502	1458	59[b]	127[b]
Total trips	1614	4023	3869	3678
Trips/rat/hour	8.844	1.531		

[a] Only nonvacillating trips included.

[b] Vacillating trips and trips at whose end an object was transported home are not included since the termination of trips determined was solely by the number of transported objects.

terminations during both the initial 150 minutes of hyperactivity and the following three, 6 P.M. to 6 A.M., 12-hour periods of normal heightened nocturnal activity. The frequency, y, of terminating trips as a function of distance, x, from home is described by the equation:

$$y = \exp (a + bx) \tag{9}$$

where b is the slope. The slope for trip-terminations during the hyperactive period, b_1, is -0.2099; while b_2, the slope for trip-terminations during the 36 hours of normal nocturnal activity, is -0.1924. The t test

$$t_{32} = \frac{b_1 - b_2}{\sqrt{\text{Var. } (b_1 - b_2)}} = -0.682$$

has a p value of 0.051 which indicates that slopes b_1 and b_2 do not differ significantly.

Therefore, it is concluded that the neural mechanism producing termination of trips is unaltered by the nearly sixfold increase in the incidence of initiating trips accompanying initial exposure to a strange environment. For this reason, the mean slope of -0.20115, i.e., $(b_1 + b_2)/2$, was fitted to both these sets of data shown in Fig. 3 as trips per rat per hour for comparative purposes to emphasize the hyperactivity of initial exposure to a strange environment.

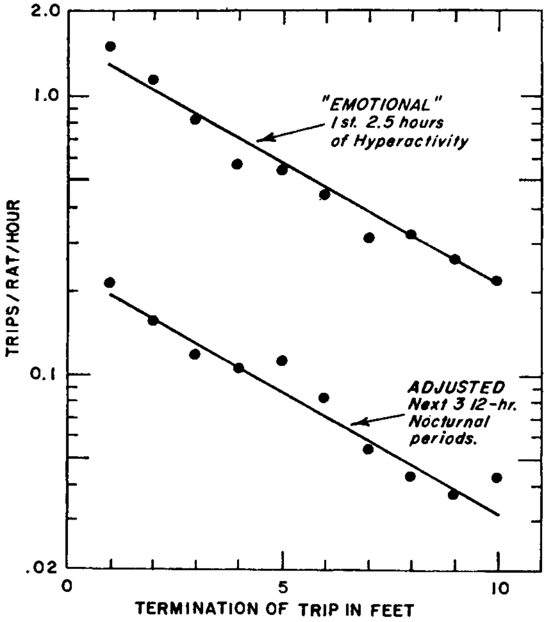

FIG. 3. Frequency of terminating trips at successive distances from the home compartment in the unstructured Ferguson Alley. See Table Ia.

2. THE ROLE OF A STRUCTURED ENVIRONMENT ON THE TERMINATION OF TRIPS

Natural habitats possess structures which elicit responses. Items of food and nesting material represent structures normally causing animals such as rats to terminate trips. When such items are transported home the trip resembles the nonvacillating ones in the one-dimensional alley in the sense that there is a direct outward phase, terminated by the object being picked up, followed by a direct homeward trip transporting the item. In order to explore the effect of such structuring in the one-dimensional habitat upon termination of trips, one of two procedures was followed: At each one-foot interval from home along the alley, there was placed a pad of paper strips or an open hopper of food pellets. During any particular rat's stay of 3–12 days in the alley, only nesting material or only food pellets were available. Periodic replenishment of each source ensured a continuous supply at each distance. Nevertheless, the rats removed items from each distance (Table Ia) even though this necessitated passing by opportunities to respond while on the outward journey. Each item removed at a particular distance from home is considered to indicate a trip-termination at that distance. Examination of the oscillograph record confirmed this interpretation.

The frequency of termination of such trips as a function of distance is also described by the equation, $y = \exp(a + bx)$. The slope for trips terminated by picking up paper strips, b_3, is -0.3027; while b_4, the slope relating to securing food pellets, is -0.2481. The t test,

$$t_{32} = \frac{b_3 - b_4}{\sqrt{\text{Var. } (b_3 - b_4)}} = -2.128$$

has a p value between 0.05 and 0.01 which indicates a statistically significant difference between these two slopes. However, examination of Fig. 4 reveals a marked dispersion about the best-fit line of the observed points relating to nesting material. For this reason, the interpretation that the b_3 and b_4 slopes differ statistically is open to question that this difference in slope implies biological significance. I therefore believe it wisest to assume that b_3 and b_4 are really identical, or nearly so.

If this is so, we may compare the slopes of the mean of $b_1 + b_2$ with that of $b_3 + b_4$. Here the t test

$$\frac{\frac{1}{2}(b_1 + b_2) - \frac{1}{2}(b_3 + b_4)}{\sqrt{\text{Var. } \frac{1}{2}(b_1 + b_2) - \frac{1}{2}(b_3 + b_4)}} = 4.0925$$

with a p value less than 0.001.

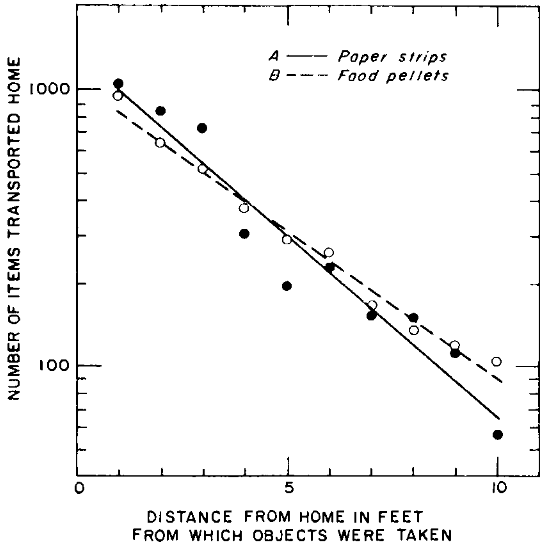

FIG. 4. Frequency of transporting nesting material and food into the home compartment from points at successively greater distance from it. *A*, 3810 strips of paper; *B*, 3551 pellets of food. See Table Ia.

It is therefore concluded that structuring the environment with items inducing responses leads to a reduction of the distance from home at which trips are terminated.

3. THE PROBABILITY OF TERMINATING TRIPS

The two prior sections merely demonstrate an effect produced by structuring the environment. They do not further our understanding of the underlying biological process.

The behavior of rats in the structured environment provides the clue. During any period of intensive transportation, one trip almost immediately followed the preceding one. And yet the distance at which a particular trip terminated bore no relationship to the distance at which the previous or following one terminated. It was as if the rat was blind to its surroundings on the outward trip until some neural switching mechanism became activated in a random fashion with reference to the time of the trip's initiation. This switching on (or off?) placed the rat in a perceptive phase at which time it responded by picking up the nearest relevant object and transporting it into the home compartment. Therefore, it will be helpful to determine the probability of this switching, which is synonymous with the probability of terminating a trip.

Let: t_j = the number of trips reaching any jth distance from home.
N_j = the number of trips that stop at the jth distance.
p_j = probability of stopping at the jth distance.

Then:

$$t_{j-1} - t_j = p_{j-1}t_{j-1} \tag{10}$$

$$N_j = p_j t_j \tag{11}$$

$$N_j - N_{j-1} = p_j t_j - p_{j-1}t_{j-1} \tag{12}$$

If $p_j = p$ (a constant independent of j), then:

$$\begin{aligned} N_j - N_{j-1} &= p(t_j - t_{j-1}) \\ &= -p(t_{j-1} - t_j) \end{aligned} \tag{13}$$

$$N_j - N_{j-1} = -p(pt_{j-1}) \tag{14}$$

And by analogy to Eq. (11):

$$N_{j-1} = pt_{j-1} \tag{15}$$

Substituting Eq. (15) into Eq. (14):

$$N_j - N_{j-1} = -pN_{j-1} \tag{16}$$

Therefore

$$p = (N_{j-1} - N_j)/N_{j-1} \tag{17}$$

This p represents a constant probability of terminating trips which arrive at a point regardless of the distance from home. Rigorous proof that this p actually is a constant is difficult from present data because of the barrier produced by the relatively short alley. However, the validity of a constant p, independent of distance, may be arrived at intuitively since an equation of the form $y = \exp(a + bx)$ best represents the observed data. In other words, log y plotted against x forms a straight line. Whenever this is so, Eq. (17) must be true.

Utilizing Eq. (9) stated in the form:

$$\log_e y = a - bx \tag{18}$$

the expected number of trips terminating at N_{j-1} and N_j, where $j = 2$, were found to be as shown in Table Ib, along with the p values calculated from Eq. (17). Thus, the probability of 0.182 of terminating trips arriving at any distance in the unstructured alley is increased to 0.24 by structuring.

TABLE Ib

PROBABILITY OF TERMINATING TRIPS WITH RESPECT TO ENVIRONMENTAL STRUCTURE AND LEVEL OF ACTIVITY

Alley	Secondary condition	Expected number of trips terminating at: N_{j-1}	N_j	p	Mean $\bar{p}$
Unstructured	During first 2.5 hr. of hyperactivity	237.5	194.3	0.182[a]	0.182
	During normal nocturnal activity	510	417	0.182[a]	
Structured	Paper transportation	999	783.3	0.261	0.240
	Food transportation	837	653.5	0.220	

[a] The mean b value of -0.20115 used in the calculation of p.

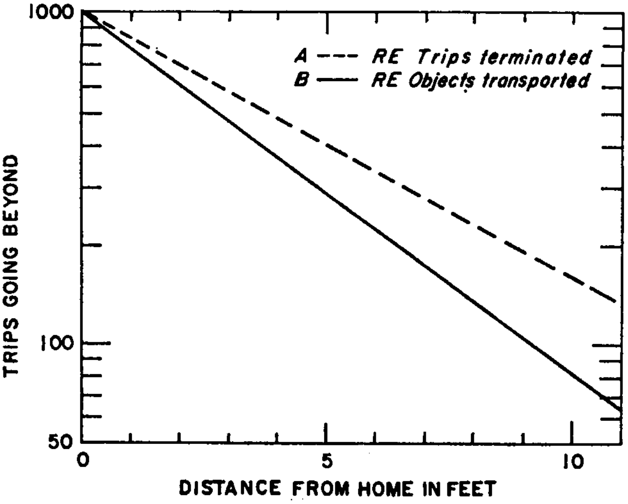

FIG. 5. Theoretical curves depicting relative likelihood of trips going beyond successive distances from home based upon an initial 1000 departures. *A*, in an unstructured alley (see Fig. 3); *B*, in an alley structured with objects available for transport back home.

The amount of structuring used here increased the probability of stopping by 32% [i.e., (0.240 − 0.182)/0.182]. The extent to which this difference modifies the use of a field may be visualized by considering the following: Of every 1000 trips arriving 1 foot from home in the unstructured alley, 30 would stop at the tenth foot and 134 would continue farther, whereas in the structured environment only 20 would stop at the tenth foot and only 64 would continue farther (see Fig. 5).

In closing this section it should be emphasized that the probability of stopping is basically a function of time. In the particular situation, the p's refer to the time required for the rats to travel a distance of 1 foot.

A further question may be asked: "How does structuring increase the probability of stopping if the animals are perceptually 'blind' to specific stimuli to the extent of being unable to exhibit directed responses to them?" One may visualize the situation in general terms: There is some assembly of neurons which provides a signal terminating an ongoing behavior, such as outward locomotion from home. The magnitude of this signal necessary for behavioral termination requires simultaneous firing of some x number of neurons. This assembly of neurons may be called a "governor." It must be located anatomically in some subcortical portion of the brain precluding conscious awareness of its functioning. During any ongoing behavior all perceivable stimuli unrelated to the ongoing behavior initiate impulses which arrive at the behavior terminating governor. Each unit of impulse causes an increase in the rate of firing of the neuronal net forming the governor. The greater the intensity of such stimuli, or the greater the number of stimuli of a given intensity, the more rapidly will the neurons of the governor fire and thus the shorter will be the interval between emission of effective signals by the governor. This signal both terminates the ongoing behavior and produces awareness of stimuli appropriate to eliciting those responses appropriate to initiating some other behavior.

4. Initial Hyperactivity in a Strange Environment

For the rats discussed in Section III, A, 1 the level of activity in terms of trips per rat per hour (Fig. 3 and Table Ia) was approximately six times as high during the first 150 minutes of exposure to a strange environment in comparison with the later periods following adjustment. This observation requires postulation of a second governor, one which determines the probability of initiating trips. Initiating trips is here considered to be synonymous with initiation of periods of diffuse undirected motor activity. Examination of the expression of hyperactivity during the first 2–2½ hours of exposure to a strange environment provides insight into the functioning of this governor of trip-initiations.

For 71 of the 73 rats previously discussed with reference to the distance of trip-terminations, a count was made of the total feet traveled each half-hour during the first 2½ hours of exposure to the alley. A similar analysis was prepared for the 26 rats, considered further in Section III, A, 5, which emerged into the alley more than momentarily and for which the recording system functioned properly.

For each set of data, results are quite similar (Fig. 6). Activity continuously declines during initial exposure to a strange environment. But the important point is that this decline begins from an extremely elevated state of hyperactivity. From Table Ia it may be calculated that the average round trip approximates 10.44 feet. During the normal nocturnal period of activity, trips occur at the rate of 1.53 per hour. This means that in this one-dimensional alley rats travel 8 feet per half-hour on the average when adjusted to their environment. As may be seen from Fig. 3 the activity is increased nearly twenty times normal during the initial half-hour in this strange environment. Projection of the curves, shown in Fig. 6, indicates that a normal level of activity will be reached by 3–4 hours of adjustment.

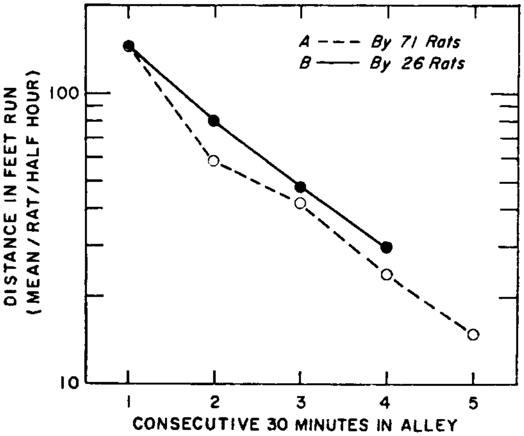

FIG. 6. Hyperactivity in a strange environment: Curve *A* represents the mean activity level of 71 rats immediately after first exposure to the Ferguson Alley. Curve *B* similarly gives the mean response of 26 rats to the NIH Emotional Activity Alley.

Such decay curves of hyperactivity suggest that the rats secrete some humoral agent upon their initial exposure to strange stimuli such as represented by the activity alley. This humoral substance increases the rate of firing of the neuronal net comprising the governor which determines onset of diffuse motor activity, such as trips out into the alley. As this substance is degraded, the frequency with which this governor emits signals initiating trips decreases until normal behavior is achieved.

5. AVOIDANCE OF A STRANGE FIELD

During the pursuit of these studies on behavior in a one-dimensional habitat, a few rats failed to emerge into the alley until after the lapse of several hours. Most frequently such rats were members of subgroups having had less opportunity to adjust to novel stimuli. This suggested that the less opportunity an animal had to make adjustments to strange stimuli, or the more novel was the strange environment, the more likely it would be avoided.

New alleys were constructed to permit exploration of this hypothesis. These alleys consisted of an 8 × 8-inch channel 15 feet long. At one end a home nest box could be attached from which the rat gained access to the alley by way of a 3 × 3-inch door. At the opposite end of the alley, light from two 60-watt lamps shone through a ground glass plate. Unless otherwise modified, the floor was stationary. A photoelectric cell at each 3-foot interval along each alley initiated a signal to an Esterline–Angus event recorder each time a rat passed. This apparatus is called the "NIH Emotional Activity Alley."

Each of the 76 subjects, Osborne–Mendel male rats, was housed alone for 3 months from weaning in a small cage precluding the visual perception of any object outside the cage. Cages were not opened. Food and water were delivered into the cage through channels making it unnecessary to open them. These procedures minimized opportunity for adjusting to new configurations of stimuli. In the terminology of Section XIV, G, 1, the isolation cage represents an E_1 configuration of stimuli. Under this terminology $E_1 \cdots E_n$ represent a series of discrete configurations of stimuli which an individual may encounter for the first time in that order.

Twenty rats were transferred directly from the isolation cages into the activity alley for a 2-hour exposure. Of the remaining 56 rats, 24 were exposed to an E_2 configuration for 2 hours for 10 days prior to being placed in the alley. Similarly, 16 others were exposed to an E_3 configuration, while the remaining 16 were exposed to E_2 for 2 hours, then immediately exposed to E_3 for 2 hours for 10 days. Three days after these exposures, which provided opportunity to adjust to the new stimuli of E_2, E_3, or E_2 and E_3, each rat was given a 2-hour trial in the activity alley, which represented an E_4 configuration. Half of each of these four groups were placed in the alley with a stationary floor, an E_{4A} configuration; while for the other half the alley contained sections of tilting floor, an E_{4B} configuration, which clanged when the rats passed over them.

Greater detail of these studies are presented in Section XIV, G, 4 and in Table IIb. However, the results presented in Table IIa suffice for the present purposes. Both aspects of the hypothesis were confirmed. The

TABLE IIa

EFFECT OF TRAINING AND DEGREE OF STRANGENESS OF A FIELD UPON ITS BEING ENTERED DURING 2 HOURS OF EXPOSURE BY EACH OF 76 RATS[a]

Response to alley	A "Training" in adjusting to strange stimuli		B Degree of strangeness of alley	
	Yes	No	High (tilting floor)	Low (stationary floor)
Entered	37	4	13	30
Avoided	19	16	25	8

[a] A data: $\chi^2 = 10.8045$; p less than 0.001; B data: $\chi^2 = 13.7110$; p less than 0.005.

stranger a field or the less opportunity there has been to adjust to novel stimuli, the greater will be the tendency for an animal to avoid that field.

6. PROBABILITY OF VACILLATING AT THE TERMINATION OF TRIPS

In the unstructured Ferguson Activity Alley, rats usually went directly out to the point where the trip terminated, then turned around and went directly back to the home compartment. Yet occasionally when a rat made an excursion out into the alley, it would wander back and forth

TABLE IIb

EFFECT OF KIND AND SEQUENCE OF "TRAINING" IN ADJUSTMENT TO STRANGE STIMULI UPON AVOIDANCE OF AN ACTIVITY ALLEY

Group[a]	E_{4A} Alley			E_{4B} Alley		
	Total trials	Trials entered	Proportion entered	Total trials	Trials entered	Proportion entered
A	40	11	0.275	40	2	0.050
B	48	33	0.688	48	24	0.500
C	32	31	0.969	32	22	0.688
D	32	24	0.750	32	6	0.188
Total	152	99	0.651	152	54	0.355

[a] See Section XIV, G, 4 for details of treatment of the four groups.

about the place where the trip terminated. Two hundred and fifty-six of the total 2357 trips studied with reference to the initial period of hyperactivity, terminated in such vacillations. As graphically shown in Fig. 7 the probability of vacillating is proportional to the length of the trip.

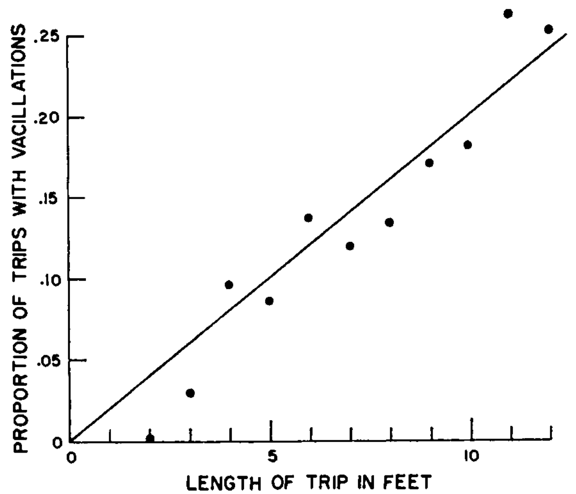

Fig. 7. Probability of trips including a period of vacillation, wandering back and forth about the point of termination. Curve based on 2357 trips by 136 rats during their first 150 minutes in the Ferguson Activity Alley.

These results are given here because of their bearing on the question of the proportion of time an animal is capable of responding to static components of its environment. As I have stated above, I am proceeding with this formulation, utilizing the hypothesis that directed responses can be made only at the ends of periods of diffuse activity, which are represented here by the outward termination of trips. If this responsiveness at ends of trips persists throughout the wandering about at the end of trips, then it follows that the farther a familiar type of object is from home the more likely it will be responded to in proportion to trips terminating there. This conclusion is subject to the qualification that the object is so sparsely distributed in space as to require more searching than mere detection of the surroundings at the point of terminating a trip.

IV. Use of a Two-Dimensional Field

A. Theoretical Origin

We are here considering animals whose movements emanate from a fixed home base. For them a two-dimensional field differs from a one-dimensional one in that in a two-dimensional field the area available at successive radial distances from home increases with radius. Considering this fact, will the behavior exhibited by rats in a one-dimensional field lead to an equation for home range closely resembling the bivariate normal distribution [Eq. (3)]?

When Casby and I originally found that the bivariate normal distribution did conform with the observed home range resulting from captures, we were merely culminating a search for a means of describing the distribution of captures about the mean coordinate point of capture. This conformity revealed nothing about the biological mechanisms involved. We shall now inquire whether the phenomena of (a) decreasing frequency of arriving at successively greater distances from home, and (b) the probability of wandering increasing with distance from home suffice to explain the origin of the bivariate normal type home range.

A critical issue concerns the origin of the observation or "capture." Two types of observation are possible. First, the observer may record the physical presence of the animal at successive points independent of the activities of the individual. Second, the observation may arise as a consequence of the animal responding to an object placed by the investigator. Captures in traps represent this type of observation.

An assumption is made regarding where responses, such as entering baited traps, will be made. This is that such responses to continuously present and unvarying stimuli occur only during the period of wandering at the end of trips. This assumption implies that the animal remains in a perceptually blind state during the outward and return phases of a trip. The circumstantial evidence suggesting this assumption will not be considered here.

Let: P_1 = probability of terminating a trip at radius r.
t = time spent wandering at r if it stops there.
C = probability of capture at r, which equals tP_1 times geometry factor of two-dimensional space.

Then:

$$P_1(r) = Ae^{-r/\alpha} \tag{19}$$

$$t(r) = Br \tag{20}$$

These two equations, in which A, B, and α are constants, represent the two basic assumptions regarding use of one-dimensional space. Then considering the geometry factor:

$$C = Kre^{-r/\alpha} \cdot rdrd\theta \tag{21}$$

And normalizing, it is found that:

$$C = \frac{1}{2\alpha^3} r^2 e^{-r/\alpha}\, dr \tag{22}$$

Where $r/\alpha = R$, the cumulative probability of capture, Cum, as a function of the radius R from home becomes:

$$\mathrm{Cum}_{\mathrm{II}} = 1 - \left(\frac{R^2}{2} + R + 1\right) e^{-R} \tag{23}$$

Equation (23) above will be called Curve II as shown in Table III and Fig. 8. It may be compared to a similar cumulative probability curve for the bivariate normal distribution, which will be called Curve I, and which has the form:

$$\mathrm{Cum}_{\mathrm{I}} = 1 - \exp\,(-r^2/2) \tag{24}$$

Curve II, Eq. (23), may be compared to Curve I, Eq. (24), by converting R into units of r, where r, the radius from the center of the home range, is measured in the σ units of the bivariate normal distribution, provided the constant α of $R = r/\alpha$ is known. This conversion was arbitrarily accomplished as follows: It can be shown that the cumulative probability of "capture" of Eq. (23), when expressed in terms of α and r, has the form:

$$\mathrm{Cum} = 1 - \frac{1}{2\alpha^2}\,(r^2 + 2\alpha r + 2\alpha^2)e^{-r/\alpha} \tag{25}$$

By Eq. (24), Curve I, when $r = 1.2$, Cum $= 0.513$. Therefore, by successive approximations, utilizing Eq. (25), it was found that when $\alpha = 0.44$, $\mathrm{Cum}_{\mathrm{II}} = 0.511$ at $r = 1.2$. Therefore, 0.44 is the α conversion factor applied to $R = r/\alpha$, so that Curves I and II may be compared in terms of the bivariate normal home range σ distance.

The values for these two curves, as shown in Table III, are shown in Fig. 8. Note that up to about 2σ radius these two curves are so nearly identical that they are either likely to approximate actual field data equally well. There is considerably more "tail" to Curve II, but since so few observations occur in the greater than 2σ range, it will still be difficult to decide which of these two curves most nearly approximates actual field data for the longer recapture radii.

However, the objective was to determine how well phenomena observed in the use of one-dimensional space could lead to a curve approximating the bivariate normal distribution. One of the assumptions was that the wandering responsive phase was proportional to radius from home. In the analysis of wanderings, vacillations at ends of trips in the one-dimen-

TABLE III

CUMULATIVE PROBABILITY OF "CAPTURE" WHERE r IS RADIAL DISTANCE FROM HOME IN σ UNITS OF THE BIVARIATE NORMAL DISTRIBUTION

Radius, r in σ units	Observed Captures[a]	Curve I $1 - \exp(-r^2/2)$	Curve II $1 - (\frac{1}{2}R^2 + R + 1)e^{-R}$	Curve III $1 - (1 + R)e^{-R}$	Curve IV $1 - (\frac{1}{6}R^3 + \frac{1}{2}R^2 + R + 1)e^{-R}$
0.3	0.0574	0.044	0.032	0.150	0.0152
0.6	0.1667	0.165	0.157	0.395	0.1207
0.9	0.3621	0.333	0.337	0.607	0.3136
1.2	0.5489	0.513	0.511	0.755	0.5162
1.5	0.6839	0.675	0.662	0.8541	0.6882
1.8	0.8247	0.8021	0.7766	0.9155	0.8096
2.1	0.8966	0.8897	0.8555	0.9514	0.8977
2.4	0.9483	0.9439	0.9032	0.9724	0.9409
2.7	0.9741	0.9739	0.9435	0.98447	0.9685
3.0	0.9914	0.9889	0.9668	0.99163	0.9837
3.3	0.9971	0.99568	0.98055	0.99530	0.9918
3.6	1.0000	0.99846	0.98793	0.99740	0.9971
3.9	—	0.99950	0.99300	0.998595	0.9998
1.0	—	0.3935	0.397	0.663	0.3807
2.0	—	0.8647	0.8314	0.9411	0.8698

[a] The 348 captures shown in Fig. 1 are here presented as the proportion the accumulated forms of the total.

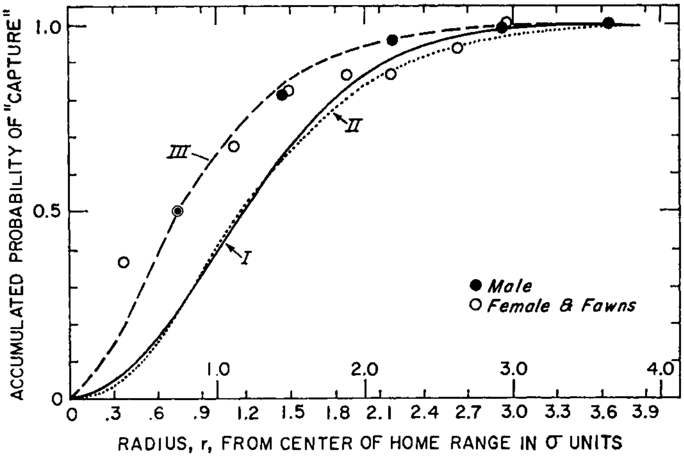

FIG. 8. Accumulated probability of "capture." Curve *I* is the expected from the bivariate normal distribution function. Curve *II* is the expected based upon (a) termination of trips according to the equation, $y = e^{a+bx}$ in which the slope b is negative, (b) probability of wandering at end of trips is proportional to radius, and (c) captures only occur during the wandering phase at end of trips. Curve *III* is the accumulated travel path with no wandering at end of trips and "captures" represented by observation of the animal in motion.

sional alley shown in Fig. 7, it was only recorded whether or not a wandering occurred at the end of trips. No measure was made of the length of the wandering. However, it is my impression that the longer a trip, the greater will be the amount of wandering at the end of a trip if wandering is initiated. This would mean that the amount of responsive wandering at the end of trips is proportional to r^2 rather than just to r. If this is really the case, then we can derive a fourth cumulative probability curve, Curve IV, which has the form:

$$\mathrm{Cum}_{\mathrm{IV}} = 1 - \left[\frac{R^3}{6} + \frac{R^2}{2} + R + 1\right] e^{-R} \tag{26}$$

By successive approximations utilizing Eq. (25), it was found that when $\alpha = 0.32$, $\mathrm{Cum}_{\mathrm{IV}} = 0.516$ at $r = 1.2$. Therefore, 0.32 is the α conversion factor applied to $R = r/\alpha$, so that Curves I and IV may be compared in terms of the bivariate normal home range σ distance. Note that thus there is forced conformity of both $\mathrm{Cum}_{\mathrm{II}}$ and $\mathrm{Cum}_{\mathrm{IV}}$ to $\mathrm{Cum}_{\mathrm{I}}$ at the 1.2 value of r.

Near the home range center, Curve IV predicts fewer captures than is implied by Curve II or found by observed captures, Table III. However, at the longer radial distances from the home range center, Curve IV more closely approximates Curve I and the observed data than does Curve II. At present parsimony demands assuming only that the farther an animal moves from his home range center, the more likely it will terminate an outward trip and respond to stimuli near the place of stopping. Extremely careful observation is required to determine if animals tend to wander still farther about the points of termination of trips as these points occur farther from home.

B. Travel-Path Home Range

Captures or responses represent only one method of assessing home range. I have indicated that one assumption regarding behavior is that on the outward trip from home and on the return trip to home, the animal is in a preceptually blind state during which static stimuli fail to elicit responses. And yet it is possible to observe and record the presence of such nonresponsive individuals on this outward and return trip. Utilizing Eq. (19) and considering the effect of the geometry factor in the sense that the observer in a two-dimensional field can record an animal only if it passes directly by the observer, and assuming that the amount of wandering at end of trips is minimal, the equation for the cumulative probability of observing an animal during its travels, Curve III, becomes:

$$\mathrm{Cum}_{\mathrm{III}} = 1 - (1 + R)e^{-R} \tag{27}$$

Data for Curve III with the α constant $= 0.44$ are shown in Table III and on Fig. 8. Obviously, if "captures" represent such observations, the animal will appear to spend more time closer to home. Leopold *et al.* (1951, Fig. 50) provide data on home range based upon visual observation of marked mule deer. They presented their data in terms of number of observations within successive 100-yard bands from the site of capture. The actual home range center will be on the average somewhere to the right or left of the line of length d connecting the point of capture and the point of later observation. the actual radial distance from the true home range center would be $K \cdot d/2$ when K is between 1.0 and 1.414. Without going into the origin of K, it is still apparent that the distances given by Leopold *et al.* (1951) can be utilized as approximating proportionality to radial distances of observation from the home range center. The cumulative probabilities of observation for 102 observations of males and 103 observations of does and fawns are with distance, respectively: 100 yards (0.363, 0.495), 200 yards (0.500, 0.815), 300 yards (0.678, 0.952), 400 yards (0.726, 0.980), 500 yards (0.862, 1.0), 600 yards (0.862,—), 700 yards (0.932, —), 800 yards (1.0, —). Noting that 0.50 of the males were observed within 200 yards of the point of capture, and that 0.495 of the females and fawns were observed within 100 yards of the point of capture, and utilizing Eq. (27) and the fact that $R = r/\alpha$, σ, in the sense of *d*, for males is 270 yards and for females and fawns is 137 yards. On this basis the observed cumulative probabilities of observation were converted into sigma units of distance from the point of capture and posted on Fig. 8.

There is forced conformity with Curve III, Eq. (27), at 0.74σ. However, the further proximity of the observed points, up through 1.5σ, to Curve III provides credence to the general formulation of Eq. (27). Observations may occur when the animal is on either the outward or return portions of a trip or during the wandering at the end of a trip. The more an animal wanders at ends of trips relative to the cumulative travel path, excluding wandering at the end of trips, the farther the observed points may be expected to diverge from Curve III and approach Curves I and II. In fact, were it possible to obtain adequate assessments of home range in terms of observations made of the individual during its travels as well as of data derived from responses such as entering traps, it would be possible to calculate wandering distance at *r*.

V. Summary of the Concept of Home Range

Developing an attachment to a restricted region to which an animal returns after wandering outward from it requires that the individual belong to a species which has evolved the capacity to retain the memory of prior experience. If an animal remains at the site of its birth there is no question that the immediate surroundings of this site will be known better than more distant ones. However, many individuals are forced from the site of their birth. The term "forced" is here used as a postulate derived from the observed avoidance of fields containing strange stimuli. Parsimony demands the assumption that an animal will remain at home unless forced away, until it can be shown that an animal will change its home in the absence of any factors which might tend to expel it.

Even if an animal is expelled from the site of its prior residence and begins to wander at random, it will be chance cover some areas more frequently than others. As it thus becomes familiar with a restricted area, it will increase its avoidance of less frequented areas. This process will lead to a repeated frequenting of a particular restricted location which can be defined as "home." Home may acquire other attributes, such as the construction of a den, but such additional attributes are not necessary for a site to become a home.

At irregular, probably random, intervals the individual engages in excursions from home. During these outward excursions the animal remains in a refractory state during which it is unable to respond to stimuli encountered. Only at the termination of trips, including the period of wandering at end of trips, will the animal be able to respond to objects or situations such as it had already passed on the outward trip. However, those objects which were bypassed on the outward trip do alter the probability of terminating trips. The greater the number of such objects, or the greater the intensity of stimuli emanating from them, the greater will be the probability of a trip stopping after reaching every distance from home. Should novel stimuli be encountered during a trip, the shorter will be the interval after reaching home before initiating another trip. This holds in so long as the novel stimuli are not excessive. In this case, the animal will remain at home for unusually long periods before again venturing forth. The probability of wandering increases with distance from home. These several aspects of locomotion and responsiveness to stimuli lead to a probability of responding within the region about an animal's home, which so closely resembles that of the bivariate normal distribution function that the latter may be used to represent home range.

VI. Continuous Removal Trapping of Small Mammals

When a large number of snap-traps are set within a habitat where mice and shrews live, it is usually observed that more individuals are captured on the first than on the second or third day, and that fewer animals enter traps on the third than the second day. It has generally been assumed that this decline in catch through time would continue were the traps left set for a longer period. Based upon this assumption, various equations (e.g., Zippin, 1956; Calhoun and Casby, 1958) have been developed for estimating the number of individuals which would eventually enter the traps.

Furthermore, it has also generally been assumed that the catch for a 3- or 4-day period would reflect the relative species composition of the community being sampled. This assumption served as the basis for establishing the North American Census of Small Mammals (Calhoun, 1949–1957). During the nine years, cooperators provided results (see NACSM Release No. 9) for 1615 standard trap-lines consisting of 20 stations, usually 50 feet between stations, 3 traps per station, run for three consecutive nights. Despite the laudable objectives of this cooperative endeavor, this tremendous effort has, for reasons we shall shortly see, provided inadequate data for insight into either relative density or species composition.

Questioning the usefulness of short-term removal trapping developed slowly. It began in 1950 when I asked A. Dexter Hinckley, then a summer student at the Jackson Memorial Laboratory, to continue eight NACSM lines for 15 days (see Section VI, E and Fig. 13A). Despite the expectation of a continually declining catch after the first 3 days, it turned out that the number taken from day 4 onward actually increased each successive day until on day 15 three times as many individuals entered traps as did on day 1.

These results initiated an intensive effort to explore the results obtained from prolonging the period of removal trapping. I am particularly indebted to Drs. William L. Webb and Earl F. Patric of the Huntington Wildlife Forest, and to my colleague, Dr. Kyle R. Barbehenn. Without their permission to utilize here some of the data from their extensive studies of removal trapping, it would have been impossible to develop the concepts elaborated in succeeding sections of this paper. I have also profited from a number of 30-day census contributed by other NACSM cooperators.

Our concern here will be with the contribution of this program, and allied research developing from it, to furthering our understanding of home range and the organization of small mammal communities. The following few sections merely present results. Note that within each study presented, the several species present markedly different patterns of capture by traps over time. Interpretations based upon the data in Section VI are given in Sections VIII, IX, and X.

A. Rich Lake Island, New York, 1952, Sixty-Day Removal Study—Data Contributed by William L. Webb

Four NACSM traplines were run on this island in the Huntington Forest for 60 consecutive days, beginning August 16. The red-backed mouse, *Clethrionomys,* and the shrew *Sorex* formed the majority of the catch. Figure 9 gives the results for the first 30 days. Note that *Clethrionomys,* which entered the traps in large numbers during the first few days, was by the end of 30 days represented by only half the total catch as that for *Sorex,* whose peak in catch per day did not come until the ninth day. Both species exhibited a secondary minor period of increase in captures.

During the same summer, 34 NACSM lines were run for the standard 3-day period in similar forests on the mainland (Table IV). As on the island, comparatively few *Sorex* entered traps on mainland areas during the first 3 days of trapping. And yet, continuous removal trapping for an 80-day period (Section XI) in one tract of the mainland forest produced 617 *Clethrionomys* and 1225 *Sorex.*

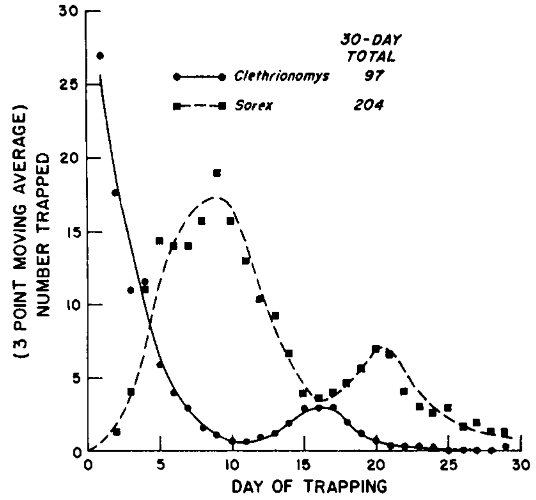

FIG. 9. Daily removal captures of the two most abundant species inhabiting a 30-acre island; recorded by Dr. William L. Webb.

TABLE IV

COMPARISON OF RESULTS BETWEEN SHORT-TERM AND LONG-TERM REMOVAL TRAPPING ON THE HUNTINGTON FOREST DURING 1952

Location	Genus		
	Clethrionomys	*Sorex*	*Peromyscus*
80-Day total for continuous removal trapping on a 30-acre mainland area (see Section XI)	617	1225	77
34 NACSM lines each for 3 days on mainland	753 (22.1)[a]	17 (0.5)	38 (1.1)
4 NACSM lines on Rich Lake Island			
60-day total	133	243	27
Total 1st 3 days	53 (13.3)	4 (1.0)	0

[a] Mean 3-day totals shown in parentheses.

B. Chadwick Woods, Montgomery County, Maryland, Removal Study, 1958–1959—Data Contributed by Kyle R. Barbehenn

Five circular traplines, each with a radius of approximately 300 feet, were used. The number of traps per station and the interval between stations varied among the lines. However, for the present purposes these differences are unimportant. As with the Rich Lake Island study, the genus, here *Peromyscus*, with the initial most rapid input was represented by only half as many (57) captures as another genus, *Blarina*, which entered the traps more slowly (116 taken) (see Fig. 10). A third genus, *Sorex*, began its period of maximum captures only after the majority of the other two genera had been removed, but only 48 were captured. Note that *Peromyscus* exhibited a fairly rapid rate of capture until approximately 65% of the 30-day total had been taken. Following an intervening period with very few captures, there ensued a secondary period of increased captures.

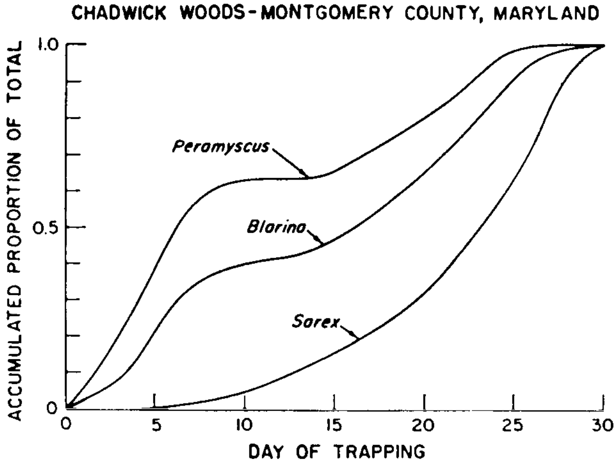

FIG. 10. Differential "schedules" of entering traps expressed by the three species recorded by Dr. Kyle Barbehenn in his study of continuous removal trapping in an upland hardwood forest.

C. Comparative Catches, Huntington Wildlife Forest, 1952–1953—Data Contributed by Earl F. Patric and William L. Webb

During these two years *Peromyscus* and *Blarina* were universally scarce on the Huntington Forest. In order to determine the general pattern of their input, data from five separate plots must be pooled.

Four plots consisted of concentric circular traplines, 75 feet between circles, with one trap each 10 feet along the lines. Two plots consisted of three lines, and two of four lines. The fifth plot is represented by the first 15 days' results of the Rich Lake Island study presented in more detail in Section VI, B. All areas were sampled for at least 15 days (Fig. 11). Each day all animals captured were removed.

Note that whereas the catch of *Clethrionomys* initially declines through time, all other species exhibit an increase in catch per day for the first 4 or 5 days.

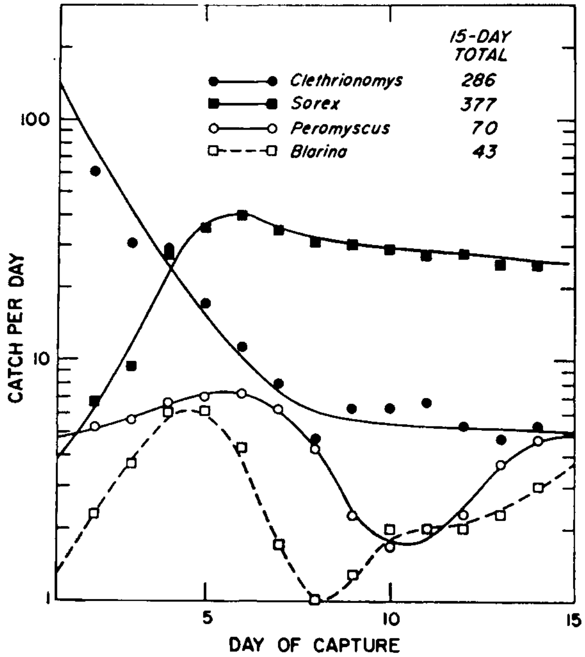

FIG. 11. Summated results from five continuous removal studies conducted by Dr. Earl Patric and Dr. William Webb during 1952 and 1953 on the Huntington Forest, New York.

D. Comparative Catches, Huntington Wildlife Forest, 1951—Data Contributed by William L. Webb

Nine NACSM lines were each run for at least 24 days during September of 1951 (Fig. 12). In contrast to the following two years, *Peromyscus* nearly equaled *Clethrionomys* in abundance. Likewise, *Blarina* was abun-

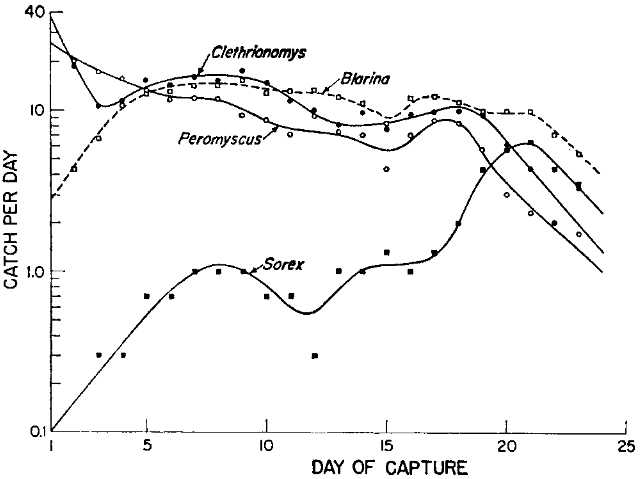

FIG. 12. A continuous removal study conducted by Dr. William L. Webb on the Huntington Forest in 1951. This year represented a time when the dominance relationship of the three most abundant species was not yet clarified, the small mammal community was in a state of social flux. See Table V. Points shown are 3-point moving averages.

dant. Only *Sorex* was rare. The relative likelihood of capture during the initial and terminal days of trapping forms a most interesting series (Table V). Initial and terminal likelihood of capture are inversely related despite the fact that usually over 50% of each genus were taken during the middle period of trapping.

TABLE V

HUNTINGTON FOREST (1951) 24-DAY CONTINUOUS REMOVAL TRAPPING

Genus	24-Day total	Proportion of 24-day total during	
		First 5 days	Last 5 days
Peromyscus	217	0.418	0.042
Clethrionomys	267	0.311	0.079
Blarina	229	0.188	0.166
Sorex	41	0.024	0.585

E. Comparative Catches in Maine (1950) and Maryland (1953)

Eight NACSM lines within an 80-acre tract of a much more extensive continuous forest opposite the Hamilton Station of the Jackson Memorial

Laboratory on Mt. Desert Island formed the trapping procedure in the Maine study. Four concentric circular traplines, each of a 75-feet greater radius than the next innermost one, having one trap each 10 feet along the lines, formed the trapping procedure in the Maryland study. During the years these studies were conducted, I was still working under the assumption (see Calhoun and Webb, 1953) that the large numbers of animals taken shortly after the first 3 days of trapping resulted primarily from invasion from beyond the periphery of the trapping area. These relatively short-term removal studies are presented here (Fig. 13) since they provide further insight into the differential rate of input for the several species making up the small mammal community. Total 15-day catch by genus for the Maine study (Fig. 13A): *Clethrionomys* 80, *Sorex* 53, *Peromyscus* 75, and *Blarina* 132. Total 14-day catch by genus for the Maryland study (Fig. 13B): *Peromyscus* 45, *Blarina* 76, and *Pitymys* 62. The Maine study was conducted by A. Dexter Hinckley under the author's direction, and the Maryland study was conducted by the author.

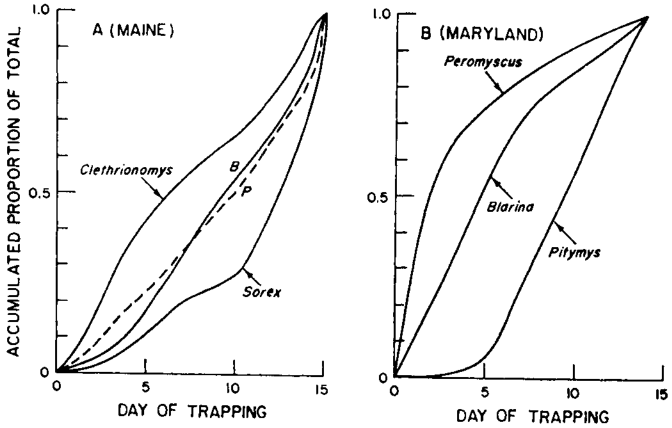

FIG. 13. Two short-term removal studies. The more dominant a genus happens to be the sooner will 50% of its members be trapped. In Fig. 13A: *B* = *Blarina*; *P* = *Peromyscus*.

F. Comparative Catches of *Peromyscus* and *Clethrionomys*

Relationships between these two genera, revealed by NACSM census data, have been particularly helpful in developing insight concerning community organization. Census from three localities, where both genera occur, are represented by a large number of traplines. Those run in each locality encompass a period of several years, and so should provide a representative picture of relationships in the respective habitats. Results in Table VI derive from 37,080 "trap-days" of effort.

Drs. Earl F. Patric and William L. Webb provided the New York data from the Huntington Wildlife Forest at Newcomb, New York. The majority of the animals shown were taken in the years of high density, 1953–1954, although the few taken during the low density years of 1955 and 1956 are included. Dr. J. E. Moore of the University of Alberta, Edmonton, provided the Alberta census including the years 1948–1956. Dr. John A. King and two U. S. National Park Rangers, Clifford Senne and L. S. Winsor, and the author conducted the Maine census on Mt. Desert Island between 1949 and 1952.

TABLE VI

COMPARATIVE CATCH OF TWO GENERA IN THREE LOCALITIES

Genus	Location	Number of lines	Day[a] 1	2	3	Total, days 1–3	Mean per line
	New York	90	586 (0.408)	470 (0.327)	380 (0.265)	1436	16.0
Clethrionomys	Alberta	36	117 (0.390)	103 (0.338)	83 (0.272)	303	8.5
	Maine	80	90 (0.489)	58 (0.315)	36 (0.196)	184	2.3
	New York	90	93 (0.274)	117 (0.344)	130 (0.382)	340	3.8
Peromyscus	Alberta	36	241 (0.577)	122 (0.292)	55 (0.132)	418	11.6
	Maine	80	132 (0.434)	103 (0.399)	69 (0.227)	304	3.8

[a] Proportion of 3-day Σ shown in parentheses.

Figure 14 shows the decline in catch from day 1 through day 3 for these two genera for Maine and New York.

In Maine where both genera have low densities, their respective patterns of decline in catch through time are very similar. However, the relatively greater catch of *Clethrionomys* on day 1 should be noted with reference to the trends of the 15-day trap-out as shown in the left-hand graph of Fig. 13 for eight NACSM lines also run on Mt. Desert Island.

In New York, where *Peromyscus* had the same density as in Maine but *Clethrionomys* was four times as numerous as *Peromyscus*, a striking difference in the trends resulted. *Clethrionomys* exhibited a typical, though somewhat slow, decline through the three consecutive days. In contrast, despite removal trapping and thus fewer deer mice available for entering traps, a greater number of *Peromyscus* entered traps each successive day. I wish to emphasize that competition for entering traps contributed negligibly to these trends. Three times as many traps were set each day as there were total animals caught for the entire 3-day period.

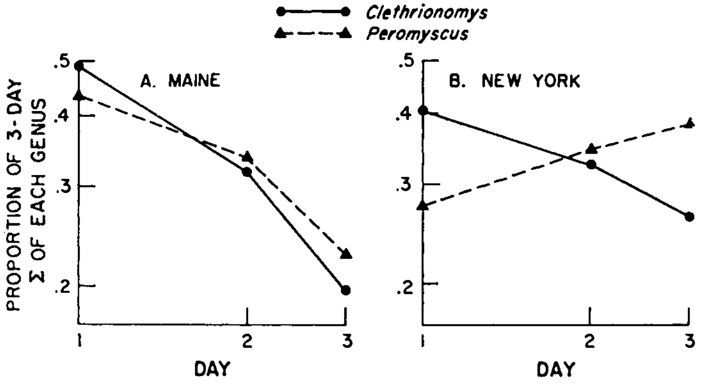

Fig. 14. Capture rates for *Clethrionomys* and *Peromyscus* in Maine and New York. Nearly codominance, or lack of dominance, is reflected by the Maine data, whereas in New York *Peromyscus* is clearly subordinate to *Clethrionomys*. See Table VI.

In Alberta, where both species are on the average relatively abundant (Table VII), there exists a marked seasonal difference (Fig. 15) in the trend of input over time between these species. During the spring, when low densities characterize both species, each exhibits a rapid rate of decline. In contrast, by fall when high densities have developed for both species, *Clethrionomys* shows a relatively constant input. Note the reversal of the trends of input for *Clethrionomys* and *Peromyscus* when Fig. 11 and Fig. 15B are compared.

VII. Toward a General Theory of Interspecific and Intraspecific Use of Space

The data presented in Section VI reveal that a continuous decline in catch from one day to the next during removal trapping is the exception

TABLE VII

MEAN CATCH PER TRAPLINE ON DR. MOORE'S ALBERTA STUDY AREA

Genus	Season		Fall/Spring
	Spring	Fall	
Clethrionomys	5.00	11.90	2.18
Peromyscus	8.06	15.56	1.93

rather than the rule. Even where the numbers taken per day do initially decline, a secondary increase usually ensues by the fifteenth day of trapping. Furthermore, many species actually exhibit an increase in catch per day as their associates are removed. Any trend of increase in catch after previous removal of associates can only mean that the survivors have in some way altered their behavior so as to increase their exposure to traps. Furthermore, we must conclude that those caught earlier in time must, while still alive, have suppressed this change of behavior. We shall now consider how these results make possible a conceptualization of spatial, temporal, and social organizations of the small mammal community.

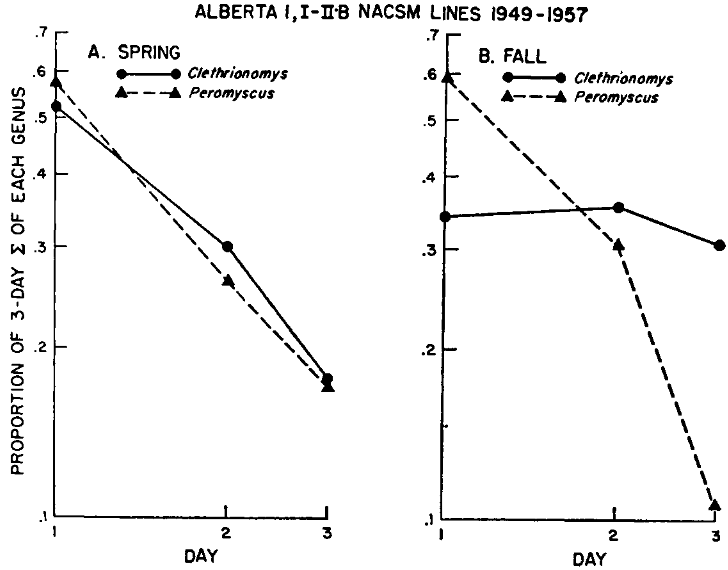

FIG. 15. Seasonal capture rates for two species. With the increase in density from spring to fall (see Table VII) *Peromyscus* apparently becomes dominant to *Clethrionomys*.

A. A Two-Species System

The relationship between *Clethrionomys* and *Sorex* on the Rich Lake Island (Section VI, A, Fig. 9) and between *Peromyscus* and *Blarina* in the Chadwick Woods study (Section VI, B, Fig. 10) form the basic data leading to this formulation. The shrews—*Sorex* and *Blarina*, respectively,—in these two studies exhibited a delay in entering traps until many of the mice, *Clethrionomys* or *Peromyscus*, had been removed. Yet despite this slowness of entering traps, twice as many shrews as mice were taken during the 30 days of trapping in each study.

These data pose two questions:

1. Why were there twice as many shrews as mice?
2. In what way (and why) did the behavior of the shrews change so that after several days of trapping they were more exposed to traps than initially?

The first assumption will be that the larger the home range the greater the likelihood an animal will encounter a trap and be caught. Since during the first few days of trapping many mice but few shrews were taken, despite the greater abundance of shrews, the mice must have had considerably larger home ranges than the shrews. Furthermore, since the number of shrews taken per day increased during the first 10 days of trapping, it follows that their home range expanded as the mice were killed off. This leads to the conclusion that the mice in some way inhibited the extent of home range of these shrews. We may now designate the mice as being dominant or alpha species and the shrews as subordinate or beta species.

Formulation of a theory depicting the social and spatial aspects of such a two-species system requires the assumption of a uniform distribution of centers of home range for the alpha species. This represents the simplest assumption leading to a 1:2 ratio of number of alpha and beta species. In the preparation of Fig. 16, a field of uniformly spaced dots (not shown in Fig. 16) was plotted. These dots represented home range centers for members of the alpha species. A circle of radius half the distance between centers was drawn about each center. Each of the larger circles in Fig. 16 encompasses some portion of an alpha individual's home range.

Now we can ask: Where is it most logical to find the home range centers of beta species? They should be located at points minimizing encounter by members of the beta species with members of the alpha species. The interstices formed by juncture of each set of three neighboring home ranges of alpha species represent such locations.

Here a beta individual is equidistant from three alpha individuals. Displacement of the home range of a beta species member from such a point will increase its probability of encountering at least one member of the alpha species. About each such home range center a smaller circle was drawn (Fig. 16). This smaller circle represents the same proportion of the beta species home range as does the larger circle for the alpha species.

Examination of Fig. 16 shows that according to this formulation there will be in an ideal steady state exactly twice as many individuals of the subordinate beta species as there are of the dominant alpha species. This is because there are twice as many interstices between uniformly distributed alpha home ranges as there are alpha home ranges.

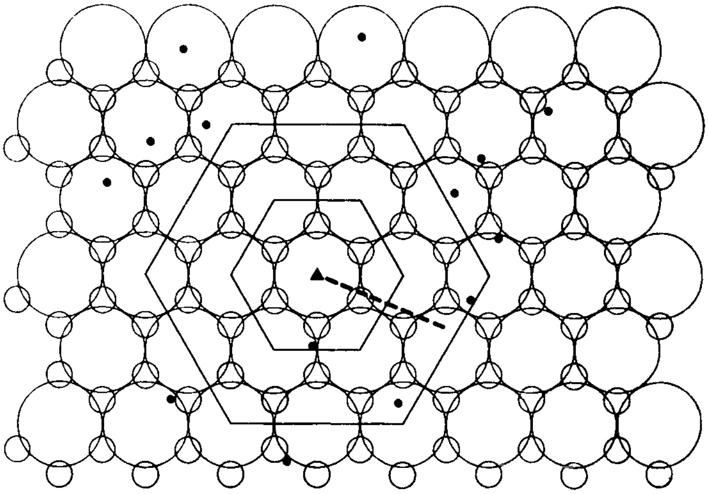

FIG. 16. Spatial distribution of a dominant and a subordinate species. Large circles represent a uniform distribution of one sigma radius portions of the home ranges of a dominant, alpha, species, while the smaller circles represent a similar proportion of the home range for members of a subordinate, beta, species. See text for other details, Section VII, A.

Now, suppose that a few traps are placed at random within a habitat characterized by inhabitation by such an alpha and a beta species. The fifteen dots in Fig. 16 represent such random points. It is readily seen that there is an alpha individual exposed to nearly every trap, but few individuals of the beta species are exposed to traps.

Now suppose we do set traps in such a system and remove the individuals caught. It is the general experience in continuous removal trapping that 25–50% of the members of the alpha species which are taken during 30 days are actually taken during the first 3 days.

This can only mean that by the end of 3 days there must be many members of the beta species whose neighbors of the alpha species are then no longer present. In the absence of the inhibiting influences emanating from the former alpha neighbors, the beta individuals then make a complementary expansion of their home range. As they do so, some beta individuals come into contact with traps and are also removed. Inspection of a number of continuous removal census in which there is an alpha species and one or more subordinate species indicates that maximum expansion of home ranges of the subordinate species is generally reached by the fifteenth day of trapping. After this time, the catch by day for subordinate species also declines over time since fewer and fewer remain to be caught.

B. The Nature of the Inhibitory Influence

Both *Sorex* and *Blarina* in Fig. 10 and *Sorex* in Fig. 9 exhibit an increase in catch even beginning on the second day of removal trapping. Similar results apply to the subordinate species included in Figs. 11–14, although not so apparent in those graphs where the ordinate represents accumulated catch. These results indicate that even removal of a small proportion of the alpha species is sufficient to induce home range expansion by subordinate species. Thus, the means of communication through which inhibition operates must be sufficiently effective and repetitive that a change in the general field intensity (or frequency) of stimuli emanating from an alpha species is detected within a few hours at least by subordinate species.

Bodily contact by random movement is unlikely to be effective. By the same token that it takes several days before all alpha species are taken in traps, it follows that in many instances subordinate species would be unaware of the absence of their alpha neighbors if this detection were a consequence of a change in frequency of contact. Production and detection of scent, at least where scent signposts are concerned, would likely operate to inhibit home range expansion because of the persistence of scent beyond the death of alpha individuals. Sight is unlikely to be an effectual means of detection of alpha by beta species, both because of concentration of activity during the night by many species and because many of these beta species actually spend considerable time under the leaf mold.

There remains vocalization and audition as the means of communication. Although there is as yet no proof that such is the means of communication whereby individuals can detect the presence of unseen neighbors, it stands out as the most likely possibility. Most small mammals do vocalize.

Fewer barriers exist that might prevent or distort the passage of sound through the environment than is true with regard to light stimuli or odors. In the following discussions vocalization and audition will be assumed to be the means of communication within and between species. However, identification of the means is unessential to the general argument; only recognition of the existence of some effective means of communication is necessary.

C. The Learning of Signals

There exists the possibility that the response of one individual to a signal emitted by another has become through evolutionary processes one which does not require a learned association between the signal and some act on the part of the emitter for its development. In the prior history of such species there must have been the opportunity for associating the signal with its emitter and there must have been survival value in the receptor developing an innate response to detection of the signal. However, until such responses to signals are demonstrated to be innate, it shall be assumed that they are learned.

We may now ask, "How may the members of a species learn a signal when the individuals are characterized by fixed home ranges which may be described by the bivariate normal distribution function?" In order to gain insight into this question, we shall consider two neighbors, *A* and *B*. *A*'s home range center is fixed whereas *B*, who lives some distance away, gradually shifts its home range center toward that of *A*. When the home range centers are six home range sigma or more apart, it is apparent that the probability of their meeting by chance will be extremely remote. This relative probability of meeting is proportional to the product of their density functions at any particular point (see Table 2 in Calhoun and Casby, 1958).

However, as the home range center of *B* approaches that of *A*, these two individuals will meet by chance on very rare occasions. Three examples of the relative probability of *A* and *B* contacting are given in Fig. 17. When the home range centers (HRC's) are 3.9 sigma apart, one peak is 1.5 sigma from *A*'s HRC and the other is 1.5 sigma from *B*'s HRC. In examining Fig. 17 it is well to keep in mind that we are considering the probability of contact at points along the line connecting the two home range centers. At all distances intervening between home range centers, from slightly over 3 sigma up to 6 sigma, there are always two peaks in this curve of probability of contact between two neighbors. As the home range center of *B* approaches 3 sigma to that of *A*, these two peaks approach each other until at 3 sigma they coincide for the first time. This single peak of highest probability of contact of two neighbors, which lies exactly halfway between the two home range centers, characterizes all distances less than 3 sigma intervening between the home range centers.

Let us assume that when *A* and *B* meet there is some interaction between *A* and *B*. That is, *A* responds to *B* and *B* responds to *A*. At the same time, each emits a signal. If such chance contact occurs frequently enough there exists the opportunity of each individual associating the other with the signal emitted at the time of interaction. Furthermore, we may assume that learning is enhanced by other factors of the environment being constant at the time of interaction. When home range centers are more than 3 sigma apart, the two points of greatest probability of contact are separated from each other and therefore are unlikely to have identical surroundings. This nonidentity of surroundings, that is the absence of identical secondary reinforcers, may be expected to retard learning.

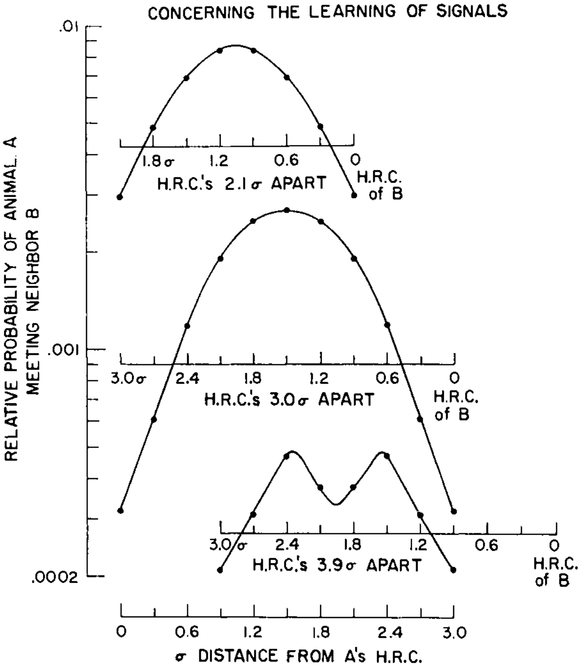

FIG. 17. Concerning the learning of signals. Not unless home range centers are 3 sigma or less apart will there be a single point of most probable contact of two animals meeting by chance. This point lies halfway between the line connecting the two home range centers. The closer home range centers approach, the higher will be the probability of chance contact and thus the more likely the association of any simultaneous signal with the consequences of meeting.

However, at a 3-sigma interval between home range centers, there is only a single point of greatest probability of contact; thus, at this intervening distance between home range centers there is not only an increased probability of contact because the home range centers are closer together, but there exists a greater constancy of secondary reinforcers at the single point of greatest probability of contact. It is for this reason that I suspect that learning of signals is not likely to be effective unless home range centers are 3 sigma or less apart.

Once an animal has learned to associate a signal with the animal which emitted it, there then exists the opportunity that the detecting individual can perceive (hear) the signal at some distance from the emitter and make the appropriate response of approach or withdrawal. How far the signal may be detected depends upon both the intensity of the signal emitted and the ability of the detector to hear it. Presumably, sensory capacities for detection and motor capacities for emission have evolved simultaneously and in harmony. We may then wonder as to the distance over which such evolution of capacities permits the detection of an emitted signal. In the absence of any experimental data, introspection suggests that one might anticipate evolution of capacities to the point that an individual can just detect a signal emitted at the maximum distance between home range centers which still permits the learning of such signals. As we have seen, this distance is equivalent to 3 home range sigma. In other words, when animal *A* is at its home range center, a signal emitted by animal *B* at the border of *A*'s home range (as represented by a 3-sigma distance) reaches *A* in just the sufficient intensity to elicit a response by *A*. As *B* moves farther than 3 sigma away from *A*, the signal exhibits further decrease in intensity. Such reduced intensity may well be perceived by *A* until *B* gets at least 6 sigma away. Thus, between 3 and 6 sigma, it is suspected that the signal itself is perceived but is below the threshold necessary for eliciting a response by the receptor. Signals arising between 3 and 6 sigma from the receptor are here designated as contributing to what I shall call "hum."

These characteristics of the signal are represented schematically in Fig. 18. A signal emitted by one animal when nearly in contact with another may be given a rating of 1.0. For the purpose of later calculations, it is assumed that there is an inverse decrease of intensity of the signal at successive distances from the emitter until at a distance of 3 sigma it has reached one-tenth of the intensity that might be recorded at the emitter.

Investigations of this formulation requires that the sound signals emitted by typical individuals of a species be recorded and other individuals of the same species trained to exhibit a response upon perception of a recorded vocalization. Then, in the native habitat of the species, the trained subject must be moved continually farther away from the sound source until it no longer exhibits the characteristic response which it had been trained to perform following presentation of the signal. This distance may then be compared with the animal's home range sigma, as determined by live trapping and related observational procedures.

D. The Distance between Neighbors of the Same Species

From the observed tendency of a 1:2 ratio between alpha and beta species when coexisting in the same habitat, it was concluded that the home range centers for the alpha species should approximate a uniform distribution. However, this analysis provided no insight into whether there might be some ideal distance which should intervene between home range centers. In order to seek this insight we shall consider a single species community in which all individuals have exactly the same-sized home range, centers of home range are uniformly distributed, and the bivariate normal distribution function describes the home range.

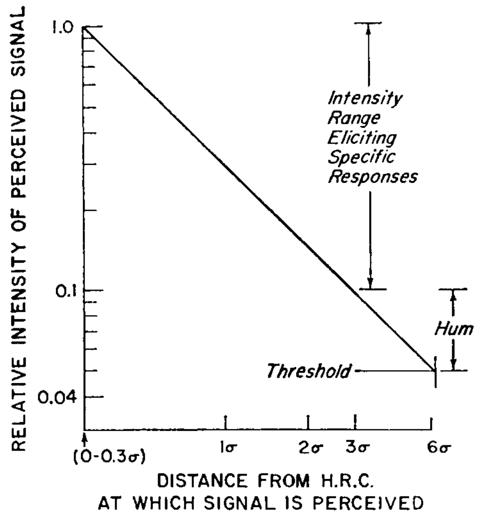

FIG. 18. Theoretical conceptualization of signal characteristics with reference to emission at a constant intensity at the home range center and detection and response by others at distances from it.

Answers to two questions will be sought with reference to the relative distance between home range centers:

1. How does distance between home range centers affect the impact of the community on the environment?
2. How does the interval between home range centers affect the probability of one individual meeting or detecting its neighbors?

The impact of an individual upon its environment should be proportional to the amount of time per unit area it spends at successive distance from its home. This relative impact is described by the bivariate normal distribution function (Fig. 2). For any particular animal this means that at 3 sigma distance from its home its impact per unit area will be only 0.011 of what it was adjacent to its home. We may visualize the impact of any one animal upon its environment as having a mountain-shaped topography. Where home range centers are at least 6 sigma apart, there lies between them a "valley" where neither animal has a significant effect on the environment. As soon as home range centers get closer than 6 sigma to each other, the home ranges overlap and neighbors can both affect those portions of the environment falling within both neighbor's home ranges. As soon as home range centers become less than 3 sigma apart, some portion of the environment can be affected by more than two individuals.

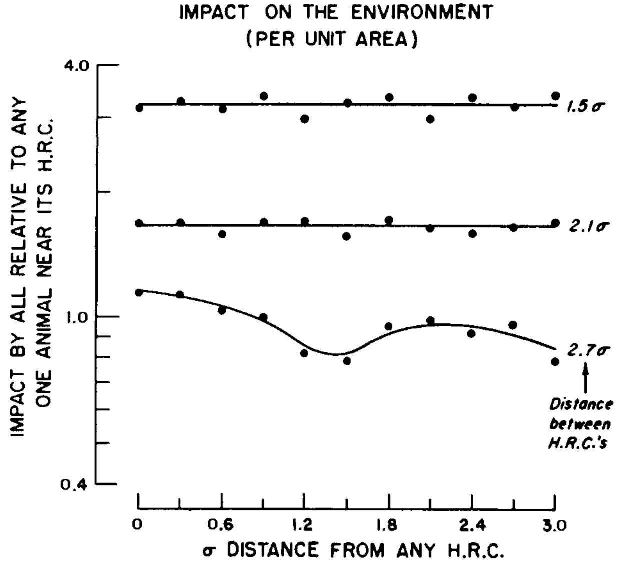

FIG. 19. Impact on the environment (per unit area). The value 1.0 represents the effect one individual will have near its home range center. Since home ranges increasingly overlap as their centers approach each other, i.e., density increases, the summated impact of all animals on any one point not only increases, but the relative impact on all points becomes more nearly equivalent.

At any point in the environment, the impact of all animals which can arrive at that point during this normal ranging about their home is proportional to the sum of their separate density functions at that point. Utilizing the normative data of density function as a function of the sigma radius from home, given in Table 2 of Calhoun and Casby (1958), several curves of summated density function were calculated (Fig. 19).

E. Methods of Calculating Data Relative to the Distance between Neighbors

In Fig. 16, which illustrates the uniform distribution of an alpha species and of a beta species lying in the interstices between the home ranges of the alpha individuals, we can select any single alpha individual and note certain characteristics of the geometric distribution of its alpha neighbors. One such individual, whose home range center is indicated by a triangle, is shown in Fig. 16. A line drawn between the home range centers of its adjoining nearest neighbors forms a hexagon about this individual. Just as there are six nearest neighbors, there are twelve next-nearest neighbors. Lines connecting the home range centers of these next-nearest neighbors also form a hexagon. Successively more distant neighbors form concentric hexagons, each containing six more individuals than the next innermost hexagon. For the purpose of investigating the effect of neighbors on each other or upon the environment, a system of four "concentric" hexagonal sets of neighbors was prepared on a large sheet of graph paper. This procedure was repeated three times, forming spatial sets in which home range centers between nearest neighbors were respectively 1.5, 2.1, and 2.7 sigma apart. Ruler scales representing density functions (Table 2, Calhoun and Casby, 1958) at successive sigma distances from the home range center, as well as ruler scales representing intensity of signal (Fig. 18) were prepared. Using these ruler scales, several types of events were calculated with regard to their changes in intensity or frequency along a 3-sigma route such as is shown by the heavy dashed line in Fig. 16.

At each of eleven points along this typical route of travel, a sum of the density functions of all neighbors whose home ranges overlapped one or more of these eleven points was calculated (see Fig. 19).

F. Further Comment on the Impact of All Individuals on the Environment

Each of these sums of density functions were divided by 0.159, the relative density function of an animal near its own home range center. By so doing we can obtain a fairly good idea of the impact of all individuals who may arrive at any particular point with reference to the effect that one individual would have near its home range center. It may be seen that when home range centers are 2.7 sigma apart, considerable inequality between points exists. In other words, points near home range centers are relatively intensively used in comparison to distances about halfway between home range centers. This inequality of usage of the environment is even more pronounced when home range centers are more than 2.7

sigma apart. However, by the time home range centers are uniformly distributed at 2.1 sigma apart, all portions of the environment are approximately equally utilized although every point is more intensively utilized than when home range centers were farther apart. Every further increase in density, as represented by home range centers coming closer together, merely increases the intensity of usage of every part of the environment and all parts continue to be equally utilized.

These curves (Fig. 19) are particularly instructive in gaining an insight into an "ideal" interval between home range centers. It is logical to assume that portions of the environment which are less utilized than others serve as a trap to catch wandering individuals who have not yet established a home range. As long as the process of equalizing distance between adjoining home range centers continues, no remaining pockets of less utilized habitat will occur by the time adjoining home range centers are nearly 2.1 sigma apart.

Any increase in density, that is any shortening of the interval between home range centers below 2.1 sigma, will merely increase the probability that available objects will be overutilized.

At the maximum interval between HRC's at which uniform utilization of the environment arises, aggressive actions exhibited by individuals with resident home ranges may be expected to prevent excess members of the populations from settling down within such an established area. Such wandering individuals may be expected to wander through and out of such established areas and into marginal habitats.

Thus, if minimizing the opportunity for aggressive encounters and the development of a uniform utilization of resources represent forces affecting evolution, we may anticipate development of capacities for communication which will most readily assure that the members of a population of a single species will be able to distribute themselves uniformly through space with an approximate 2.0 home range sigma distance intervening between any two adjoining home range centers.

G. Contacting Neighbors

The product of the density functions of any two individuals at a particular point determines the relative probability that these individuals will meet by chance. Similarly, the product of the density function of any one individual at a point with the sum of the density functions of all other individuals determines the relative probability that this one individual will contact neighbors at that point. Such latter calculations were made for uniformly distributed home range centers at 2.7, 2.1, and 1.5 sigma (see Fig. 20). As might be expected, as home range centers get closer together the probability of any individual contacting neighbors at every distance from its home range center increases. There may be some frequency of contacting neighbors which becomes so unbearable to the individual that his resultant aggressive actions prevent further contraction of the interval between home range centers. However, we have no basis for gaining insight as to what this frequency might be.

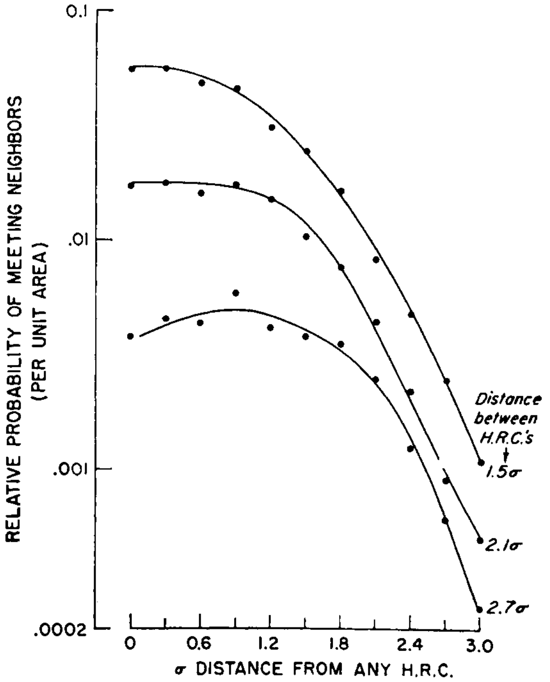

FIG. 20. Contacting neighbors. The relative probability of any one individual meeting others with reference to its distance from its own home range center, and to the distance between home range centers of all individuals.

One characteristic of these curves of relative probability of contacting neighbors does lend itself to suggesting a condition leading to an optimum interval between home range centers. When HRC's are 2.1 sigma apart the probability of contacting neighbors up to half the distance between home range centers is for all practical purposes constant. Applying this insight to all members of the population, it is apparent that with HRC's this distance apart, the probability of contact between neighbors becomes relatively constant everywhere. If we accept the principle elaborated by

Fredericson (1951) that animals attempt to make their environment predictable, and if we accept constancy of consequences as assuring greater predictability, then it follows that where the members of a community have their home range centers approximately 2.1 sigma apart, greatest predictability with regard to contacting neighbors characterizes this interval.

H. Sign Field of All Neighbors

Urination, defecation, and activities relating to the removal of materials used for food or nests represent signs by which one individual might recognize the presence of neighbors. Signs left by neighbors may be expected to be proportional to the sum of the density functions of neighbors at points considered. Unless home range centers are extremely close together, there will arise a noticeable increase in signs of neighbors as the individual moves away from its own home range center. Obviously, the closer home range centers are to each other the relatively greater will be the sign of neighbors at any particular radius from the individuals's own home range center. We may then wonder what standard a particular individual may utilize in judging the intensity of signs left by its neighbors. Any individual's own sign is maximal near its own home range center. Therefore, an individual may resort to comparing the relative amount of sign of neighbors at any point to that which it would leave in a similar area near its own home range center.

Dividing the sum of the density functions of all neighbors at a particular point by the density function of a particular individual near its home range center provides such an index of the relative intensity of sign of neighbors (Fig. 21). The optimum interval between home range centers with regard to the sign field should be that interval at which throughout the home range of a particular individual the total sign left by neighbors nearest approximates that individual's own standard and in which there is greatest predictability with regard to sign, that is in which there is the least variation in intensity of neighbors' signs from point to point. Judging from the three curves presented in Fig. 21 an inter-home range center interval of somewhere near 2.1 sigma would lead to the development of an optimum sign field.

I. Signal Field of Neighbors

Following the formulation presented in Section VII, C, it is assumed that the signal emitted by one individual can be perceived by another individual with sufficient intensity to produce a response by the latter in so long as the individuals are separated by a distance no greater than 3 home range sigma. In all probability, signals in the sense of vocalizations are emitted by each individual periodically as they wander through their home range. In order to simplify calculation of the signal field of neighbors, the particular condition was taken where all signals are emitted only from the home range centers. Thus, along a typical route of travel, as shown by the heavy dashed line in Fig. 16, the sum of the intensity of signals from all neighbors was calculated.

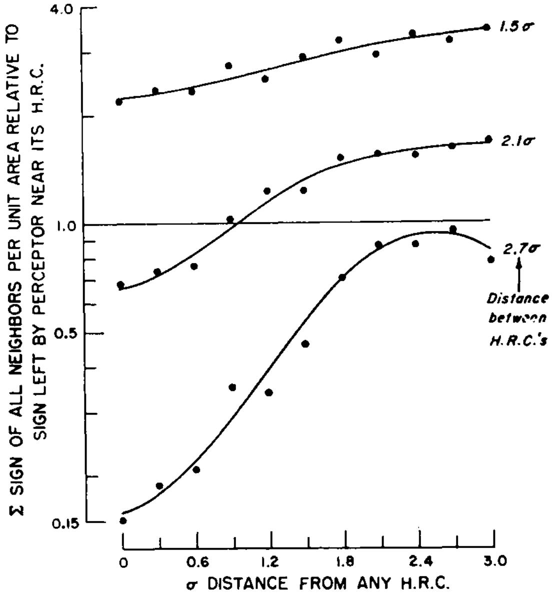

FIG. 21. Sign field of neighbors. Signs are considered as any persisting indication of an animal having made a response, i.e., defection, gnawings, or removal of food items. Thus Fig. 21 essentially represents the subtraction of the density function of one individual from the sum of the density functions of all individuals as shown in Fig. 19.

Again, we might wonder what standard the individual might utilize in judging the total intensity of signals received. Since the learning of the signal presupposes emission by one individual and detection by the other when they are in contact, this level of intensity with an assigned value of 1.0 may be taken as the standard. Since the intensity of signals probably drops off inversely proportional to distance, the sum of signals at any point in place and time may be less than 1.0. A further complication to the problem is that all neighbors may not emit signals simultaneously. Simultaneity other than by chance will arise regularly only if the detection of the signal by one individual elicits a similar response by the perceiver. However, if this is so, and if each individual after emitting a burst of sequential signals enters a refractory period (see Section XIII, A) of some given mean length before it can emit signals again, then we have a situation in which there occur recurrent periods during which most nonsleeping individuals in the community emit signals nearly simultaneously. Although no proof of the validity of this assumption can be offered at present, my formulation will accept the existence of such a process. Such an assumption is inherent in the utilization of Fig. 22 in arriving at some insight as to the

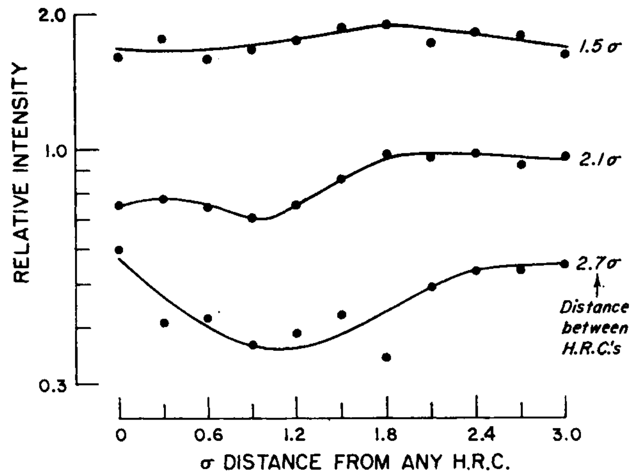

FIG. 22. Signal field produced by neighbors. If all neighbors emit signals simultaneously at their home range centers, and these signals have the properties shown in Fig. 18, then their summated intensity will form a "topography" as here shown with reference to any particular animal moving through its home range. The value 1.0 represents the intensity of a signal at the point of emission.

influence of the signal field on determination of an optimum interval between home range centers.

As with the sign field of neighbors, the signal field of neighbors is presumed to influence interval between home range centers through the members of the community seeking that interval between home range centers which will ensure most closely attainment of both constancy of the signal field, leading to predictability and to approximation of the standard signal intensity. Judging by the three curves in Fig. 22, operation of these two criteria indicates an optimum interval between home range centers slightly less than 2.1 sigma.

J. Hum Field

In Section VII, C it was suggested that when the emitter is between 3 and 6 sigma from the receptor the signal given by the emitter can be perceived by the receptor but is insufficient in strength to elicit the appropriate responses. The sum of all such signals below threshold for inducing a response is here termed "hum." When this value exceeds the standard intensity of 1.0 (see Section VII, I), the receptor will become restless even though perhaps not exhibiting a specific response to the signals. What effect this general state of restlessness may have upon the receptor is unknown, but it is logical to assume that the members of the community will attempt to adjust the interval between the home range centers in such a way as to reduce the likelihood of the "hum" exceeding 1.0. To do so implies that home range centers must be of the order of 2.4 sigma apart (Fig. 23).

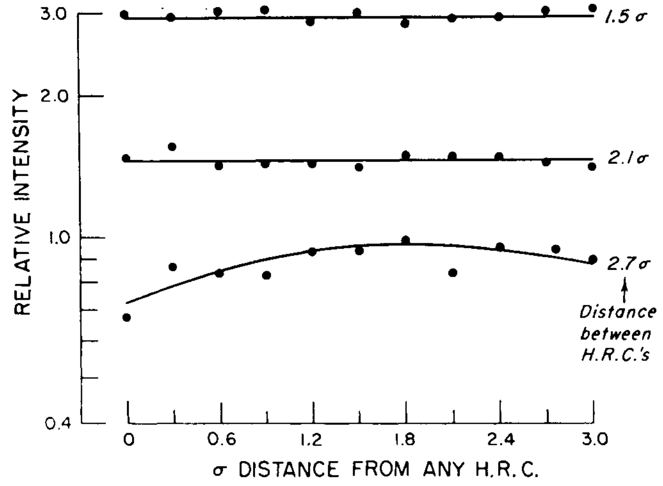

FIG. 23. Hum field refers to the sum of the intensity of all signals, any one of which is below that minimum intensity required to elicit a specific response. The value, 1.0, denotes the intensity of a signal at the point of emission.

K. General Conclusion Concerning the Distance between Neighbors

Effective learning of signals probably does not begin until home range centers come at least 3.0 sigma from each other, and even further shortening of this interval must increase the effectiveness of learning. Several factors examined all suggest that the optimum interval between home range centers should be of the order of a 2 home range sigma distance. From an evolutionary standpoint, the most important of these probably is the fact that utilization of the environment becomes uniform at slightly more than 2 sigma distance between home range centers. This factor should have been the major one in the evolution of those characteristics of individuals pertaining to the frequency of trips, the velocity of the individuals, and the aggressive acts elicited when two individuals meet. It is probably strictly coincidental that the properties of the sign and signal field are also likely to be such as to make an interval of about 2 sigma between home range centers optimum. It is at this distance between home range centers that both signs and signals become most constant and thus more predictable. Also, the intensity of the signs and signals most nearly approximate any receptor's own behavior near its home, which can serve for it as a standard in evaluating the intensity of the actions of its neighbors impinging on it.

L. The Number of Neighbors Perceived

When home range centers are 2.7 sigma apart, an individual at its home range center can just perceive all its six nearest neighbors. However, as it begins to move away from home it begins to lose contact with those nearest neighbors lying on the opposite side of its home range center. By the time it reaches half the distance to its nearest neighbors in the direction in which it is traveling, it can detect only three of its nearest neighbors. Toward the periphery of its home range, it can detect only two of its nearest neighbors. In addition, it can detect one, and only one, of its next-nearest neighbors, which are members of the group of twelve forming the second hexagonal tier of neighbors about its home range center. Thus, with this fairly large interval between home range centers, any one individual has poor contact with its associates. When home range centers are 2.1 sigma apart, any one individual can maintain contact with all six of its nearest neighbors out to about 0.75 sigma. Even when an individual has journeyed halfway in a direction of a nearest neighbor it is still in contact with four of its six nearest neighbors, in addition to one of the twelve neighbors lying in the next tier. As he proceeds still farther, losses of nearest neighbors are compensated for by next-nearest neighbors. Thus, at all times when home range centers are 2.1 sigma apart, an individual is in contact or potential contact with five or six of its neighbors.

By the time home range centers are of 1.5 sigma apart, an individual is in potential contact with ten other individuals though not always the same ten, no matter where it is in its home range. Since the dynamics of the use of space relating to uniformity of utilization of resources and the characteristics of the sign and signal field all point to an optimum interval between home range centers of somewhere near 2 sigma, it follows that there should have been evolutionary adjustment of tolerance to simultaneous or near simultaneous communication with five to ten others.

VIII. Interpretations of Observed Data Derived from Removal Trapping of Small Mammals

At this stage in the development of a concept of community organization, one must resort to a certain amount of quasi circular reasoning. Regularities in observed results lead to theoretical formulations. Then these formulations can be used to reexamine the data for further insight. This is my present intent. In time, many aspects of the concept may be subjected to more rigorous study. However, for the present we must content ourselves with a search for a best approximation to a very complex set of phenomena.

Section VI, "Continuous Removal Trapping of Small Mammals," presented results from several extensive studies. Specific interpretations follow.

A. The Relationship between Two Dominant Species

The dominant species in the community reveals itself during removal trapping through its members having such large home ranges that every individual living near a trap has a high probability of encountering it. Thus, for them, fewer days lapse from initiation of trapping until 50% of the population is caught. As can be seen from the two Maryland studies presented (Fig. 10 and Fig. 13B), *Peromyscus* fulfills this criterion. For species associated with *Peromyscus*, whether they be *Blarina* and *Sorex*, or *Blarina* and *Pitymys*, the dates of 50% removal arrive much later. The later the date of 50% removal, the more subordinate a species, and the more slowly its members expand their home ranges as the dominant species is removed.

In more northern forest habitats, *Peromyscus* rarely is found in the absence of *Clethrionomys*. In fact, it is as if the red-backed mouse is just superimposed upon the simpler *Peromyscus–Blarina–Sorex* community of more southern forests. Typical dominance of *Clethrionomys* over *Peromyscus* may be seen in Figs. 9, 11, and 13A. Although I am convinced that *Clethrionomys* usually can develop the ability to inhibit the home range of

Peromyscus, there exist conditions limiting the extent to which this ability may develop.

The typically low relative density of both species (Table VI) on Mt. Desert Island, Maine, represents such a condition. As revealed in Fig. 14, both species decline at about the same rate from day 1 through day 3. This can happen only when no alteration in home range size transpires over time or when the survivors of each species make equivalent but slight increases in extent of home range. Appreciation of why inhibition of home range fails to develop at low densities demands knowledge of variables we lack.

It demands that we know actual densities. The NACSM census provide only relative densities. However, we can make approximations. Run long enough (30 days), the 950-foot-long B-type NACSM census procedure should take all residents within 3 home range sigma on either side of the trapline and for a radius of this distance about the end of the line. If we take 50 feet as approximating the average home range sigma of small mammals, uninhibited by dominants, then approximately 8 acres are exposed to such a trapline. Furthermore, examination of 30-day censuses reveals that for species with uninhibited home ranges, 25–50% of the residents are taken during the first 3 days of trapping. On this basis, there was on the average less than one *Clethrionomys* and less than two *Peromyscus* per acre in this Maine study. Since juveniles, with as yet probably little influence on the spatial distribution of associates, comprised a portion of the catch, it is quite likely that the average distance between home range centers for each species exceeded 3 sigma. As shown in the prior theoretical sections, learning of signals would most likely be fairly ineffective here because contact between neighbors would be infrequent.

Under these circumstances the signals emitted by each species should have acquired little in the way of negatively stimulating characteristics for its own members. It follows that inhibition of home range size will have been negligible and thus the two species, which probably have nearly the same size home range, should encounter traps with nearly equal frequency, and thus the rate of decline in catch from days 1 through 3 should be nearly equal. However, in the one Mt. Desert Island, Maine, study where eight NACSM lines were run for 15 days (Fig. 13A), it is apparent that home ranges of *Peromyscus* were slightly contracted. Fifty per cent of the 15-day total for *Clethrionomys* was attained by day 6, but not until day 10 for *Peromyscus*. Thus, where both species regularly occur at low densities, *Peromyscus* is only moderately subordinate to *Clethrionomys*.

In the Adirondacks, where *Peromyscus* most frequently has a low density and *Clethrionomys* a much higher one (Table VI), *Peromyscus* is markedly subordinate. Its home ranges not only are markedly contracted, but also they expand immediately as *Clethrionomys* are removed. The validity of this interpretation is revealed in Fig. 14B, which shows that during the first 3 days of trapping as the *Clethrionomys* population is reduced, as indicated by fewer numbers taken on successive days, the numbers of *Peromyscus* taken increases. This increasing catch can only result from sufficient expansion of home range by survivors to bring about an increased probability of encountering traps.

One might argue that these latter data for *Peromyscus* merely indicate that the snap-trap is initially a sufficiently strange object to elicit avoidance. As time elapses these mice become accustomed to the presence of the trap and thus later in time more individuals will enter traps. Two lines of evidence of reasoning suggest the fallacy of this interpretation. If it were correct, we must conclude that *Peromyscus* in Maine lack this strange object response but those in New York have it highly developed (see Fig. 14). There exists no logical basis for believing that such a difference characterizes the populations of these two areas. Furthermore, in the trapping of both *Peromyscus* and *Clethrionomys* it is not an uncommon experience to find either of these mice dead in a trap with a bloody stump of one hind leg, while another trap, 2–5 feet away, is covered with fresh blood and fur. The conclusion as to what happened is clear. The mouse happened to get caught in one trap by one leg, it chewed or pulled itself loose, then went fairly directly to another trap, bit at the bait on the treadle and was thus killed. If these mice have a strange-object reaction it must be of a sufficiently low order of magnitude that even the recent loss of a leg in one trap fails to increase it to the point of avoiding the next trap encountered.

In the third area, Alberta, from which adequate data are available for these two genera, both are relatively abundant but *Peromyscus* exceeds *Clethrionomys* (Table VII). During the fall season, nearly twice as many of each genus are trapped as during the spring. During the period of low spring densities, these genera exhibit nearly identical rates of decline (Fig. 15A) accompanying removal trapping. As with the Maine data, such trends may be interpreted as indicating that at such densities neither species is capable of markedly inhibiting the home range of the other. However, by fall many *Clethrionomys* have contracted their home ranges as a response to their exposure not only to more of their own kind but also to more *Peromyscus*. Home ranges of *Peromyscus* remained unaltered, as indicated by the similarity of rate of decline during both spring and fall (Fig. 15). However, the daily catch for *Clethrionomys* remained nearly identical through three successive days of removal trapping. Sufficient enlargement of home ranges by surviving *Clethrionomys* must have taken place each day to lead to an equivalent frequency of traps being encountered on the following day by red-backed mice, despite their fewer numbers than on the preceding day. At this Alberta site, the inhibition of *Clethrionomys* home ranges by *Peromyscus* must have been less than the inhibition of home ranges of *Peromyscus* by *Clethrionomys* in the Adirondacks.

Despite the paucity of areas from which extensive comparable data are available, it looks as though *Clethrionomys* has a slight advantage over *Peromyscus* in gaining psychological ascendency. At this point one may suspect that the characteristics of some environments will markedly favor the reproduction and survival of one of these genera. Whichever genus this happens to be will then become psychologically dominant to the other, as evinced by the contraction of home range of the less numerous genus. Consideration of other aspects of the relationship between these two genera requires familiarity with the concept of the constellation dealt with in the following sections.

B. Removal Captures of Socially Dominant Species

In several studies already presented (Figs. 9–13) we have seen that one species tends to be caught in large numbers during the first few days, and that the time of maximum input for the remaining species comes during a successively later period. Very frequently a secondary increase in daily catch starts near the 15th day of trapping for the species with initially the greatest rate of capture. Such species will henceforth be designated as the socially dominant or alpha species of the small mammal community. For example, see *Clethrionomys* in Fig. 9 and *Peromyscus* in Fig. 10. Where there are several species taken, usually only one is characterized by this secondary input. Four censuses examined included one such species and a fifth included two with definite secondary inputs.[1]

Although several species are involved in this phenomenon, the assumption is here made that they all so behave because of similar properties leading to their alpha rank in the community. If this is so, we are justified in pooling the data. A table of the total catch per day of trapping was

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[1] The five censuses utilized in preparing Fig. 24:

1. By Dr. J. E. Moore, Sept. 1959, Edmonton, Alberta: 128 *Peromyscus maniculatus borealis*, 65% of 30-day total by day 14–15.
2. By Dr. A. I. Roest, Oct.–Nov. 1959, San Luis Obispo, California: 75 *Dipodomys heermanni*, 65% of 30-day total by day 15–16.
3. By Dr. William L. Webb, Fall 1952, Rich Lake Island, Newcomb, New York: 97 *Clethrionomys g. gapperi*, 65% of 30-day total by day 7.
4. By Dr. Earl F. Patric, Fall 1953, Arbutus Area, Newcomb, New York: 86 *Clethrionomys g. gapperi*, 65% of 30-day total by day 12–13.
5. By Dr. Kyle R. Barbehenn, Nov.–Dec. 1959, Chadwick Woods, Montgomery County, Maryland: 57 *Peromyscus leucopus*, 65% of 30-day total by day 14; 116 *Blarina brevicauda*, 65% of 30-day total by day 20–21.

prepared. These data are shown as a three-point moving average in Fig. 24. There results a continuous decline in catch until about the 12th day. After this, the daily rate of capture increases, reaching a second maximum five to seven days later. Following this, the number of animals taken continuously declines, but it is not until about the 27th day of removal trapping that the numbers taken per day reaches the low level characterizing the 12th day.

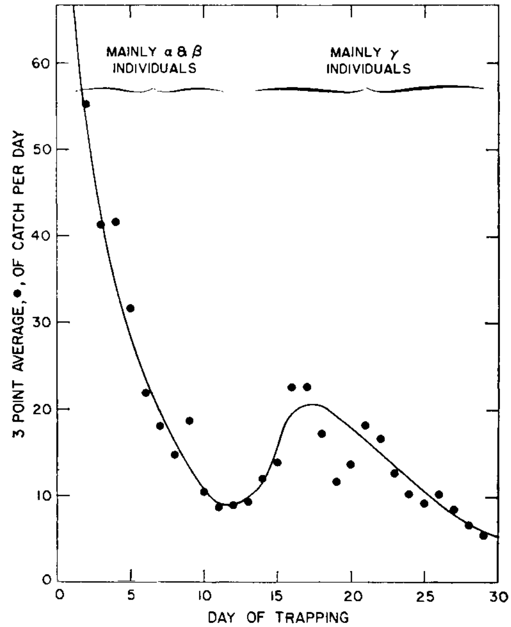

FIG. 24. Removal captures of 559 small mammals who are representatives of species, socially dominant in their community. Alpha and beta represent the intraspecific dominant individuals with large home ranges. The gamma individuals represent the intraspecific subordinates which enlarge their home ranges following removal of the alphas and betas.

If the assumption that practically all the resident population exposed to the traps is removed during 30 days of trapping is correct, then the accumulated catch plotted as the proportion of the 30-day total over time will reveal both the proportion of the total comprising the initial input and the time at which the secondary input begins (Fig. 25). This shows that the intersection of the two rates of input occurs on day 15 after removal of 64% of the resident population.

C. Constellation Formation—An Intraspecific Phenomenon

After the removal of 64% of the resident population of socially dominant species, whose home ranges are sufficiently large to give them a higher probability of encountering traps, there arises a secondary input. These latter individuals must have enlarged their home ranges as a response to the absence of their former associates. It follows that certain individuals have the ability to restrict the home ranges of other members of their own species. At this point in my analysis I began to wonder whether there were circumstances relating to the spatial distribution of the population which might lead to a 64:36 ratio of larger:smaller home ranges.

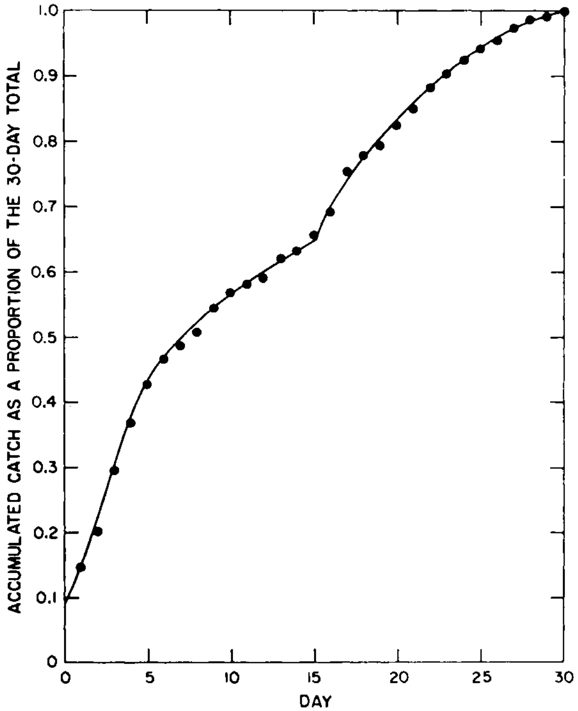

FIG. 25. Removal captures of socially dominant species. Same data as in Fig. 24, but here shown as an accumulated total.

In the previous discussion we have seen that one possible spatial equilibrium is that in which home range centers become uniformly distributed with an inter-home range center interval of about 2.0 sigma. It was further pointed out that the mechanics of moving through space are such as to favor the evolution of a signal emitted by one individual which has the potentiality of eliciting a response by another up to a maximal distance of about 3 sigma between individuals. We may then ask, "How many other individuals in such a uniformly distributed population can any one individual know?" Figure 26 shows that a line connecting the home range center of any one individual's six nearest neighbors forms a hexagon. With the hypothesized communication system operating, this one individual can remain in constant communication contact with all its six nearest neighbors except under the condition when it and one of them happen to move in opposite directions away from the line connecting their respective home range centers. Such actions can increase the distance between them to greater than 3 sigma.

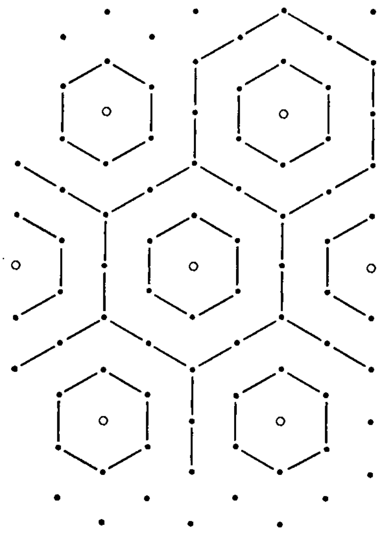

FIG. 26. Spatial distribution of home range centers during the preconstellation phase. Small open circles represent centers for individuals destined to become alpha members. Dots represent home range centers for all other individuals. Home range centers are uniformly distributed.

Lines connecting the home range centers of this individual's next-nearest neighbors also form a hexagon. Home range centers for all these twelve next-nearest neighbors lie nearly 4.0 sigma from the selected individual. Therefore, each of these next-nearest neighbors can be in contact with the selected individual when they approach each other, such that the distance intervening between them becomes less than 3.0 sigma. Any more-distant neighbors, those living 6.0 or more sigma from the selected one, will have such a low frequency of communication with the selected individual that mutual effects will be of little significance.

Examination of the spatial distribution of home range centers in a uniformly distributed population reveals that one-twelfth of the members each have six nearest neighbors whom they can influence without competitive influence being exerted by any other individuals in this one-twelfth population. Such individuals will hereafter be designated as alpha individuals. Home range centers for these alpha individuals are designated by small open circles in Fig. 26. It will further be noted that two such alpha individuals, who live closest to each other, share next-nearest neighbors.

Antagonistic relations, uniform utilization of the environment, and attainment of uniform sign and signal fields approximating in intensity the sign and signal intensity expressed by an individual at its own home range center, and equalization of contact rate with all neighbors throughout any one individual range, all serve as forces leading to a uniform distribution of home range centers at near 2.0 sigma between centers (Section VII, K). Yet, we may anticipate an opposing force of attraction between members in close communication with each other. This will lead to all nearest neighbors shifting the centers of their home ranges slightly toward their single alpha associate. Such nearest neighbors will hereafter be designated as beta individuals.

Now we can turn our attention to the alpha's next-nearest neighbors. It may be seen from Fig. 26 that in each group of twelve next-nearest neighbors, six are equidistant to two neighboring alphas. Therefore, since the probability of each of these six nearest neighbors is 0.5 of being attracted to either of two alpha individuals to which they are equidistant, each alpha on the average will have attracted to it three of these next-nearest neighbors. The remaining six next-nearest neighbors to any alpha are equidistant to three alphas. It similarly follows that on the average any one alpha will have attracted to it two of six such next-nearest neighbors. Next-nearest neighbors which so move toward an alpha associate will hereafter be designated as gamma individuals. Thus, each alpha will have attracted toward it six beta individuals and on the average five gamma individuals. This process leads to a clumping of the population into groups ranging in size from 7 to 19, with a mean of 12 (see Section VIII, D).

The central alpha individual because of its more favored position in the communication network may be assumed to be dominant to both its beta and gamma associates. Gamma individuals, because of their peripheral location in the developing clump, here designated a constellation, will be subordinate to both the beta and alpha associates. Now let us consider the situation where home ranges contract as individuals become more subordinate.

How much beta and gamma members may be expected to contract their home ranges requires consideration of phenomena treated in Section XIV, E, titled "Velocity and Home Range." There, it is shown that in terms of σ_α units of distance, the home range sigmas for alpha, beta, and gamma individuals become, respectively, 1.0, 0.9575, and 0.6457. Since an optimum uniform utilization of the environment requires a 2σ interval between home range centers, the distance between alpha and beta home range centers will become $1.9575\sigma_\alpha$, and $1.6032\sigma_\alpha$ between beta and gamma home range centers.

The periphery of each constellation (Fig. 27) may be arbitrarily designated as that radius from the center of the alpha member's home range extending to one σ_α beyond the center of each gamma individual's home range. This radius is $3.1478\sigma_\alpha$. And since the home range centers of the alpha members of adjoining constellations are $6.92\sigma_\alpha$ apart, it is obvious that between constellations there lies what may be called an interconstellation matrix, receiving very little usage from the dominant species forming constellations. Furthermore, this interconstellation matrix must markedly reduce communication between members of adjoining constellations. How extensive this reduction becomes must be viewed against the requirement of a 2σ inter-HRC interval for an optimum state. Yet, the HRC of any beta or gamma member of one constellation will lie on the average 4σ units of distance away from the nearest beta or gamma members of an adjoining constellation with reference to their own reduced home ranges.

On the average, such constellations will consist of twelve individuals, 1 alpha, 6 betas, and 5 gammas. Of these, the gammas with smallest home ranges form 0.417 of the population. These are the individuals who, after removal of their dominant alpha and beta associates, will enlarge their home ranges. Actually, some gammas will be trapped before the 15th day and some alphas and betas will be taken after it. Furthermore, Fig. 25 clearly shows that a few more gammas would have been taken after the 30th day of trapping. Therefore, the observed proportion of the population consisting of gamma individuals, estimated at about 36%, reasonably well approximates the theoretical expected of 41.7%.

To date, this approximation stands as the only direct supporting proof (see Section XI) that populations of dominant species of small mammal communities do, in fact, tend to form such constellations. If they really do, we may anticipate that there has been evolution relative to physiology such that its optimum state is most compatible with interactions among individuals transpiring in groups with a mean size of twelve adults. In later sections, I shall present data which support the hypothesis that a group size of twelve has been phylogenetically retained in more highly evolved forms.

For the present, let us examine further implications of constellation formation upon the structure of the small mammal community. Con-

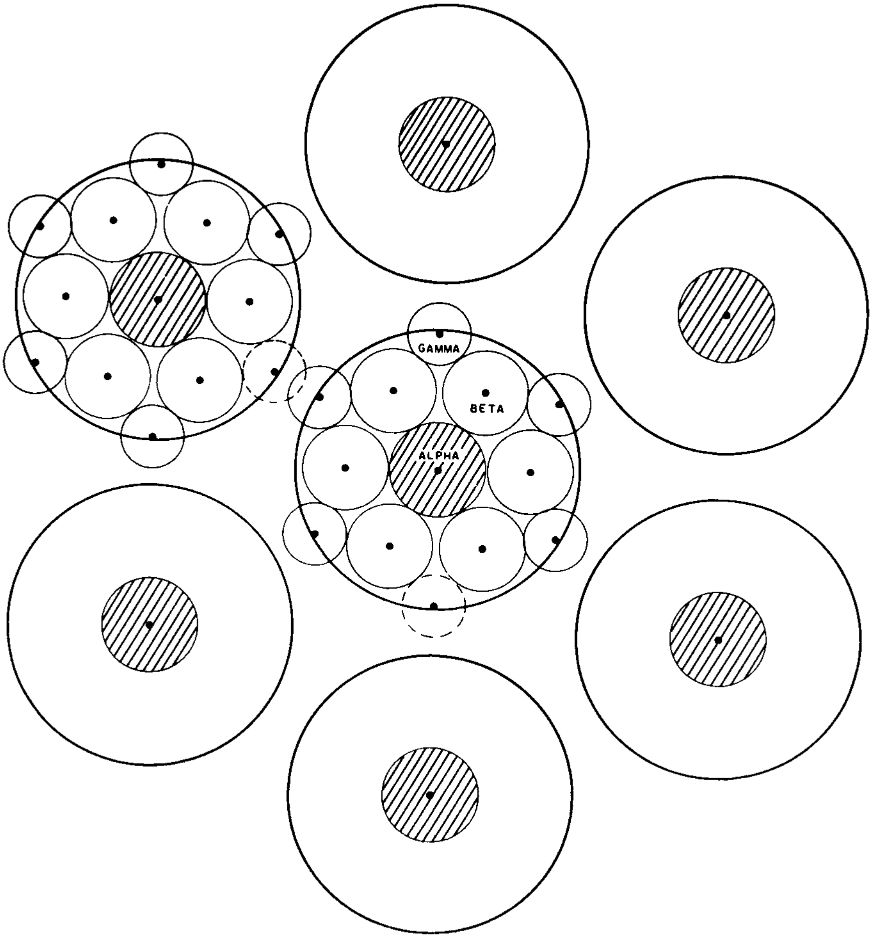

FIG. 27. The theoretical constellation phase of intraspecific community organization of dominant species. A 3-sigma radius home range for alpha individuals is represented by the large circle. Small circles represent 1-sigma radius portions of all members of a constellation. Contraction of home range by beta and alpha members permits the more intensively used portion of the home ranges of all individuals to fall mostly within the 3-sigma radius home range of the dominant alpha members. Crosshatched circles represent the 1-sigma portion of the home range of alpha individuals.

stellation formation presupposes passing through a stage of uniform distribution of home ranges. In the interstices between the home ranges of alpha species there is the opportunity for very subordinate species with highly contracted home ranges to establish themselves. As the constellation forms, certain members of the subordinate species will be retained within the interstices of the constellation while others will lie at its periphery. However, as constellations form, there develops an interconstellation matrix rarely frequented by members of the alpha species. We may then wonder what members of the community will live here.

At this point, the Huntington Forest censuses of 1952 and 1953 (Fig. 11) are particularly instructive. The red-backed mouse, *Clethrionomys*, is obviously the alpha species. Just as obviously, the shrew *Sorex* is the most subordinate species, which has highly contracted home ranges lying in the interstices between those of *Clethrionomys*. Had all these census been run for longer than 30 days, it looks as though the 2:1 ratio of the alpha species to one of its most subordinate associates would have been realized. Censuses shown from other areas indicate that both *Peromyscus* and *Blarina* are dominant to *Sorex* in the community. And yet, in these Huntington Forest censuses, relatively few of either were caught. What I suspect has happened is that as the constellations developed, both species were relegated to the interconstellation matrix, where they existed in somewhat contracted home ranges, as indicated by the catch per day increasing from day 1 to days 4–6. In fact, for both these species it looks as though a certain portion of their members had even more markedly contracted home ranges. This is indicated by the secondary increase in catch per day starting between days 8 and 10.

D. Expected Variability in the Number of Individuals Forming Constellations

In terms of the formulation of Section VIII, C the six nearest neighbors to any alpha individual will always be attracted toward it as the members of a population with a uniform distribution of home range centers begin to form diffuse clumps, termed constellations. The twelve next-nearest neighbors to any alpha individuals may be divided into two types, *a* and *b*, according to their probability of being attracted toward any given alpha neighbor.

Let: a represent the six individuals who have a probability, $p_a = \frac{1}{2}$, of being attracted to any given alpha.

b represent the six individuals who have a probability, $p_b = \frac{1}{3}$, of being attracted to any given alpha.

The probability, $p_a(i)$, that i number of the six a individuals will be attracted to the given alpha will be:

$$p_a(i) = \binom{6}{i}\left(\frac{1}{2}\right)^6 \tag{28}$$

Similarly the probability, $p_b(i)$, that i number of the six b individuals will be attracted to the given alpha will be:

$$p_b(i) = \binom{6}{i}\left(\frac{1}{3}\right)^i\left(\frac{2}{3}\right)^{6-i} \tag{29}$$

Therefore, the probability, $p(m)$, where $m = 0$ to 12, of m members of the 12 next-nearest neighbors joining any given alpha and its six nearest neighbors to form a constellation will be:

$$p(m) = \sum_{i=0}^{m} p_a(i) \cdot p_b(m - i) \tag{30}$$

For example, if $m = 4$ this becomes:

$$p(4) = p_a(0) \cdot p_b(4) + p_a(1) \cdot p_b(3) + p_a(2) \cdot p_b(2) + p_a(3) \cdot p_b(1) + p_a(4) \cdot p_b(0) \tag{31}$$

$p(0) \cdots p(12)$ were calculated and are shown in Table VIII as $p(7 + 0)$

TABLE VIII

EXPECTED VARIABILITY IN THE NUMBER OF INDIVIDUALS FORMING A CONSTELLATION

Number of animals in group	Probability of group developing
7	0.00137200
8	0.01234568
9	0.05041152
10	0.12345679
11	0.20190329
12	0.23225308
13	0.19266546
14	0.11612654
15	0.05047582
16	0.01543210
17	0.00315072
18	0.00038580
19	0.00002143
	Σ 1.00000023

$\cdots p\ (7 + 12)$ since the constellation becomes composed of the addition of these next-nearest neighbors, or gamma individuals to the basic core of the one alpha and its six beta nearest neighbors.

E. Social Rank and Intraspecific Associations

In the 14-day removal study shown in Fig. 13B, trapping results indicated large home ranges for *Peromyscus*, moderate-sized ones for *Blarina*, and highly contracted home ranges for *Pitymys*. Estimated home range sigmas, σ, of 50, 25, and 12.5 feet, respectively, probably closely enough approximate the real values to permit their use in a study of these data. If we knew the actual home range centers of all animals trapped, a 1-sigma radius circle plotted about each on a map of the study area should provide more insight into spatial relationships.

Since such centers were not known, they were approximated by making the following assumptions:

1. *Peromyscus* maximize inter-home-range-center distance from other *Peromyscus*.
2. *Blarina* similarly maximize distance, not only from others of their own kind, but also from *Peromyscus*.
3. *Pitymys* maximize distance from both *Peromyscus* and *Blarina*, as well as from others of their own kind.
4. The later an animal was trapped the farther its home range centers were located from the trapline.

For *Peromyscus* some of the HRC's were shifted to one side of the line of capture, and the remaining to the other side, until every adjacent 3 HRC's approximated equilateral triangles. A similar procedure was applied to *Blarina* captures except that where possible their HRC's also were placed in the center of triangles formed by the HRC's for *Peromyscus*. Then the HRC's for *Pitymys* were, insofar as possible, placed in the centers of triangles connecting the HRC's of the other two species.

Utilizing these assumptions, centers of home ranges for *Peromyscus* were plotted first, *Blarina* second, and *Pitymys* last. Originally these were all plotted on a single figure, but for the sake of greater clarity in examining intraspecific relations the home ranges, in terms of 1-sigma circles, are shown separately in Figs. 28–30.

Moisture conditions in the habitat varied markedly. Steep xerophytic slopes of oak and pine covered the three sectors encompassed between the E and SW radii. The sector between the N and NW radii was quite steep and dry. A damp drainage area lay roughly along the W and NE radii.

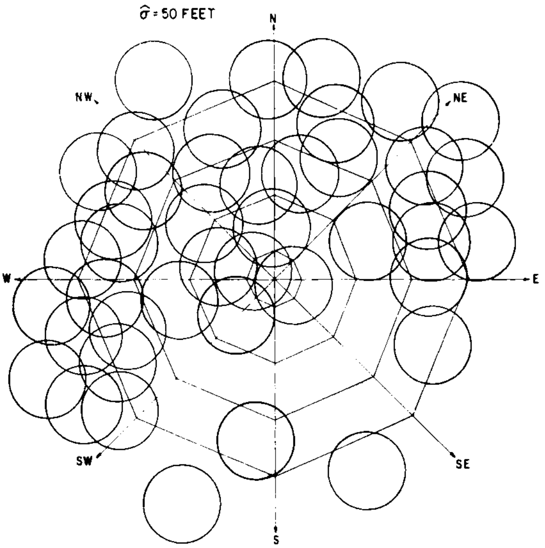

FIG. 28. Schematic home ranges for *Peromyscus*. The octagons represent traplines along which removal trapping was conducted.

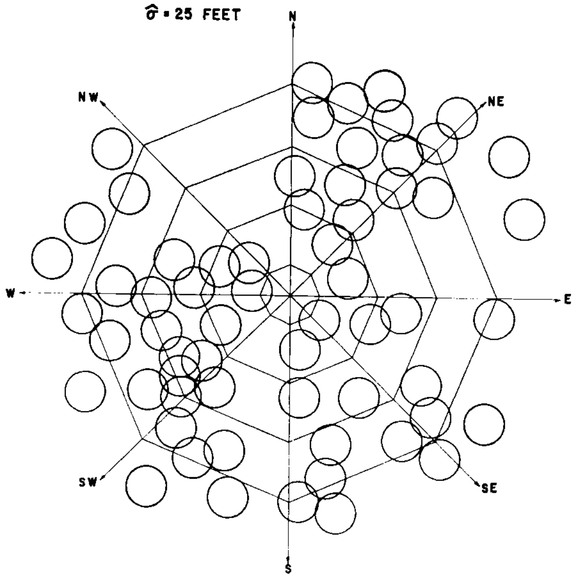

FIG. 29. Schematic home ranges for *Blarina*.

Away from the narrow drainage area the other four sectors were moderately mesophytic. Deep leaf mold covered the entire forest floor. No attempt was made to obtain a detailed cover map. Total timbering a year later for a housing development revealed that many of the trees in the forest exceeded 150 years in age.

It may be noted that both *Peromyscus* and *Blarina* tended to avoid the more xerophytic areas, whereas *Pitymys* was more abundant in these drier areas. However, it is interesting to note that no *Blarina* occurred in the N to NW sector and yet quite a number were taken in the even more xerophytic E to SW sectors. The marked clumping of *Pitymys* in the N to NW sector suggests that a tendency toward colony formation in this very subordinate species may actually serve to exclude from that region the more dominant *Blarina*.

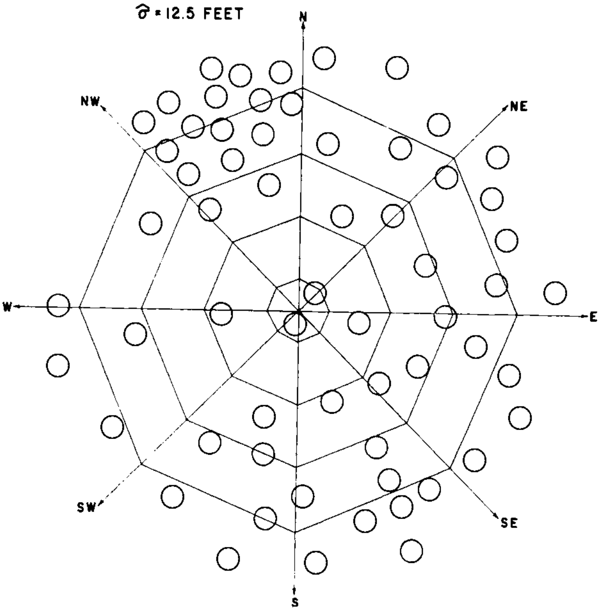

FIG. 30. Schematic home ranges for *Pitymys*.

However, despite such a local tendency for *Pitymys* to cluster, no overlapping of the 1-sigma radius home ranges occurred anywhere in the study plot. In fact, the mean interval between home range centers of nearest neighbors is of the order of 4 sigma. This must mean that the probability of one *Pitymys* associating with a neighbor is very low. With their larger home ranges, there is more opportunity for *Blarina* to associate with others of their own kind. Yet even with them their movements are sufficiently inhibited as to reduce contacts far below that otherwise possible. However, with *Peromyscus* so much overlapping of home ranges existed that most individuals must have had frequent associations with others of their own kind. Reduction of communication with others of their own kind accompanies interspecific social subordination. The lower the rank of a species, in terms of the degree other species in the community cause it to restrict its home range, the more its intraspecific systems of communication will be reduced. Even, as the analyses shown in Figs. 28–30 suggest, if there develops some compensatory clumping of home ranges by members of subordinate species, there must still be a greater degree of isolation between such clumps than between any comparable number of groups of the dominant species.

F. The Instability of Social Relations

Results from the extensive censusing of small mammals conducted by Drs. Patric and Webb and their associates at the Huntington Forest form a major key in unraveling the process involved in community structure. Fortunately, their records (Patric, 1958) include some of the years before 1952 (see Table VI for 1952–1956).

An effort of 9650 trap-nights during 1940 and 1941, in which traps were set for five consecutive nights, caught 173 *Clethrionomys* and 1280 *Peromyscus*, or 7.4 *Peromyscus* for each *Clethrionomys*; in contrast, during the years of 1952–1956, 4.1 *Clethrionomys* were captured for each *Peromyscus* taken (Table VI). However, during these two years the trends of capture over time were so nearly identical that only the greater numbers of *Peromyscus* can argue for its having been more dominant. Actually, both showed increases in catch per day as associates were removed. The day 1 to day 5 captures were: for *Peromyscus*, 117, 225, 313, 317, 308; for *Clethrionomys*, 17, 19, 61, 46, 30. Apparently many members of both species were characterized by reduced home ranges, which they expanded as associates were removed. There being so few *Clethrionomys* present, they could not represent the species producing the inhibition of home ranges. Thus at this time we must suspect that actions by members of the genus *Peromyscus* not only caused many of its own kind to contract their home ranges, but also caused similar contraction by *Clethrionomys*. In the light of the apparent reversibility of social roles of these two genera, previously discussed when comparing different localities, these comparisons between different eras within the same habitat suggest that *Peromyscus* and *Clethrionomys* in this habitat are really codominants, but that one will nearly exclude the other. At such times whichever one became more numerous than the other would cause members of the less numerous species to contract their home ranges and live within the interconstellation matrix of the more abundant species.

A small amount of trapping during 1946–1948 revealed that *Peromyscus* still held a 3:1 relative abundance over *Clethrionomys.* The intensive trapping was resumed during 1951, an apparently critical year in the social balance of the population. Forty-one NACSM traplines, each run for three consecutive days, for a total of 7380 trap-nights of effort (NACSM Release No. 5) provided total catches for the three consecutive days as follows: *Clethrionomys:* 143, 114, 77; *Peromyscus:* 167, 132, 108; *Blarina:* 52, 58, 50; *Sorex:* 2, 0, 2. Although *Peromyscus* was slightly more numerous than *Clethrionomys*, 9.93 versus 8.15 per trapline per three days, its slower rate of decline in captures from days 1 through 3 suggests that it was slightly subordinate and that some of its members were enlarging home ranges as their associates were being trapped off. However, the nearly constant total catch per day for *Blarina* clearly indicated its subordinate status to the other two genera.

The 24-day continuous removal study of 1951 (Table V, Fig. 12) provided further insight into this realignment of social relations. Despite nearly equal numbers taken for the three most abundant species, *Blarina* is clearly subordinate to both *Peromyscus* and *Clethrionomys.* Its more marked contraction of home ranges is revealed by the continuously increasing daily catch over the first few days of trapping (Fig. 12). Comparison of the proportion taken the first 5 days with that during the last 5 days provides an index of expansion of home range. The relatively more that are taken during the first 5 days, the less has been the expansion of home range, and thus the more dominant the species. On this basis, the four genera are listed in order of decreasing rank in Table V.

One of the most remarkable aspects of this set of data is the nearly constant daily catch for each of the three more abundant genera between the 4th and 17th day of trapping. This means that within each genus, survivors increase their home range each day sufficiently to result in as many encountering traps as on the previous day despite their fewer numbers. Furthermore, an individual member of each of these genera must be receptive to the inhibitory signals from the other two genera as well as of others of its own kind. Otherwise, the capture curves would have resembled that for clearly alpha species (Fig. 9).

This set of data also suggests that in the presence of several more dominant species actively contending for rank status, the very subordinate *Sorex* not only is markedly reduced in numbers, but also is much slower in expanding its home ranges. Peak captures, and thus maximum expansion of home range, did not take place until day 21, which was just after the final maximum expansion of home range for the other three species.

By the following year (Table Ib, NACSM Release No. 6) this uncertain social state had completely clarified. Three-day totals for 34 NACSM lines were *Clethrionomys* (753), *Peromyscus* (38), *Sorex* (17), and *Blarina* (1). Other details of the resultant social organization have already been treated in Section VIII, A.

The studies (e.g., Figs. 10 and 13B) conducted during the past few years in Montgomery County, Maryland, by Dr. Barbehenn and me, further substantiate the indeterminancy of the small-mammal community as a dynamic system. We have mostly sampled woodlands of 50 to 1000 acres. *Peromyscus*, *Blarina*, *Sorex*, and *Pitymys* are the more abundant species. In every case *Peromyscus* is the dominant species. For it, the largest catches per day occur during the first few days, and usually from day 1 there is a continuously declining catch per day with the exception of the slight secondary increase resulting from expansion of home ranges by gamma individuals (Fig. 10). *Blarina* is also nearly universally present. The date by which 50% of the total is trapped consistently arrives several days later for *Blarina* than for *Peromyscus*. In actuality, peak numbers taken per day usually occur several days after initiation of trapping. Thus, in these communities the home ranges of most *Blarina* are socially contracted. When either *Sorex* or *Pitymys* is present, they are definitely subordinate to both *Peromyscus* and *Blarina* in terms of the degree to which their home ranges are contracted. Their peak captures per day never occur until after most of the two dominants have been removed. Relative numbers are quite another matter. It seems to be purely a matter of chance whether either *Pitymys* or *Sorex* is present in any particular woodlot. Either, both, or neither may be present. Their absence appears not to be due to absence of requirements for food and shelter, but merely due to failure to reproduce under circumstances of spatial isolation, when the processes of social adjustment within a particular woodlot happens to markedly reduce the numbers of some one species. These woodlots in suburban to semirural Montgomery County, adjacent to the district of Columbia, exist as ecological islands which must be characterized by a rather low probability of receiving colonizers of these subordinate species. Furthermore, any one of the three subordinate species can become the most abundant species in the community. In each case the most abundant species has small home ranges whose centers lie within the interstices of the larger home ranges of the dominant *Peromyscus* (as shown in Fig. 16). *Blarina* was such a species in the study shown in Fig. 10. Had trapping been continued longer in the study shown in Fig. 13B, *Pitymys* would undoubtedly have had a nearly 2:1 ratio of abundance to the dominant *Peromyscus*.

In other unpublished studies by Dr. Barbehenn, *Sorex* catches nearly doubled those of *Peromyscus.*

IX. A Theoretical Conceptualization of the Evolution of a Social Hierarchy among Species in the Utilization of Space

The concept of social inhibition of home range represents an inference derived from the observed differential probability of capture by snap traps. Reduction of extent of home range must result from an increase in the probability of terminating trips away from home. We have seen that an increase in the structuring of the environment, with stimuli which elicit responses, does lead to an increase in the probability of terminating trips. This structuring of the environment represents an increase in the amount of stimuli impinging on the organism. For this reason I believe that one is justified in making the following tentative generalization: Any increase in the frequency or intensity of stimuli to which the animal has responded in the past will lead to an increase in the probability of terminating trips.

It follows that genera such as *Sorex* or *Pitymys* frequently are characterized by such small home ranges that we may conclude that they experience a high frequency or intensity of relevant stimuli. At the same time their associates, *Peromyscus* or *Clethrionomys,* have large home ranges. This being so, we may conclude that the latter are not unduly exposed to an excess of relevant stimuli. And yet we may suspect that any stimulus which *Sorex* or *Pitymys* can detect can also be detected by *Peromyscus* or *Clethyrionomys.* Thus, their differential response to stimuli must involve some internal mechanism through which stimuli produce an effect indicating relevancy or irrelevancy.

So far it has appeared that auditory stimuli of the class represented by vocalizations of members of the small mammal community might represent the class of stimuli producing alterations of home range. If this inference proves correct, it means that some species respond to a broad spectrum of different auditory stimuli whereas others "ignore" all except those emitted by their own species.

Broadbent (1958) elaborates a theory of perception and communication which may serve in conceptualizing how vocal communication functions in leading to an organization of the small mammal community. Briefly this theory is as follows:

The central nervous system may be conceptualized as a signal flow system possessing the following connections and characteristics. Stimuli impinging upon the sense organ generate signals which pass into a temporary store. Storage here is in terms of seconds only. From this short-term store, signals must pass through a limited capacity channel before they can serve to initiate immediate responses or reach a long-term store where the signal can be preserved to affect later action. Signals passing through the limited capacity channel from the temporary store may be passed back through another circuit and reenter the temporary store. Likewise, responses made to a stimulus or a sequence of stimuli, in turn, serve as stimuli which generate signals entering the temporary store. Furthermore, several signals may arrive simultaneously at the temporary store through separate sensory channels. Only a portion of these signals in the temporary store can get through the limited capacity channel.

There has evolved a neural mechanism which Broadbent calls a "filter," intervening between the temporary store and the limited capacity channel. This filter "selects" which signals may get through the limited capacity channel and thus be available for (a) recirculation into the temporary store, (b) inducing immediate response, or (c) entering the long-term store.

The following conditions affect the probability of signals passing through the filter:

1. The signal is of the same class as that of the prior signal. That is, the related stimulus has similar characteristics in terms of frequency, intensity, pattern, or location of origin. In other words, the filter tends to pass in sequence several signals from stimuli with related characteristics.
2. However, the longer a given category of signals has been passing the filter, the more likely the filter will switch to signals arriving from a different sensory channel.
3. Signals generated by intense or infrequent (novel) stimuli exhibit a high probability of passing through the filter.
4. Given any three signals in the temporary store and one is passed through the filter, the one of the remaining two most likely to follow it is the one which followed it most frequently on prior occasions.

A special case will particularly concern us. An animal may exhibit both bodily response and vocalization to a given external stimulus. Each of these responses also becomes a stimulus with a high probability of association, each with the other, and each with the external stimulus. As the external stimulus becomes weaker, only the bodily response is preserved. Presumably the reason for this is that the bodily response represents a more intense stimulus and for this reason develops a higher conditional probability of association with the external stimulus. That is, the signal from the bodily response stimulus is more likely to pass through the filter immediately after the signal from the external stimulus.

Although I have treated Broadbent's theory only sketchily here, its importance in the context of the present discussion is his documentation of the necessity for postulating the existence of some neural mechanism having the properties he attributes to the "filter." His thesis evolved primarily from studies with human subjects, and to a much lesser extent from studies of rats and dogs. He accepts the existence of a filter, and even that there are intraindividual differences in the effectiveness of its maturation. His concern with the evolution of the filter extends only to his belief that animals with a smaller cortex probably also have a less well developed filter. He does not discuss how a less well developed filter would differ from a more highly evolved one. We might anticipate the four attributes of filters listed above to be less well developed. That is, signals sequentially passing the filter represent a class of stimuli having a wider range of variability; shifts from one sensory channel to another occur with greater frequency; a stimulus need be only slightly more intense or novel to generate signals capable of having priority over other signals in passing through the filter, and two stimuli must be associated in time much more frequently for their signals reaching the temporary store to have a higher conditional probability of passing in sequence through the filter.

Let us turn to a consideration of how the social use of space may have encouraged the evolution of animals with more efficient neural filters. At the dawn of mammalian evolution, we can visualize a type having close equivalence both morphologically and physiologically to contemporary shrews of the genus *Sorex,* with the exception that they had developed essentially no neural filter mechanism for screening signals passing from the temporary store to the limited capacity channel. All stimuli arriving separately would get through the limited capacity channel and it was purely a matter of chance which of two simultaneously arriving stimuli might find passage. Under these circumstances, no discrimination may be made between aversive stimuli emitted by neighbors at a distance. This would lead to a uniform distribution of home range centers at approximately 2.0 sigma distance between centers.

Paleontological evidence suggests that these early diminutive mammals preyed upon insects and other small invertebrates. Furthermore, since among present day shrews *Blarina* is dominant to *Sorex* in the hierarchy of use of space, it follows that evolution permitting such differential control of space must have proceeded prior to further marked alteration with reference to feeding habits. Therefore, it appears that early in the history of shrew-like mammals there was sufficient evolution to permit one species to inhibit the extent of home range of another. For simplicity's sake let us designate the earlier form as *A*, and the later derived one as *B*. Two characteristics gradually become fixed in *B*. It evolved an altered vocalization. This vocalization preserved much of the characteristics of *A*, but entailed an addition of components. Following Broadbent's analysis of stimulus characteristics we may suspect that an attribute of some portion of the added vocal components included an increase in intensity. Likewise, *B*'s filter developed alterations which enabled *B* to filter out selectively those vocalizations not including the new attributes developed by *B*. Thus, members of the new species *B* could develop conditioned associations with the vocal signals emitted by its own kind while ignoring those emitted by species *A*. At maximum stability of such a two-species community there would exist a 2:1 ratio of *A*:*B* in a similar fashion exemplified by the *Blarina*:*Peromyscus* community previously described for Dr. Barbehenn's Chadwick Woods study (Section VI, B) and Dr. Webb's Rich Lake Island study (Section VI, A) for *Sorex*:*Clethrionomys*.

The interesting aspect of this 2:1 ratio of species *A*:*B* is that it enabled three animals to live where only one lived before. In other words, the evolution of dominant species *B* not only enabled as many of species *B* to live in the habitat as was formerly the case with reference to the time when species *A* only existed there, but it also enabled twice as many of the more primitive species *A* to live in the habitat as had been the case when *B* was absent. For such a pattern of evolution to have transpired, it means that intraspecific dispersal of home range centers in a one-species community as a consequence of the repulsive character of vocal stimuli must have been sufficient to ensure an average utilization of resources far below maximum carrying capacity. To clarify further what is intimated above: Members of *A*, as a result of antagonistic interactions with others of its own kind, develop conditioned avoidance responses to intraspecific vocalizations. Furthermore, the greater the frequency of these vocalizations, as represented by increases in density of the species, the greater is the probability of outward excursions from home being terminated, thus the smaller home range. Lacking a sufficiently effective neural filter, *A* responds to *B*'s vocalizations as if they were their own. If *B* emits signals with the same frequency as does *A*, it follows that in a stable two-species system *A* will be responding to three times the signal load as *B*. For this reason, *A*'s home range becomes markedly reduced in contrast to its area when *B* was absent.

The next step in the evolution of the social hierarchy of space utilization, resulting in species *C*, entailed similar alterations to vocalizations and to enhancement of the filter in restricting the spectrum of stimuli which would likely be associated with intraspecific interactions. Judging by the fact that the omnivorous mouse *Peromyscus* is dominant to both *Sorex* and *Blarina*, one may conclude that evolution of altered food preference facilitated further evolution of interspecific social domination of space.

In fact, it was this difference in food preference which led me to conclude that the interspecific aspects of dominance in the utilization of space most likely fails to involve direct physical interaction between members of different species. Objects desired by species holding opposite ranks in the hierarchy gradually became more and more different. At this level of evolution species *A* responds not only to vocalizations of its own kind but also responds to vocalizations of both *B* and *C* as if they were by members of species *A*. Species *B* can ignore signals from *A* but treats both its own signals and those from *C* as *B* signals, while *C* "filters out" *A*'s and *B*'s signals and responds only to those of its own species. In other words, *C* functions as if it alone were in the environment.

The fourth step involving evolution of species of type *D*, which is similarly dominant to species types *A*, *B*, and *C*, again is accompanied by further specialization toward a nearly total use of plant material as food. Judging by the results of field studies presented earlier in this paper, the red-backed mouse, *Clethrionomys*, represents a species at the D level. In most situations where both it and *Peromyscus* are present, *Clethrionomys* dominates. Following the previous line of reasoning we may anticipate that such a *D*-type species emits vocalizations having not only the basic characteristics of species *A*, *B*, and *C*, but, in addition, possesses vocalization characteristics peculiar to itself.

At each level a species responds not only to its own vocalizations, but also to those of all species ranked above it, as if they were emitted by its own kind. The lower the rank of a species, the greater are the number of vocal stimuli to which it responds and thus the smaller its home range. Reasoning back from present day small-mammal communities to the probable course of evolution, it appears that there is a correlation between (a) social rank in the domination of the use of space, and (b) the shift from carnivorous to herbivorous diet. I do not believe that an herbivorous diet per se contributes in any way to social dominance. Rather, it has relevance only because of the later development of flowering plants and grasses. Evolution of more advanced types of plant permitted evolution of small mammals specialized to utilize these new resources. To a certain degree such feeding specialization would enable an incipient species to avoid direct competition with its progenitor. Once removed from overt competition with its progenitor, psychological dominance by the incipient species could then proceed through the process of increased complexity of vocalization and development of a more effective filter.

A major aspect of my thesis is that psychological dominance, resulting from a greater complexity of vocalization and an increased effectiveness of the neural filter, far outweighs all niche specializations in determining the relative abundance of species comprising the small mammal community.

Such psychological dominance also develops among members of a single species, at least at the higher levels of the interspecific hierarchy. We have already presented the data and logic which gave rise to the concept of constellation formation. On the average, each constellation has one central alpha member with a very large home range, six beta members with home ranges slightly smaller than for alpha individuals, and five gamma members with markedly restricted home ranges. Such intraspecific differences in home range size suggests that, among alpha (*C* or *D* types in above discussion) species at least, developmental alterations in vocalization arise. Gamma members of alpha species exhibit a minimum complexity of vocalization. Successively beta and alpha members increase the complexity of their vocalizations. All members of the species presumably have the same level of filter development. Even so, the differences in complexity of vocalization should result in alpha members mainly ignoring vocalizations of beta and gamma individuals insofar as these signals have a negative valance. Beta members respond not only to other beta individuals but to their alpha associates. Gamma members not only treat the vocalizations of other gamma members as inhibitory stimuli, but are likewise similarly influenced by those from their beta and alpha associates.

It must be borne in mind that this whole discussion of vocalizations and filters in the context of the small mammal community is strictly theoretical. However, it not only provides a conceptual framework offering one interpretation of empirical data, but also enables formulations capable of experimental analysis.

A study of the complexity and intensity of vocalizations is suggested as having priority in testing the theory. *Sorex, Blarina, Peromyscus,* and *Clethrionomys,* respectively representing theoretical types *A, B, C,* and *D* discussed above, should serve as particularly useful subjects, especially since they all may occur in the same small-mammal community. The vocalization of each higher member of the series should include the basic characteristics of all lower ones and in addition possess characteristics not held by lower members in the series. Furthermore, if each of these species is experimentally exposed to a conditioned avoidance situation where vocalizations of their own species serve as a conditioned stimulus, one may anticipate that vocalizations of the other members of the series will equally well induce avoidance upon their replacement of the intraspecific stimulus only if the vocalization represents a higher member of the series. Unfortunately, the extreme paucity of our knowledge of vocalizations of small mammals necessitates these suggestions in lieu of any firm experimental evidence.

Development of cryptic behavior forms an ancillary aspect of this concept. The lower-ranked shrews typically spend much of their time in underground runways. Presumably such behavior enables these species to reduce the frequency or intensity that they experience by the vocalizations of their dominant associates. When Dr. Barbehenn first joined me in these studies of small-mammal communities he insisted that the only effective way of trapping *Blarina* was to set traps at points where excavations in humus revealed underground runways. However, it had been my experience with continuous removal trapping, where traps were set at fixed intervals from stations without any regard to underground runways, that once the dominant *Peromyscus* has been removed *Blarina* were caught on surface sets with equal ease as earlier for *Peromyscus*. Therefore, when he initiated his Chadwick Woods study (Fig. 10) he set his traps on the surface without regard to runways. During the initial days while many *Peromyscus* still survived, most *Blarina* were taken only by traps accidentally set by underground runways. As the number of *Peromyscus* became fewer and fewer by the removal trapping, not only were more *Blarina* caught, but also an increasing percentage of these had so entered traps as to indicate clearly that they had been wandering about the surface and were not emerging through the leafmold below the trap. Thus, a reduction in crypticism accompanied enlargement of home range. This same change in behavior characterizes the typically subterraneous mouse *Pitymys* following removal of its dominant associates. The prior discussion of the special case of both bodily movement and vocalizations of another individual become important here. We might thus expect that vocalization of shrews would become reduced as they become more cryptic in the presence of dominant mice. Also as mice are removed from the habitat, shrews should not only spend more time out on the surface, but they should vocalize more.

This section cannot be closed without brief reference to the meadow mouse *Microtus*. Data from a recent unpublished study by Dr. Barbehenn in an abandoned orchard in Maryland suggest that this genus represents one terminal phase in this evolution of types, which on the psychological level enables successively evolved types to acquire a more dominant position with reference to the use of space. At points isolated from each other by at least 600 feet he placed covered feeding stations which contained rolled oats mixed with dyes which stained the fur of animals eating there. Daily removal of food increased for nearly a month, after which the daily removal fluctuated about an asymptote for another month. At the end of this time removal trapping was conducted along a circular trapline having a radius of 150 feet from the feeding station. Practically all the *Peromyscus* taken were marked with the red dye, but no *Microtus* were so marked. This indicated that *Microtus* living at this distance from the feeding stations were not only unaffected by it, but their home ranges were unaffected by *Peromyscus*, even those living much farther out in the habitat, altering their movement and passing with increasing frequency and in an altered pattern through the home ranges of *Microtus*. This trapping was followed by additional removal trapping along several concentric circular traplines between the original one and the bait station. Many more *Microtus* were trapped, but practically all *Peromyscus* had been removed in the initial trapping. Furthermore, the drop-off in catch of *Microtus* in this later trapping, as the concentric lines came nearer the initial one, indicated that only *Microtus* living within 37 feet of the initial circular line had been taken by it. It furthermore indicated that *Microtus* were not wandering about, as we had supposed they might be, but regardless of distance from the feeding stations had maintained fixed home ranges despite many strange *Peromyscus* focusing their movements toward this one central spot. Parenthetically, it might be added that this altered behavior by *Peromyscus* did disrupt *Sorex* home ranges. They were taken in relatively large number beginning with the very first day of trapping along the initial circular trapline.

Now the question arises, "What do these data indicate?" Since *Peromyscus* altered its behavior by readjusting its movements toward the feeding station as if *Microtus* was not there, I conclude that one of *Microtus*'s adaptations has been the loss of vocalization. On the other hand, since *Microtus* appears to be unaffected by the altered movements of *Peromyscus* and the periodic concentration of many *Peromyscus* in one spot, which must increase the vocalizations at that spot, I conclude that *Microtus* has evolved a filter system so effective that they can ignore signals from other species. This leads me to suspect that *Microtus* represents what might be called a secondary herd-type species. See later discussion on the evolution of colonialism and herding.

X. Psychological Dominance as the Primary Component of the Niche

Hutchinson (1957) includes the relationships one species has with others as comprising aspects of its niche requirements equally to be considered along with food, shelter, and climatic factors. Implicit in his inclusion of interspecific social factors in niche characterization is the relative capacity for any two given species to compete for some given environmental commodity or condition. The more nearly the identity of their nonsocial niche requirements, the more important become social relationships both as a component of the niche and in leading to the elimination of one species by the other via the principle of "competitive exclusion" (Hardin, 1960).

In terms of this viewpoint and the marked difference in diet, morphology, and behavior of such distantly related genera as *Clethrionomys, Peromyscus, Blarina,* and *Sorex,* we would suspect minimum niche similarities and thus little influence of one genus upon the other.

If their niche requirements are really quite dissimilar, if within any individual's home range each requirement is represented at many points, and if in most home range-sized plots most of the niche requirements for each genus abundantly occur, then, depending upon the intraspecific factors leading to fluctuations in density, we might in fact anticipate that one or several of these genera might occur simultaneously in high densities. In fact, observed relative densities do behave in such a fashion. Were we content to rest our case solely on relative densities, we would remain content with the satisfactoriness of such logic in revealing true relationships.

However, the time sequence analysis of removal captures leads to a formulation of community dynamics suggesting the nearly complete invalidity of the concept of lack of influence of one species upon another if their niche requirements markedly differ. In fact, the concept of competition has little relevance. Instead, "home range inhibition" becomes the most useful concept. Home range inhibition is the consequence of processes through which the individual reacts to a signal as if it were identical to a different signal with which it shares certain physical characteristics. In other words, an animal may react to a signal emitted by a member of another species as if it were the signal emitted by another member of its own species with whom its interactions have led to its characterizing the signal as noxious. Such a species becomes a subordinate member of the community.

Signals of the dominant species must contain not only the basic characteristics of the subordinate but some characteristics peculiar to itself. Thus, when both a dominant and a subordinate species occur simultaneously in a habitat, members of the dominant species will come to associate noxious qualities only to that portion of the signal which is species-specific since it is the only portion of the signal which always accompanies a negative intraspecific interaction. If we consider a community composed of four species A, B, C, and D (following the nomenclature of Section IX) in which D is most dominant and A most subordinate, and signal components a, b, c, and d are observed, then D's signal should include components a, b, c, and d; C's should include a, b, and c; B's only a, and b; and A's only a.

Even though A learns to define signal a as noxious only by reacting with other A associates, he will respond similarly to detection of the a components of his B, C, and D associates. I have cited data indicating that the greater the frequency of relevant stimuli in the environment the greater will be the probability of the origin of a neural signal leading to termination of the behavior of outward movement from home. In this situation, every time A emerges and starts on an outward excursion he experiences a bombardment by so many a signals that his trip is shortly terminated and he returns home. In a similar fashion, B's home range will become contracted but not so much as A's because A does not emit b signals, whose sum at any one time is contributed to only by species B, C, and D. C will have only a slightly inhibited home range since it is responsive only to signals contributed by itself and D. At the apex of the system members of species D are influenced only by d.

At the psychological apex of the community, further differentiation occurs among the members of the dominant, D species. According to the formulation developed in Section VIII, C, members of this species have the capacity to differentiate into alpha, beta, and gamma members. Their basic d-type signal becomes differentiated into d_α, d_β, and d_γ components. Alpha individuals possess all three; beta members only d_β and d_γ; while gamma members emit only d_γ.

This purely theoretical formulation predicts that home range size and complexity of signals emitted are positively correlated. The observed data on removal captures lead to inferences of home range expansion following removal of associates. Intra- and interspecific inhibitions are so apparent as to demand the minimum assumptions made above for maintaining such a complex spatial organization of the small-mammal community. Compare these formulations with those of "velocity" developed in Sections XIII, A; XIV, A; and XIV, E and F. Such comparison leads to the conclusion that the greater an individual's velocity, the more complex will be the pattern of signals he emits.

Psychological dominance is then the ability to inhibit the home range of others resulting from the fact that the dominant shares certain signal characteristics with the subordinate, but in addition possesses signals which the subordinate lacks. The sharing of a signal by a species with another species which it usually dominates may lead to mutual inhibition of home range or actual reversal of roles.

Consider the *Clethrionomys* and *Peromyscus* relationship. The greater frequency with which *Clethrionomys* appears to be dominant to *Peromyscus* suggests that it has the c-d-type signal while *Peromyscus* has only c. We may ignore other shared characteristics of their signals. In fact, we may focus only on the shared c component. Chance vagaries of the system may from time to time, after a crash in the populations of both species, result in a marked preponderance of *Peromyscus* over *Clethrionomys*. Similarly, at the southern periphery of its range, we can expect *Peromyscus* frequently to be more dense than *Clethrionomys*. *Clethrionomys* will then meet too infrequently to make any associations with their own species' specific signal. However, encounters will occur more frequently between *Clethri-*

onomys and the more numerous *Peromyscus*. Regardless of which species dominates in the actual encounter, the interspecific common characteristic of the signal may be expected to assume only a negative quality by *Clethrionomys*. Some interactions among *Peromyscus* must be of a positive nature. Thus, even though both species may detect the interspecies common component of their signals with equal frequency, *Peromyscus* might be expected to exhibit less contraction of its home range because this signal is less aversive than it is for *Clethrionomys*.

This line of reasoning applies also at times to relationships among three species. In the unusual situation (Fig. 12) in which *Blarina, Peromyscus,* and *Clethrionomys* were all quite abundant, the sequential trapping data clearly indicate that inhibition of home range nearly equally characterizes all three species.

In such a system, the extent and center of an animal's home range depends not so much on characteristics of the habitat as on the current density and origins of signals, and the temporal and spatial history of interaction among members of the community during the most recent generations. The absence of an animal in a locality cannot be construed to mean unsuitability of the habitat. It is conceivably possible to delineate microhabitat characteristics contributing to the animal's niche even under such circumstances. However, it requires that we know an individual's home range center and that we mark out stations along a circumference of a circle having a radius which will result in a high probability of the animal crossing that circumference. A 1-sigma radius should prove effective. Examination of stations from such a series, which have a greater than chance frequency of visitation, might lead us to isolate those conditions which do contribute to an animal's niche.

XI. An Induced Invasion

The major portion of this section presents the author's interpretation of a study conducted by Webb and Rosasco (1953). It describes the response of the red-backed mice, *Clethrionomys,* surrounding a 30-acre tract within which continuous removal trapping was conducted for 80 consecutive days. In this account it will become apparent that the concepts elaborated remain inconclusive. Even so, their implications, when taken in conjunction with the other sections of this paper, warrant their presentation.

A brief history of events leading up to Dr. Webb's study provides a background for appreciating the objective. During the summer of 1950, while I was in residence at the Roscoe B. Jackson Memorial Laboratory as a National Institute of Mental Health Special Fellow, Dr. A. Dexter

Hinckley, then a sophomore at Yale University, was assigned to me for supervision on a research project. I assigned him the task of placing eight NACSM traplines in an 80-acre central portion of a much more extensive tract. He ran the 480 traps for 15 consecutive days. At that time it was generally accepted that if one plotted a regression line through points representing catch per day as a function of total prior catch, this line would intersect the abscissa at a point denoting the total population (see Calhoun and Casby, 1958, pp. 15–16 for a summary of this procedure). Previously, Hayne (1949) had made such estimations on the basis of 3 days of consecutive trapping as employed by the North American Census of Small Mammals. Thus, it was my anticipation that Hinckley's longer-term trapping would merely result in the anticipated continuous decline from day to day, and that by the 15th day essentially no more animals would be entering the traps. Furthermore, by the end of the 15th day the total should approximate that predicted by the intersection of the abscissa by the regression line as noted above. During the first 3 days the catch per day did decline. However, on the fourth day Hinckley reported a larger catch than on the first day. Well, I thought this was just due to the vagaries of chance or some unrecognized climatic factor. On every successive day his report was the same—more animals than yesterday. On the 15th day, three times as many animals were taken as on the first day. All of this was very perturbing.

After several months of reflection I came up with this formulation: During the first 3 days the number of residents in the 80-acre tract had been drastically reduced. Animals at the periphery of this tract would then find themselves with the normal number of neighbors centrifugal to the trapped area but with very few remaining centripetally. Now, suppose that in the normal state maintenance of a uniform distribution through the environment is facilitated by vocalizations and audition. Each individual's customary state would be that of detecting an equal intensity of signals in all directions from the center of its home range. In these terms mice and shrews at the periphery of the trapped area would detect few signals toward it but comparatively many away from it. Their normal response being to move so as to equalize signals coming from all directions, their response to the neighboring depleted area would be to move in toward it. They then became exposed to traps still set in the central area and many of these invaders were killed. This left the next peripheral group of animals in the same situation so that they also began moving inward toward the trapped depleted area. By this process, a chain reaction was set in motion in which the entire population for a great distance from the trapped area began moving toward it. If we visualize the trapped area as a circle, rather than its actual rectangular shape, it becomes apparent that if animals are moving in at a constant speed of travel per day, those invading the trapped area each day will represent residents from successive bands of equal width. Each successive day the majority of the captures will be from a more distant band than on the prior day. In a system of concentric bands of equal width, each band more distant from the center contains a larger area than the next innermost one. Thus, with density proportional to area and invasion into the central area transpiring from a constant rate of movement toward it, catch per day should increase with time.

At the time when this formulation was just crystallizing in the fall of 1950, Dr. Webb wrote me concerning their developing plans for long-range studies of small-mammal populations of the Huntington Forest near Newcomb, New York. I mentioned the interesting results obtained by Hinckley, and the hypothesis generated by them. His response was to replicate Hinckley's study.

Details of these two studies have been included here (Figs. 12 and 13A). However, at the time of these two studies the failure of catch per day to decline over time blinded us to the story which the differences of input for different genera could tell us. That is, it was not realized at that time that expansion of home range by subordinate members of the dominant species and by all members of the remaining subordinate species could lead to results by removal trapping in which catch per day did not decline even though there were no invasions. Not recognizing this possibility the results of these two studies were described (Calhoun and Webb, 1953) as supporting the hypothesis that continuous removal trapping did in fact lead to invasion of the trapped-out area by residents from surrounding areas.

By that time I had become associated with the Neuropsychiatry Division of the Walter Reed Army Institute for Medical Research. If this hypothesis were correct it might have relevance both to lemming migration (Elton, 1942) and to certain panic phenomena of troops (Ranson, 1949; Caldwell, *et al.*, 1951). In order to explore this phenomenon in more detail, it was possible for Dr. Webb to negotiate Contract Number DA-49-007-MD-325 between the Medical Research and Development Board (Office of the Surgeon General, Department of the Army) and the College of Forestry, State University of New York. This enabled him and his associate to execute a large series of studies on the response of small mammals to removal trapping. The major details of these studies will be published elsewhere by Dr. Webb. I merely wish here to present a brief outline of one of these studies because of its importance to the general theme being developed in this paper.

In the center of an extensive forested tract they established a circular trapline with a 562-foot radius. Along this trapline 781 snap-traps were placed, one at approximately every 5 feet. Along two diameters at right angles to each other, 156 additional traps were placed, 3 to a station and with a 50-foot interval between stations. This central cross of traps was intended to facilitate removal of residents and afterward capture any invaders "filtering" through the peripheral circular trapline. All 937 traps were run for 80 consecutive days. No *Clethrionomys* entered the traps on the 21st day. Prior to that, 101 were caught and, in addition, six died in a preceding period of live trapping. These 107 individuals presumably represent the majority of residents. Between the 21st and 80th day of trapping, 501 additional redbacks entered traps. Furthermore, these 501 represented four fairly definite waves, roughly 15 days elapsing between the beginning of each wave and the start of the next one. Each later wave exceeded in numbers that of the preceding one (Fig. 31).

Let us now return to a consideration of the hypothesis, originally conceived from reflecting upon the results of Hinckley's 1950 Maine study. Although it is now recognized that the hypothesis does not apply to the study from which it originated, we shall now ask the question: "Does it

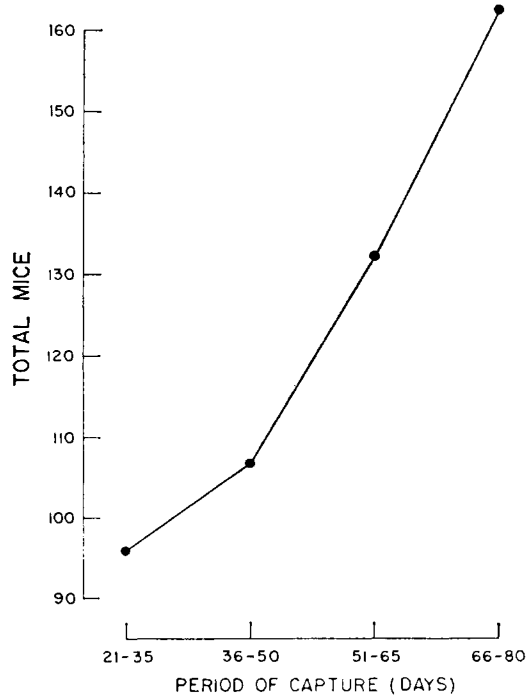

FIG. 31. Invasion of redbacked mice into an area from which most of the residents had presumably been removed.

apply to the present data with regard to captures following presumed removal of all residents during the first 20 days?" If it does, we shall also wish to know whether the apparent waves might reflect some basic property of intraspecific social organization.

The first problem concerns determination of the area inhabited by those animals taken during the first 20 days. It must include all the πr^2 area delimited by the trapline. Furthermore, animals from some distance outward from the trapline must also have been caught. On first thought, it might be logical to anticipate that all mice whose home range centers lay within 3.0 home range sigma of the circular trapline, and away from it, would be the only ones to exposed. However, as we shall see, the distance outward from the trapline to which animals are affected by it more likely approximates the maximum distance at which they can perceive signals from other mice.

But, this is getting ahead of the analysis. For the present let us assume that each wave of mice entering the traps represents the inhabitants of a band of width w. Furthermore, assume that during the first 20 days mice from a band of width, w, immediately outward from the trapline, get caught by it in addition to those internal to the circular trapline.

The radius from the center of the area being trapped to the trapline was 562 feet. Thus, the area sampled during the first 20 days equals $\pi(562 + w)^2$. Since each wave of invaders is presumed to represent a band of equal width, w, then the entire area sampled during the entire 80 days equals $\pi(562 + 5w)^2$. One hundred and seven mice were taken from the central area, and 608 from the total area. Thus, to the extent that number of mice is proportional to the area they inhabit, 5.626 as many mice inhabited the total area as the central area. It follows that:

$$5.626[\pi(562 + w)^2] = \pi(562 + 5w)^2$$

Thus $w = 302$ feet.

Radii to the limits of the central area and the four successive bands become 864, 1166, 1468, 1770, and 2072 feet (Table IX). From these the areas within the central area and the four bands may be calculated. These are areas as proportions of the total within a circle having a radius of 2072 feet as given in Table IX. These proportions can then be utilized to calculate the expected number of mice residing within the central area or invading it during later successive periods.

The assumptions force identity between observed and expected for the central area, but not for the four bands. However, the observed catch for the four bands will approximate that of expected only to the extent that the formulation is in harmony with reality. As may be seen from Table IX, observed and expected numbers approximate each other so closely as to

TABLE IX

INVASION OF REDBACKED MICE INTO AN AREA SUBJECTED TO CONTINUOUS REMOVAL TRAPPING

Location	Radius to outer edge of area	Proportion of total area from which trapped mice originated	Catch	
			Expected	Observed
Central area, $r = w + 562$ ft.	864	0.174	107	107
Band No. 2	1166	0.145	88	96
Band No. 3	1468	0.183	111	107
Band No. 4	1770	0.227	138	135
Band No. 5	2072	0.271	165	163
		1.000	609	608

make a test of significance superfluous. This, of course, only proves that the formulation is not wrong; it does not prove its validity. In the absence of any evidence to the contrary, the formulation will be accepted as approximating reality, and I will proceed with exploring further questions.

First, what about $w = 302$ feet? Webb and Rosasco (1953) and Patric (1958) offer considerable evidence indicating that the home range sigma for *Clethrionomys* must be close to 50 feet. Thus, $w = 6.0\sigma$. According to the independently arrived at formulation, vocal signals can be detected up to a distance 6.0σ from the emitter (Fig. 18 and Section VII, C). Also, the diameter of the constellation approximates 6.0σ (Fig. 27, Section VIII, C). Recall that the constellation represents the inferred basic unit of social organization among such animals. Thus all members of constellations which overlap the circular line, or even just touch it although the home range centers of their members all live peripheral to the trapline, can detect a signal void centripetal to the trapline.

Before going on, I would like to emphasize that the diameter of 1124 for the circular trapline was dictated by the desire to ensure that mice arriving at the trapline would not be able to hear others across the void on the other side. In fact, if 302 feet does represent the threshold distance of perception, then the angle of signal void facing a mouse arriving at the trapline would be that angle subtended by chords of 302 feet from that point, in this case 159 degrees.

The existence of constellations assumes prior development of bonds of attachment among its members. Once the central cross of traps and the circular trapline had removed all mice exposed to it, survivors of constellations in contact with the trapline would then tend to move simultaneously toward it. There would then arise the situation in which out to a *w* distance from the trapline few mice remained. At this time the mice in the second band would begin moving more or less together after a lag in time resulting from their attachment to home and to each other. No mouse could leave home until several of its associates were ready to move together. Similarly, residents of bands 3, 4, and 5 would start inward as soon as most of their neighbors of the adjoining inner band had moved *w* distance toward the central trapping area. In this way a "chain-reaction" was set in motion in which several bands simultaneously were moving toward the central area.

For the present this interpretation seems the most likely one. Whether the phenonemon has any analogies to lemming migrations or troop panic need not concern us here. Of importance are the indications that the influence of a signal void extends for approximately 6.0 home range sigma. The wavelike nature of invasion suggests that most of the mice from a band of 6.0 sigma move together. That they should do so is in harmony with the concept of constellation formation into groups whose mean size is 12 individuals and whose spatial diameter is about 6.0 home range sigma.

In the context of the present paper this additional support of the concept of a constellation as a real phenomenon represents the prime importance of this study on an induced invasion. For it is the evolution of the constellation and its later condensation into the compact colony way of life that I believe represents the reason why a basic group size of 12 adults is the most important one in the mammalian series.

XII. Derivation of Compact Colonies from Constellations

Accentuation of the social bonds among members of a constellation must have increased reproductive effectiveness and permitted survival of individuals exhibiting a decreased antagonism toward those neighbors who become familiar through repeated contacts. As the aggressiveness became reduced, beta and gamma members gradually shifted their home range center toward that of their dominant alpha associate until at last theirs coincided with his. A compact colony will then be formed in which all individuals share the same home range. Furthermore, the aggressive actions of the single dominant alpha individual of a compact colony serves to protect the other members of his colony from intrusion by extracolony members of the same species. Whereas constellation formation may be observed to take place within one or a few generations from a prior uniform distribution of home range centers, the development of compact colonies from constellations must have entailed considerable genetic change over sufficient generations to permit the evolution of a new species or genus. Stages intermediate between that of constellations and compact colonies may be recognized by the mean interval between adjoining home range centers decreasing from 2 sigma toward zero sigma.

A. Compact Colony Formation in the Norway Rat

Over a 27-month period I observed the development of social organization in a population of Norway rats confined in a one-quarter acre enclosure. Preliminary details have already been presented (Calhoun, 1949, 1952), and further details will shortly be published (Calhoun, 1963). By the end of the study the population had increased essentially from a single reproducing female to 120 adults. These formed 11 clear-cut local colonies (Table X). Each colony inhabited a single burrow or group of neighboring boxes, placed below the surface, to which the rats had access by a drain tile from the surface. Each such burrow or cluster of inhabited boxes was separated from adjacent ones by an average distance of about 35 feet. These are rank-ordered from *a* to *k* in a descending order of social rank. For the present purposes we may equate social rank with sex ratio and reproductive success. High-ranking colonies had few males and many females, most of whom successfully reared litters or were pregnant at the time of terminating the study. As social rank of the colony decreased there

TABLE X

CHARACTERISTICS OF NORWAY RAT COLONIES

Colony	Number of rats	Proportion female	Mean weight, males (gm.)	Mean weight, nonpregnant females (gm.)	Proportion of females reproducing	$\bar{x}$ young per female
a	14	0.928	548	457	0.769	4.3
b	6	0.666	511	449	0.750	3.8
c + d	11	0.600	500	488	0.428	3.4
e	14	0.642	512	435	0.555	2.3
f	15	0.534	456	427	0.250	2.0
g	16	0.812	432	413	0.153	0
h	8	0.500	477	357	0	0
i	13	0.000	442	—	—	—
j	10	0.100	448	—	1.0	0
k	13	0.000	429	—	—	—

gradually ensued a change toward more males per female, and these females were less successful in reproduction. At the lowest level a colony consisted of only males, or if females occurred they were essentially asexual with regard to reproductive effectiveness. The lower the colony's rank, the lower the mean weight.

Members of each colony represented more than one place of birth in the pen. Members of the highest-ranked colony, *a*, mostly still lived at the place of their birth or had come there from adjacent colonies. As social rank of the colony decreased, its members represented ever more different places of birth. Despite this disparity in places of birth characterizing each colony, the total number of adults forming each colony varied little from the mean number of 12 characterizing the loosely knit constellation of such simple social types as *Peromyscus* and *Clethrionomys*.

At this point we may consider possible events which fostered the evolution of the compact colony from the loosely knit constellation. The major impact of the constellation way of living is that the most frequent group size would be 12 individuals. It might, therefore, be anticipated that evolutionary processes would adjust the physiology and behavior of such species to be most effective and appropriate to interactions transpiring in such a sized group. In accordance with the conservatism of evolution we might anticipate restriction of group size about this optimum of 12 as other factors caused the constellation to contract into a compact colony. Restriction of location of food stands is the most likely candidate for an appropriate environmental change. Provided the location of food became restricted but abundant and relatively permanent at these locations, we could expect types like the Norway rat to develop. They build burrows not too far away from such spatially restricted sources of food and all members of the colony participate in transporting this food into the burrow where large caches are formed.

Compact colony evolution produced a situation which necessitated further evolution of the nervous system. If groups of 12 adults assembled, either as a consequence of being born at the same place or from random mixing, a more nearly equal sex ratio would characterize most colonies than was the case in my study within the experimental enclosure. This presents the opportunity for development of marked aggression among males and consequent stress experienced by associated females. Actually this was the initial situation always characterizing an incipient colony of Norway rats. In the process one or more males were driven off and sufficient females remained, although some always left to keep the colony at near 12 individuals. The rejected males either joined another developing colony lacking a male as dominant as the one at the colony they left or they joined to form an all-male colony. Where there was a single very dominant male (as in colony *a*, Table X) his actions kept away most other males at times when his harem females were in estrus. This reduced the stress experienced by females in estrus, such as followed the thousands of mountings or attempted mountings experienced by females in colonies lacking such dominant males. In this sex-ratio restructuring of the population, a few colonies contribute most of the young.

Although this readjustment ensures the survival of the species, it is not the consequence most important with regard to further social evolution. Each time a rat is excluded from one colony it attempts to join another aggregate *in order that* it will again find itself in a group of a size most compatible with its physiology. As soon as a group exceeds the optimum size, some of its members are excluded from it. This results in a marked reshuffling of the population from the time of puberty of young born in one season up to the beginning of the next breeding season. At this time the population is relatively stable with regard to membership of each colony.

In the process of attaining colony stability, the social environment is in a constant state of turmoil. Each individual is forced to make many adjustments to such changes. It continually has to learn new social relationships. These are learned so well that a group can shift its place of residence over a sufficient distance that passage by or through other colonies is necessitated. Even so, they can maintain their group integrity. I am convinced that the necessity of making such changes of membership from one colony to another required for reproductive survival of the species has resulted in the evolution of the Norway rat into a species which is not only highly perceptive of changes within the environment but has the capacity to learn required adjustments of behavior.

Although such capacities for perception and learned adjustment must have arisen in the context of a changing social environment, these same capacities then become available for perceiving and adjusting to nonsocial changes in the environment. Among ecologists this extreme awareness to changes in their environment by Norway rats has been termed the "strange object reaction" (e.g., Chitty and Southern, 1954). Among psychologists it is reflected in the studies falling under the broad rubric of "open-field emotional behavior" (e.g., Hall, 1934, Schneirla and Tobach, 1962).

If I were to make my evolving thesis concerning the social use of space complete, I should substantiate the role of vocal communication at the compact colony level of social evolution. Unfortunately, I cannot cite any adequate proof regarding the nature of its function. Norway rats do have a wide scope of vocalization ranging from the loud signal accompanying the termination of a fight to the low chirping and whining one can detect if one lies on the surface of a burrow with his ear at an entrance hole. Many other vocalizations also occur when rats are on the surface near their burrows and also while at the source of food. I can only suspect that among these there is specific communication among alpha members, the dominant males, neighboring colonies, and that rats at the food source emit a signal which might be termed a "here is food" signal. Unless there are such signals, it is difficult for me to understand many of the observed behaviors of rats which clearly indicated that they were aware when other rats were or were not at the food source, even though they could not see it.

B. Howler Monkeys, a Compact Colony Living Species

Carpenter (1962) summarized the results of field research on this species (*Alouatta palliata*) during the past thirty years. Tabular data on 136 distinct groups show the number of adult males and females and the number of immature individuals in each group. I derived Fig. 32 from these data. Two large groups containing 27 and 31 adults, respectively, were omitted from the analysis.

Regardless of group size all groups contained more females than males. Excluded males live in a state of near isolation and have very little association either with each other or the organized groups. As with the Norway rat, reproduction within compact colonies apparently requires a reduction in the number of males in groups for effective reproduction to take place.

One of the central hypotheses in my formulation of the social use of space is that constellation formation must have served as a mold which so guided evolution that behavior and physiology would become fixed so that they would have optimum expression in a group of 12 adults. For howler monkeys, groups of 9 to 11 are encountered more frequently than smaller and larger ones (Curve *A*, Fig. 32). And although the decline in frequency of groups containing more than 11 adults is not so rapid as expected (Table VIII), the observed data do reveal a marked decrease in frequency of larger groups. Furthermore, only 3% of the 136 groups exceeded the maximum of 19 anticipated by the theory. The theory indicates no expectation of groups containing less than 7 adults, yet 26.5% of the 136 groups of howler monkeys did contain less than 7 adults. However, it must be pointed out that such theory presupposes completion of all social processes culminating in a group having considerable stability of membership. Incipient groups formed from the fragmentation of larger ones and larger ones approaching the point where fragmentation is imminent should logically both be excluded in comparing observed and theoretical frequencies of group sizes. However, present knowledge prevents such a comparison.

Production of young is fairly ineffective in small groups in comparison with those containing 10 or 11 adults (Curve *C*, Fig. 32). In general, the trend of young per female also decreases as groups get larger than 12 individuals. The two very large groups not included in this figure and which had 27 and 31 adults were characterized by only 0.18 and 0.29 young per female, respectively. We must conclude that group size does affect those behaviors and physiology culminating in the production and survival of young.

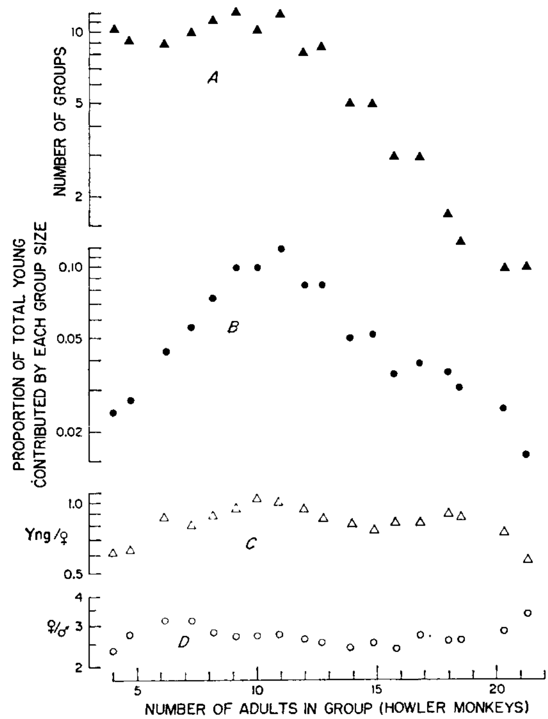

FIG. 32. Group dynamics of howler monkeys based upon Carpenter (1962).

Another way of looking at this problem is to ask: "What proportion of the total young are contributed by each group size?" For any group size the proportion will depend upon (a) the proportion of females in the group (Curve *D*, Fig. 32), (b) the number of young per female (Curve *C*, Fig. 32), and (c) the number of groups of each size (Curve *A*, Fig. 32); where such data for each group are weighed against similar data for all other group sizes. Resultant data are given in Curve *B*, Fig. 32. This curve clearly shows that more individuals gain their initial social experience in groups of about the size anticipated by theory as most nearly optimum than they do in any smaller or larger sized groups. In fact, the mean number of adults with which the 838 young in these 136 groups had their early social experience was 12.22!, even though Curve *C*, Fig. 32, is flatter than predicted by the theory of Section VIII, D and Table VIII.

My selection of the Norway rat and the howler monkey as examples of compact colony types is open to the criticism that I selected those species which would support my theory that group size in higher evolved types is dependent upon their evolution from species which had been characterized by the loose constellation form of social use of space. At present, this criticism cannot be avoided. I wish merely to say that my intensive study of a few groups of Norway rats, and the extensive study by Carpenter and his colleagues of a large number of howler monkey groups, are the only ones known to me that appear adequate for the present purpose.

All we can really say at present is that available data show that optimum group size in some compact colony living species appears to approximate 12 adults and that this number is in harmony with that number anticipated by the physics of communication characterizing more primitive and more dispersed types.

C. Behavioral Sink Development by the Norway Rat

Much of the prior sections have been devoted to documenting theory and evidence supporting the hypothesis that groups of 12 individuals represent a major category of optimum density. Yet many species customarily live as aggregates much larger than this. Why such large groupings should have evolved remained a puzzle until insight developed from an unexpected phenomenon arising in the situational content of some experimental populations of rats I was studying (Calhoun, 1962a).

The upper portion of Fig. 33 presents in diagrammatic fashion the salient aspects of the environment affecting the rats. Four 35 square-foot pens, separated by 2-foot high partitions, formed a linear communication network through the opportunity of access between adjoining pens via the V-shaped ramps, *R*, surmounting barriers between pens. *F* and *W* represent a superabundant supply of food and water in each pen. "Apartment" houses, *H*, connected to the floor by ramps provided ample place of retreat and rearing young by most residents. The *H*'s of the left-hand pens I and II were 3 feet from the floor, while in pens III and IV a 6-foot distance separated the *H*'s from the floor. Height formed an intentional environmental factor designed to produce a 2:2:1:1 ratio of density across pens I:II:III:IV as a consequence of the inverse-proportionality-to-effort usage principle.

In addition the endedness of the environment biased movement. After some period of time every rat tended to leave the pen it was then in and go into an adjoining pen. Rats in an end pen could only go to the adjoining center pen, while a rat in one of the two center pens could go to the other center pen or to the adjoining end pen. In other words, when a rat is in an end pen it has a probability of 1.0 of going into the adjacent center pen, but if it is in a center pen it has a probability of 0.5 of going into the adjacent end pen or 0.5 of going into the other center pen. Repetition of shifting by all members by the operation of this principle alone soon leads to a steady state in which a 1:2:2:1 ratio will characterize the density of rats across pens I:II:III:IV. See pages 298–299 of Calhoun (1962a) for details of the mathematics involved in the origin of this ratio.

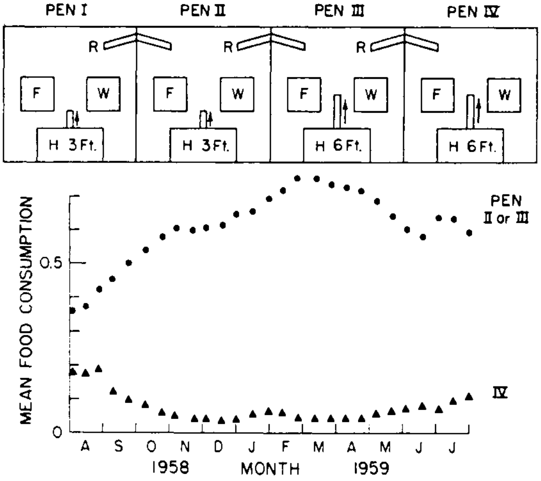

FIG. 33. The upper portion of the figure represents in schematic fashion the environment in which large social groups of albino rats were maintained. See text for details. The lower figure contrasts the amount of food consumed in the most used and the least used pen from the inception of the behavioral sink during the sixth month (August, 1958) of the study.

Populations in four such 4-pen environments were studied from February 1958 to July 1959. By the eighth month, September 1958, each population consisted of three generations, each artificially fixed at near 30 individuals. The first and second generations were sexually adult, and the third was recently weaned. Distribution of adults at this time proved to be of considerable importance in producing a phenomenon I have termed a "behavioral sink." Five surveys of place of residence gave a total count by pen of 343 for pen I, 467 for pen II, 331 for pen III, and 245 for pen IV.

If the two movement biasing principles described above operated independently and equally, the expected ratio of density would be 3:4:3:2 across pens I:II:III:IV, thus giving an expected distribution for the September 1958 observation of 347:462:347:232. The observed and expected values are so nearly the same as to support strongly the belief that these two movement biasing principles were in fact the only effective ones operating at this time. These same factors also affected the third generation then maturing.

Taking mortality into consideration, each population consisted of about 80 rats with on the average 20 living in pen I, 27 in pen II, 20 in pen III, and 13 in pen IV. Only in pen IV did the density approximate the ideal of 12. Elsewhere, particularly in pen II, density far exceeded this. From this time on a remarkable change in the differential use of space, particularly as reflected by food consumption, set in. In one pen (in three instances it was in pen II and in the fourth in pen III) food consumption increased at the expense of that in the other three pens. See the lower half of Fig. 33. By the time seven months had elapsed, most rats were eating all their food in this "favored" location and all rats were doing most of their eating there.

The explanation for this change appears rather simple. Gnawing food through the wire mesh of the food hoppers required considerable time. In the one pen where more rats fed than in the other pens, the probability of two rats eating side by side increased. Gradually rats redefined the eating situation as requiring presence of other rats. Thus, all rats shifted most of their eating to that pen where this condition was most likely to be met. It must be kept in mind that such a system is stochastic and not deterministic, so it was not unexpected that pen III became the favored place of eating by one of the four groups. However, the likelihood of pen IV ever becoming the favored pen is extremely remote.

The learned need for social proximity while engaging in an act which might have been expressed alone assumed priority over the simple original hunger drive. Food was not food without the presence of a comrade. This whole process of developing excessive aggregations in order to satisfy a secondarily acquired social drive is what I mean by a "behavioral sink." Gradually more rats also shifted residence to this favored place of eating. Such behavioral sinks result in every member encountering more associates than the ideal, and even more than necessitated by the operation of those principles of spatially structuring the environment which biases movement.

In this situation marked alterations in mortality and behavior resulted. Males became pansexual in the sense that they mounted other rats irrespective of sex or age. Nest building and maternal behavior became so disrupted in most females as to preclude the possibility of most young surviving. In each experimental setting the rats experienced less disturbance in one pen, usually pen IV, than elsewhere, since they were somewhat less trapped in the behavioral sink. And yet even here only half the young born survived to weaning and their growth was markedly retarded. In contrast, in the pen where most rats assembled only half as many young were born and only 1% of these survived to weaning.

In addition, the abnormal frequency of social interaction resulted in marked disturbance to female reproductive physiology. Near-term fetuses died. Some females with such dead fetuses shortly succumbed from apparent toxemia. Others died from massive hemorrhaging in many organs, an accentuation of the event likely to have been associated with fetal death. Many females who survived such events later died as a consequence of a site of resorption of a near-term fetus becoming the focal point for the development of a large abscess. Normally death occurred by the time the abscess reached a diameter of 50 mm. As an example of this scourge, 56% of second-generation females died by a year of age, by which time only 10% of males had died.

Were a species to survive for many generations in an environment fostering development of a behavioral sink, it is obvious that selection must proceed to produce individuals whose behavior and physiology were in harmony with such a heightened frequency of social interaction. Wherever an environmental resource which was formerly so widely distributed as to be readily available within each individual's or group's home range becomes restricted, then conditions are ripe for production of a behavioral sink. It is my belief that just such happenings have been the usual alterations which have forced the evolution of horde or herd type species from one previously characterized by an optimum group size of 12 adults.

D. Yarding by Deer in Northern Wisconsin

Characteristically since 1935 white-tailed deer (Dahlberg and Guettinger, 1956) in Northern Wisconsin assemble during the winter in a restricted area known as yards. These cover only 5–10% of their range. Conifers, which comprise the major cover in the yard, provide protection from deep snows. However, such cover provides only a secondary quality food. One or more feeding stations were established in most yards. During the 1930's food supplements represented a small amount of total food requirements. By 1953, when artificial feeding was largely terminated, most of the food requirements were supplied at these feeding stations in many yards. Nevertheless, many deer died of "starvation" even in yards where the most food was provided.

The restricted locations where food was provided and the striking aggregations of deer in their vicinity reaching 350 per square mile strikingly resemble my experimental populations of rats from which developed the concept of the behavioral sink. Even though many deer died in the yards, the question stands: "Is this really an instance of a behavioral sink?" Gaining insight into this question has proved to be a difficult detective job. Shiras (1921), Sanders (1939), Swift (1948), Kabat *et al.* (1953), Schorger (1953), and Dahlberg and Guettinger (1956) proved to be particularly helpful.

Before the days of lumbering, deer were so scarce in the primeval forests of Northern Wisconsin as to contribute very little to the diet of Indians. Between 1860 and 1880 a marked increase in deer followed lumbering operations with the consequent development of openings and second growth which provided abundant food. Although the deer did not reach the densities of 1935 to 1953, they supported a major industry as a commercial source of meat. There is some mention during this era of herds up to 200 being seen, of aggregations about salt licks, and about concentrations in white cedar swamps during heavy snows. However, one gets the impression from Schorger's citations that it was more customary for deer to be scattered. After heavy snows the commercial hunters trailed the deer until they found them exhausted and trapped by the deep snow. Schorger (1953, p. 210) writes, "It is stated by Harvey Braein that about Christmas, 1857, a crust about one-half inch in thickness formed on the deep snow in Buffalo County, and that nearly every deer perished. Following the spring, their bodies were found in nearly every coulee." Unfortunately, this is the sort of data one has to rely on. Even so, it suggests a typical pattern of scattering.

As early as 1920 when the Northern Wisconsin deer herd was well on its way to recovery after its prior decimation by forest fire and unrestricted hunting, private hunting clubs and the operators of tourist camps had begun the practice of feeding deer during the winter months. After 1935 Civilian Conservation Corps camps and the Wisconsin Conservation Department greatly increased this artificial feeding. However, the intensive artificial feeding characterizes only the 1943–1953 period. Swift (1948) states that yarding had not commenced very extensively until after 1941 even though astonishingly high populations existed in many locations. It is difficult to escape the conclusion that the accentuation of yarding was a direct outgrowth of the artificial feeding.

Daily movements rarely exceeded one-quarter mile from the feeding stations. Thus, available food outside the yards remained unutilized. Even with the advent of warm weather deer exhibited considerable reluctance in leaving the yard despite increasing new growth outside it. Even cessation of artificial feeding has not disrupted the marked yarding tendencies of Wisconsin deer. Through many generations they have developed a culture demanding an excessive frequency of contact with others during the winter season when they would otherwise be more scattered.

I will freely grant that this interpretation of the origin of yarding may be oversimplified. Nevertheless, available observations warrant consideration of the concept of the behavioral sink as helping us understand the historical development of yarding to an excessive degree.

E. Concerning Basic Numbers, N_b, for Man

During the past half million years, density of *Homo sapiens* has exhibited a continued increase over the inhabited portions of the earth (Deevy, 1960; von Foerster *et al.*, 1960). Most who have concerned themselves with studying such change restrict their emphasis to changes in density accompanying advance in extractive efficiency of natural resources. Less attention, even by anthropologists, has been devoted to determining sizes of social groupings forming partially closed systems. Such partially closed systems range from a male-female pair to that of a nation such as the United States among which interactions among all members may be conceived of in terms of population potential (Stewart, 1948; Calhoun, 1957). It will not be my purpose here to treat the entire range. Rather, I shall merely present a few highly selected examples of some of the smaller groupings which presumably reflect evolutionary limitations to group structure. On the assumption that these group sizes represent the consequences of underlying basic forces, they will be used in later sections (XIII, A and B) as data for developing a general formulation of group size and social interaction.

For about 98% of his history during the past half-million years, simple food gathering limited man's economy and social life. One of the earliest known settlements at the Star Carr site in east-central England of nearly 10,000 years ago consisted of five families, ten adults (Braidwood and Reed, 1957). Thus, it appears that an adult group size not diverging greatly from my hypothesized ideal of 12 may have characterized the human species up until at least 10,000 years ago.

The Australian aborigines (Birdsell, 1953, 1957) provide further insight into the basic numbers of human groups. In terms of the typical number of adults, five levels are recognizable: (a) the family with 2 adults; (b) the "horde" or extended family with 16 adults; (c) the supra-horde of 50 adults; (d) the tribe with 200 adults; and (e) the supra-tribe with 2200 adults. The horde forms the most basic social group, ranging generally between 10 and 20 adults. When the group exceeds 20 adults a budding process occurs, 10 adults forming a minimal-sized horde. These approximations of Birdsell's again suggest a basic group size not diverging greatly from the 12 presumably fixed by much earlier evolution. Occasionally, the horde may fragment temporarily into single family groups when scarcity of food demands such dispersal.

Also, occasionally an average of five hordes, 50 adults, may temporarily assemble into a supra-horde. However, this grouping appears to be a less basic one than the other four. The third grouping, the tribe, lacks any form of authority, and only on rare occasions do the 12 or so hordes forming the typical tribe assemble. However, common bonds of culture, their customs and value systems, clearly delineate the tribe as a social entity. Furthermore, marriages are primarily restricted to those between individuals of different hordes within the same tribe. Only in one local region of Australia has a higher-order grouping evolved. Three supra-tribes, averaging 2200 adults, represent an assembly of tribes bound together by a more advanced type of political organization characterized by matrilineal descent.

These data suggest that cultural evolution has proceeded by saltatorial steps, each characterized by some accretion to the culture. It will be my hypothesis, to be developed in more detail in Sections XIII, B, 2 and B, 3, that the *sole* function of culture is to provide a mold which enables interactions to transpire in a larger group such that their physiological consequences to the average individual closely approximate those that would result were the individuals still living in a closed social group of about 12 individuals.

Hallowell (1960, pp. 345–346) states that ". . . a normative orientation becomes an inherent aspect of the functioning of all socio-cultural systems, since traditionally recognized standards and values are characteristic of them. Techniques are appraised as good or bad; . . . . Knowledge and beliefs are judged true or false. Art forms and linguistic expression are evaluated in relation to ethical values. All cultures are infused with appraisals that involve cognitive, appreciative, and moral values," and "if the total ramifications of the normative orientation of human societies are taken into account, we have a major clue to the kind of psychological transformation that must have occurred in hominoid evolution which made this level of adaptation possible and some measure of its depth and significance for an understanding of the dynamics of human social systems of social action." Culture so conceived as normative orientation in which individuals play sanctioned roles provides the structure which allows individuals to reap the maximum rewards (the theta, θ, of Section XIII, A) from participation in the social system.

If culture really does permit individuals to function in the context of a larger social group as if they were still only in the basic $N_b = 12$ group compatible with their physiology, then any disruption in the culture should reduce the group size since its unstable state would then no longer buffer the individuals from the excessive contacts with their associates. I am assuming that, depending upon the extent of the cultural disturbance, physiological disturbances comparable to those of my rats caught in the behavioral sink (Section XII, C) would arise.

In fact, Birdsell (1953) demonstrates that such a phenomenon has characterized Australian aborigines in recent times. Tribes which have recently adopted the rites of circumcision or subincision generally have a size less than one-third that of tribes which have either not been exposed to these practices or adopted them long ago. Furthermore, the historical records indicate that tribes once reduced in numbers after they first adopted these rites now after several generations have recovered their typical numbers.

These data on the Australian aborigines further suggest that an individual can shift his participation from one level of social organization to another, provided there are cultural means for channeling such participation. Duff and Kew (1957) provide an account of the recently extinct Kunghit Haida Indians of British Columbia, which enables similar insights into basic group sizes in a food-gathering people.

Their winter village consisted of 16 to 20 large houses (1600 sq. ft. of floor space each). From various of the accounts it appears that the tribe totaled about 500 individuals, of which slightly over 200 were adults. This means about 10–12 adults on the average per house. Each house was inhabited by a kinship group or lineage. During the warmer months of the year each lineage group left the winter village for its own hunting territory. Like the Australian aborigines, these British Columbia Indians also appear to have a basic group size not diverging far from 12 and an assembly of these into a tribe of around 200 adults.

Incipient agriculture, in which plow and draft animals are absent, represents an even more advanced efficiency of food extraction, characterized by a permanent village. The Jarmo site in Iraq, inhabited some 6700 years ago, presumably represents a typical village at this level (Braidwood and Reed, 1957). Braidwood and Reed estimate that 150 persons (50 adults) inhabited the 25 houses located there. This type of village structure extends into the present. The mean size of 185 villages in this part of Iraq is 140, which presumably represents 46–56 adults.

From the scanty examination of lower-order basic group sizes in man we shall skip to the urban society of a modern nation, the United States. The social organization represented by Australian aborigines and the

Kunghit Haida suggests that each larger semiclosed social system includes within it all the culturally limited basic group numbers. But even if some are skipped or unrecognizable, the one group structure which must be preserved is that of 12 adults. Recent studies by Zimmerman and Broderick (1954) and Zimmerman and Cervantes (1960) confirm this suspicion. Their approach has been to focus on any given family, designated the ego family, and then to determine with how many other families its members have frequent and close associations. These latter are designated as friend families. Absence of divorce or desertion, juvenile arrest, or children not completing high school comprised criteria for judging a family as "good" or "successful." Presence of these traits were used to delimit the "bad" or "unsuccessful" families. Values held by a family were judged on the basis of their religion, region of origin, income level, and kinship bonds. The good ego families typically have five friend families with whom they have a high coincidence of values, and furthermore, if the ego family is characterized as good most of the friend families are likely also to be so characterized. On the other hand, bad ego families generally have fewer friend families and they are likely to differ from them with respect to the value traits. The fewer the values shared by the several families forming such a cluster, the smaller the cluster will be and the greater the probability that each family will be characterized by one or more of the traits denoting it as an unsuccessful family.

The ideal state then appears to be six families, 12 adults, composed of an ego family and five friend families. Shared values bind such a cluster despite the dispersal of the member families through the local community. Furthermore, each friend family in a particular cluster is, as an ego family, the center of another cluster. In this way an extension of the cluster develops to include 26 total families. Although similar bonds between families may include a larger network, insofar as any particular family is concerned the 25 friend families and extended friend families form the limit of dependence and social support relationships. This approximation of 50 adults of the family-friend cluster further argues for the reality of $N_b = 50$ as a basic grouping revealed also in Birdsell's supra-horde of Australian aborigines and of the incipient agricultural village of the Jarmo type. Reduction of the size of the family cluster below the optimum of six when values held by member families diverge from each other represents another example of the principle of group fragmentation, enunciated by Birdsell, which follows a clash in values. Zimmerman and Cervantes refer to this conflict as a "confusion of values."

All the information in this section, when viewed as a whole and in the context of the earlier sections concerning the evolution of a basic group size, suggests the following tentative generalization: Modern man derived from his primate and preprimate ancestors a physiology transpiring in groups within the range of 10–20 adults. This physiology was fixed some half a million years ago and has not significantly diverged from it since. Development of a larger social group is made possible by a culture in which a normative orientation prescribes values, and sanctions roles of behavior such that the total effect of participation in a larger group so buffers the individual that at any particular time the individual functions socially as if he were a member of a group of 12 individuals. Furthermore, genetic changes of the central nervous system making learned value systems of cultures possible must have arisen under circumstances which prevented division of the basic group size when it reached twice this level. Either an ecological-psychological trap like the behavioral sink (Section XII, C) or any isolated but very abundant source of a needed resource would be adequate to demand either a genetic change of physiology making life in large groups tolerable, or a genetic change endowing the central nervous system with the capacity to learn and culturally transmit values. Each increase in group size is associated with a reorientation of the value system. Such increases in group size are saltatory. The theoretical basis of why such changes must be saltatory and not transitional is discussed in Section XIII, B, 3.

XIII. A Formulation of Group Dynamics

Twelve individuals represent the approximate optimum group size for certain species (Sections VIII, C and XII, E). Furthermore, such a sized group might be expected to have evolved from home range dynamics. Evidence could readily be assembled that other basic N's, N_b's, characterize other mammalian species. Some typically live as pairs while others assemble in herds exceeding 100 or 1000 individuals. However, circumstances may force N to diverge markedly from N_b. Elaboration here of the model of social interaction presented in pages 349–354 of Calhoun (1957) provides insight into the consequences of such divergence of N from N_b.

A. The Model of Social Interaction

On a presumptive basis there are three variables which should determine the mechanics of contact and interaction. These are (a) the number of animals moving about and having opportunity of contacting each other, (b) the length of the refractory period following the response of one animal upon contacting another until it is again capable of exhibiting a similar response, and (c) the amount of space in which the movement of N individuals takes place. Random distribution of positions of individuals at any moment in time is assumed. We choose to ignore a small correction factor arising from the fact that all individuals move. Velocities of all individuals are initially assumed to be a constant. Furthermore, we assume that all individuals are identical. Thus our concern is not which individuals meet, but rather which state, responsive or refractory, the contacting individuals happen to be in.

N = Number of animals forming the group.
d = The diameter of interaction for each animal, that is, that distance between the centers of two individuals at which a physical or psychological collision or contact occurs. In the simplest case animals may be considered equivalent to billiard balls. Then d represents the diameter of the ball, the individual. See Section XIII A, 1 for further elaborations.

Assume an animal moving in some direction on the plane in a population, $N - 1$, of other animals.

Each of these other individuals presents a target of dimension d, normal to the x direction. The expectation that the incoming animal will make a collision while moving a distance Δx (in time t) is the ratio,

$$\frac{d(N - 1)\Delta x}{A}$$

of surface covered by the targets to the total surface, where A is the area available to the animals.

It should be emphasized that the unit of time must be sufficiently large so that the number of collisions in that time interval is large enough to justify using the statistical law of large numbers in the derivation. For similar reasons, it must be assumed that the mean free path of the individuals must be large in comparison with the target diameter.

Since the velocity v may be considered equal to $\Delta x/t$, the average number of contacts n_c, per individual in time t is

$$n_c = \frac{d(N - 1)vt}{A} \qquad (32)$$

For present purposes we are concerned only with the average n_c in t and not in the variability in contacts in t. The frequency of contacts by a given individual will be:

$$f_c = \frac{n_c}{t} = \frac{d(N - 1)v}{A} \qquad (33)$$

Since d, v, and A will be considered constants for this presentation, we set

$$(dv/A) = \mu \qquad \text{so that} \qquad f_c = \mu(N - 1) \tag{34}$$

μ reflects the ease of communication in the sense of contacts per unit of time. Basically, d, v and A may be specified in terms of linear unit, L. Therefore,

$$\mu = \frac{dv}{A} \approxeq \frac{L \cdot Lt^{-1}}{L^2} = \frac{1}{t} \tag{35}$$

The symbol $\approxeq$ is here used in the sense of "dimensionally equivalent to." So by selecting appropriate units of time, μ can be made equal to 1.0. In following discussions μ will be considered equal to 1.0 in this sense whenever the basic N, N_b, of a species is in an evolutionarily steady state.

We will assume that the population of individuals can be divided into two classes: $[N_a]$, those individuals who are in a responsive state, and $[N_p]$ those individuals who are in a refractory state. We further assume that the individuals in $[N_a]$ will be rendered refractory either after a contact with a member of the same class or with a member of $[N_p]$. After any such contact, an individual will remain in the refractory state for a length of time, α, the refractory period, and after this time has elapsed return to membership in $[N_a]$. It is also assumed that any contact that an individual undergoes while it is in the refractory state has no influence on the duration of its refractory period.

The duration of such refractory periods must be a function of the behavior of each member of the contacting pair toward the other. It is assumed that the critical aspect of this behavior is its intensity. At the steady state of an N_b we shall first consider every individual to be identical with reference to the intensity of its behavior toward others.

Let:

i_a be the intensity of action of any member of $[N_a]$ toward every associate it encounters.

i_p be the intensity of action of any member of $[N_p]$ toward every associate it encounters.

It is further assumed that the most likely way that the duration of the refractory period, α, becomes a function of the behavior of two individuals toward each other is that it results from the product of the intensities of their behaviors. Furthermore, there must be some factor, which will be called B, which governs whether a refractory period will result from the interaction.

Let:

B_a = 1.0 be the value of this factor in all members of $[N_a]$.
B_p = 0 be the value of this factor in all members of $[N_p]$.
α_{aa} represent the refractory period resulting in each of two members of $[N_a]$ who meet.
α_{ap} represent the refractory period resulting in each member of $[N_a]$ which encounters a member of $[N_p]$.
α_{pa} represent the refractory period resulting in each member of $[N_p]$ which encounters a member of $[N_a]$.
α_{pp} represent the refractory period resulting in each of two members of $[N_p]$ which meet.

It follows that:

$$i_a i_a = \alpha_{aa} B_a = i_a i_p = \alpha_{ap} B_a, \qquad \text{and all are real values} \tag{36}$$

and that:

$$i_p i_a = \alpha_{pa} B_p = i_p i_p = \alpha_{pp} B_p = 0 \tag{37}$$

In all following discussion B_a and B_p will be omitted in discussing α, but every mention of α_{aa} and α_{ap} will assume the action of B_a, and likewise any mention of α_{pa} and α_{pp} will assume the action of B_p.

It may be objected that no distinction is being made between the two kinds of contacts, responsive–responsive, and responsive–refractory. It is perfectly feasible to introduce two refractory periods, α_{aa} and α_{ap}, of different duration to answer this objection. At the present juncture the experimental data are so scanty that it does not appear to be fruitful to introduce additional complexity, and we have chosen to consider $\alpha_{aa} = \alpha_{ap}$ for the working model insofar as duration is concerned.

An alternative model would have been to choose $\alpha_{ap} = 0$, that is, the only contact inducing a refractory period being a contact between two individuals both of whom are responsive. Under such an assumption the number of contacts between responsive individuals in a unit interval of time would increase asymptotically to the value $1/\alpha$, whereas, as we shall show, the model adopted provides that the number of contacts between responsive individuals passes through a maximum as N increases.

Given sufficient proximity of an individual in the responsive state to some other individuals requisite to the usual elicitation of an interaction or response to denote a contact, evidence from certain mammals suggests a mechanism capable of blocking a social response. Such a mechanism which defines the probability of a contact being socially "perceived" shall be called μ'.

n_a = number of contacts made while the given animal is in the "responsive" state.

f_a = (n_a/t) is the frequency of responsive contacts when the animal in question is in the "responsive" state over all time.

Since each contact between two individuals, at least one of whom is in the responsive state, is followed by a refractory period α, characteristic of each of the responsive individuals, and since there are n_a such contacts in time t, then the individual is in the refractory state for a total time αn_a. Clearly, the total time t_a in which the individual is in a responsive state is $t - \alpha\mu' n_a$.

Since $n_a = tf_a$ then

$$t_a = t - \alpha\mu' n_a = t - \alpha\mu' tf_a = t(1 - \alpha\mu' f_a) \tag{38}$$

In this sum of refractory intervals, t_a, contacts will be made at frequency f_c, but all such contacts are made while the animal is responsive so that

$$n_a = f_c t_a = f_c t(1 - \alpha\mu' f_a) = tf_a$$

or, since $f_a = n_a/t$

$$f_a = f_c(1 - \alpha\mu' f_a) \tag{39}$$

Thus

$$f_c = \frac{f_a}{1 - \alpha\mu' f_a} \tag{40}$$

It will also be helpful to rearrange Eq. (39) to obtain f_a as a function of f_c:

$$f_c = f_a + \alpha\mu' f_a f_c = f_a(1 + \alpha\mu' f_c)$$

So

$$f_a = \frac{f_c}{1 + \alpha\mu' f_c} \tag{41}$$

We may also define the frequency of refractory contacts by each individual over all time

$$f_p = f_c - f_a \tag{42}$$

Contacts between individuals will be of three kinds: (a) both individuals responsive; (b) both refractory; and (c) one individual responsive and the other refractory. A given individual meets f_c other individuals in unit time. Of these f_c contacts, f_a are with individuals in a responsive state. Hence, the probability p_a that any given encounter will be with a responsive individual will be

$$p_a = (f_a/f_c) \tag{43}$$

Therefore, of all the encounters f_a in unit time which the given individual makes while it is responsive, the number

$$f_{aa} = p_a f_a \tag{44}$$

will be with other responsive animals. Thus, f_{aa} may be considered the (absolute) frequency of responsive-responsive encounters. Substituting (43) into (44) we obtain

$$f_{aa} = \frac{f_a^2}{f_c} \tag{45}$$

Using Eq. (41)

$$f_{aa} = \frac{f_c^2}{f_c(1 + \alpha\mu' f_c)^2} = \frac{f_c}{(1 + \alpha\mu' f_c)^2} \tag{46}$$

In like manner we can define f_{pp} as the frequency of contacts of individuals both of whom are refractory and of f_{ap} for the frequency of contacts in which one individual is responsive and the other refractory.

By an argument analogous to that given above we arrive at the formulation

$$f_{pp} = \frac{f_p^2}{f_c} = \frac{(f_c - f_a)^2}{f_c} \tag{47}$$

Using Eq. (41)

$$f_{pp} = \left[f_c - \left(\frac{f_c}{1 + \alpha\mu' f_c}\right)\right]^2 \Big/ f_c = f_c\left(\frac{1 + \alpha\mu' f_c - 1}{1 + \alpha\mu' f_c}\right)^2$$

$$= \frac{\alpha^2 f_c^3 (\mu')^2}{(1 + \alpha\mu' f_c)^2} \tag{48}$$

Again:

$$f_{ap} = \frac{2f_a f_p}{f_c} = \frac{2f_a(f_c - f_a)}{f_c} \tag{49}$$

And using Eq. (41)

$$f_{ap} = \frac{2f_c}{1 + \alpha\mu' f_c}\left[f_c - \left(\frac{fc}{1 + \alpha\mu' f_c}\right)\right] \cdot \frac{1}{f_c}$$

$$= \frac{2}{1 + \alpha\mu' f_c}\left[\frac{f_c(1 + \alpha\mu' f_c - 1)}{1 + \alpha\mu' f_c}\right]$$

$$= \frac{2\alpha f_c^2 \mu'}{(1 + \alpha\mu' f_c)^2} \tag{50}$$

We can obtain an explicit relation between f_{ap} and N and f_{aa} and N by substituting Eq. (34) respectively into Eqs. (50) and (46):

$$f_{ap} = \frac{2\alpha\mu'\mu^2(N - 1)^2}{[1 + \alpha\mu\mu'(N - 1)]^2} \tag{51}$$

And

$$f_{aa} = \frac{\mu(N - 1)}{[1 + \alpha\mu\mu'(N - 1)]^2} \tag{52}$$

The function $f_{aa} = 0$ when $N = 1$ and also f_{aa} approaches 0 as N tends to infinity. Since f_{aa} is continuous and differentiable for all positive values of N, it has a maximum N_m for some value of f_{aa} at which the derivative of f_{aa} with respect to N is zero

$$\frac{\mathrm{d}f_{aa}}{\mathrm{d}N_m} = 0 = \frac{\mu[1 + \alpha\mu\mu'(N - 1)][1 - \alpha\mu\mu'(N - 1)]}{[1 + \alpha\mu\mu'(N - 1)]^4} \tag{53}$$

and

$$1 - \alpha\mu\mu'(N_m - 1) = 0 \tag{54}$$

Hence

$$N_m - 1 = \frac{1}{\alpha\mu\mu'} \quad \text{or} \quad \alpha\mu\mu' = \frac{1}{N_m - 1} \tag{55}$$

Thus, the larger α, the smaller N_m. In other words, the position of the maximum shifts to the left as α increases. In order to find the maximal value of f_{aa}, $f_{aa}^{(m)}$, we may substitute Eq. (55) into (52) obtaining

$$f_{aa}^{(m)} = 1/4\alpha\mu' \tag{56}$$

In other words, the number of responsive-responsive contacts in unit time decreases as the refractory time increases. Since the refractory time,

α, is assumed to increase when the intensity of interaction, i^2, increases, f_{aa} decreases as intensity of interaction increases.

When the N of a species has attained an evolutionary steady state, designated as N_b, μ and μ' will each have values of 1.0. When $\mu = 1.0$ it will be designated μ_b. Existence of an N_b steady state does not mean that the temporal N cannot fluctuate within the lifetime of a species or the history of a population. Rather, it means there is a particular N compatible with μ_b. At this N_b, with its μ_b, all contacts are perceived. That is, $\mu' = 1.0$, and whenever $\mu' = 1.0$ it will be designated μ_b'. Not only will all contacts by responsive individuals be perceived, but each member of N_b will interact with the same average intensity and, thus, α becomes α_b. Obviously N_b is the N_m toward which a species "strives." In this "striving," which may be either maturational or evolutionary in terms of units of time, N may vary as a function of α, or α may vary as a function of N. At that N it follows from Eqs. (55) and (56) that:

$$\alpha_b f_{aa}^{(m)} = 0.25 \tag{57}$$

This holds for all N_b.

$\alpha_b f_{aa}^{(m)}$ defines the maximum satisfaction from social interaction and will hereafter be referred to as θ_b.

The usual intensity, i, of interaction, which determines α, since $i^2 = \alpha$, may be considered as basically under genetic control. Similarly, μ and μ' may be considered to be normal expressions of genetic factors in so long as N_b is approximately realized and the members of N experience conditions in harmony with their genetic constitution, that is to say that the environmental conditions approximate those usually experienced by the species for many prior generations. However, abnormal environmental circumstances may so alter physiology and condition behavior that i, μ, and μ' diverge from the i_b, μ_b, and μ_b' appropriate to N_b. In these circumstances μ and μ' no longer each equal 1.0, nor is i_b in harmony with N_b in the sense that αf_{aa} will lead to maximum satisfaction from social interaction. Yet, regardless of how i, μ, and μ' have diverged during maturation, this maximum may be attained if the species adjusts by attaining that N, different from N_b, such that:

$$\alpha f_{aa}^{(m)} = 0.25 = \theta_a^{(o)} \tag{58}$$

Theta, the maximal and also optimal satisfaction from social interaction, is here designated as $\theta_a^{(o)}$ or just θ_o to indicate its possible attainment at some other N than N_b.

Interactions whose frequency has been designated by f_{ap} require special consideration.

For clarification: $f_{ap} = f'_{ap} + f'_{pa}$

And f'_{ap} = frequency with which a *given* responsive individual interacts with refractory individuals, while it is itself in the responsive state.

And f'_{pa} = frequency with which a *given* refractory individual interacts with responsive individuals, while it is itself in the refractory state.

It can be demonstrated that $f'_{ap} = f'_{pa}$.

Therefore

$$f'_{ap} = 0.5 f_{ap} \tag{59}$$

If we let α_m represent that α appropriate to N_m and $f_{aa}^{(m)}$, then from Eq. (55)

$$\alpha_m = \frac{1}{\mu_m \mu_m'(N_m - 1)} \tag{60}$$

Similarly, for N_b with μ and $\mu' = 1.0$

$$\alpha_b = \frac{1}{N_b - 1} \tag{61}$$

If we assign $f_{ap}^{(m)}$ as the f_{ap} characterizing N_m when $f_{aa}^{(m)}$ represents the maximal value of f_{aa} (e.g., see Eq. (56)), then by utilizing Eqs. (51), (52), (55), and (60) and considering the fact that $\mu' = 1.0$, it follows that

$$f_{ap}^{(m)} = 2 f_{aa}^{(m)} \tag{62}$$

And from Eq. (59) it follows that, when μ and μ' each equals 1.0,

$$f'^{(m)}_{ap} = f_{aa}^{(m)} \tag{63}$$

For clarification, it is to be noted that Eqs. (62) and (63) refer to the condition when μ and μ' remain unchanged at the μ_b and μ_b' values appropriate to N_b, but α adjusts to the existing N according to Eq. (60) so that the existing N becomes an $N^{(m)}$ differing from N_b in most instances.

As already demonstrated

$$\theta_o = \alpha f_{aa}^{(m)} \tag{64}$$

where θ_o represents the maximal, and for this special case also the optimal, amount of time an individual can remain in that refractory state denoting satisfaction from social interaction. At N_m, where θ_o is realized $\alpha f'^{(m)}_{ap}$

amount of time is spent in frustrating refractory periods.
Here

$$\theta_f^{(m)} = \alpha f_{ap}'^{(m)} \tag{65}$$

And from Eqs. (63), (64), and (65) it is obvious that

$$\theta_f^{(m)} = \theta_o^{(m)} \tag{66}$$

Since N_b is a special, and the most important, case of N_m, Eq. (66) represents a significant consequence of evolution, as well as adjustment to current group size different from N_b. It means that when members of a group attempt to maximize satisfaction from social interaction, they will of necessity spend an equivalent amount of time experiencing frustration from social interaction. Evolution having transpired in such a system of social physics, physiology must be in harmony with this normal degree of frustration. Likewise, any marked decrease or increase of f_{ap}' from $f_{ap}'^{(m)}$ should prove stressful.

From Eqs. (51), (59), and (61), when $\mu\mu'$ and α remain appropriate to N_b but N fluctuates, it follows that

$$f_{ap}' = \frac{\alpha_b(N - 1)^2}{[1 + \alpha_b(N - 1)]^2} \tag{67}$$

As N approaches zero, f_{ap}' approaches zero. As N approaches infinity, f_{ap}' approaches the f_c characteristic of N_b, that is when $f_c = N_b - 1 = 1/\alpha_b$. Yet at the same time (see discussion following Eq. (52)) f_{aa} approaches zero as N approaches infinity with reference to its divergence from N_b. At N's much larger than N_b the frequency of contacts resulting in refractory periods (i.e., f_{aa} and f_{ap}') comes to approximate the total contacts transpiring in N_b; however, practically all of such contacts are of the type frustrating to individuals having returned to the responsive state.

1. TERMS AND EQUATIONS

The following assembly of definitions will facilitate understanding later discussions. Insofar as possible the N animals in the group will serve as the basis of the definitions. Some terms utilized in later sections will also be included here.

N = Total number of individuals in the group. In the strictest sense, a group is defined by habitation of an exclusive area in which each resident member has a good chance of contacting all others.

d = Target diameter of an individual. In the simplest sense, d specifies the actual physical diameter with the "animal" having no more d properties than a billiard ball. Included under d are any characteristics such as bright color, vocalizations, odor, or upright posture which enhance the likelihood of an individual being perceived by its associate. Through evolution and maturation certain species, particularly man, acquire the capacities to utilize nonphysical characteristics to alter target diameter. These nonphysical characteristics include attitudes and values whose possession influences the likelihood of the holder being perceived and responded to by his associates.

v = "Velocity" with which an individual "moves" through its environment. It includes all properties which enhance the likelihood of one individual approaching its associates. Thus, in addition to including actual velocity, it includes all sensory mechanisms which extend the individual's perception of others in any direction along its travel path. Thus, where r is the radius of perception beyond the physical bounds of the individual, v becomes rLt^{-1}, see Eq. (35). Furthermore, $v = rLt^{-1}$ must actually become more complex than this. Animals further vary in the number of trips per unit time. See previous discussion in Sections III, A, 1 and A, 4 which deal with how emotionality alters the frequency of trips. Therefore, if we let:

$v_1 = r =$ radius of perception
$v_2 =$ number of trips per unit time; or any time or place pattern of movement which alters probability of contacting others
$v_3 \approx Lt^{-1} =$ actual velocity

Then biological velocity, v, becomes:

$$\begin{aligned} v &= v_1 v_2 v_3 \\ &= v_1 v_2 Lt^{-1} \end{aligned}$$

Note: Here *the product* is used in the sense of *a function of*.

When v is considered in later discussions it will have all these connotations.

r = radius of perception as discussed above.
A = area inhabited by the N individuals, each of whom has a good opportunity of contacting any other member of N.
$\mu = (dv/A)$ is a communication-enhancing or contact-producing factor. By considering v in its simplest sense, μ becomes (drv/A) as soon as the *perception swath*

determined by the individual's capacity to perceive beyond its own physical bounds comes into play.

μ' = A communication-inhibiting or contact-blinding factor. It reflects a psychological property permitting the individual to ignore a contact resulting from μ. μ' must derive from $(d'r'v'/A')$ factors. See Section XIII, B, 4 for further treatment of μ'.

i = Intensity of action of one individual toward another upon contact.

α = i^2, the duration of the refractory period following the contact of a responsive individual with some other individual. Contacts made by an individual while it is in a refractory state have no influence upon its α. In some way the refractory period is a consequence of the intensity of interaction. It is thus the result of the interplay between the action of each individual toward the other. I have, therefore, assumed that the product of these intensities of action represents a first approximation of a proportionality to the duration of the refractory period.

f_{aa} = The frequency with which one individual, while in the responsive state, meets other individuals, who are also in the responsive state.

f'_{ap} = The frequency with which an individual, while in the responsive state, meets nonresponsive ones (i.e., those in the α refractory state).

α_{aa} = Refractory period produced in each individual after each of the f_{aa} interactions in which it is involved. α_{aa} produces satisfaction.

α_{ap} = Refractory period produced in the responsive individual after each f'_{ap} interaction. α_{ap} produces frustration at least in the sense of being a nonspecific stressor of physiology.

α_{aa} = α_{ap} with regard to duration.

θ_a or
$\theta^{(a)}$ = αf_{aa}, the amount of time per unit time spent in satisfying refractory periods. θ_a represents the consequences of positively affective interaction.

θ_f or
$\theta^{(f)}$ = $\alpha f'_{ap}$, the amount of time spent in the frustrating and physiologically stressful state.

θ_f approaches zero as N approaches 1.0

θ_f approaches 0.25 at N_b

θ_f approaches 1.0 as N approaches infinity with reference to N_b.

θ_f represents the consequences of negatively affective interactions.

$\theta_a^{(m)} = \alpha_m f_{aa}^{(m)}$ = maximal $\theta_a = 0.25$; see Eq. (57).

$N^{(m)}$ = That N at which $\theta_a^{(m)}$ results. In other words, at N^m satisfaction from social interaction is maximized, but at $N^{(m)}$, $\theta_f^{(m)} = \theta_a^{(m)}$, that is, there is as much frustration as satisfaction from social interaction.

N_b = The basic group size of a species living under those conditions to which it is most adapted. N_b is a special case of $N^{(m)}$. $\theta_a^{(b)}$, $\theta_f^{(b)}$, α_b, i_b, μ_b, and μ_b' represent values appropriate to N_b. Here $\theta_a^{(b)}$ and $\theta_f^{(b)}$ always $= 0.25$, as may be seen from Eqs. (57) and (63). At N_b both μ_b and μ_b' must equal 1.0. $\theta_a^{(m)}$, $\theta_f^{(m)}$ represent values appropriate to $N^{(m)}$ in which $\theta_a^{(m)} = \theta_a^{(b)}$ and $\theta_f^{(m)} = \theta_f^{(b)}$.

However, $\alpha^{(m)}$, $i^{(m)}$, $\mu^{(m)}$ and $\mu'^{(m)}$ at $N^{(m)}$ may all differ from comparable values appropriate to N_b.

$\theta_a^{(o)} = \theta_a^{(m)}$ for all N other than N_b, although quantitatively $\theta_a^{(o)}$, $\theta_a^{(m)}$, and $\theta_a{}^{(b)}$ all $= 0.25$.

N_o = Any N when $\theta_a = \theta_a^{(o)}$. N_o may equal N_b, but when it differs from N_b, some alteration in μ, μ', or α permits attainment of the optimum θ_a, that is $\theta_a^{(o)}$.

2. INTERACTION FUNCTIONS STATED IN TERMS OF N

The number of individuals inhabiting an area is more readily measured than any other function relating to this model of social interaction. Therefore, it will be helpful to state all other functions in terms of N:

$$f_c = \mu(N - 1) \tag{34}$$

If intensity of interaction is labile to the point that $\theta_a^{(m)}$ can always be attained, then

$$\alpha_m = \frac{1}{\mu_m \mu_m'(N_m - 1)} \tag{60}$$

which means that:

$$i_m = \left(\frac{1}{\mu_m \mu_m'(N_m - 1)}\right)^{1/2} \tag{68}$$

A core aspect of this thesis is that whenever μ increases above μ_b there will be compensatory shifts in μ' such that $\mu\mu'$ will again equal 1.0. Therefore, α and i will gradually become a function of N_m, or we might rather say that the members of the group attempt to adjust their intensities of interaction to make any existing N, regardless of how much it has diverged from N_b, become N_m. Thus, Eqs. (60) and (68) become:

$$\alpha_m = \frac{1}{N - 1} \tag{69}$$

$$i_m = \left(\frac{1}{N - 1}\right)^{1/2} \tag{70}$$

At N_b it follows from Eqs. (56) and (69) that the maximum frequency of interaction of one responsive individual with other responsive ones becomes:

$$f_{aa}^{(m)} = \frac{N_b - 1}{4} \tag{71}$$

Accepting the logic above that in time all individuals will attempt to adjust their intensity of interaction compatible with any existing N, it follows that:

$$f_{aa}^{(m)} = \frac{N - 1}{4} \tag{72}$$

It further follows from Eqs. (52) and (69), where $\mu\mu'$ tend to adjust to 1.0 and i adjusts to maximize θ_a regardless of change in N, that:

$$f_{aa}^{(m)} = \frac{\mu(N - 1)}{[1 + \alpha(N - 1)]^2} = \frac{\mu(N - 1)}{4} \tag{73}$$

And similarly at $f_{aa}^{(m)}$, it follows from Eqs. (51), (59), and (69) that:

$$f_{ap}^{\prime(m)} = \frac{\alpha\mu^2(N - 1)^2}{[1 + \alpha(N - 1)]^2} = \frac{\mu^2(N - 1)}{4} \tag{74}$$

Equations (73) and (74) must be kept in mind while reading Section XIII, B. It has already been pointed out in the discussion following Eq. (66) that in the evolutionary steady state $\theta_f^{(m)} = \theta_o^{(m)}$. Here [see Eq. (63)], $f_{aa}^{(m)} = f_{ap}^{\prime(m)}$. This is a major premise of this paper, that animals "strive" to experience equal amounts of satisfaction and frustration from social interaction. But note what happens according to Eqs. (73) and (74) when μ varies. If μ increases and the members attempt to optimize satisfaction, to attain $\theta_o^{(m)}$, then

$$\frac{\theta_f}{\theta_o^{(m)}} = \mu, \qquad \text{or} \qquad \theta_f = \mu\theta_o^{(m)}.$$

Thus, excess frustration will increase proportional to the increase in μ. For this reason, animals will always be conservative in that they will attempt to reject any changes leading to an increase in μ.

Where $\mu = \mu_b = 1.0$ and N becomes N_m [also refer to Eq. (25)]

$$f_{aa}^{(m)} = f_{ap}^{\prime(m)} = \frac{N-1}{4} \tag{75}$$

In some circumstances μ may be more labile than i as an adjustive mechanism to changes in N from N_b. Where intensity of interaction remains constant at that level appropriate to N_b, α remains α_b. And yet Eq. (55) reveals that the N differing from N_b can become N_o provided:

$$N_o = 1 + \frac{1}{\alpha_b\mu_o\mu'} \tag{76}$$

Also by analogy to Eq. (69):

$$\alpha_b = \frac{1}{N_b - 1} \tag{77}$$

Then substituting Eq. (77) into (76):

$$N_o = 1 + \frac{N_b - 1}{\mu_o\mu'} \tag{78}$$

Therefore:

$$\mu_o\mu' = \frac{N_b - 1}{N_o - 1} \tag{79}$$

In the original change of N_o from N_b, μ and μ' were μ_b and μ_b' and each was therefore equal to 1.0. However, we are here concerned with the case when μ is labile, that is, it can become different from μ_b. Furthermore, μ_b' can be ignored since any change in μ_b' must await some stability in the change of μ. Thus, when α remains at α_b

$$\mu_o = \frac{N_b - 1}{N_o - 1} \tag{80}$$

Where intensity of interaction remains constant, and N_i represents the value of N at the inflection point of f''_{aa}, that is at the point where the second derivative of f_{aa} as a function of N is zero, it may be shown that

$$N_i = 1 + \frac{2}{\alpha_b \mu_o} \tag{81}$$

Then inserting Eq. (77) into Eq. (81)

$$N_i = 1 + \frac{2(N_b - 1)}{\mu_o} \tag{82}$$

Then inserting Eq. (80) into Eq. (82)

$$N_i = 1 + 2(N_o - 1) \tag{83}$$

Where N is N_i, Eq. (83) becomes

$$N_i = 1 + 2(N_b - 1) \tag{84}$$

$$= 2N_b - 1 \tag{85}$$

B. Basic Processes Involved in Social Interaction

1. SATISFACTION AND FRUSTRATION AS A FUNCTION OF GROUP SIZE

Satisfaction and frustration from social interaction are by definition measured, respectively, by θ_a and θ_f. Full satiation attains at $\theta_a^{(m)}$ and optimum frustration at $\theta_f^{(m)}$. These equivalent quantities are equally necessary for the individual to persist in an optimum state. We shall here be concerned with the effects upon θ_a and θ_f resulting from varying N when α_b, μ_b, and μ_b' remain constant and appropriate to N_b. It must be recalled from the statement preceding Eq. (65) that $\theta_f^{(m)}$ is not used in the sense of the maximum $\alpha f'_{ap}$ but rather as the amount of time spent in frustrating refractory periods at N_m, that N where the maximum amount of time, $\theta_a^{(m)}$, is spent in satisfying refractory periods. As implied in Table XI, B and Fig. 35, $\alpha f'_{ap}$ attains a maximal value when N = infinity.

As N_b increases i and α must decrease in order to maintain $\theta_a^{(m)}$ [see Eqs. (56), (61), and (69–71)]. Likewise, for any arbitrary series of α, such as 1.0, 0.75, 0.5, 0.25, 0.1, 0.05, 0.025, and 0.01, there must be respective N_b at which $\alpha f_{aa}^{(m)} = \theta_a^{(b)}$. Each such α with its corresponding N_b might be considered as representing a distinct species. For each species circumstances may cause N to diverge from its N_b. In any such divergence θ_a diminishes, and for the species where α remains constant, f_{aa} will exhibit changes proportional to θ_a. Thus, f_{aa} may be taken as an index of the degree to which changes in N from N_b diminish satisfaction from social interaction. Such reductions of f_{aa} are shown in Fig. 34; $f_{aa}^{(m)}$, Eq. (75), is that f_{aa} denoted by the point where the dashed line intersects each solid line curve. Dropping vertically to the abscissa from each such intersection defines the N_b for which that α is appropriate in the sense of optimizing satisfaction, $\theta_a^{(m)}$. In each case, regardless of the size of N_b, $\alpha f_{aa}^{(m)} = 0.25$.

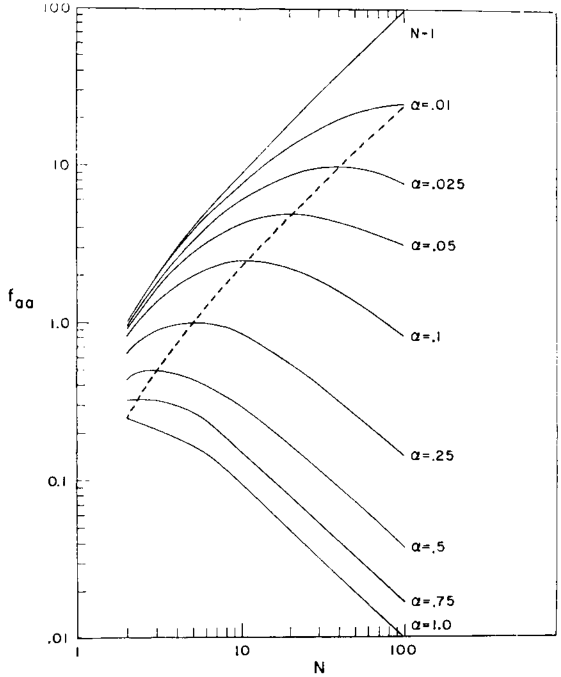

FIG. 34. Frequency of satisfactory social interactions (f_{aa}) as a function of density (N) and refractory period (α). The intersection of the dashed line and any solid line curve defines the basic group size, N_b, appropriate to that α. All αf_{aa} defined by these intersections represent a constant, $\theta_a^{(b)}$, which defines the optimum amount of satiation which can be experienced by any member of an N_b. The values on the ordinate indicated by N intersecting the dashed line represent $f_{aa}^{(m)} = (N - 1)/4$ when μ and μ' each equals 1.0 or $\mu\mu' = 1.0$. For any given $f_{aa}^{(m)}$, α can be determined by finding the N at which f_{aa} intersects the dashed line. Here $\alpha = 1/(N - 1)$.

Each N_b, so defined, represents a distinct species in the sense that there have arisen genetic alterations in i, such that there exists the highest probability of a steady state in which αf_{aa} optimizes satisfaction from social interaction.

Some of the insights revealed in Fig. 34 may be more explicitly comprehended by examining Table XI. In the left-hand part A of this table, successive doublings of N_b are presented. For each N_b those values for f_c, i_b, α_b, and $f_{aa}^{(m)}$ are given which are requisite for each member to attain on the average an optimum satisfaction, $\theta_o = \alpha f_{aa}^{(m)}$, from social interaction. It is apparent that as N_b increases, α_b and i_b decrease, while f_c and $f_{aa}^{(m)}$ increase. As the N_b group size increases, each individual will have more f_c contacts with associates, of which one-fourth will be satisfying (i.e., $f_{aa}^{(m)}/f_c = \frac{1}{4}$). For clarification, I might add that for each individual on the average at every N_b, another one-fourth of the contacts are of the frustrating f'_{ap} type, while the remaining one-half of the contacts transpire while in the refractory state which involve f'_{pa} or f_{pp} contacts. Values for $N_b = 12$ are shown in italics for reference because of the apparent importance of groups of this size. It may be seen that i for $N_b = 12$ is only one-third that for $N_b = 2$. N_b must increase from 12 to 121 for a similar decrease in intensity of interaction to be necessary.

In the now voluminous literature on "stress," many papers deal with the physiological repercussions accompanying change in group size. Yet these reveal little concerning how much physiological disturbance might be expected to result from a given change in group size. The prior model of social interaction will now be examined to determine what insight the model provides, under the assumption that it approximates reality.

TABLE XI

NORMATIVE RELATIVE VALUES OF INTERACTION FACTORS[a]

	A. When $N = N_b$				B. When $\alpha = 0.091$[b]				
N	f_c	α	i	$f_{aa}^{(m)}$	f_{aa}	$0.5f_{ap}^{c}$	θ_a	"θ_d"	θ_f
2	1	1.000	1.000	0.25	0.84	0.08	0.07644	0.1736	0.007
4	3	0.333	0.577	0.75	1.85	0.51	0.16835	0.0816	0.046
8	7	0.143	0.378	1.75	2.62	1.67	0.2384	0.0116	0.142
12	*11*	*0.091*	*0.302*	*2.75*	*2.75*	*2.75*	*0.250*	*0.00*	*0.25*
16	15	0.067	0.258	3.75	2.68	3.66	0.2439	0.0061	0.333
32	31	0.032	0.180	7.75	2.12	5.99	0.1929	0.0571	0.545
64	63	0.016	0.126	15.75	1.39	7.97	0.1265	0.1235	0.725
128	127	0.008	0.089	31.75	0.80	8.71	0.0728	0.1772	0.793

[a] All values are relative to the intensity of interaction, 1.0, appropriate to a group of 2 individuals, when $\mu = 1.0$.

[b] The α appropriate for $N_b = 12$.

[c] $0.5 f_{ap}$ when α remains constant approaches $1/\alpha$ as N approaches infinity. In this case with $\alpha = 0.091$, $1/\alpha = 11.0$. In other words $0.5 f_{ap}$ approaches $N_b - 1$. $0.5 f_{ap}$ is used in the sense of f'_{ap}.

Two deviations from the consequences of social interaction appropriate to N_b stand out as the logical candidates as physiological stressors. First there is the situation in which an existing θ_a is less than the optimum $\theta_a^{(m)}$ or θ_o. This difference is designated as the satiation deficit, θ_d, where

$$\theta_d = \alpha_b f_{aa}^{(m)} - \alpha_b f_{aa} = \theta_o - \theta_a \tag{86}$$

The second stressor is θ_f. It presents a philosophical problem with regard to its assessment as a stressor. At N_b, $\theta_f = \theta_o$. The mechanics of interaction according to the model are such that optimizing (i.e., maximizing) satisfaction from social interaction leads to an equivalent amount of frustration. During evolution, physiology must have been altered such that it became compatible with this amount of frustration. θ_f may be thought of as a nonspecific stressor whose presence in $\theta_f^{(m)}$ amount, that is the amount which will arise when N_m is also N_b, is necessary for stimulating physiology to an optimum level. When θ_f is below optimum, $\theta_f < \theta_f^{(m)}$, there will be a deficit in the nonspecific stressors required to maintain physiology at normal levels. Above optimum levels, when $\theta_f > \theta_f^{(m)}$, θ_f may be considered truly as a stressor to the extent that it exceeds $\theta_f^{(m)}$. As N becomes greater than N_b, θ_f becomes greater than the optimum value of 0.25, and as N approaches infinity θ_f approaches 1.0. This means that nonspecific stressors in the sense of frustration from social interaction can never exceed four times the optimum level. For these reasons I choose to examine merely how θ_f varies as a function of N rather than making any effort to evaluate any possible differential effect resulting from θ_f being greater or less than the optimum.

To see directly how these two stressors, θ_d and θ_f, vary as N changes, a specific case for $N_b = 12$ is given in Part B of Table XI. Here again, as in Fig. 34, it may be seen that the frequency of satisfactory interactions, f_{aa}, declines following either decreases or increases in N from N_b. However, frustrating interactions, f'_{ap} decline as N declines below N_b, and likewise increase as N increases above N_b. There results an approximately 70% deficit in satiation when N declines to 2 or increases to about 122 from the $N_b = 12$. Somewhat more marked changes from the optimum frustrations follow changes in N from N_b.

In order that the change in θ_f as a function of the deviation of N from N_b may be visualized, they were calculated (Fig. 35) for $N_b = 2$ and $N_b = 12$, for which appropriate intensities of interaction are, respectively, 1.0 and 0.302. Only increases in θ_f at N's above N_b are shown. As N_b increases from 2 to 12, the respective intervening curves for θ_f shift to the right, that is, it takes slightly greater relative increases from N_b to produce an equivalent increase in θ_f. For all practical purposes the θ_f curves for all N_b above 12 are identical with that of $N_b = 12$. Initial increases in N

above N_b produce the greatest increase in θ_f. Later equivalent increases in N produce less and less increments to θ_f, frustration.

Satiation deficit, θ_d, increases (Fig. 35) in a somewhat similar fashion as θ_f, but it takes somewhat larger increments in N to produce comparable increments in θ_d. Whereas θ_f most likely represents a quantity of social nonspecific stressors, θ_d most likely reflects emotion of a kind which on the human level we call sadness, foreboding, apprehension, or home sickness. It represents the physiological consequences resulting from needed and perhaps known social interaction.

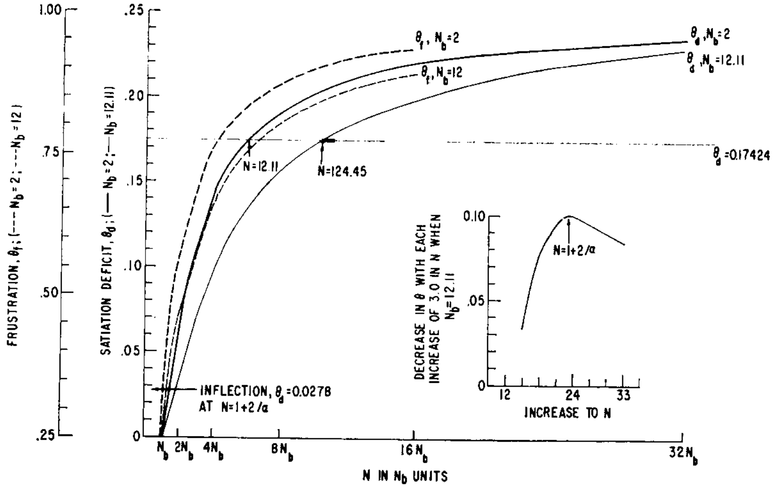

FIG. 35. Satiation deficit and frustration at greater than optimum group size. The inset figure defines the N of maximum decrease in the satiation θ, per unit increase of N.

A word of explanation is in order to reveal why I selected the nonfinite $N_b = 12.11$ instead of 12.0 for examining θ_d in Fig. 35. In brief, I reasoned that there must be some θ_d not compatible with maintaining social life at that corresponding N. When this N is reached there must be some genetic change transpiring which so reduces intensity of interaction that θ_o may be restored. On a rather arbitrary basis, I selected $\theta_d = 0.174$, which is equivalent to a 70% decrease in θ_a from θ_o. Reacquisition of θ_o at this N requires i to decrease to 0.3 of its former level. By such criteria, successively larger N_b, starting with $N_b = 2$, will form a series of 2, 12.11, 124.45, etc. Any such saltatorial series of N_b's may be designated $N_b^{(1)}$, $N_b^{(2)}$, $N_b^{(3)}$, . . ., $N_b^{(n)}$. The θ_d curves for all N_b of 12.11 and above will cross the 0.174 horizontal θ_d line within the small black rectangular area superimposed on this line in Fig. 35. Further elaboration of such saltatorial series of N_b is given in Section XIII, B, 3.

It must be kept in mind that a basic assumption underlying this general formulation of social interaction is that the mean free path of an individual must be large in comparison with the target diameter represented by any other individual. That is, animals must not be so crowded that one individual becomes so physically hemmed in or surrounded by a few others that opportunity to contact many of its associates becomes markedly reduced. When an experimental study violates this condition, what has been said in the above statements will not apply.

2. THE BUDDING OFF OF SOCIAL GROUPS

As the group size increases beyond N_b both the deficit in satiation, θ_d, and the amount of frustration, θ_f, increase in so long as intensity of interaction remains constant. Members of the group will find participation in it both less and less satisfactory and more and more stressful. The question arises, "At what point will members find conditions so unbearable that they will leave or at which the group will split?" Changes in θ_a, or θ_d, as a consequence of changes in N, are proportional to f_{aa}. Therefore, we would like to know if there is some N from which any given change in N brings about a greater change in f_{aa} than a similar change from any other N. The second derivative, $f''_{aa} = 0$, occurs when: $N = 1 + 2/(\alpha_b\mu_o)$ [see Eq. (81)]. This N shall be referred to as N_i.

For $N_b = 12.11$ this arithmetic inflection point comes at $N = 23.22$. As may be seen from the inset graph in Fig. 35 this N marks the point of maximal change in θ_a with a given change in N. At this point an increase in N produces a greater decrease in θ_a than a similar change at any other N greater than N_b. Furthermore, at N_i, θ_d, as calculated by Eq. (86), for any N will always be 0.0278, which represents an 11% deficit in θ_o.

For howler monkeys and man, where the basic N appears to be about 12 adults, the social group size rarely exceeds $2N_b$ unless, as in the case with man, the next well-defined larger group is much larger. It is for this reason that I suspect that N will split or bud off another group when N approaches $(2N_b - 1)$, the point of maximal rate of change in satiation deficit as given by Eq. (85). In essence, this line of reasoning says that by the time a group nearly doubles in size from its basic N, its members will begin to feel uncomfortable in the sense that they do not find participation in the group sufficiently satisfactory. This will lead to enough members leaving the former group so that within each of the two new groups interaction will produce near optimal results.

3. SALTATORIAL CHANGES IN THE BASIC GROUP SIZE

Within most orders, and many lesser taxonomic categories, related species may be found between which there exist marked differences in the typical group size. Caribou and elk characteristically maintain large herds in contrast to the small groups or even isolated pattern of living by mule deer or moose. During the active breeding season, bats of the species *Myotis lucifugus* and *M. yumanensis* roost singly or in small clusters, whereas *M. grisescens* and *M. velifer* maintain large assemblies even during the breeding season. Woodchucks, *Marmota monax,* tend to live in isolation, whereas black-tailed prairie dogs, *Cynomys ludovicianus,* live in large colonies.

Obviously these represent a select group of comparisons. Although I shall not attempt to substantiate here the typical group sizes found within any fairly closely related series of species, examination of many series suggests that there are within each series several discrete basic group sizes with an extensive range between any two nearest sizes not represented by any species. For the present purpose, this conclusion will be accepted as approximating reality. Then the question follows: "What characteristics of physiology and group interactions might lead to saltatorial steps in group size which become fixed by natural selection or cultural evolution?"

In the first place, there must be some condition which induces animals to assemble in far greater group sizes than their N_b, and this condition must remain sufficiently strong to prevent splitting of the group as it approaches $2N_b - 1$ [see Eq. (85)]. Any spatially restricted but locally abundant resource might well so act, particularly if response at the source favored the establishment of a behavioral sink as described in Section XII, C. Increase in group size beyond $2N_b - 1$ would accentuate social discomfort and stress in the sense of increasing θ_d and θ_f (Fig. 35). At some point these factors must become so intense as to produce sufficient decrements in reproduction and survival to threaten the survival of the species. There is no *a priori* basis for judging what this threshold might be. Beyond $2N_b - 1$ each increment in N produces a smaller increment of θ_d and θ_f. Examination of the curves in Fig. 35 reveals that when θ_d is about 0.70 of its maximum and θ_f is slightly over twice its optimum level, any further increments to N produce little further change in θ_d and θ_f. The horizontal line through all curves defines this point on each curve and shall be considered empirically as a limit beyond which further increases in N cannot be tolerated.

If $N_b^{(1)} = 12$, the limit is $N_b^{(2)} = 82$ for θ_f and $N_b^{(2)} = 123$ for θ_d. It will be recalled from Section XII, A that N_b for the Norway rat appeared to be about 12. Although local colonies approximated this number, all members of all colonies were forced to interact at the single source of food and water. Furthermore, the entire population in the quarter-acre pen surrounded by a rat-proof fence made a closed system out of the entire population. At 123 adults (Table X), marked disturbance was in evidence, with only a minority of the females reproducing successfully. In the closed systems contained within a smaller area, described in Section XII, C, severe reproductive disturbance characterized an N of slightly less than 80 adults. Therefore, for the Norway rat at least, when the actual N approaches the increase above N_b presumed to represent the tolerance limit, a degree of physiological disturbance of sufficient magnitude arise as to indicate a necessity for some evolutionary adaptation to the increase in group size for continued survival. Parenthetically, I might add that this tolerance limit for θ_d and θ_f was arbitrarily assigned simply with reference to the slope of the curve, and without prior knowledge that this level would lead to tolerance limit N's so closely approximating those observed in my experimental studies.

One type of evolutionary change which will reinstate θ to its optimum level, that will eliminate θ_d, involves reducing intensity, i, of interaction. It will be recalled that $i^2 = \alpha$, the refractory period following interaction. Now if $N_b = 12$, and the tolerance limit N is 123, a reduction of α from 0.091, the α appropriate to $N_b = 12$, to 0.0082, the α appropriate to $N_b = 123$, will return θ to its optimum value of 0.25. The change in i is 0.3 of its level at the former N_b, that is, from $i = 0.3$ to $i = 0.09$.

With a hereditary change in behavior amounting to a reduction of i to 0.3 its former level, N_b changes from 12 to 123. These would then represent two species, the stem one having an $N_b^{(1)} = 12$ and residing under those environmental conditions not necessitating an evolutionary change in physiology and behavior, and the derived one having an $N_b^{(2)} = 123$ and residing in the presence of those environmental conditions forcing the maintenance of group size far above that of the stem species. If this process is repeated each time θ_d reaches a tolerance limit of approximately 0.607 of the minimum θ_d possible, there arises what might be termed a "satiation deficit saltatorial series of basic N's" which are as follows, starting with $N_b^{(1)} = 12$.

$N_b^{(1)}$	12
$N_b^{(2)}$	123
$N_b^{(3)}$	1,359
$N_b^{(4)}$	15,088
$N_b^{(5)}$	167,645
$N_b^{(6)}$	1,862,544
$N_b^{(7)}$	20,695,365
$N_b^{(8)}$	229,937,917

Each successive N_b will have an intensity of interaction approximating 0.3 that of the preceding. At the 8th and last listed N_b, intensity of interaction would be only 0.0002 that when $N_b = 12$. It seems rather patent that no meaningful behavior could transpire with such a reduced intensity (duration) of interaction. Two-hundred thirty million adults in a semiclosed social system can only apply to the world as a whole for the human species. Reduction of intensity of activity as a means of recovering satiation from social interaction could, in evolutionary terms, likely suffice in mammals to the third stage of 15,000 adults which entails a reduction of i to 0.09 of that appropriate to $N_b = 12$.

A similar series of N_b can be calculated with reference to $\theta_f = 0.775$ or the tolerance limit involved in shifting N_b from 12 to 82. Optimum $\theta_f = 0.25$ can be regained if at this limit i is reduced to about 0.36 of its intensity at the former N_b. Such a "frustration saltatorial N_b series" becomes:

$N_b^{(1)}$	12
$N_b^{(2)}$	82
$N_b^{(3)}$	597
$N_b^{(4)}$	4,491
$N_b^{(5)}$	32,343
$N_b^{(6)}$	238,153
$N_b^{(7)}$	1,753,772
$N_b^{(8)}$	12,914,892

Again this series becomes rather absurd at the upper limit because of the great demand for reducing intensity of interaction. Since semiclosed systems, at least on the human level, and occasionally with other mammals do approach some of these N_b, we must ask what other avenues of evolution exist.

For this we must assume that intensity of interaction remains constant at some level approximating that for $N_b = 12$, but that a tolerance limit for θ_d and θ_f exists. At the N of these limits a change in behavior may take place which insulates the individual by producing subaggregates in which, for all practical purposes, the individual at any particular time is a member of a subgroup in which $N_b = 12$, even though many other subgroups exist in the environs. The individual may be a member of several such groups but participates in only one at a time. Such changes in behavior can be considered to be of either genetic or cultural origin. In either case, so long as any tolerance limit for θ_f and/or θ_d exists, there must be saltatorial steps between successive N_b, and only a few such steps are possible even if the tolerance limit arises at a somewhat lower level than hypothesized above.

If later research supports this hypothesis it will have considerable bearing on our understanding of the course of evolution involving change in group size. It will mean that gradual changes in heredity or culture will rarely have transpired. Rather, from the pool of gene variability accumulated in the species, there will be rapid shifts in gene frequencies of many genes, thus resulting in a new phenotype. In so long as environmental conditions facilitate maintenance of its N_b by a species, its gene pool may become quite diverse through the accumulation of mutant genes. Then, once environmental circumstances force the species to maintain an elevated N near its tolerance level for θ_d or θ_f, an extreme selection pressure will arise for reducing the frequency of all genes except those which adapt the species to its new N. A genetically variable $N_b^{(1)}$ species will thus rapidly be transformed into a genetically rigid $N_b^{(2)}$ species.

On the cultural level such a process of saltatorial change in basic group size demands that the value system which dictates acceptable roles of action and communication be preserved even after the usual group size has far exceeded the N_b appropriate for that value system. At the same time, under the pressure of increases in θ_d and θ_f, small segments of the closed system will develop values divergent from the main group. At the tolerance limit of θ_d and θ_f, when N has so diverged from $N_b^{(1)}$, there will arise a marked and rapid shift to the prevalence of those newer values appropriate to $\theta_o^{(m)}$ and $\theta_f^{(m)}$ at $N_b^{(2)}$. Value frequencies and gene frequencies become isomorphic in these two avenues through which there can be a saltatorial evolution from one basic group size to another.

Basic group size for adults only in the primary steps of human cultural evolution seem to include the 10–16 range, 50, 200, and 2,000. This series resembles neither of the hypothetical saltatorial group size series except in its saltatorial character. The hypothetical series merely demonstrated the kind of changes following from stated assumptions. The exact series followed by any line of change depends upon the threshold tolerance limit for θ_d and θ_f as well as three factors ignored in our discussion up to the present. Discussion up to this point assumes $\mu = (dv/A) = 1.0$, where d represented the target diameter of other individuals, A the area inhabited by the N individuals, and v the velocity of movement of individuals. In essence, μ represented the likelihood in time t of one individual encountering another.

It can readily be shown from Eqs. (52) and (60) that θ_a, the satiation from social interaction, i.e., αf_{aa}, can remain constant regardless of changes in μ. At least this is so if the physiology and behavior of the species is completely adjustive. From the general form of Eq. (60) where $\mu' = 1.0$, $\alpha = 1/[\mu(N - 1)]$, it follows that each doubling of μ, that is doubling the likelihood of one individual meeting another, necessitates a halving of α, and thus reduces intensity of interaction from $(\alpha)^{1/2}$ to $(\alpha)^{1/2}/2$. If we follow the prior assumption that each species has an optimum intensity of interaction, then each increase in μ will have an analogous effect to increasing group size. In other words, increasing μ above 1.0 will increase θ_d and θ_f. When we are concerned with the effects of changes in μ but assume α remains static at the value appropriate to $\mu = 1.0$, then α must be calculated from Eq. (60) with $\mu' = 1.0$ and f_{aa} calculated with this α by using Eq. (52) above and some value of μ different from $\mu_b = 1.0$.

For example, consider $N_b = 12$. Then $\alpha_b = 0.091$, and $\theta_b = 0.25$ (see Table XI). If N doubles and μ remains 1.0, θ_a becomes 0.219, but if N remains constant at N_b but μ doubles to 2.0, θ becomes 0.195. Thus, a comparable increase in μ produces a greater deficit in satiation, θ_d, from social interaction, than does a double of N.

Thus, saltatorial evolution of $N_b^{(1)}$ to $N_b^{(2)}$ may be necessitated either by an increase in N or an increase in μ. The rate of change in N and μ may well offset the tolerance limit of θ_d or θ_f and thus affect the magnitude of the shift from $N_b^{(1)}$ to $N_b^{(2)}$. dv essentially measures the rate of communication and A the space within which this communication takes place. Thus, μ will increase if A remains constant and dv increases, or if dv remains constant and A decreases. If both the rate, that is means, of communication increases and the distance over which communication must take place decreases, μ will increase very rapidly. Detailed consideration of communication is given in the following section.

4. THE μ COMMUNICATION FUNCTION

We have already seen that $\mu = (dv/A)$, as defined by the previous Eqs. (35) and (80), is a communication-enhancing or contact-producing factor. (See prior discussion under Terms and Equations, Section XIII, A, 1.) Other than for pointing out in the latter part of Section XIII, B, 3 that altering μ has much the same consequences as altering N, we have been content to consider consequences of variability in other functions when μ remains constant at that value $\mu_b = 1.0$ appropriate to N_b.

I was led to examine the question of the consequences of varying μ as a result of the observation by Birdsell and by Zimmerman and Cervantes, cited in Section XII, E. They observed that where a conflict of values arises in a group there results a reduction in group size. Here, we are concerned with the special case where attitudes or values comprise a major aspect of the target diameter d. Each member of the group holds some n number of values by which others recognize it as an appropriate object for interacting. When some particular value is shared by all members, it may be said to possess a unitary value in contributing to target diameter. In other words, under this circumstance all individuals possess the same target diameter, $d = 1.0$. With reference to Eq. (35), a unity value for target diameter merely means that there has been genetic or cultural adaptation to the actual magnitude of d, such that $\mu = dv/A = 1.0$. However, if an individual expresses a value shared by only a few of his associates, he will by this fact be much more likely to be perceived by his associates, and thus more likely to be reacted to by them. His target diameter will be increased. Furthermore, it is logical to assume that the larger an individual's target diameter, the greater will be the response evoked from associates. In so long as all other d value characteristics remain identical among the members of the group, the one which does vary among members will assume the sole role of influencing target diameter. As a first approximation this response-evoking capacity, which I will call S, of a particular d value can be taken as being inversely proportional to the probability p of its being encountered among the members of the group of N individuals.

Therefore:

$$S = 1/p \tag{87}$$

Where only one component of d varies, and since those shared components of d may be ignored, $d \approx S$. For the special case where all members have the same d:

$$\mu = (dv)/A = (Sv)/A = 1.0 \tag{88}$$

Furthermore, where area, A, remains unchanged at the value appropriate to N_b it has the relative value of 1.0. Therefore:

$$Sv = 1.0$$

$$S = 1/v \tag{89}$$

And considering Eqs. (87) and (89)

$$v \approx p \tag{90}$$

Lastly:

$$v = 1/S \tag{91}$$

Variability of the target diameter d among individuals means that d comprises an assembly of traits, physical size, color, vocalizations, behavior, and attitudes or values. d is the total complex. Components shared by all members will be referred to as (d). Those remaining traits, through which an individual differs from its associates, represent a genetically and culturally determined phenotype to which the response evoked from associates is a function. By *response* I here refer solely to actions reflecting the choosing or rejecting of an associate. Such a response may be a function of the trait itself or may be a function of a recognizable degree of difference between one individual and its most similar associate. I believe that such degrees of difference form the primary basis for the maturation of social behavior and social organization within a group. Further treatment of this topic follows in Sections XIII, B, 5, a and b; XIV, A and B.

Such traits or degrees of difference comprise the units influencing social behavior. These units will here be called d-genes. As stated above they may be of either hereditary, or cultural origin. Any d-gene, $g^{(1)}$, may develop an allelic series of differing or "mutant" forms $g_1^{(1)} \cdots g_n^{(1)}$. When degrees of difference, and not the absolute amount or kind of difference, forms a d-gene there can only be two forms of a particular d-gene, $g_A^{(1)}$ and $g_a^{(1)}$, where $g_{(a)}^{(1)}$ represents a degree of difference from the ideal type, the ideal d, and $g_A^{(1)}$ represents the retention of the ideal traits for which $g_a^{(1)}$ represents the divergence. d-genes of the type $g_A^{(1)}$ will be called dominant d-genes, while those of the type $g_a^{(1)}$ will be called recessive d-genes. d-genes of the latter type are treated in detail in Sections XIII, B, 5, a and b. Without specifying the allelic nature of any d-gene it is obvious that the target diameter d is a function of (d), $g^{(1)}$, $g^{(2)}$, $\cdots$, $g^{(n)}$.

Let

$S_i{}^A$ represent the response-evoking capacity of any ith individual with reference to the probability of its being chosen by associates as an object of affection. $S^{(A)}$ is related to Schaeffer's *love-acceptance* referred to in Section XIV, C.

$S_i{}^{(a)}$ represent the response-evoking capacity of any ith individual affecting the probability of his being rejected by associates. $S^{(a)}$ is related to Schaeffer's hostility-rejection referred to in Section XIV C.

$S^{(A)}$ is a function of both (d) and the assembly of dominant d-genes, while $S^{(a)}$ is solely a function of recessive d-genes. The probability of encountering the common (d) assembly of traits will be 1.0. Therefore, from Eq. (87) the positively affective stimulus-evoking capacity of this commonly held assembly of traits will contribute to the $S^{(A)}$ of an individual inversely proportional to the probability of its being encountered within the N individuals forming the group. Thus where p_g represents the probability of encountering a particular d-gene and A, B, C, $\cdots$, represents the dominant "allele" of d-genes (1), (2), (3), $\cdots$, and there are $N - 1$ d-genes of the degrees of difference type, then:

$$S_i^{(A)} = \frac{1}{p_{(d)}} + \frac{1}{p_g{}^{(\,)}} + \frac{1}{p_{g\mathrm{B}}^{(1)}} + \cdots + \frac{1}{p_{g(N-1)}^{(N-1)}} \qquad (92)$$

Similarly where a, b, c, $\cdots$, $N - 1$ represent recessive d-genes of the degree of difference type:

$$S_i^{(a)} = \frac{1}{p_{g_\mathrm{a}}^{(1)}} + \frac{1}{p_{g_\mathrm{b}}^{(2)}} + \cdots + \frac{1}{p_{g_{(N-1)}}^{(N-1)}} \tag{93}$$

Equation (92) applies strictly only for that single individual which has preserved all the dominant or ideal traits. For every other individual one or more terms in Eq. (92) will be missing, depending upon replacement of the dominant *d*-genes by recessive ones. Similarly Eq. (93) applies strictly only to that individual in which all traits, other than those commonly held (*d*), have diverged from the ideal, that is in that individual in which all non-(*d*) *d*-genes are recessive. For all other individuals one or more terms in Eq. (93) will be missing.

Consider the case where all *d*-genes in a group had been identical up until a particular point in time, at which a particular *d*-gene, $g^{(1)}$, "mutated" to $g_2^{(1)}$ in half the members. In this mutation $g_2^{(1)}$ diverged sufficiently from $g_1^{(1)}$ to make quite distinct the derived from the original. Then the probability of each in the group will be only 0.5 and thus the response-evoking capacity of each will rise to a relative value of 2.0. For the average individual S will have increased from 1.0 to 2.0.

The total N_b members of a basic sized group will consist of N_1 type 1 individuals possessing $g_1^{(1)}$ and N_2 type 2 individuals possessing $g_2^{(1)}$. Thus $N_b = N_1 + N_2$. Any individual will be considered as being able to encounter itself in the sense of being aware of its own characteristics.

Considering this premise it follows that the probability p_1 of any type 1 individual being met by associates becomes:

$$p_1 = N_1/N_b \tag{94}$$

Similarly, the probability, p_2, of type 2 individuals being met by associates becomes:

$$p_2 = N_2/N_b \tag{95}$$

From Eq. (87) it follows that response-evoking capacity, S_1, of any type one individual, and S_2 of any type two individual will be respectively:

$$S_1 = N_b/N_1 \tag{96}$$

$$S_2 = N_b/N_2 \tag{97}$$

Therefore, the mean response-evoking capacity, $\bar{S}$, of the N_b individuals becomes:

$$\bar{S} = \frac{N_1 S_1 + N_2 S_2}{N_1 + N_2} \tag{98}$$

Substituting Eqs. (96) and (97) with (98)

$$\bar{S} = 2.0 \tag{99}$$

The S of Eqs. (96) to (99) is essentially that of Eq. (93) in which $g_1^{(1)}$ and $g_2^{(1)}$ become, respectively, recessive d-genes, $g_a^{(1)}$ and $g_b^{(2)}$.

As may be seen from Eq. (98), whenever N_1 or N_2 is zero, that is, all members of N_b have the same target diameter, the response-evoking capacity of each member of the group has a relative value of 1.0. However, Eq. (99) shows that as soon as N_b becomes divided into subgroups N_1 and N_2, even though the divergent N_2 has only one member, the average response-evoking capacity doubles. The probable consequence of this doubling depends upon the relative numbers of N_1 and N_2. Consider $N_b = 12$, then when N_1 and N_2 have the sizes given below, members of each will have S_1 and S_2 as shown in Table XII.

TABLE XII

THE INFLUENCE OF RELATIVE SIZE OF SUBGROUPS OF $N_b = 12$ ON RESPONSE-EVOKING CAPACITY

N_1	N_2	$\bar{S}_1$	$\bar{S}_2$	$\bar{S}$
12	0	1	0	1.0
11	1	1.0909	12	2.0
10	2	1.2	6	2.0
9	3	1.3333	4	2.0
8	4	1.5	3	2.0
7	5	1.7143	2.4	2.0
6	6	2.0	2.0	2.0

The S of the members of larger subgroups can never exceed twice the optimum level, but the S of the members of smaller subgroups has a maximum of N times that where all members of N_b have the same target diameter. To understand the consequences to an individual resulting from possession of a large S, we must inquire further as to its implication. In the first place, it may evoke more frequent responses from associates. If the group is essentially an N_b one, such an individual will experience more contacts than otherwise would be anticipated. This will have the same deleterious consequences to him of being in too large a group. S in this case may be thought of as increased target diameter, d. On the other hand, a heightened S may evoke more intense reaction, i, from associates at time of contact. This will have the consequence of increasing the refractory periods, α, and thus with frequency of contacts maintained harmonious with N_b, the thetas, both those of satiation and frustration, will be increased. In this situation the critical point becomes the attitude of associates toward such individuals. If the attitude toward this individual possessing rarely encountered characteristics is one in which the desired characteristic is venerated or desired by the majority not possessing it, then the resulting intense interaction will have the consequence of more frequently resulting in an α_{aa} satiation type refractory period. However, it is much more likely that the strange, rare characteristic will elicit an aggressive or rejection type response leading to an α_{ap} frustrating type refractory period for the individual with the heightened S.

When the N_1 subgroup represents a majority, they can achieve a return of their μ and θ's to more nearly normal levels by ejecting the aberrant N_2 individuals. However, the minority N_2 members of the $N_1 + N_2$ group suffer most from heightened μ and θ's. Therefore, their seeking escape from the group becomes a motivating force greater than that of ejection by their associates.

If neither N_1 or N_2 form a clear majority, the most likely result will be a splitting of the group in half, but with retention of both N_1 and N_2 type individuals in each smaller group. This consequence derives from the following:

When S doubles, μ_b doubles, the new $\mu = 2.0$.

The "effort" of the group will be to make the easiest adjustment which will make $\mu = 2.0 = \mu_o$. This route lies in reducing the N which was an N_b to an N_o. From Eq. (78) it follows that:

$$N_o = 1 + \frac{N_1}{2} + \frac{N_2}{2} - \frac{1}{2} \qquad (100)$$

The best approximation any group can make is to divide in half. Each half must contain nearly equal numbers of N_1 and N_2. If all N_1 formed a group spatially distinct from the N_2 members of the former N_b, the μ of every member in each group would automatically return to 1.0 since within each new and smaller group all members would have the same target diameter. Thus, with the N of each new group being only $0.5N_b$, every member would experience a marked reduction in satisfaction and frustration thetas below optimum since the frequency of contacts f_c [Eq. (34)] would automatically be reduced.

In discussing this concept of a few divergent individuals or even a single one doubling the μ of the entire group, one of my colleagues remarked that such an increase appears unreasonable. Three examples will suffice to demonstrate the reasonableness of this assumption. Barnett (1955) maintained established groups of Norway rats in large cages. Despite or because of the existing hierarchy characterizing the group, all rats exhibited relative amicable relations, one to another. All presumably had developed nearly identical target diameters. Introduction of a single alien rat immediately produced a state of turmoil within the group, particularly intense actions being directed toward the alien by all members of the established group. In such experiments the alien rat, the one with the markedly differing target diameter, frequently died within a day or two. This death came, not as a result of wounds received, but as a result of inability to accommodate physiologically to the intense action directed toward him. His θ_f exceeded a threshold compatible with survival.

Or we may take any one of the several incidents publicized by the press and television during 1960 and 1961 in which "Freedom Riders" engaged in action which challenged the established value systems of certain segments of the socially dominant whites in the Deep South of the United States. Such actions frequently evoke drastic reaction, including physical violence, from members of the established group. Furthermore, many cross currents of elevated intensity of interaction became generated within members of the established group as they considered appropriate adjustments to the threat to their held values and to their prior target diameter.

The point I have been making in both the theoretical formulation and in these examples is that a qualitative change in the target diameter of a portion of the group will produce both an increase in μ and an increase in intensity of interaction. Another pertinent example is one I have previously given (Calhoun, 1956, pp. 87–88). That example concerns the establishment of a new group, designated as "C57 Colony 1B," from two smaller groups of mice not previously having contact with each other. After provision of an access door through the wall previously separating the two groups, the males from the socially more integrated group invaded the living space of the other males. Not only did the former attack the latter, but the males from the more socially integrated group began a period of intense fighting among themselves such as had never previously been observed.

Admittedly, all three of these examples include introduction of aliens into an established group rather than the hypothesized divergence in target diameter of a portion of a single group. However, it is difficult to imagine a portion of a group altering their target diameter without temporary partial isolation from the remainder. So, in effect, the consequences of divergence of target diameters among members of a group will be the same regardless of how the group is assembled.

In actuality

$$\mu = (Sv/A) \tag{101}$$

However, in most instances, I shall continue to consider $\mu = (dv/A)$ as previously. But when so doing, it must be understood that d is used in the sense of its S response-evoking capacity.

When S changes from 1.0 to 2.0 for the reasons relating to Eq. (99), μ will no longer be $\mu_b = (dv/A) = 1.0$, but μ will then become $(2dv/A) = 2.0$. Inserting $\mu = 2.0$ into Eq. (78), in which μ' remains 1.0, for the special case where $N_b = 12$, then N_o becomes 6.5. This means that in the presence of conflicting values group size must be reduced for each individual to maintain its θ_o, its optimum level of satiation from social interaction. Increase in μ follows increases in d or v, or decrease in A. Regardless of the origin of the increase in μ, reduction in group size should follow.

Such reduction in group size should not be instantaneous. Consider $N_b = 12$, $\alpha_b = 0.091$ and $\mu = 2.0$ and the group has not yet fragmented. From Eq. (82) it is obvious that $N_b = N_i$, when $\mu_o = 2.0$ and $\alpha = \alpha_b$, and that θ_d, the deficit in satiation from social interaction, will be as great as if μ had remained unchanged at 1.0 and N_b increased to $[1 + 2(N_b - 1)]$. [Refer to Section XIII, B, 2.] This is a very interesting consequence for it means that when μ increases to 2.0, $N_b = N_i$. Recall that N_i is that N at which an increment in N brings about the greatest change in θ_d. Since groups do resist division and since any increase in μ is likely to be gradual, the most likely time for fragmentation of the group is when μ becomes 2.0 and $N_b = N_i$. Then N_b will divide into two groups approximating N_o determined by Eq. (78). Roughly, this says that when the ease of communication doubles as a result of a doubling of the response-evoking capacity S, the group will approximately divide in half if it is to optimize satiation from social interaction.

This process of halving the basic group size each time the ease of communication becomes twice as efficient cannot continue long if $N_b = 12$, because by the fourth doubling of μ, sexual reproduction could no longer be tolerated. That is, N_o would be less than two individuals. The practice of divorce by the human animal reflects this process. We now have another question raised: "What avenue of adaptation or adjustment is open if N_b remains 12 and i remains unchanged at i_b?"

Although μ theoretically may be defined in terms of attributes of d, v, and A external to the organism, any solution to this question demands that μ must in effect be reduced back to 1.0 by some compensating mechanism.

This mechanism which alters the probability of a contact being socially perceived has been called μ'. In Eqs. (38) to (55) it was shown that $\mu\mu'$ represents the appropriate interaction between these two factors. So far μ' has been elaborated no further. $\mu\mu'$ then becomes the communication constant, more explicitly stated as $(dv/A)\mu'$. Since μ can vary as a result of any one of its contained factors, d, v, or A, fluctuating alone, one cannot escape the conclusion that during evolution a separate compensating mechanism for each must have arisen. This means that there is a d', a v', and an A', and that $\mu' = (d'v'/A')$. Furthermore, when $\mu\mu' = 1.0$, $\mu' = 1/\mu$. Having arrived at these insights, one is logically lead to ask: "What do d', v', and A' most likely represent biologically?" Although answering this question is not necessary for the general theoretical formulations, an attempt to specify their more likely nature may be helpful in searching for their identification.

d' represents the degree to which the stimuli emanating from any configuration *pass unselectively* from the sense organs into the memory store of the central nervous system (CNS). Thus, an increase in d' means facilitation of passage of stimuli into the CNS, while a decrease in d' indicates impeding or preventing stimuli from getting to the CNS. When the target diameter of associates increases through evolution by acquiring more d-genes, a compensating evolution of a d'-mechanism will permit a discrimination among the d-genes such that in that brief span of time required for psychological contact only a portion of the d-genes of the other individual will be responded to. It must be kept clearly in mind that an increase in the efficiency of the mechanism which serves to alter d', decreases d'. Such a decrease in d' implies the evolution of a filtering device which reduces the amount of information about others per unit time arriving at the sense organs, which is permitted to pass from them into the integrative centers of the nervous system. Without specifying what CNS structure serves the d' function, it meets the requirements hypothesized by Broadbent for his CNS "filter." See Section IX.

v' also represents a process internal to the individual. It cannot have any influence upon the motor component of v. Therefore it must affect the consequences of those sensory capacities which enable the individual to achieve a psychological contact prior to an actual physical one. This is the r component of velocity mentioned in Section XIII, A, 1. Just as an increase in r increases v by decreasing the time required for a contact, so must a decrease in v' function to increase the time from the moment of input of a signal from a d-gene at the sensory organ until this transformed signal reaches and evokes a response at an effector. Thus v' could represent either a structural or biochemical alteration in the time required for an impulse to pass over a synapse, or it could be represented by an alteration in the number of neurons in the circuit which will also alter transmission time. But we must not confuse the magnitude of v' with the efficiency of the mechanism involved. An increase in v' means a decrease in the efficiency of the mechanism, that is increased synaptic transmission, while a decrease in v' follows from an increase in the efficiency of the mechanism in impeding the passage of the signal along the circuit between the sense organ to the effectors.

A word is required to differentiate clearly d' from v'. d' governs the probability of a signal relating to d-genes getting through the Broadbent type hypothesized "filter," while v' applies to the speed of transmission from the filter to effectors.

In a similar fashion, conceptualization of A' must be in terms of counteracting A. Where an N_b group is living under optimum conditions, A may be considered to be equal to 1.0. Optimum conditions will continue even though A changes in so long as $AA' = 1.0$. For the sake of simplicity we are considering the case where the only change in the system pertains to A. Recall that A represents the area which the group shares. In essence then A alters the time between contacts. Therefore A' must operate in a similar but opposite direction to A. Suppose that A increases. In effect this is equivalent to a decrease in density. Under such circumstances there can be no internal mechanism enhancing the probability of an *actual* contact. Therefore, when A increases, an A' compensating mechanism involves an imagined contact. To the extent that such an imagined contact leads to an equal α refractory period, an A' mechanism will be effective. Since an increase in A implies a decrease in A', a decrease in A' means an increase in the capacity to store memories of associates, which can compensate for their absence. Such an increased storage of memories implies an increase in cortical mass.

On the other hand, suppose that A decreases. This will reduce the time elapsing between contacts, and since this will have the same consequence as increasing N when we are concerned with an N_b group, its members will experience an increased θ_d and an increase in θ_f above the optimum level. In this situation A' must function to increase the relative time between contacts. The only way for this to happen is for the intensity, i, of interaction to decrease. Recall that intensity of interaction has been measured in terms of its duration, and that $i = (\alpha)^{\frac{1}{2}}$ when α represented the duration of the refractory period following interaction. Furthermore, Eq. (60) becomes:

$$\alpha = \frac{1}{\mu\mu'(N - 1)} \tag{102}$$

when we consider the several factors in the general sense where a variation in one may influence any other.

Then

$$\alpha\mu' = \frac{1}{\mu(N - 1)} \tag{103}$$

The reason for stating the equation in this fashion is that μ' cannot alter μ as such but can only alter its effects through changing something else.

What Eq. (103) implies is that where A' is the factor which produces the variability in μ', it can be effective in maintaining θ_o but not necessarily an optimum θ_f (see discussion following Eq. (74)), provided it acts as a governor on the intensity of interaction independent from the influence upon i exerted by d. A decrease in the A component of μ indicates a decrease in the home range σ (see Sections II–V). The significance of this line of reasoning is that this A governor, which controls i, is likely to be identical to the one previously postulated for determining the duration of an outward trip from home. In the general sense, this governor controls the duration of behaviors. Social interaction merely represents one specific category of behaviors. Related to the above discussion, it may be noted that Eqs. (69) and (103) are equivalent since $\mu' = 1/\mu$, so long as $\mu = 1.0$ or $\mu > 1.0$. As originally formulated in the discussion before Eq. (38), μ' simply operated as a probability of an actual contact being perceived. However, the above and following discussion indicate that μ' can exceed 1.0. By imagining contacts, which actually do not occur, through a decrease of the A' component of μ', μ' can exceed 1.0.

In terms of the model proposed in Section III, A, whenever A decreases, the rate of firing of the neuronal net of the governor will increase. Thus, an increase in A' represents an increased rate of firing of the neuronal net of the governor.

Previously I pointed out that a decrease in A' to compensate for an increase in A might be visualized as an hallucinatory process. There is no reason why A' cannot equally involve the governor of intensity of activity when A increases above A_b normally appropriate to N_b; a decrease in A' would represent a slowing of the firing of the neuronal net of the governor, which change would then permit a longer duration of interaction. This longer duration of interaction would compensate for the fewer f_{aa} interactions possible in a larger A.

The concept of social perception of contacts subsumed under μ' thus includes a wide variety of processes. It includes (1) selective acceptance of stimuli to be integrated in the central nervous system; (2) impedance or facilitation of passage of signals across neuronal synapses; (3) alteration in the length of a neuronal circuit; (4) hallucinating a contact; and (5) governing the intensity of interaction. These μ' capacities for adjustment are most likely to be found farthest advanced in those species in which d, v, and A fluctuate most markedly with reference to all members of a group within the life span of every individual. However, over long spans of time encompassing many generations, a gradual increase in d, v, and A should increase the complexity of social life possible. At least this conclusion holds to the extent that enhanced synaptic transmission, increased duration and intensity of behavior, and increased discriminatory capacity foster more effective social behavior.

The following summary of presumed relationships may serve as a basis for evaluating the consequences of change in the components of μ and μ'.

External change	*Internal change*	
Increase in	*Decrease in*	
d	d'	= Increase in discriminatory capacity
v	v'	= Impeded synaptic transmission
A	A'	= Increased duration and intensity of behaviors, or Increased memory storage of social stimuli permitting hallucinated interactions which indicate increase in cortical mass
Decrease in	*Increase in*	
d	d'	= Decreased discriminatory capacity (i.e., less selection of stimuli passing the "filter")
v	v'	= Enhanced synaptic transmission
A	A'	= Decreased duration and intensity of behavior, or decreased memory storage of stimuli which are available for producing hallucinated social interactions which indicates decrease in cortical mass

These relationships represent intuitive logical deductions. d' and A' serve as fairly satisfactory first approximations. With progressive social evolution, d and A generally increase. Along with this trend, discriminatory capacity increases, cortical mass increases, and ability to maintain a behavior for longer periods of time increases, all of which tend to harmonize with the model. However, I am less satisfied with my formulation of v' (Section XIII, A, 1). The reason for this opinion is that with advancing social evolution there presumably arises an increase in v_1, that sensory extension of the self to produce psychological contact before bodily contact. This should produce the opposing phenomenon of impeded synaptic transmission. For the present, I can see no rational basis for reconciling impeded synaptic transmission with social advances.

v' merely connotes alteration of sensory perceptions of others involving some distance between the two individuals concerned. My supposition that alteration of synaptic transmission subserves v' may well be wrong. The important point for the present is simply recognition of the likelihood of some such mechanism whose evolution is influenced by social conditions.

I have pointed out that since μ can change as a result of independent change in d, v, and A, consequently there must be discrete phenomena in the individual representing what I call d', v', and A', which can change independent of each other. Nevertheless, it is quite likely that the components of μ and μ' do have interactions. The concept of intensity (duration), i, of social action includes control of i by both internal and external factors. The internal factor is A', the "governor" previously discussed. The external factor is the d of the other. The greater d, the greater i. Thus, d can influence the governor. This means that an increase in the d of associates can decrease the A' of self.

In studies with rats recently completed (Calhoun, 1962b) some rats develop a high v while others develop a low v. Those with a very high v exhibit high i in terms of both intensity and duration. This suggests that in some way an increase in v leads to a decrease in A'. Furthermore, male rats with very low v commonly respond as though they did not make adequate discrimination of the cues emanating from associates. They sexually mount associates without regard to their age, sex, or sexual receptivity. These observations suggest that lowering of the motor components of self's v increases self's d', which suggests that somehow when an animal decreases its velocity its ability to discriminate among available social stimuli also becomes reduced. All I have attempted to do in the preceding paragraphs is to lay the groundwork for understanding the meaning of the contact-modifying factor μ'.

Decreases of μ *re* increase in N: We are here concerned with the special case where the area, A, remains constant as numbers of individuals, N, increase. This means that density increases. We have already seen that an increase in N with μ held constant leads to a deficit, θ_d, in satisfaction from social interaction as well as an increase above optimum of the frustration, θ_f, from such interaction. As density increases one should anticipate μ changing before μ'. Therefore we shall consider μ' as remaining constant at the 1.0 value appropriate to N_b but let N increase. In each instance we wish N to become N_o, which means that θ_o and $\theta_f{}^{(m)}$ will be optimum. Consider the case where $N_b = 12$ and intensity of interaction remains at i_b, it may be seen from Eq. (80) that successive doublings of N_o demands successively slightly more than halving of μ_o:

N_o	μ_o
12	1.0
24	0.478
48	0.234
96	0.116
192	0.057
384	0.028

Where $\mu = \mu_o$ and $N = N_o$ it may be seen by substituting Eq. (80) into Eq. (34) that the frequency of contacts will remain constant at $(N_b - 1)$ regardless of the increase in density. Since we are considering the special case where area, A, remains constant, the constancy in the absolute number of contacts despite increases in density can only derive from decreases in the d or the v component of $\mu = dv/A$.

Where decreases in μ transpire within the lifetime of an individual as an adjustive change to increase in density, and where this decrease in μ results solely from a decrease in the target diameter, d, this change must be reflected through reductions in the frequency of usage of signaling mechanisms or of the intensity of such signals. Vocalizations should occur less frequently, be less complex, and of reduced intensity. Bodily display characteristics under voluntary control should similarly be reduced, as should also the use of chemical signals. Similarly, when a species, A, now exhibits an N_b of 80–120 or 800–1400 (see Section XIII, B, 3) but there is reason to suspect that at some earlier era it had had an N_b of 2 or 12, such as is still expressed by a related species (or genus), B, then a comparative examination of species of types A and B should reveal that members of species B more frequently resort to the utilization of vocal, display, and chemical signals and that these are of greater complexity and intensity than in species A. In making any such comparisons it is well to keep in mind the earlier hypothesis that the change of an $N_b = 2$ to an $N_b = 12$ may lead to an increase in complexity of the signal. For this reason, it is more appropriate to compare a species whose N_b has a typical range of 7–19 with one which rarely falls below 80. Such comparisons will provide critical tests of the general formulation.

In like fashion, velocity, v, may be the factor which becomes reduced as density increases. This reduction may be expressed in any of the three aspects of v listed in Section XIII, A, 1. Sense organs may become less effective with reference to the animals' perception. This reduces v_1. Such a tactic must be effective only through genetic changes and so can serve only as a long-term adaptive mechanism. The animal may also reduce its v_2 by way of reducing the number of trips it makes, or by altering the time and place of its activities. This strategy includes initiating activity while others are resting, or by becoming cryptic in the sense of becoming arboreal or subterranean. Finally, the animal may reduce its v_3, its actual rate of movement.

Although such reductions in d and v will lead to a reduction in μ which will compensate for increase in density, it is obvious that μ must decline so markedly as to present biological limits of effectiveness. Further accommodation to increases in density must require μ' to decrease also. Reduction in this communication-inhibiting or contact-blinding factor means (a) decreased duration or intensity of behaviors or decreased memory storage (i.e., increase in A'); (b) increase in discriminatory power in the sense of screening out portions of those stimuli of the d of others requisite for eliciting responses (i.e., decreasing d'); or (c) impeded synaptic transmission (i.e., decreasing v').

5. Behavioral Origin of Response-Evoking Capacity, S

a. The target diameter genotype as determined by varibility of behavioral traits. I now wish to present the logic of why variability of behavioral traits becomes inevitable. In fact, as aminals become more social, variability in physical traits must become of less importance in determining the kind and intensities of interaction. So let us start with the case where all individuals possess identical heredity and therefore identical physical characteristics. Even for so simple an organism as the house mouse, marked differences in capacities for social involvement develop despite the fact that the members of the group come from a stock made genetically homozygous by nearly a hundred generations of brother-to-sister inbreeding (Calhoun, 1956).

The initial formulation of social interaction dealt with a deterministic model in which all individuals were identical. It showed that half the time an individual was in the responsive state it would meet another responsive individual and half the time it would meet another in the refractory state. Thus, even under ideal conditions, an individual would be frustrated as frequently as it would be satisfied from social interaction. But satisfaction will not likely precisely alternate with frustration. Furthermore, if we consider some arbitrary relatively short span of time when the group first forms, determined by the average individual having, for example, a total pool of interactions equivalent to 2–5 times the number of individuals in the group, then something like the following will have transpired:

Each individual's behavior toward another may be characterized by its form or pattern and by its timing with regard to whether the other individual involved in the interaction is also in the responsive state (the a state) or whether it is in the opposite or nonresponsive state (the p state). Initially the form of the behavior of all individuals in the responsive state will be identical. Identical form denotes possession of the entire assembly of traits, d, by every individual. With each individual contacting its associates in a random sequence over time, it is inevitable that some, who are in the responsive a state, will purely by chance more frequently encounter others who happen to be in the nonresponsive p state. Each such encounter will throw the responsive individual into an α'_{ap} frustrating type refractory period. Thus, the appropriate behavior of this individual will not only not be rewarded, it will actually be punished. After this individual passes through its α'_{ap} refractory period and again enters the responsive state, some random change may typify its behavior. The more frequently it is frustrated, the more likely will its behavior become deviant simply because there has been so infrequent reinforcement of its original appropriate form. Conversely, those individuals which, when they are in the responsive state, have met another also in the responsive state, will have the original appropriate behavior rewarded or reinforced. The behavior of such individuals will remain much in its original form.

In this way the members of a group may be rank ordered according to the degree to which their behavior has deviated from the original. Each recognizable unit of deviation represents a recessive *d*-gene. Each unit of retention of the original behavior pattern from which theirs has been a deviation represents a dominant *d*-gene. The more dominant *d*-genes an individual possesses, the more intensely will associates respond to him in a positive affective manner, and the more likely will he be chosen as a partner or leader. Conversely, the more recessive *d*-genes an individual possesses, the more intensely will associates impose restraints or sanctions on him, and the more likely will they reject him.

It is useful to borrow terminology from genetics which deals with heredity. Let upper case letters represent dominant *d*-genes, and lower case letters represent recessive *d*-genes. Such a system for an $N = 11$ is shown in Table XIII. Here (d) represents the common traits shared by all members of N. (d) plus the remaining dominant and recessive genes specify an individual's *d*-genotype. That individual which has been exposed to the least number of circumstances producing changes in its *d*-genotype may be said to possess the "ideal" *d*-genotype. All other individuals will diverge more or less from this ideal. They may be rank ordered from the alpha individual with the ideal *d*-genotype to the omega *n*th ranked individual, which differs most from the alpha one. Each can then be assigned a similarity rank, R. The alpha individual is represented by R_1; the one who differs least from the alpha has R_2; while the individual who differs most from the alpha has R_n. In Eqs. (92) and (93) $i = R$ (Tables XIII to XV).

Consider R_4. By utilizing Eq. (93) its *d*-genotype, by which we simply mean its d, becomes:

$$d = (d) + g_a^{(1)} + g_b^{(2)} + g_c^{(4)} + g_D^{(5)} + g_F^{(6)} + g_{\mathrm{G}}^{(7)} + g_{\mathbf{H}}^{(8)} + g_{\mathbf{I}}^{(9)} + g_{\mathbf{J}}^{(10)} \quad (104)$$

Obviously the d for each similarity rank, R, will be different for every other one. Therefore S for each individual will be unique. This response-evoking capacity, S, represents the *d*-phenotype.

TABLE XIII

TRAIT, *d*-GENE, DIFFERENTIATION IN A SIMILARITY RANK HIERARCHY

Similarity rank, *R*	N_i	N_J	Common traits (*d*)	Differentiating traits, *d*-genes									
				Dominant *d*-genes									
1	11	1	(*d*)	A	B	C	D	E	F	G	H	I	J
2	10	2	(*d*)	*a*	B	C	D	E	F	G	H	I	J
3	9	3	(*d*)	a	b	C	D	E	F	G	H	I	J
4	8	4	(*d*)	a	b	c	D	E	F	G	H	I	J
5	7	5	(*d*)	a	b	c	d	E	F	G	H	I	J
6	6	6	(*d*)	a	b	c	d	e	F	G	H	I	J
7	5	7	(*d*)	a	b	c	d	e	f	G	H	I	J
8	4	8	(*d*)	a	b	c	d	e	f	g	H	I	J
9	3	9	(*d*)	a	b	c	d	e	f	g	h	I	J
10	2	10	(*d*)	a	b	c	d	e	f	g	h	i	J
11	1	11	(*d*)	a	b	c	d	e	f	g	h	i	j
				Recessive *d*-genes									

b. Response-evoking capacities. Prior formulations regarding the typing of behavior and personality, exemplified by Schaefer (1959, 1961), suggest that the nature of one's own S and the nature of the response evoked from others is influenced by the mood or attitude of the other individual involved. This mood or attitude determines how one views the target diameters of others. It determines whether one focuses on the dominant d-genes or the recessive d-genes of others. That is, when an individual responds to another does he look at the other's desirable or undesirable characteristics. It will be a prime premise of my formulation that one can be affected only by the good or by the bad side of another at a particular moment in time, but not by both simultaneously. Furthermore, I shall show that there are two ways of assessing the good qualities, the dominant d-genes, of another. Likewise, there are two ways of assessing the undesirable qualities, the recessive d-genes, of another. Any individual's d-genotype in a social setting produces four types of d-phenotypes, that is four kinds of S.

Let

$S^{(A)}$ represent the response-evoking capacity of an individual affecting the probability of his being chosen by associates as an object of affection. S_A is related to Schaefer's *love-acceptance*. S_A depends upon both the common target diameter, (d), and on dominant d-genes.

$S^{(a)}$ represent the response-evoking capacity of an individual affecting the probability of his being rejected by associates. $S^{(a)}$ is related to Schaefer's *hostility-rejection*. $S^{(a)}$ depends solely on recessive d-genes. It is dependent in no way upon the common traits, (d).

$S^{(V)}$ represent the response-evoking capacity of an individual affecting how intensely he will be loved or approved of by associates. Love here implies intensity of positive response and thus connotes increase in probability of an individual realizing the objective of his behavior. $S^{(V)}$ determines the extent to which an individual's desires will be facilitated by associates. In this sense, $S^{(V)}$ is related to Schaefer's *autonomy*. $S^{(V)}$ depends upon both the common target channels, (d), and on dominant d-genes.

$S^{(v)}$ represent the response-evoking capacity of an individual affecting the degree to which its velocity is altered. $S^{(v)}$ is related to Schaefer's *control*. $S^{(v)}$ is dependent solely upon recessive d-genes. It influences the intensity of negative sanctions imposed by associates.

Equations for $S_i^{(A)}$ and $S_i^{(a)}$ have already been given; i.e., Eqs. (92) and (93) subject to the restrictions there stated.

Let:

$p_i^{(A)}$ = the probability of choosing any *i*th individual.

$p_i^{(a)}$ = the probability of rejecting any *i*th individual.

Then

$$p_i^{(A)} = \frac{S_i^{(A)}}{\sum_{i=1}^{N} S_i^{(A)}} \tag{105}$$

$$p_i^{(a)} = \frac{S_i^{(a)}}{\sum_{i=1}^{N} S_i^{(a)}} \tag{106}$$

i here, and in Eqs. (92) and (93) and (105) to (113), refers to specification of individuals by similarity rank, R. See discussion before Eq. (104).

Equations (105) and (106) in essence state that the probability of any other individual choosing or rejecting the *i*th individual depends upon what proportion of the total dominant *d*-gene pool, or recessive *d*-gene pool, of the entire N individuals is encompassed by this *i*th individual. Note that these equations include evaluation of one's entire experience with members of the group, including awareness of one's own traits. This topic of self-awareness will be discussed later.

Conceptually, it is somewhat more difficult to understand $S^{(V)}$ and $S^{(v)}$, although the equations for their calculation are rather simple. Let us consider $S^{(v)}$ first, since earlier reference simply to S was usually in the restricted sense of $S^{(v)}$.

Consider the individual in Table XIII with similarity rank 6, R_6. When individuals R_1 to R_5 are in that state where they tend to impose restraints or sanctions on others, they will view R_6 as being more different from the ideal type than they themselves are. In this sense, R_1 to R_5 are type 1 individuals, in the sense of Eq. (94). Similarly, R_7 to R_{11} will perceive R_7 as being like themselves in that they all share the recessive *d*-gene, $g_e^{(5)}$. Thus, they along with R_6 may be considered as type 2 individuals, in the sense of Eq. (95), with reference to calculating the $S^{(v)}$ of R_6 by Eq. (97). N_j for R_6 is 6. By a similar logic the $S^{(v)}$ of each individual may be calculated. See Table XV for $S^{(v)}$ calculated for every member of an $N = 11$ as depicted in Table XIII.

Each individual will belong to a different-sized N of type 2 individuals. This N will hereafter be referred to as N_j to differentiate it from the N_2 given in Eq. (97). By analogy to Eq. (97):

$$S_i^{(v)} = N/N_j \tag{107}$$

And from Eq. (91) it follows that

$$v_i = N_{\mathrm{j}}/N \qquad (108)$$

Equation (108) has proved a most useful one in the study of social groups of experimental animals because it leads to predicting the degrees of social withdrawal expected among any group of known size. In the discussion following Eq. (99) I pointed out that where μ increases as a result of $\bar{S}^{(v)}$ becoming greater than 1.0, accommodation might be through ejection of those members with the largest $S^{(v)}$ or by a splitting of the group. Each of these possibilities presumes unused area A into which the appropriate individuals may immigrate. However, when surrounding groups maintain territories, or other circumstances preclude emigration, then the A component of $\mu = (Sv/A)$ remains constant. Thus, reduction in velocity, v, becomes the only avenue for reducing μ back to the 1.0 value appropriate to N_o.

By a similar line of reasoning to that leading to Eq. (107), N_J represents the number of individuals with which the individual in question possesses a given uniqueness of dominant *d*-genes.

Reference to Table XIII will clarify the meaning of N_J. For example, R_5 belongs to an $N_J = 5$ since it may be recognized by sharing the dominant *d*-gene, E, with four other individuals. N_J and the similarity rank, R, will always have identical numerical values.

By analogy to Eq. (107)

$$S_i^{(V)} = N/N_J \qquad (109)$$

And although I do not for the present see how one identifies V in biological or social terms, although it may represent the seeking for positive affection, it is obvious that

$$V_i = N_J/N \qquad (110)$$

In this sense behavioral *d*-genes do not represent retention or deviation from specific behaviors. Characterization by two individuals of possessing at least three degrees of deviation does not mean that these degrees of deviation are identical.

Now consider a group consisting of four individuals, the pertinent data and calculations for which are given in Table XIV. The probabilities of the dominant and recessive *d*-genes are:

$$\begin{array}{rlrl} p_A &= 1/4 & p_a &= 3/4 \\ p_B &= 2/4 & p_b &= 2/4 \\ p_C &= 3/4 & p_c &= 1/4 \\ p_{(d)} &= 4/4 & & \end{array}$$

TABLE XIV

RESPONSE-EVOKING CAPACITY AND VELOCITY IN RELATION TO BEHAVIORAL DEVIATION IN A GROUP OF FOUR INDIVIDUALS. THE NUMBER FOR RELEVANT EQUATIONS APPEARS IN PARENTHESES ABOVE COLUMNS

(106) $p_i^{(a)}$	(93) $S_i^{(a)}$	(107) $S_i^{(v)}$	(108) v_i	R	N_j	Dominant d-genes				N_J	(105) $p_i^{(A)}$	(92) $S_i^{(A)}$	(109) $S_i^{(V)}$	(110) V_i
0	0	1.00	1.00	1	4	A	B	C	(*d*)	1	0.521	8.33	4.00	0.25
0.136	1.33	1.33	0.75	2	3	a	B	C	(*d*)	2	0.271	4.33	2.00	0.50
0.218	2.33	2.00	0.50	3	2	a	b	C	(*d*)	3	0.145	2.33	1.33	0.75
0.646	6.33	4.00	0.25	4	1	a	b	c	(*d*)	4	0.063	1.00	1.00	1.00
1.000	10.00	8.33	2.50	—	—	Recessive *d*-genes				—	1.000	16.00	8.33	2.50

The pool of shared behaviors, (d), acts as a single dominant d-gene. Where R represents the rank of the animal in terms of the degree of retention of dominant d-genes, that is how closely it expresses the ideal prototype manner of behaving, $S^{(A)}$ and $S^{(a)}$ may be calculated by Eqs. (92) and (93) utilizing the above probabilities of dominant and recessive d-genes.

$$\begin{aligned}
S^{(A)}_{R=1} &= (4/1 + 4/2 + 4/3 + 4/4) &&= 8.33\\
S^{(A)}_{R=2} &= (4/2 + 4/3 + 4/4) &&= 4.33\\
S^{(A)}_{R=3} &= (4/3 + 4/4) &&= 2.33\\
S^{(A)}_{R=4} &= (4/4) &&= 1.00
\end{aligned}$$

Then

$$\sum_{R=1}^{N} S^{(A)}_i \qquad \overline{16.00} = 4N$$

Restatement of the concept of behavioral d-genes in the context of a hypothetical example of their relationship to the origin of the various stimulus-evoking capacities and of velocity, v, will assist in clarifying the relationships. As described in Section XIII, B, 5, a the members of an established group may be ranked in terms of the degree to which deviation has developed from the ideal prototype. This ideal prototype will always be that individual characterized by the least absolute deviation. There will be $N - 1$ degrees of deviation in a group of N individuals.

Let:

$S_1, S_2, \cdots, S_{N-1}$ represent the characterization of an individual by 1, 2, $\cdots$, $N - 1$ degrees of deviation

$\Delta_1, \Delta_2, \cdots, \Delta_{N-1}$ represent the absence of deviations $\delta_1, \delta_2, \cdots, \delta_{N-1}$

Then:

$$\begin{aligned}
\delta_1 &= \text{recessive } d\text{-gene a}\\
\delta_2 - \delta_1 &= \text{recessive } d\text{-gene } b\\
\delta_3 - \delta_2 &= \text{recessive } d\text{-gene c}\\
&\text{etc.}
\end{aligned}$$

And

$$\begin{aligned}
\Delta_1 &= \text{dominant } d\text{-gene A}\\
\Delta_2 - \Delta_1 &= \text{dominant } d\text{-gene B}\\
\Delta_3 - \Delta_2 &= \text{dominant } d\text{-gene C}\\
&\text{etc.}
\end{aligned}$$

$$\begin{aligned}
S^{(a)}_{R=1} & &&= 0\\
S^{(a)}_{R=2} &= (4/3) &&= 1.33\\
S^{(a)}_{R=4} &= (4/3 + 4/2) &&= 2.33\\
S^{(a)}_{R=4} &= (4/3 + 4/2 + 4/1) &&= 6.33
\end{aligned}$$

Then

$$\sum_{R=1}^{N} S^{(a)}_i \qquad \overline{10.00} = 3N - (N/2)$$

N_J and N_j in the sense of type one and type two individuals discussed in relation to Eqs. (94) and (95) and (107) are given in Table XIV. When $N_J = 2$ it means that the second ranked, $R = 2$, individual is a member of a subgroup of two individuals which share the dominant *d*-gene B. Likewise when $N_j = 2$ it means that the third ranked, $R = 3$, individual belongs to a subgroup of two individuals each of whom possesses recessive *d*-gene b. Every individual belongs to a unique N_J and N_j. Given these uniquenesses of N_J and N_j as shown in Table XIV, the respective $S_i^{(V)}$, $S_i^{(v)}$ and v_i were calculated respectively by Eqs. (109), (107), and (108) and presented in Table XIV.

Up to the present I have intentionally maintained the discussion of response-evoking capacity, S, on a nearly strictly theoretical plane for the purpose of clarifying concepts. Even though such theoretical formulations may be justified in their own right, regardless of how well they approximate reality, still it is desirable to ascertain whether they are in harmony with observed data. To this end I selected two sets of empirically obtained data. One involves measurements for mice from which velocity, v, may be derived. The second involves the choosing of table partners among groups of delinquent girls. These latter data permit determination of how well the observed choosing can be predicted by Eq. (105).

XIV. Consequences and Examples of Social Interaction Systems

A. Velocity Reduction in a Hierarchy of Mice

I have previously described (Calhoun, 1956) the patterns of social relationships which develop among members of small groups of inbred domesticated mice. Whenever two mice passed within a few inches of each other they were recorded as having a contact, regardless of whether or not a detectable social interaction could be detected. During a "contact" two mice merely came within that range of each other for which contentions for status did at times develop. We shall consider the example provided by a group of eleven C57 black, inbred male mice which had developed a stable hierarchy prior to recording the frequency and kind of associations of each individual with his associates. Some pairs of mice contacted each other much more frequently than anticipated on a chance basis, while members of other pairs very infrequently met. These mice are rank ordered in Table XV according to the number of contacts each had with associates. For all practical purposes this order also represents the observed ability to dominate an encounter which precipitated in a fight or flight. That is, the most active mouse was the most dominant one and the least active one the most subordinate.

It can readily be shown that with N's as large as eleven, the number of contacts, n_c, is so nearly proportional to velocity, v, as to justify utilizing number of contacts as a measure of velocity in the present example. From Eq. (91) it is seen that $S_i^{(v)}$ varies inversely with v_i, and therefore on a theoretical basis mice with few contacts should be those with large response-evoking capacities.

TABLE XV

VELOCITY IN A HIERARCHY OF MICE

1	2	3	4	5	6	7
			Number of contacts, n_c, expected			
Mouse's number	Rank R	N_j	Obs.	Exp. Eq. (113)	v Eq. (108)	$S^{(v)}$ Eq. (107)
315	1	11	123	128.17	1.000	1.00
311	2	10	116	116.63	0.910	1.10
282	3	9	109	104.84	0.818	1.22
286	4	8	93	93.18	0.727	1.38
319	5	7	85	81.52	0.636	1.57
303	6	6	65	69.85	0.545	1.83
321	7	5	51	58.19	0.454	2.20
317	8	4	46	46.65	0.364	2.75
290	9	3	35	34.99	0.273	3.67
288	10	2	26	23.33	0.182	5.50
301	11	1	20	11.66	0.091	11.00
Σ			769		$\Sigma = 6.001$ $= (N+1)/2$	

Where v represents relative velocity as calculated by Eq. (108) for any N, empirical calculation will show that:

$$\sum_{i=1}^{(N)} v_i = \frac{(N+1)}{2} \tag{111}$$

Then where $n_{ci}^{(\text{obs})}$ and $n_{ci}^{(\text{exp})}$ represent respectively, observed and expected number of contacts in any arbitrary period of time, the number of contacts, n_{ci}, for any ith animal becomes:

$$n_{ci}^{(\mathrm{exp})} = \left[\frac{v_i}{(N+1)/2}\right] \sum_{i=1}^{N} n_{ci}^{(\mathrm{obs})}$$

$$= v_i \left[\frac{2\sum_{i=1}^{N} n_{ci}^{(\mathrm{obs})}}{N+1}\right] \tag{112}$$

And by substituting Eq. (108) into Eq. (112) we obtain an equation more convenient for calculation:

$$n_{ci}^{(\mathrm{exp})} = \left[\frac{N_{ji}}{N}\right] \left[\frac{2\sum_{i=1}^{N} n_{ci}^{(\mathrm{obs})}}{N+1}\right] \tag{113}$$

$n_{ci}^{(\mathrm{exp})}$, so calculated, are given in Table XV. Where

$$\chi^2 = \sum_{R=1}^{N} \left[\frac{(n_{ci}^{(\mathrm{obs})} - n_{ci}^{(\mathrm{exp})})^2}{n_{ci}^{(\mathrm{exp})}}\right]$$

$\chi^2 = 8.001$, which with 10 degrees of freedom has a p of 0.629. On this basis the observed certainly does not deviate significantly from the expected.

1. AWARENESS OF SELF

Three-fourths of the contribution to the above χ^2 come from the single omega, nth ranked individual. Considering only the highest ten ranked individuals, $\chi^2 = 2.006$ which with 9 degrees of freedom has a p of 0.99! I have already shown (Calhoun, 1956) that the paired contacts in this group diverged markedly from randomness, and so the divergence must reflect some fixed social system such as elaborated here with regard to reduction in velocity. Therefore, the marked divergence of this single omega individual is likely to reflect a basic process, not just a random variation; so I asked, "How would self-awareness affect the present formulation?" By self-awareness I mean that an individual recognizes and imposes self-sanctions which are of sufficient intensity to reduce his velocity just as much as do the sanctions imposed upon him by his associates. For this to happen it means that an individual can "meet" himself.

Equations (96), (97), (107), and (109) imply that an animal can meet itself. That an individual meets himself means that he must recognize himself. This raises the question of how an individual recognizes himself. One way is by comparison. Considering degrees of difference depicted by Table XIII, an individual can say, "I am at least as different as those which possess certain recessive d-genes that I possess." By this method of comparison with individuals who differ more than he does, an individual can know the entire extent of his difference. This is true for all except the nth ranked omega individual. As may plainly be seen from Table XIII, R_{11} has no basis for comparing his d-gene $g_j^{(10)}$ since no other individual shares it. He can only be aware of his divergence including $g_a^{(1)} \cdots g_i^{(9)}$ shared in entirety by R_{10}. Therefore, by Eq. (107) his

$$S^{(v)} = 11/2 = 5.50$$

and by Eq. (108) his

$$v = 2/11 = 0.182$$

Therefore, by Eq. (113) his

$$n_c^{(\text{exp})} = 23.33$$

Using this value in Table XV the χ^2 for the entire group of 11 mice becomes 2.522, which with 10 degrees of freedom has $p = 0.99$. I realize that this is only one case and I may justifiably be accused of making a "conceptual mammoth out of a mouse." Yet if animals do recognize their individuality, the only confirmation of such recognition can come through observing that the omega individual in an N_b group exhibits twice the velocity or twice the number of contacts he would otherwise be expected to have.

It is realized that if the N_j of the Nth ranked animal, the omega individual, is equivalent to that of the $(N - 1)$th ranked animal, the $n_c^{(\text{exp})}$ for the omega animal will actually be slightly less than 23.33. Likewise the $n_c^{(\text{exp})}$ for all higher ranked animals would be slightly less than stated in Table XV, since

$$\sum_{R=1}^{N} n_{ci}^{(\text{exp})} = \sum_{R=1}^{N} n_{ci}^{(\text{obs})}$$

2. Sanctions and Facilitations

When the target diameters of all members of N are identical, then the S, in the sense of $S^{(v)}$, is identical for all individuals and is equal to 1.0. As target diameters vary in accordance with the system illustrated in Table XIII, S increases except for the alpha first-ranked individual. Such increases in S mean that the intensity (duration) of the response evoked from others will be greater. Therefore, intensity of response, the i of the prior formulation, will increase by a factor $= S^{(v)}$.

Let $i_e^{(v)}$ represent the intensity of response evoked from every member,

e, of N compatible with one's own $S^{(v)}$. Then it follows from Eq. (70) that for the ith individual

$$i_e^{(v)} = S_i^{(v)} \left[\frac{1}{N-1}\right]^{1/2} \tag{114}$$

$i^{(v)}$ represents the imposed restraint or sanction. Sanctions in this sense lead to velocity reduction as exemplified by the mice. $i_e^{(v)} = i_i^{(v)}$ with reference to self action.

Where the target diameters of all individuals are identical, Eq. (70) with an N of 11 gives an $i = 0.316$. However, where target diameters differ as given in Table XIII, it may be seen from column 7 in Table XV that $S^{(v)}$ increases from 1.0 to 5.5. (Here, I am also assuming that the Nth ranked individual has the same S as the $(N - 1)$th ranked individual for reasons discussed in Section XIV, A, 1.) The mean $S^{(v)}$ will be 2.52. There fore, the mean $i^{(v)}$ becomes $2.52 \times 0.316 = 0.816$.

We are considering intensities of interaction involved during imposition of sanctions in the sense of restraints. Therefore, when we consider any individual in the a responsive state, the other individuals from which it evokes an $i^{(v)}$ sanction-type interaction must be considered to be in the p nonresponsive state since the resulting interaction will not contribute to this individual's satiation from social interaction. Every member, e, of N, which is in the responsive state, a, will exhibit an $i_{ei}^{(v)}$ intensity of response toward any ith individual, also in the a responsive state, where

$$i_{ei}^{(V)} = S_i^{(V)} \left[\frac{1}{N-1}\right]^{1/2} \tag{115}$$

$i^{(V)}$ represents the intensity of interaction of the individual searching for satisfaction. Similarly the mean $i^{(V)}$ will also be 0.816 instead of the 0.316 which exists when all individuals in an N of 11 have the same target diameter.

$$\begin{aligned} i_i^{(V)} i_{ei}^{(v)} &= \alpha'_{ap} \\ &= 0.666 \end{aligned}$$

This α'_{ap} represents the mean frustration-type refractory period resulting from the imposition of sanctions in an $N = 11$. Since when all individuals have the same target diameter, $i^2 = (0.316)^2 = 0.1$, hierarchy formation increases the average amount of stress more than sixfold. No wonder that the $i_{ei}^{(v)}$ elicited from others became so effective in reducing velocity so that each individual's μ again equals 1.0. That is, $vS^v = 1.0$. Although intermittent application of sanction, $i^{(v)}$, may be required to reinforce the v behavior, sanctions still must be primarily a phenomenon of hierarchy formation or role assumption.

When two individuals, x and y, are both in the a responsive state, their resulting interaction, $i_x^{(V)} i_y^{(V)}$ will lead to a satisfying α_{aa} refractory period. Being in the responsive state implies a need for satisfaction from social interaction. Furthermore, during such interactions each must be focusing its attention on the $S^{(V)}$ aspects of the other's target diameter. In like fashion, when individual x in the responsive state approaches y in the nonresponsive state, x exhibits behavior appropriate to y's $S^{(V)}$, while y retaliates with a response appropriate to x's $S^{(v)}$.

One individual which is in the responsive phase will have its behavior toward another judged by the latter as appropriate or inappropriate, depending upon whether or not the individual approached is also in the responsive state. Appropriate social behavior becomes synonymous with what I have termed "dominant *d*-genes." These behaviors must be appropriate both in form and in timing, such that the approached individual will be in a similar need state for obtaining satisfaction from social interaction. Even though a social behavior may seem appropriate with regard to form, if the timing of its expression is not harmonious with the refractory nonresponse state of the individual approached, then the approached individual will judge this behavior as being inappropriate. Inappropriateness in this sense becomes what I term a "recessive *d*-gene."

In a perfectly random system, with all individuals exhibiting identical behavior with regard to its form, some individuals will by chance more frequently encounter others who are in a refractory nonresponsive state. Thus, such individuals will be responded to by their associates in identical fashion as they would have been if the form of their behavior were actually inappropriate. To the degree that such structurally appropriate behaviors fail to be reinforced by similar behavior from associates, they may be expected to vary in some random fashion until their form becomes relatively distinct from the original. To the extent that these alterations in behavior become established, they represent clearly recognizable recessive *d*-genes. Due to this modification of behavior $S^{(v)}$ will increase and $S^{(V)}$ decrease, so even when the approached individual is also in the responsive state the approaching individual will experience less satisfaction from the interaction than it would have had these random processes not transpired.

Once μ becomes restabilized to 1.0 following the reductions in velocity accompanying hierarchy formation, it will then be possible for two individuals, each in the socially receptive a state, to encounter each other and mutually contribute to each other's need state by an $i^{(V)} i^{(V)} = \alpha_{aa}$ interaction. In this case, each individual's own $i^{(V)}$ represents its searching for social satiation, while the other's $i^{(V)}$ represents a social facilitation, the opposite of a social sanction.

I shall leave the concept of social facilitation at this theoretical level without seeking empirical confirmation. However, excellent data have been presented by Moreno (1953; Moreno and Jennings, 1960) which permit an exploration of the probable validity of $S_i^{(A)}$, Eq. (92).

B. The Choosing of a Partner

We have already seen that $S_i^{(v)}$, Eq. (107), and $S_i^{(V)}$, Eq. (109), relate to those response-evoking capacities of an individual's target diameter which determine the *intensity* with which associates will respectively impose sanctions or facilitations. $S_i^{(A)}$, Eq. (92), and $S_i^{(a)}$, Eq. (93), likewise represent aspects of one's target diameter influencing the response of others. One's own $S^{(A)}$ determines the probability of being chosen by others as an appropriate object for social response, while one's own $S^{(a)}$ similarly determines the probability of being rejected. No doubt there are excellent empirical data for testing the validity of $S^{(a)}$. However, I shall confine myself to $S^{(A)}$. If I can show the likelihood of $S^{(A)}$ being an approximation of reality, it follows that $S^{(a)}$ can be similarly justified as a concept.

Moreno (1953, 1960) presents a set of data for which there has been no adequate formulation of their origin. In seven cottages each containing exactly 26 delinquent girls, he asked each girl to choose three others in their own cottage whom they would most like to sit close to at the dining table. This instruction presents marked complications in determining whether Eq. (105) will account for the observed results. However, Eq. (105) includes the possibility that one will choose oneself as a partner; that is, one will choose to eat alone. Moreno by his instructions excluded this possibility. Further, Moreno's instructions precluded the possibility of choosing the same person two or three times, which Eq. (105) permits on successive independent choices. Dr. Clifford Patlak worked out for me the full set of equations required to determine how many times each individual would be chosen, considering Moreno's restrictions, after the probability, p, of being chosen was calculated by Eq. (105) for each ith individual in an $N = 26$. Moreno's restrictions so complicated the calculations that it was concluded that a simple lottery would adequately test the applicability of the present theory, and at the same time avoid the time-consuming job of developing a computer program to the same end. This was done as follows:

1. $S_i^{(A)}$ was calculated by Eq. (92) for each of the 26 members of N, from $S_1^{(A)}$ for the alpha-ranked individual to $S_{26}^{(A)}$ for the omega-ranked individual.

2. Then the p of being chosen was calculated for each individual by Eq. (105). For example:

$$p_1^{(A)} = 0.152, \qquad p_2^{(A)} = 0.121$$

$$p_3^{(A)} = 0.092, \qquad p_{10}^{(A)} = 0.039$$

$$p_{20}^{(A)} = 0.012$$

3. We then prepared $1000 \cdot p_i$ tokens for each individual.
4. All these 1014 tokens were placed in a large glass jar. For any "individual" to make three choices, three squares at random were picked out. If an "individual" picked himself, the token was returned to the jar and another "choice" made at random. Similarly, if another individual was chosen twice, one of the two tokens was returned to the jar and another selection made until each "individual" had chosen three different "others." Between drawings all tokens were returned to the jar and the contents mixed. Each such test consisted of 78 "choices." At the end of each test it was possible to tally how many of the 26 "individuals" had never been chosen, chosen once, chosen twice, etc.
5. Fourteen such independent tests were performed and the mean number of individuals in each choice category was calculated. This mean represents an estimate of the expected.

These data in Table XVI are plotted in Fig. 36. A smoothed curve approximating the means of the observed and the lottery presumably approximates that conforming to Eq. (105), considering the restrictions imposed by Moreno. This smoothed curve is called "theoretical" in Fig. 36. Each of the two sets of points varies so closely about this curve as to provide confirmation that my formulation is adequate to account for the observed sociometric phenomenon of choice.

Moreno and his associates make much of the chains, triangles, etc. of reciprocal or nonreciprocal choices that became apparent in such a sociometric system. While such patterns may become fixed realities, there is no reason to attribute any condition other than chance to their origin.

C. The Response-Evoking Capacity Circumplex

Schaefer (1959, 1961) presents a conceptual model capable of describing the attitudes, personality or behavior of an individual in a two-dimensional space. This latter is determined by two orthogonal axes of polar opposites. As may be seen in Fig. 37, one axis consists of the polar opposites love and hostility, while the other is represented by control and autonomy. About

TABLE XVI

EMPIRICAL AND THEORETICAL DATA REGARDING THE CHOOSING OF A PARTNER

Times chosen	Mean number of individuals		"Theoretical" mean of A and B
	A Moreno (1953, 1960)	B Present Lottery based on $S^{(A)}$	
0	5.00	5.36	5.18
1	4.15	5.36	4.76
2	4.29	3.82	4.06
3	3.72	2.29	3.01
4	2.29	2.50	2.40
5	2.00	1.79	1.90
6	1.14	1.50	1.32
7	1.43	0.86	1.15
8	0.86	0.72	0.79
9	0.57	0.57	0.57
10	0.14	0.50	0.32
11	0.43	0.36	0.40
12	0.00	0.29	0.15
13	0.00	0.07	0.04

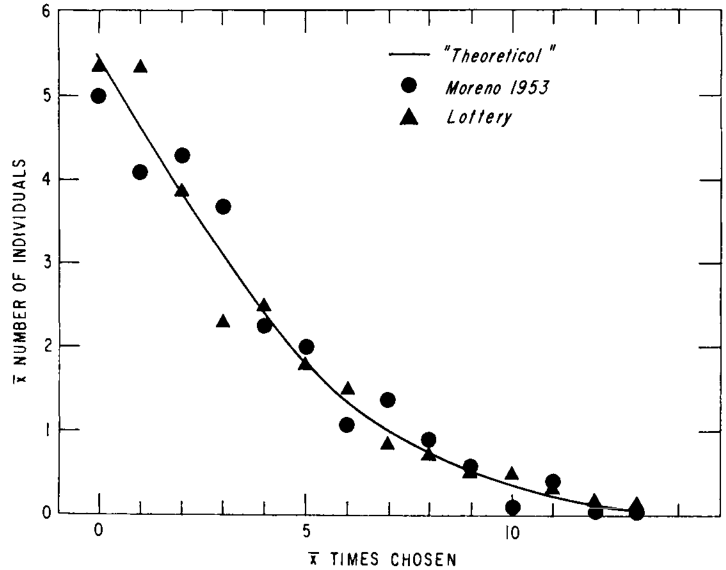

FIG. 36. The choosing of a partner. Moreno's empirical data are compared with a lottery conforming both to Moreno's procedure and the probabilities of being chosen as predicted by Eq. (105) in the present paper.

or within the circle determined by the extremes of these polar opposites, the typical characteristic of an individual may be oriented.

There exist remarkable similarities between Schaefer's model and that implied so far by my concept of response-evoking capacity, S, and the resultant or concomitant change in the behavior of the individual, such as reflected by change in velocity.

$S^{(v)}$, $S^{(V)}$, $S^{(A)}$, and $S^{(a)}$ represent factors not specifically treated by Schaefer. They relate to his formulation as follows: They represent those characteristics of the individual that determine the probability of acceptance or rejection as a social object and that determine the kind and intensity of response elicited. Schaefer considers the second logical step, the evoked response, such as the mother's response toward her children. He also considers the third-order phenomenon, that of the personality developed as a result of being the target of such responses.

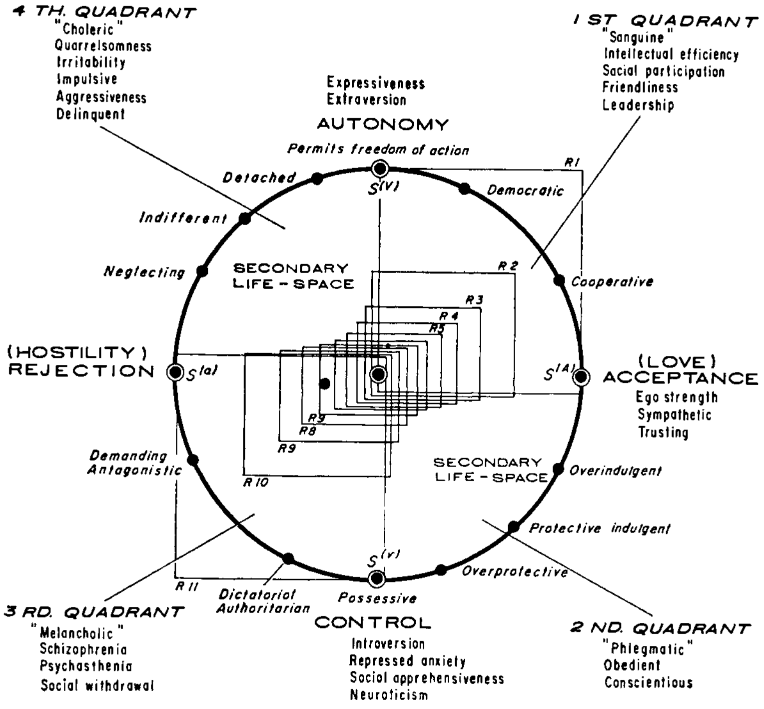

FIG. 37. The circumplex depiction of behavior and personality superimposed upon the coordinates of response-evoking capacity, S.

I shall now attempt to place these three orders of phenomena in perspective. For an $N = 11$, $S^{(v)}$, $S^{(V)}$, $S^{(A)}$, and $S^{(a)}$ were calculated by the above equations. These values were then recalculated as proportion of the maximum value. For examples, see tabulation.

Similarity rank	$S^{(v)}$	$S^{(V)}$	$S^{(A)}$	$S^{(a)}$
1	0.091	1.000	1.000	0.000
6	0.166	0.166	0.244	0.220
11	1.000	0.000	0.030	1.000

$S^{(v)}$ and $S^{(V)}$ with values of 1.0 form polar opposites, as likewise do $S^{(A)}$ and $S^{(a)}$. These polar opposites are shown as a two-dimensional coordinate system in Fig. 37. The four "response-evoking capacity" coordinate points for each individual are connected by lines. Thus, a square may be delineated for each ranked individual which represents its "life-space" with regard to eliciting responses from associates.

Schaefer's two-dimensional circumplex description of behavior and personality replaces the relative intensity values of my axis of correlation coefficients. In most comprehensive sets of measures of behavior or personality, he regularly found that two measures which can be equated with the terms love (acceptance) and hostility (rejection) are highly negatively correlated and so form polar opposites which may thus be plotted as polar coordinates at 180 degrees from each other. Similarly, concepts identified by the terms "control" and "autonomy" form polar coordinates opposite each other. Control and autonomy have zero correlation with acceptance and rejection and so the control-autonomy axis lies at right angles to the acceptance-rejection axis. From the center zero point each of the four axes extend outward to represent a maximum correlation coefficient of 1.0 at its extremity. Every other concept in the set is then correlated with each of the four "key" concepts. It is regularly observed that every other concept in the set has positive correlations with two of the neighboring polar concepts, and so each may be plotted in this two-dimensional behavior-personality field.

Such points approximately fall on the circumference of a circle intersecting the polar coordinates. Schafer calls such a set of points a circumplex. His schematic representation of types of maternal behavior is shown by dots in Fig. 37. Terms connected by arrows to these points denote various kinds of maternal behavior. These maternal behaviors are the types I would anticipate as being directed toward, and derived from, the response-evoking-capacity circumplex determined by $S^{(V)}$, $S^{(v)}$, $S^{(A)}$, and $S^{(a)}$.

Schaefer also reviews many studies by others which harmonize with this conceptualization of behavior and personality. I have included selected terms in boxes which carry the "flavor" of what each pole or each quadrant represents.

It will be noted that the response-evoking-capacity life-spaces of the members of any group, as I have described their origin, mainly fall in the first and third quadrant of this two-dimensional space. I shall, therefore, call these two quadrants the "primary life-space." We may inquire how individuals become identified with the other two quadrants, the second and the fourth, which may be called the secondary life-space.

My colleague, Dr. Kyle Barbehenn provided the solution. In examining Table XIII he noted its bilateral symmetry with reference to dominant and recessive *d*-genes. In any group recessive *d*-genes merely represent degrees of divergence from some ideal prototype. The alpha-ranked individual possesses only dominant prototype characteristics, whereas the omega-ranked individual, except for commonly held (*d*) traits, possesses only divergent and therefore recessive *d*-genes. But suppose in the history of the group some circumstance led the omega's associates to consider his characteristics as being more desirable than the alpha's. Such a change in attitude would reverse the roles of all individuals, except for the median-ranked individual. The individual who formerly was socially withdrawn and had a low velocity would immediately become a high velocity individual, participating in many social interactions. Likewise, the former alpha individual would become the omega one, losing his "leadership" role and becoming socially withdrawn.

This transformation of recessive *d*-genes into dominant ones, and vice versa, will still place most of the individuals again within the first and third quadrants of the circumplex life-space. The critical question involves the transition period. In this transition Eqs. (92) and (93) change roles with reference to their application to dominant and recessive *d*-genes, as likewise do Eqs. (107) and (109). There arises the likelihood that previous to this transition choosing and rejecting will be a more predominant activity than controlling or granting autonomy. If so, $S^{(A)}$ will switch to pertain to recessive *d*-genes and $S^{(a)}$ to dominant *d*-genes while $S^{(V)}$ and $S^{(v)}$ will retain their orientation toward dominant and recessive *d*-genes, respectively. Or the reverse could happen if the group were primarily oriented toward the control-autonomy axis. The consequence of these changes are summarized in Table XVII.

1. Shifts into the Second and Fourth Life-Space Quadrants by Rats

No intent is here implied of proving the validity of the general formulations. All I have hoped for is to evolve a logical and reasonable formulation that may later prove to be a fair first approximation of processes that do in fact exist. This elaboration of Schaefer's circumplex life-space immediately brought recall of a striking transitory change in behavior which regularly occurs in structured, dense, socially closed systems of domesticated Norway rat populations.

When these populations have been permitted to attain a density of 60 to 100 adults in a space ideal for 40 or fewer adults, an extremely rigid social structure develops. All rats "know" their place and aggressive actions terminating in some individuals receiving even moderate-sized wounds become markedly reduced. Threat and avoidance becomes the predominant pattern where aggression and imposition of sanctions directed toward maintaining status roles is involved. And yet in six of seven such populations studied, one or several males went temporarily berserk. Each such male abruptly began attacking all other members of the population except those that behaved as they did. They inflicted deep slashing gashes on the bodies and tails of associates of all ages and both sexes until fresh blood could persistently be observed splattered about the habitat.

TABLE XVII

CHANGE OF "ATTITUDE" TOWARD *d*-GENES AFFECTING SHIFTS INTO THE SECONDARY LIFE-SPACE OF THE 2ND AND 4TH QUADRANTS

Initial change	*d*-Gene involved	Interaction of neighboring poles	Quadrant
$S^{(A)}$ oriented to recessive *d*-genes	Recessive	Control-acceptance	2nd
$S^{(a)}$ oriented to dominant *d*-genes	Dominant	Autonomy-rejection	4th
$S^{(V)}$ oriented to recessive *d*-genes	Recessive	Autonomy-rejection	4th
$S^{(v)}$ oriented to dominant *d* genes	Dominant	Control-acceptance	2nd

For any particular rat such episodes persisted from one to several days and since usually several males were involved the total period of such disturbance might last up to 6 weeks. In every instance these bursts of males going berserk followed a period of at least three months during which the investigator had removed all young prior to weaning. Then a new generation of young were permitted to survive. The period of males going berserk coincided with the initial post-weaning integration of these young rats into the society when they ranged between 45 and 90 days of age.

All the males going berserk belonged to the high velocity, generally dominant, segment of the society, and so belonged in the "sanguine" most desirable first quadrant of the life-space circumplex. This meant that dominant *d*-genes predominated in their target diameter. The juvenile rats emerging into the society, being less differentiated, were therefore now prototypic and therefore resembled dominant adult males in their possession of mostly dominant *d*-genes. And yet these juveniles would still possess traits lost during maturation by most adults.

Due to the typical response of rejecting strange objects, the young would be rejected while still being permitted autonomy of action due to dominant *d*-genes shared with high-ranking adults. There being more juveniles in the population than adults belonging clearly in the first quadrant of the life-space circumplex, the general response of rats to these adults would be to react to them as they did to juveniles by rejection. This rejection triggered the release of the muted aggressive capacities of dominant males to the extent that it was expressed with great intensity even toward others, such as juveniles and adult females, who normally were not bitten.

Such an origin of an aberrant behavior in a rat society is patently an interpretation lacking the complete documentation to carry the conviction of its reality. Yet my intensive studies of rat societies permit identification of so many behavior-personality types as to suggest that rats are equally as complex as humans in this regard. The eight societies previously studied have been commented upon in general terms elsewhere (Calhoun, 1962a, b).

In the early history of a rat society, while its numbers and density are low, most individuals seem rather clearly to fall into quadrants one and three of the circumplex. This is a typical expectation when a straight-line hierarchy develops, as it always does in initial stages of social organization. Later on, histories and situations become more complex. Other types develop which may clearly be assigned to the second and fourth quadrant.

For example, there is the type I call a "prober," which appears to represent a rat having shifted from the third to the fourth circumplex quadrant. Earlier in their history they clearly belong within the lower echelons of the social hierarchy. Later on they are generally ignored by dominants with whom they live most closely. In consequence, they develop a marked persistent state of hyperactivity indicating autonomy of action. They seem to generalize this autonomy of action as permitting them freedom of action anywhere. Consequently, they persist in invading the domains of territorial males whenever members of their harems are in estrus. During such invasions they rarely contest the status of the territorial male, but in the process of being rejected by him receive wounds. These are received so frequently that their entire posterior becomes a mass of scar tissue devoid of hair. Like other males who still receive sufficient sanctions from associates to maintain their velocity at a low level, they become pansexual in the sense of including adult males and juveniles of both sexes as objects for sexual advances. They also share with the berserk males of quadrant four the property of heightened intensity of interaction. Theirs, however, reveals itself in sexual behavior toward adult females. Mounts, instead of lasting the usual 1 to 3 seconds, may continue for several minutes. This persistence of the mounting, without intromission, resembles that of frogs.

Low velocity male rats, those which belong in circumplex quadrants two and three, fall mostly into two distinct categories, those which have received many wounds and those which have received very few. The former, which belong in quadrant three, present no conceptual problem as to their origin. Straightforward operation of the four S factors will always place the lower-ranked members of the hierarchy in the third quadrant. However, the latter, "phlegmatic" types must have arisen from a secondary 180 degree shift in response evoked by the d-genes. Their lack of wounds during their entire history indicates $S^{(A)}$ involves dominant d-genes. Their low velocity indicates that now as adults $S^{(v)}$ also involves dominant d-genes. They are rats for whom we may infer that their associates have always been "overindulgent" and "overprotective." Such rats are quite fat and have relatively small adrenals, ventricles, and kidneys. Though they exhibit some displaced sexual behavior, their "personality type" is one most characteristically involving failure either to elicit or initiate social interaction. They are types lacking social involvement.

This brief discourse on rat types suggests that my elaboration of Schaefer's (1959, 1961) circumplex behavior-personality complex may prove to be a fruitful framework for pursuing studies in comparative social psychology.

D. Conformity, Withdrawal, and Creativity

When N increases above N_b or μ increases above μ_b it has been shown that fragmentation of N to appropriately sized discrete subgroups may lead to reacquisition of $\theta_a^{(o)}$ and $\theta_f^{(o)}$. Even when N remains at N_b, the unavoidable variability in the four types of S leads to μ differing among members of the group. Reduction of v as $S^{(v)}$ increases enables the individuals to prevent excessive increments of θ_f above $\theta_f^{(o)}$. Even so, many individuals with reduced v must experience either reduced θ_a or excessive θ_f. We may inquire as to possible avenues for escaping these deviations from $\theta_a^{(o)}$ and $\theta_f^{(o)}$ without leaving the group.

For those individuals who in their behavior do not differ markedly from the alpha-ranked, R_1, member, there exists the possibility of adopting the outward behavior of R_1. Such acquired conformity should permit elevation of velocity to basic levels and should produce a discontinuity in the range of velocities observed among members of the group. Whyte (1956) in his "The Organization Man" has emphasized the role of conformity as an adjustive mechanism accompanying increases in N.

At the opposite extreme of original behavioral divergence there exist individuals with such reduced velocity that their contacts with higher-ranked individuals proves insufficient to permit their developing conformity through emulating the behavior of their superiors. Recently I have had the opportunity of studying the behavior of all members of three populations of domesticated Norway rats for every member of which assessments of velocity had been made. Low-velocity rats develop the capacity to move about without engaging in interactions with their associates. They rarely initiate interactions nor do they elicit actions from associates. This social withdrawal becomes so complete that, despite being in the presence of many associates, they are characterized by small adrenals and small ventricles, just as are rats which have lived all their lives as members of N's of 3. David Riesman *et al.* (1953) has movingly described such isolation and oblivion of surroundings among humans in his "The Lonely Crowd."

In between the velocity levels producing conformity and withdrawal, there lies a narrow but important range of velocity permitting a process which can terminate in creativity. Why this is so requires recall that according to my model or social interaction, interaction with self must be included along with interaction of self with others. One can choose oneself, one can reject oneself, one can facilitate one's own behavior, or one can restrain or impose sanctions on one's own behavior. All are possible.

Consider sanctions. These are mostly the $i_{ei}^{(v)}$, Eq. (114), of others directed against oneself. Let $i_i^{(v')}$ represent self-sanctions. The self-interaction becomes:

$$[i_i^{(v')}]^2 = \left(S_i^{(v')}\left[\frac{1}{N-1}\right]^{1/2}\right)^2$$

$$= \frac{[S_i^{(v')}]^2}{N-1} \qquad (116)$$

The $[i_i^{(v')}]^2$, which initially solely represents self-control but may evolve into creativity, is proportional to $[i_i^{(v')}]^2$. As may be seen from column 7 in Table XV, the intensity of this self-control mounts ever more rapidly as lower ranks in the hierarchy are approached. In so long as self-interaction only represents self-control, there can be no creativity. However, in this system what were recessive *d*-genes can become considered as dominant *d*-genes. When this happens for the whole group, a complete reversal of the social rank ordering develops. But such reversal can also take place within a single individual. In essence, this means that $[\dot{i}_i^{(v')}]^2$, which is equivalent to an α'_{ap} frustrating experience, became transformed into an $[\dot{i}_i^{(V')}]^2$, which is equivalent to an α_{aa} satisfying experience, without losing any intensity in the process.

There need not be any outward manifestation of this transformed self-control. $[\dot{i}_i^{(V')}]^2$ only implies cortical associations among stored traces of external events lacking any aura of negativism. Other than this, there are no limits to the kinds of traces which may by chance attain a high conditional probability of association. External manifestation of $[\dot{i}_i^{(V')}]^2$, that is creativity, implies sufficient contact or awareness of external events to permit symbolic or behavioristic alteration of the enivornment in harmony with these heightened conditional probabilities of association. $[\dot{i}_i^{(V')}]^2$ must not be confused with learning. I shall not attempt to go into the question of learning here other than to say that it should be most effective in high velocity individuals.

It is well recognized that a feeling of ecstasy, of extreme well being, accompanies any instance of creativity. A unit of $\theta_a^{(o)}$ arising from a single interaction represents such ecstasy. Recall that $\theta_a^{(o)} = 0.25$. Examination of Table XV reveals that not until R_8 is reached in the descent through such a hierarchy of $N = 11$ individuals will $[\dot{i}_i^{(v')}]^2 = [S_i^{(v')}]^2/(N - 1)$ exceed 0.025. It will exceed 0.25 for $R_8 \cdots R_{11}$ in an $N_b = 11$. And yet I have already indicated that some of these, probably at least the last two, will be so withdrawn from reality as to preclude any opportunity of creativity. At most, we can therefore anticipate only 2/11 or 18% of the group to possess potentialities of creativity. As N increases, proportionately more individuals will accommodate by social withdrawal and relatively fewer will possess potentialities of creativity.

Realization of these potentialities requires another set of conditions, opportunity for having made many satisfactory accommodations to new configurations of stimuli. As discussed in the later Sections XIV, G, 1 to 3, this means that there must have transpired an increase in one's psychological area, A'', as a compensation for the reduced A associated with a lowered v.

E. Velocity and Home Range

In my search for adequate formulations of the social use of space and time I have been guided by several competent mathematicians. With regard to home range, Mr. James U. Casby (see Calhoun and Casby, 1958, pp. 16–17) derived a function, $K/2\pi\sigma^2$. He called this term "visitation frequency." It describes the relative frequency of visiting a particular place in the environment. Later, though published earlier (Calhoun, 1957), Dr. Murray Eden derived the function, $\mu = dv/A$ to represent a communication function defining the relative probability of one individual meeting another. $K/2\pi\sigma^2$ concerns arrival at a stationary point, while dv/A concerns arrival at a moving point. It was only after I began this elaboration of concepts concerning social use of space that I realized the isomorphism of these two functions. A and $2\pi\sigma^2$ become equivalent expressions as likewise do K and dv. d here is used in the sense of $S^{(v)}$, Eq. (107).

I have already pointed out in the discussion pertaining to Eqs. (35), (80), and (88) to (91) that when a group is in a steady state in harmony with its heredity and environment, $\mu = 1.0$, provided appropriate units of time are considered. It followed that v, $S^{(v)}$, and A also have relative values of 1.0 at N_b, the harmonious steady state N. Therefore

$$vS^{(v)}/2\pi\sigma^2 = 1.0 \tag{117}$$

Given this relationship, can it assist us in determining relative home range σ? We have already seen in Sections VI–VIII that contractions and expansions result from both intraspecific and interspecific interactions. Let us consider home range of members of a constellation as discussed in Section VIII, C.

On the average the constellation consists of one alpha, 6 beta, and 5 gamma individuals, ranked in this order:

$$N_b = N_\alpha + N_\beta + N_\gamma,$$

where $N_\alpha = 1$, $N_\beta = 6$, $N_\gamma = 5$. The α individual represents the ideal prototype. Each beta diverges an equivalent amount from the alpha. Likewise, each gamma also diverges from the alpha, but more so than the beta. By analogy to the discussion pertaining to Table XIII, the d-genotypes of the 12 individuals in a constellation will be represented as shown in Table XVIII. σ_S in the table denotes alteration in the home range σ resulting from the individual's $S^{(v)}$.

The N_{j} for the alphas, betas, and gammas, according to the formulation of Section XIII, B, 5 become respectively 12, 11, and 5. From Eq. (107) it follows that their $S^{(v)}$ are, respectively, 1.0, 1.091, and 2.40. This increase in response-evoking capacity, $S^{(v)}$, among beta and gamma individuals will lead to their reduction of velocity, v, respectively to 0.9167 and 0.4167, as given by Eq. (108), when compared with $v = 1.0$ for the alpha member.

In terms of home range the $S^{(v)}$ function in Eq. (117) may be ignored, which means that:

$$v/2\pi\sigma^2 = 1.0 \tag{118}$$

For this relationship to maintain in the face of reduced v for beta and gamma individuals, σ must correspondingly decrease, such that

$$\sigma = (v/2\pi)^{1/2} \tag{119}$$

Since 2π is a constant we may ignore it for the purpose of determining home range σ relative to that of the alpha individual. Then

$$\sigma_S = (v)^{1/2} \tag{120}$$

TABLE XVIII

RELATIVE HOME RANGES OF CONSTELLATION MEMBERS

Constellation member	d-Genotype	N_i	v (Eq. (108))	σ_S (Eq. (120))
α	(d) A B	12	1.0	1.0
β_1	(d) a B	11	0.9167	0.9575
β_2	(d) a B	11	0.9167	0.9575
β_3	(d) a B	11	0.9167	0.9575
β_4	(d) a B	11	0.9167	0.9575
β_5	(d) a B	11	0.9167	0.9575
β_6	(d) a B	11	0.9167	0.9575
γ_1	(d) a b	5	0.4167	0.6457
γ_2	(d) a b	5	0.4167	0.6457
γ_3	(d) a b	5	0.4167	0.6457
γ_4	(d) a b	5	0.4167	0.6457
γ_5	(d) a b	5	0.4167	0.6457

In essence, this line of reasoning predicts that as velocity is reduced the area encompassed by the home range will develop similar reductions. Relative home range sigmas, derived by Eqs. (107) and (120), as given in Table XVIII formed the basis for the relative sizes of home ranges within a constellation (Fig. 27).

In considering the home range of the individual in the context of membership within a constellation of N_b individuals, it is obvious that the term "area" possesses dual meaning. ($2\pi 3\sigma_\alpha^2$) approximately measures the A

of the constellation (Section VIII, C), while ($2\pi\sigma_S^2$) represents that portion of each individual's home range within which it spends 0.394 of its time. Each individual simultaneously "inhabits" two life spaces, his own and that of the group of which it is a member.

For all members but the alpha member, qualitative differences in $S^{(v)}$ lead to reductions in v, which in turn bring about reductions in A such that the reduced A is proportional to v. This accommodation will result in μ again exceeding 1.0 and will thus expose the individual to stress from an increased frequency of contacts. Further accommodation, again reducing μ to the relative value of 1.0, can come only through quantitative reduction of the target diameter, d, since the $S^{(v)}$ qualitative aspect has become a stable factor. It will be recalled that the concept of the constellation presupposes a capacity for emitting and receiving signals sufficient for any member to gain contact with any other member despite their spatial separation. Such signals amount to an increase in d at the moment of this emission. The easiest strategy for regaining a $\mu = 1.0$ will be for each individual to reduce the frequency of signaling as much as it had reduced its velocity. This line of reasoning culminates in the conclusion that v, σ^2, and d (in the sense of frequency of signaling) will all be reduced to values inversely proportional to $S^{(v)}$. With respect to the unchanged relative values of 1.0 for the alpha individual, these values for beta members become respectively 0.9167, $(0.9167)^2$ and 0.9167, while for gamma members they become respectively 0.4167 $(0.4167)^2$, and 0.4167.

Consistent with my objective of developing formulations adequate for acquiring data in concrete experimental studies, the above theoretical conclusions may be tested for their application to groups more compact than represented by constellations. Given an experimental $N = 12$ restricted to an area A, one can estimate relative velocity be determining the proportions of a series of time samples in which each individual is active and exposed to situations where social interactions do occur. This velocity we can designate by $\hat{v}$. Velocity so estimated will reflect true velocity more accurately than the cruder measure of number of contacts, n_c, used in the specific case in the discussion pertaining to Eq. (113). This is because an animal may be active when all others are at rest.

The more velocity is reduced, as predicted by Eq. (108), the more the individual should restrict his travels to a smaller portion of the area utilized by the group. Of an originally common home range shared by members of a "compact" group, low velocity members will come to utilize only a portion. Thus, the ideal design of an area within which social organization is being studied must provide for many subareas to which visitations may be recorded. Otherwise, reduction in home range cannot be detected.

Likewise, the more an individual reduces his velocity, the more he should reduce the emission of signals eliciting social awareness of him by associates. Such signaling may involve other than vocal modes and may even involve reduction of $S^{(v)}$ itself. In the end, such reductions of d and $S^{(v)}$ will produce an individual which, when encountered, is judged by associates as being dull, lifeless, and with flat affect, lacking the attributes of an appropriate object for social interaction.

F. Velocity in High-Density Rat Societies

While these formulations of social dynamics were being developed I was simultaneously pursuing empirical studies of social dynamics revealed by large groups of domesticated Norway rats. We shall examine those data which indicate (a) that densities greater than appropriate for N_b suppress velocity, and (b) that an increase in vitamin A above normal levels buffers the social system against the velocity-suppressing force of increased density.

During a 16-month period of 1960–1961 further studies in the habitat (Fig. 33), discussed in Section XII, C, were conducted. In this second series of studies the only habitat change involved altering the method of providing food and water. This change precluded the development of the behavioral sink discussed in Section XII, C. [See Calhoun (1962b) for a general account of these two series of studies.] However, our concern here will be with results not previously presented.

During the 13th, 15th, and 16th months of this study estimates of velocity, $\hat{v}$ were made for each of the 32 adult males in each of the two societies considered here. All males were fully mature, ranging in age from 10 to 15 months of age.

Procedure for velocity estimation: As illustrated diagrammatically in Fig. 33, each of the four pens in the room defining area A contained two areas where social interaction occurred most frequently. One was on top of the elevated artificial burrows; the other was on the floor in the immediate vicinity of the sources of food and water. During each half hour of observation, each rat was given one velocity score for each of the eight locations visited. On 2 days, not more than 3 days apart, Dr. Kyle R. Barbehenn and I each recorded such velocity scores for 16 half-hour periods during each of the three months mentioned above. For a particular month, the estimated velocity thus consisted of the sum of the velocity scores for 32 half-hour periods of observation. The estimated velocity, $\hat{v}$, is here taken as the mean for three 32 half-hour sums.

The two societies were designated as 1A and 2A. Thirty-two males in 1A and 32 males in 2A survived through the 15th month. A few males died just before the third set of velocity estimations due to injections of a monamine oxidase inhibitor (Catron), which substance had no influence on the velocity of survivors. Thus, for a few individuals, $\hat{v}$ is based on the mean of only two estimates of velocity for the 13th and 15th months.

These estimates of velocity are shown as data in Fig. 38. Approximate regression lines were fitted by eye through these points for both 1A and 2A. Velocities of 1A males are markedly lower than those for 2A males. According to the general formulation of velocity, one would anticipate that males in 1A had been exposed to many more social restraints or sanctions in the form of aggressive actions from associates. This, in fact, was the case as is reflected by the amount of scar tissue developed over the lumbar-sacral area from wounds received in fighting. On the basis of a 5-point rating scale (0 = none, 5 = most), the mean scar tissue index for 1A and 2A males was, respectively, 3.24 and 2.49.

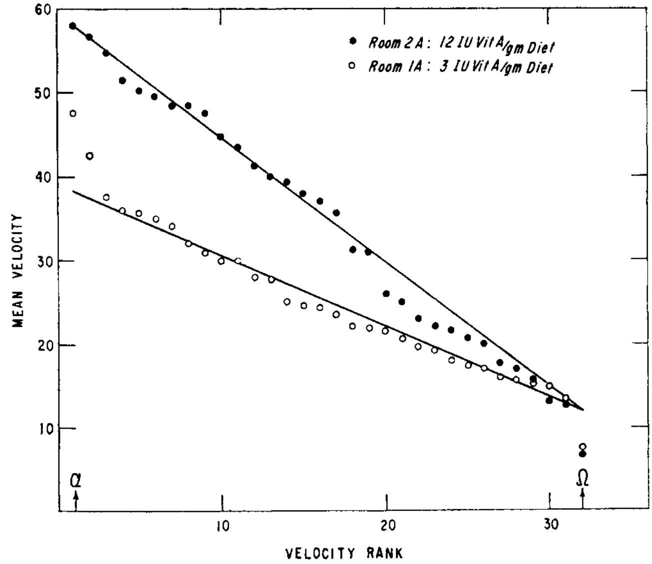

FIG. 38. Velocity, velocity-rank relationships among male rats in a closed society.

The lowered intensity of fighting by 2A males was associated with a higher vitamin A content of their diet. Both 1A and 2A rats were given an dentical synthetic diet except for vitamin A. 1A rats received 3 international units per gram of diet, a high normal level in comparison to natural foods. However, the 2A rats were given 12 international units per gram of diet, a level comparable to that given to humans in high potency vitamin pills. Although it is outside the objectives of the present discourse to detail the effects of increased levels of vitamin A on behavior, it suffices to note that increases in vitamin A above normal levels acts as a kind of "tranquilizer" which reduces fighting but increases the prevalence of abnormal behavior (i.e., females become poorer mothers while males increase the frequency of exhibiting inappropriate sexual behavior).

Previously we have seen (Section XIV, A) that in an $N = 11$ the observed velocities for mice, as calculated by Eq. (113), closely approximated the theoretical. We may ask the same equation of the present data. For 2A the sum of velocity indices $[\sum_{i=1}^{N} v_i^{(\mathrm{obs})}]$ for 16 hours of observation was 1089.2, and for 1A it was 804.7. Let $v_\alpha^{(\mathrm{exp})}$ and $v_\Omega^{(\mathrm{exp})}$ represent the velocities of the alpha, 1st-ranked, individual and the omega, Nth ranked, individual, as calculated by Eq. (113). For 1A, $v_\alpha^{(\mathrm{exp})} = 48.77$ and $v_\Omega^{(\mathrm{exp})} = 1.52$; while for 2A, $v_\alpha^{(\mathrm{exp})} = 66.01$ and $v_\Omega^{(\mathrm{exp})} = 2.06$.

Had all the intermediate $v^{(\mathrm{exp})}$ been calculated, as would have been represented by a straight line connecting these extremes on Fig. 38, it is quite obvious that the observed would differ significantly from the expected. One could drop the inquiry at this point and conclude that velocities for rats do not accord with theory as for the mice cited in Section XIV, A. However, there are two reasons for not dropping the inquiry at this stage. First, 32 males represent an N almost three times the theoretical basic N, $N_b = 12$ while the $N = 11$ for the mice closely approximated this N_b. Second, the regression curve of velocity for the 1A and 2A males converge at the omega-ranked individual. Furthermore, this convergence is at a velocity 6 to 8 times that anticipated by Eq. (113). This fact suggests a minimum velocity, v_m, below which rats cannot reduce their velocity and long survive. Two such individuals with excessively reduced velocity are shown on Fig. 38. I can only say that, on the basis of the very few individuals which did develop such unusually low velocities, such individuals usually become bloated and usually shortly died.

Accepting the indication of the reality of v_m, is there a logical basis for recognizing its relative value? In the course of evolution, where the group becomes adjusted to an N_b, there will in any stabilized group be an N_b-ranked omega individual. In terms of Eq. (107) it is readily apparent that, where R = rank in the sense used in Table XIII:

$$N_j = 1 + (N - R) \tag{121}$$

Therefore, for any ith individual where i is equivalent to its rank R, Eq. (108) becomes

$$v_i = \frac{1 + N - R}{N} \tag{122}$$

Since the rank, R_Ω, of the omega individual is N_b:

$$v_\Omega = \frac{1 + N_b - N_b}{N_b}$$

$$= \frac{1}{N_b} \tag{123}$$

Since v_Ω is the lowest velocity achieved in the normal N_b selected by evolution, v_Ω most likely also represents v_m. Given a v_m observed, $v_m^{(\mathrm{obs}}$, we may calculate a $v_\alpha^{(\mathrm{exp})}$ appropriate to N_b. Recall that from Eq. (108) $v_\alpha^{(\mathrm{rel})}$ in relative terms = 1.0 and the relative velocity, $v^{(\mathrm{rel})}$, of any other ranked individual is by this equation represented as proportions of the alpha's velocity. $v_\Omega^{(\mathrm{obs})}$ or $v_m^{(\mathrm{obs})}$ from Fig. 38 is 12. Therefore

$$12 = v_\Omega^{(\mathrm{rel})} \cdot v_\alpha^{(\mathrm{exp})}$$

And thus at N_b, and utilizing Eq. (123):

$$v_\alpha^{(\mathrm{exp\ at\ } N_b)} = v_m^{(\mathrm{obs})}/v_\Omega^{(\mathrm{rel})} = v_m^{(\mathrm{obs})} \times N_b \tag{124}$$

However, solving Eq. (124) requires that N_b be known. The rats used were a domesticated albino strain, Osborne–Mendel. N_b still might be 12, as we can expect it to be for the wild type, but we have no way of knowing directly how domestication has altered N_b. Furthermore, the artificial environment imposed possible changes on the area, A, factor in $\mu = dv/A$. So all that can be expected is that there is some optimum N, N_o, harmonious with the existing spatial structure of the environment and any changes arising through domestication. Now, using N_b in the sense of N_o, values in relative (rel) terms become:

For $N = N_b$, $R = 1$: $v_\alpha = 1$

For $N = N_b$ or $N <$ or $> N_b$, $R = N_b$ or N: $v_\Omega = v_m = 1/N_b$

$$\text{For } N > N_b,\ R = 1:\ v_\alpha{}^{(\mathrm{rel})} = 1 - \left[\frac{N - N_b}{N}(1 - v_m)\right] \tag{125}$$

When $N = \infty$: $v_\alpha = v_m = 1/N_b$

The general equation for v, where $v_m = 1/N_b$, and R = velocity rank becomes:

$$v^{(\mathrm{rel})} = R - N\left[\frac{v_m - \{1 - [(N - N_b)/N](1 - v_m)\}}{N - 1}\right] + v_m \tag{126}$$

Assuming the validity of all assumptions inherent in Eqs. (124) to (126) we can now approximate the N_o of the 1A society of rats. The regression curve for 1A shown in Fig. 38 gives $v_\alpha^{(\text{obs})} = 38$. Insertion of successive values of N_b in Eqs. (124) and (125) shows that when $N_o = 9$, $v_\alpha^{(\text{exp at } N_b)} = 108$ and $v_\alpha^{(\text{rel})} = 0.36$. Since $0.36 \times 108 = 38.9$, it follows that, for the strain of rat under the existing environmental conditions, 9 individuals approximate N_o for male rats.

Now we may return to the "tranquilizing" effect by which vitamin A "buffered" the 2A males from the velocity-inhibiting consequences of $N > N_b$. There needs to be a correction factor in Eq. (126) which, as a "tranquilizing" factor, Z, increases the slope of the velocity—velocity rank curve also increases, "pivoting" about v_m. At present there is no a *priori* basis for determining this Z factor, which can draw upon empirical evidence. However, one can visualize a likely formulation of Z. Z implies a factor "blinding" awareness of the d or $S^{(v)}$ of associates. Such perceptual blinding conforms with the d' factor of $\mu' = d'v'/A'$, previously alluded to. The critical issue concerns the influence of Z upon v_α. If the velocity of the first-ranked alpha individual never exceeds that appropriate at N_b, that is, if

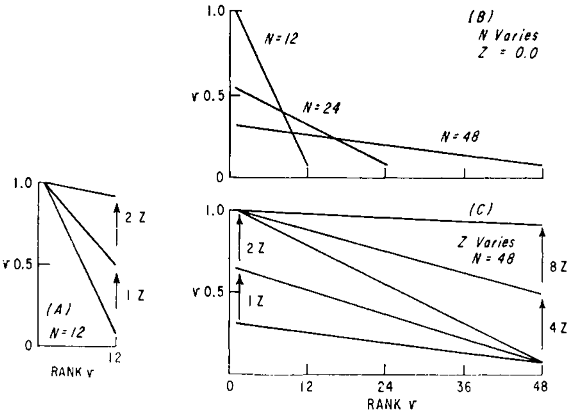

FIG. 39. Hypothetical effect of group size, N, and tranquilizer, Z, on velocity, v, when $N_b = 12$.

$$v_\alpha^{(N_b)} = v_{\max} = v_M = 1.0,$$

then we would have a partial basis for understanding how Z alters v.

In the absence of adequate empirical data regarding the function of Z on v, consideration of hypothetical relationships (Fig. 39) will facilitate our understanding to the point of enabling the design of critical experiments. First consider Eq. (125). Increasing N reduces v of all members. By the time N is only a few times N_b, velocity of all members will be so reduced as to bias the probability of the social system surviving. Minimal velocity implies withdrawal from social interaction and restriction of activities to independent acquisition of food and water.

Now, assuming a v_M, even though it might exceed 1.0, Fig. 39 suggests that increasing Z will eventually elevate v_α to v_M, while v_Ω remains at v_m as shown in Fig. 38. Once v_α reaches v_M, further increase of Z should reduce awareness of the $S^{(v)}$ of others to the point that v_Ω departs from v_m and begins to approach v_M. At $Z = \infty$, $v_\Omega = v_M$. Far before $Z = \infty$, the velocity of all members of N will be maximal for all practical purposes. A state of maximum conformity will then have been attained in which each individual views every other one as so like himself that no individual imposes restraints on the actions of any associate. All social organization must collapse, leaving a state of maximally moving independent particles, the random contact between any two of which will be equally satisfactory in consummating any interaction in which two individuals are necessary. This state demands equipotency of capacities. Complexity of behaviors will be limited to that degree possible by every individual having identical learning experience. Maximizing Z becomes incompatible with a high state of learning and culture.

The human species appears to be embarked upon a journey of both maximizing N and maximizing Z. If we are to avoid one of the other of the nirvana-like states of uniform v_m or v_M, it behooves us to seek further insight from experimentation with animal groups.

Returning from theory to reality, we may consider some correlates of velocity. Most of the 1A and 2A rats discussed above survived to autopsy during the 17th month of the study. Each set of males was divided into five velocity class intervals, with as nearly as possible the same number of rats in each velocity range. Associated conditions are graphed in Fig. 40. As velocity increases, the amount of scar tissue derived from fighting increases. The somewhat S-shaped character of this curve conforms with historical events. In general, the more rats withdrew from social interaction by reducing their velocity, the fewer wounds they received. However, a few individuals, though having a very low velocity in late adulthood, were characterized by extensive scar tissue because they failed to withdraw as early in life as had their low velocity comrades. At the other extreme of velocity, territorial males or highly dominant individuals, who were territorial in the time dimension but not in space (i.e., the "changing-of-the-guard" phenomenon through which several males share the dominant role in a particular area), by their status avoided attack and thus avoided being wounded even though they were extremely active and inflicted wounds on associates. Their lesser degree of scar tissue contributed to a reduction in the mean scar tissue index for high-velocity males.

Weights of adrenals, kidneys, and heart all tend to increase as velocity increases. Despite lack of histological studies, what I suspect has happened is that as velocity drops as animals withdraw from social interaction, organ size decreases in accordance with decreased demands made upon them.

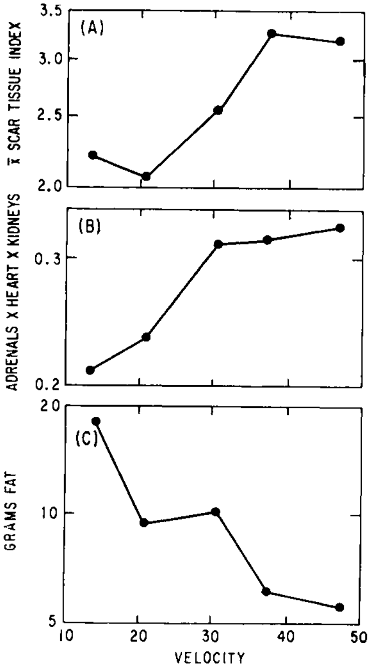

Fig. 40. Some major characteristics of rats affected by conditions that determine velocity.

Fig. 40(B) simply shows the product of the weight of these three different organs.

Most sensitive to velocity and easy to measure is fat, Fig. 40(C). Fat here represents those abdominal deposits most easily removed: the dorsal lumbar-sacral deposit, that in the genital mesentery, and those in the mesenteries of the gut. Though these deposits are rarely as large among males as for females, it is nevertheless quite clear that as rats slow down by social withdrawal they exhibit greater propensities for converting foodstuffs into fat.

G. Exploratory Behavior

Ultimate exposure to some new configuration of stimuli represents the common factor in the three phenomena encompassed by the term, "exploratory behavior." These three phenomena are: (a) the rise and decline of a hyperactive state following exposure to a new configuration of stimuli (see Section III, A, 4); (b) the rejection of new configurations (see Section III, A, 3); and (c) the seeking of new configurations. We shall now examine how the opportunity for expressing such behaviors alters an individual's attitude toward its physical and social environment.

1. THE HYPERACTIVITY PHENOMENON

In an animal's normal habitat this phenomenon may be anticipated to follow an encounter with a new configuration of stimuli at places in the normal home range where it has not occurred during customary travels. Field studies directed toward the elucidation of the consequences of such encounters are essentially nonexistent. Pearson (1960), by photographing marked mice as they move along their trailway systems, has found that, following the experience of being trapped and handled, mice not only become more active but also visit places within or near their normal home range which are normally infrequently visited. My study of the reaction of domesticated Norway rats following exposure to an activity alley (Section III, A, 4) represent this same type of situation with the exception that the induced state of hyperactivity must take place in the presence of the new configuration of stimuli represented by the alley.

Recall that the rat is placed in a compartment with an access door at one end of the alley. It does not have to enter, but many rats do so rather immediately. For example consider the 73 rats involved in the analysis of distance of termination of trips shown in Fig. 3. Analyses (Fig. 6) have been made of their hyperactivity during the initial 2.5 hours of their residence in the activity alley. From an initial high level, activity declines exponentially over an approximate 3–4 hour period nearly to a base level maintained on the average through each of the 12 hours of normal heightened activity during the next 3 days. This pattern is shown diagrammatrically in sketch (1) of Fig. 41. Such heightened diffuse motor activity lacks any aura of goal direction and will be designated by the symbol, DMA. Such a configuration of new stimuli as is represented by the alley will be designated as *E*. If a rat is placed again in the alley for 2 hours on each of several consecutive days, no appreciable amount or duration of DMA occurs on any day. This means that there has transpired an adjustment, A, to E by the end of the initial 2 hours of exposure to E. After A, motor activity persists on the average at a base line intensity, b, unless some other new configuration E is encountered. Thus, DMA represents increments of activity above b.

In the alley, E can only include nonsocial physical stimuli. And yet in a social milieu of others of an animal's own species, the responses of an associate also represent an E. Provided such a social E has not previously been encountered or if the associate is in the nonresponsive, $[p]$, refractory state, then the latter's behavior, though perhaps experienced before, amounts to a previously unencountered E in the sense that it does not permit directed motor activity leading to a satisfactory refractory period by the other individual involved in the encounter. For this reason, it will here be presumed that the period of decline of hyperactivity is equivalent to the α_{ap} frustrating type refractory period involved in normal social intercourse.

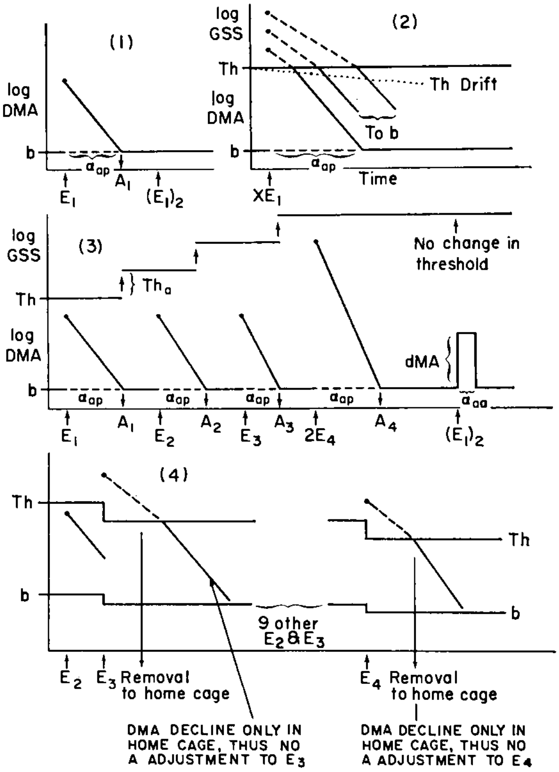

FIG. 41. Adjustment to configurations of stimuli. See text for comment.

If rats are maintained in isolation for several weeks or months and then placed in an emotional activity alley, a large proportion of them never go out into the alley from the "home" compartment. From this I infer that there is some upper threshold, Th, of DMA which "overloads" that neural circuit permitting its expression. The three dots in sketch (2) denote such overloadings. In any sample of subjects, most of whom avoid entering the alley, there are a few with various lengthened latencies, causing delays of up to nearly the end of the 2-hour test period before initiation of the initial phase of intense hyperactivity. From this fact it is apparent that the normal DMA becomes replaced by some generalized stress state, GSS, which follows a similar (but lower?) rate of decline than the DMA. GSS lacks a striated muscle component. Once it has declined to Th, GSS becomes transformed to DMA. Such subjects, owing to their having been protected from impinging external stimuli for such a long time during their isolation, view the alley configuration as an increased intensity, E. An inference from this is that there is a slow drift downward of Th toward b during the weeks of isolation when opportunities for adjustments $A_1 \cdots A_n$ in response to $E_1 \cdots$ to E_n are absent. Thus, depending upon how extensive this drift has been, any particular E, such as represented by the activity alley, raises the GSS different amounts above Th. I suspect, though my data are not conclusive, that the more elevated GSS is above Th the lower will be its rate of decline. These differences are diagrammatically shown in sketch (2) of Fig. 41. Given sufficient time with no interference by other E's, DMA will eventually reach b and an adjustment, A, transpires.

Now we may consider the more normal course of maturation, experience with a sequence of $E_1 \cdots E_n$ [sketch (3) in Fig. 41]. One general observation first. The greater has been the experience of rats in the sense of a larger number of different E's to which adjustments, A, have been made, the lower will be the probability of withdrawal in the form of failing to enter the alley from the starting "home" compartment. An explicit experiment concerning this point has already been cited with reference to Table Ib. Such results indicate an elevation of Th to Th_a following each A, and this elevation will be proportional to the magnitude of E provided E does not elicit a DMA exceeding Th. Thus, at some later time an intense E, designated as $2E_4$ in sketch (3), will result in adjustment A_4, although had a $2E$ configuration occurred earlier it would have resulted in the undesirable consequences accompanying elevation of DMA above Th. There is another conclusion, somewhat more tentative, though some of my results do support it. This is that with each successive E, the rate of decline of DMA increases. In other words, the α_{ap} refractory period decreases. Thus, the more adjustments an individual makes, the better he will be able to curtail $\alpha f_{ap} = \theta_f$. I have already mentioned the failure of a second exposure to a particular E to induce any material increase in DMA. This means that if E merely represents a configuration of strange stimuli with which the individual can interact in no meaningful way, the second exposure to E, that is $(E_1)_2$, will evoke no response. $(E_1)_2$ will merely be ignored. However, if some aspects of the E_1 configuration permit meaningful interaction, then $(E_1)_2$ will result in an interaction having an α_{aa} refractory period proportional to the evoked directed motor action, dMA. This α_{aa} will normally be of shorter duration than α_{ap} to $(E_1)_1$ since some components of the configuration are likely to be irrelevant to dMA. Furthermore, dMA may be expected to be maintained at near its initial intensity until the evoked behavior terminates. No further elevation of Th accompanies $(E_1)_1 \cdots (E_1)_n$. Persistent recurrence of any specific E merely serves to prevent the drifting downward of Th.

Each adjustment to a new E configuration resulting in an elevation in Th represents a contribution to the individual's psychological area, A''.

2. THE SEEKING OF NEW CONFIGURATIONS

Consider two groups of individuals, A and B, of which the members of each for a fairly long period merely reexperience particular sets of E's. Members of group A differ from those of B in that they are exposed to a larger assembly of different E's. Two such groups have been considered in Section III, A, 5 and Table IIa. The fact that more of the A-type individuals entered the alley when exposed to this new E configuration of stimuli indicates that reexperience of a larger assembly of different E's does maintain Th at higher levels despite some downward drift. The A-type individuals obviously have a larger psychological area, A'', than the B-type ones. A'' essentially connotes capacity to adjust. In any environment presenting frequent necessity for adjustment, a high A'' will prove advantageous. So we need to consider the question of maximizing A''.

Persistence in repeated interaction with certain E's is necessary or desirable because of acquired reward value accompanying the directed motor activity, dMA, appropriate to these E's. Such dMA can only preserve Th at a given level. Response to these E's involved in this dMA consumes time. If all waking time becomes relegated to dMA-evoking E's, the individual will develop a static A''. Furthermore, the more waking time becomes filled with repetitions of response to any given E, the more restricted will be A''. It is thus obvious that the best strategy for maximizing A'' will be to reserve a portion of one's waking hours simply for responding to new E's. Some as yet unknown but probably fairly long time, certainly of the order of several days even for rats, must elapse between one exposure to such a new E and a reexposure, permitting sufficient extinction of the A

adjustment so that at the re-exposure the *E* elicits a DMA comparable to that of the initial exposure. Because of the limitations of time and space in which any individual's activities must transpire, maximizing A'' demands an active seeking of new *E*'s. This seeking, I term v''. It represents a kind of velocity difficult to distinguish from the normal velocity, *v*, unless one is aware of the history of an individual with reference to its pattern of repeating specific dMA. In empirical experimental situations the relative magnitude of v'' may be determined by observing the probability of approaching a new *E* introduced into an individual's home range so that normal movements will produce exposure. Ecologists concerned with controlling the density of species which damage human property or serve as hosts for diseases transmittable to man have been aware of v'' in a negative sense. They (e.g., Chitty and Southern, 1954) have noted the avoidance of new objects, such as poison baits or traps. This avoidance has been termed "the strange-object response."

3. ACTIVE REJECTION OF NEW CONFIGURATIONS

Distinct from the relative attraction to or avoidance of a new configuration is the phenomenon of physically rejecting or psychologically blocking awareness of new *E*'s. Processes included under this phenomenon of rejection may be designated as d''. A grasp of the types of phenomena subsumed under d'' may be obtained through considering a case observed in my laboratory.

Large "life-space" cages, LSC, were designed to provide an optimum situation for the breeding of the very sensitive wild Norway rats in the laboratory. A 16 × 25-inch floor provided access to an activity wheel on one side and a lever on the other, which when pressed, provided a drop of water. From this floor two ramps led to a partitioned second floor of equal dimensions. From one side of the second floor rats had access to one 8 × 8 × 6-inch nest box, while two next boxes were accessible from the other side of the second floor. One male and two female adult rats lived in each of six cages. At the time in question three of these cages each also contained a recently weaned litter. Up to this time the water-providing lever apparatus had not been delivered by the manufacturer. In its place the adults were provided water through a drinking tube from a bottle, as had been the practice since they were captured in the wild as juveniles. When the lever apparatuses became available, one was inserted into each cage and the water bottle was removed. By the following morning when the cages were next examined, the situation in each cage was identical; all movable objects available to the rats, paper used as nesting material and orange peels, had been piled over the lever, completely hiding it.

In those cages containing recently weaned young, the young soon scattered the pile of objects, exposing the lever, and in so doing accidentally pressed the lever and gradually learned its function. There then followed a repeated process of covering the lever by the adults and its removal by the young. Through this process the adults were forced to face E, represented by the lever and its attached water reservoir, sufficiently to permit an A adjustment to E through the DMA decline process. Several points may be deduced from these observations. Th for the adults had previously drifted downward toward b so that the E lever configuration caused DMA to exceed it. Furthermore, at weaning Th is sufficiently removed from b that many E's will fail to evoke DMA elevation above Th. Had evolution not resulted in such a balance between neurology and physiology, animals just emerging out into the many E's of their environment would immediately be forced into a withdrawal state. Although I shall not go into this problem here, it is obvious that retardation of "weaning" increases the probability of withdrawal.

In the three cages lacking recently weaned young, the pile of material covering the levers remained undisturbed for several days until the rats were so weak from lack of water that it was apparent that their rejection of the lever was so complete that they would die before getting the opportunity to learn its function through chance depression of it. Replacing the former water bottle merely satisfied their thirst but failed to alter their rejection of E. "Teaching" the rats the lever was finally accomplished by taking all movable objects from the cage and gradually increasing the interval during which the water bottle was removed. It took 3 weeks to reach the same level of lever pressing by these rats that was obtained within 3 days by adults when young not only made rejection impossible but also set an example of adjusted interaction with the E lever configuration.

Other examples of such d'' active rejection, but toward social E's, have already been given in Section XIII, B, 4 in connection with the three examples involving Barnett's Norway rats, the "Freedom Riders," and the formation of the C57 Colony 1B of house mice. Thus, in terms of active rejection, d'' becomes essentially synonymous with intensity of action toward another, $i_{ei}^{(v)}$ as given by Eq. (114). But d'' must also encompass the more strictly psychological phenomena of psychological deafness or psychological blindness such as characterizes the "malingering type" of individual.

Note that this consideration of exploratory behavior has lead to formulations of d'', v'', and A''. As for prior comparable terms:

$$\mu'' = (d''v''/A'') \tag{127}$$

Here μ'' represents a third contact modifying function when relating to a social group. Just as with μ and μ', so it is apparent here that the magnitude of v'' and A'' will normally change by comparable degrees in the same direction and that d'' will approximately vary inversely with v''.

4. THE EFFECT OF INTERVAL BETWEEN E'S ON VELOCITY

Further examination of the data in Table IIb, in the light of the formulations relating to exploratory behavior and configurations of stimuli, provides additional insight into the origin of reductions in velocity, both v and v''. Refer to Section III, A, 3 for other comments. Presentation of the experiment in terms of the present formulations is as follows:

The subjects consisted of male albino Osborne-Mendel strain rats isolated at weaning. At this time each rat was placed in a 6 × 6 × 8 inch cage from which it could not see out. Water and food were introduced through channels from the outside which prevented the rats from seeing the experimenters or being handled by them. All rats remained in such isolation for approximately three months before further treatment. These isolation cages may be termed an E_1 configuration of stimuli. Due to the long absence of opportunity for adjustment to new configurations of stimuli, the Th of all rats probably drifted toward b.

At the end of the three months of isolation the subjects were divided into four groups: A (20 rats), B (24 rats), C (16 rats), and D (16 rats). On each of 10 days during the next two weeks each member of Group C was exposed for two hours to a new configuration of stimuli, E_2, which was a Wahman activity wheel; all rats so exposed entered the wheel and ran during each of the 10 days. Similarly, members of Group C were exposed to an E_3 configuration of stimuli. This exposure consisted of placing the rats in a 2 × 5-foot pen where they had the opportunity to climb onto a central platform where a lever could be pressed to receive a drop of water. Each day of this 10-day training period half the members of Group D were exposed for two hours to E_2 and then, immediately following, for two hours to E_3. The other half of Group D were similarly treated but were exposed to E_3 just prior to E_2. Group A remained in their isolation cages during these two weeks.

During the third experimental week every rat in all four groups was given a two-hour exposure to the NIH Emotional Activity Alley on each of four successive days. This alley represented an E_4 configuration of stimuli. For half the rats in each group E_4 had a stationary floor, a condition we may designate as E_{4A}. For the remaining rats E_4 had a tilting floor which clanged as the rats ran across it. This modification is designated as E_{4B}, which represents a much more intense or strange configuration than E_{4A}. Many rats avoided entering the alley.

Regardless of the amount of prior opportunity to adjust to novel configurations, the more intense E_{4B} elicited a more marked avoidance than did E_{4A}. (See Section III, A, 3.) However, our present concern is with a different aspect of the results in Table IIb.

Upon exposure to E_{4A} it appears that prior experiences with E_3 was much more effective than with E_2 in reducing avoidance of the E_{4A} configuration. But members of both Groups B and C evinced much less avoidance of E_4 than did members of Group A. This supports the formulation that prior opportunity to adjust to new configurations elevates Th so that at a following exposure to another new configuration of stimuli, DMA is less likely to exceed Th. Avoiding entering the alley is taken as evidence of DMA exceeding Th.

These results confirmed prior hypotheses. However, it was further assumed that rats of Group D would exhibit the most marked accommodation to E_4 since they would have had twice the opportunity for making adjustments to new E's. And yet even to E_{4A}, the rats of Group D showed little better capacity for adjustment than did members of Group B, and much less than did rats of Group C. Upon elevation of the intensity of E_4 to E_{4B}, members of Group D exhibited an extremely more marked reduction in capacity to adjust than did the rats of Groups B and C, that presumably had less opportunity for "training" in making adjustments.

These results apparently contradict the theory. But consider the following. For rats exposed to new configurations of stimuli, such as E_4, but permitted to remain for several rather than for 2 hours, it has been noted that many individuals require up to 3 hours for DMA to decline to b. In the 2000-odd tests where rats have been exposed to the E_4-type alley configuration to test for emotionality, the tacit assumption has been made that the remaining decline in DMA will take place after the return of the rats to their accustomed environment. However, this opportunity did not prevail when, after 2 hours in E_2 or E_3, rats were transferred to the opposite E.

Events presumably transpiring are diagrammed in the left-hand side of sketch (4) in Fig. 41. Upon exposure to E_3 after only partial decline of DMA following exposure to E_2, the same increment in DMA is elicited, but its rise starts at the point of a still fairly high level of DMA. Thus, this second increment in DMA forces it above the threshold, Th, where DMA is transformed from diffuse motor activity into the generalized stress state, GSS. Although GSS and DMA were not measured during E_3 (or during E_2, if it came second for Group D), both must have eventually completely disappeared after the usual return to the home cage. And yet the very failure of many members of Group D to enter the E_4 alley when given exposure to it suggests that for each degree of GSS induced by too close spacing of consecutive new E's, there had transpired a drop in Th and B such that Th drops relatively more than b. Each of the ten opportunities for consecutive exposure to E_2 and E_3 must have narrowed the gap between b and Th. Thus the later exposure to E_4 must have caused "overloading" for most Group D rats to the extent that GSS had not declined to Th by the end of the two hours in E_4. This meant that decline in DMA to base level took place in E_1. Return to E_4 for 2 hours on each of the following 3 days was characterized by persistence in avoiding entry into the E_4 alley configuration by most rats avoiding it on first exposure. Avoidance, v'', of any new E will thus be proportional to the degree of GSS "overloading" elicited by the new E's.

Although new E's have been considered above in the sense of physical nonsocial configurations, we may consider the consequences of too closely spaced new or undesirable E's in the social sense of $i^{(v)}$'s of associates. Recall that such $i^{(v)}$'s represent social restraints or sanctions imposed by associates. For such sanctions to become effective in reducing velocity, v, that is for causing a drop in baseline of activity, consecutive sanctions by the same or different associates must be sufficiently closely spaced to induce a GSS. No opportunity for v'' avoidance is possible. In fact, with the drop in velocity v (synonymous with b), psychological area A'' must be restricted through failure to make adjustments A to E while still in the presence of E. And as we have seen, as A'' declines so will v''. This means that as velocity, v, declines, the individuals have even less capacity to avoid strange stimuli. However, recall that as v'' declines d'' increases.

I can cite no quantitative data to support this conclusion of d'' increasing as v'' decreases. However, the following observations support its reality. While making the observations on velocity of rats summarized in Fig. 38, I was consistently impressed by the manner in which most very low-velocity rats moved "through" their associates. During those rare times when active, they would pass by associates as if completely psychologically blind to their presence. Furthermore, their blasé, unaffective mode of posture equally failed to elicit response from associates. The completeness of this psychological rejection of reality is reflected in their smaller organ weight and larger amount of fat (Fig. 40), corresponding to states characterizing rats maintained in approximate isolation by restrictions to groups of 1 male with 2 females in small cages or pens.

A further corroborative observation comes from the study referred to in Section XII, A. Among the wild Norway rats in that study was a small group designated as possessing an array of aberrant symptoms and behavior which I called the "syndrome of the social outcast." From comparison with rats described in Sections XII, C and XIV, F, I now know that these social outcasts must have been very low-velocity rats. Of all the rats involved in the study referred to in Section XII, A, they were the only ones ever caught in "Havahart" traps. These large, shiny wire-meshed traps with a door opened at either end and shiny metal treadles on the center floor were regularly placed on trials. All other rats invariably ran around these traps. Yet the social outcasts apparently ran into them without ever sensing their presence. This sensory unawareness is the low v'' factor characterizing low-velocity rats.

XV. Conclusion

Man did emerge from the trials, successfully overcome, of a myriad of ever more simple forms. I have attempted to formulate some phenomena which have affected man's social evolution. Some of these phenomena appear no longer directly operative on the human animal. They nevertheless left their imprint on man's capacity to adjust physiologically and psychologically to the social system in which he lives. Foremost among these presumed legacies are the limitations imposed upon him from his origin out of an evolutionary line in which optimum adjustment demanded living in small groups, not exceeding twice twelve individuals.

Only yesterday, as one may measure evolutionary time in units of ten thousand years, did man begin his attempt to escape this evolutionary bond. But cultural evolution has not produced escape from this bond, merely accommodation to it. Human society has developed the form of a many-layered chain link armor. Each link is composed of not much less than, nor many more than, twelve individuals. The links have a fluid character. Through time, any one individual shifts his membership back and forth among several joining links. This poetic view embodies the essence of reality.

In contrast to such evolutionary legacies, there exist certain principles of social physics which must affect all social animals, man included. These principles derive from certain universals I have called velocity, target diameter, area, basic group size, the social refractory period, threshold for tolerance for change, and the like. I am fully cognizant that my formulations represent only crude approximations to reality, and may in fact contain several errors of logic. Yet we must develop adequate formulations along the lines I have attempted or all efforts to gain insight into the individual's involvement in social action will prove sterile.

This sterility will crown the endeavors of both classical physiology and psychology. We can no longer afford to ignore the impact of the social setting on the individual's behavior and physiology. And without knowledge of evolutionary limitations and universal principles of social physics, consideration of the social setting will also prove of little avail. The search for conceptualizations, adequate for furthering this objective, serves as the justification for inclusion of my effort to introduce the more strictly physiological discussions by the other authors in these volumes.

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