Experimental induction of territorial behavior in the deer mouse, Peromyscus maniclatus
by James John Salonen

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Zoology
Montana State University

Abstract:
This study, through experimental induction of territorial behavior in the deer mouse within the laboratory, confirmed initial observations of territorial behavior and determined that territorial behavior was subject to seasonal variation. No relationship between territorial behavior and the reproductive state of male deer mice was discernible.' Deer mice were first habituated to the animal room and then to the interaction complex as described. Tests consisted of three series of seven experiments, each experiment with two pairs of deer mice (one male and one female per pair). Observation and quantification of sequentially related agonistic and nonagonistic behavior patterns, in the context of criteria established for territorial behavior, indicated that males more often than females exhibited agonistic behavior in defense of an area and mutual avoidance of a conspecific's terrain, while females rarely fought each other and were usually submissive to males. Male and female deer mice exhibited territorial behavior most often by attacking a conspecific in defense of a nest box. In some experiments, males utilized threats instead of fighting behavior to defend their territories from intruding conspecifics. Females rarely threatened conspecifics. As a result of compressing the home ranges of deer mice into the narrow confines of the interaction complex, the behavior patterns comprising territorial behavior were transient and usually shifted to a social hierarchy either immediately or shortly after the initial hostile encounter between the subjects of opposing pairs in each series. The failure to detect quantitative differences of spermatozoa present in the epididymides of males is thought to be the main cause for the apparent lack of a relationship between territorial behavior and the reproductive state of the males in this study. Seasonal variation in territorial behavior was determined through observed repetitions of behavior patterns of subjects. During the winter, males exhibited a reduction in agonistic and non-agonistic behavior patterns, while females exhibited an increase in agonistic and non-agonistic behavior patterns.

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at Montana State University, I agree that the Library shall make it freely available for inspection. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by my major professor, or, in his absence, by the Director of Libraries. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature James J Salomon

Date July 28, 1969

EXPERIMENTAL INDUCTION OF TERRITORIAL BEHAVIOR IN THE DEER MOUSE, *PEROMYSCUS MANICULATUS*

by

JAMES JOHN SALONEN

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree

of

MASTER OF SCIENCE

in

Zoology

Approved:

Head, Major Department

Chairman, Examining Committee

Graduate Dean

MONTANA STATE UNIVERSITY
Bozeman, Montana

August, 1969

ACKNOWLEDGMENTS

I wish to extend my sincere thanks and appreciation to the following persons for their contributions to this study: Dr. Robert E. Moore, for guidance throughout every phase of the study and for the provision of Sherman live-traps, laboratory facilities and other equipment; Dr. Arthur L. McDonald, for invaluable suggestions and encouragement; Dr. Harold Picton and Dr. Palmer D. Skaar, for critical reading of the manuscript and Dr. Kenneth J. Tiahrt, for assistance in the statistical analysis of the data. A special thanks is extended to Dr. David E. Worley, for providing the Quonset hut and the maximum-minimum thermometer used in this study.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

This study, through experimental induction of territorial behavior in the deer mouse within the laboratory, confirmed initial observations of territorial behavior and determined that territorial behavior was subject to seasonal variation. No relationship between territorial behavior and the reproductive state of male deer mice was discernible. Deer mice were first habituated to the animal room and then to the interaction complex as described. Tests consisted of three series of seven experiments, each experiment with two pairs of deer mice (one male and one female per pair). Observation and quantification of sequentially related agonistic and non-agonistic behavior patterns, in the context of criteria established for territorial behavior, indicated that males more often than females exhibited agonistic behavior in defense of an area and mutual avoidance of a conspecific's terrain, while females rarely fought each other and were usually submissive to males. Male and female deer mice exhibited territorial behavior most often by attacking a conspecific in defense of a nest box. In some experiments, males utilized threats instead of fighting behavior to defend their territories from intruding conspecifics. Females rarely threatened conspecifics. As a result of compressing the home ranges of deer mice into the narrow confines of the interaction complex, the behavior patterns comprising territorial behavior were transient and usually shifted to a social hierarchy either immediately or shortly after the initial hostile encounter between the subjects of opposing pairs in each series. The failure to detect quantitative differences of spermatozoa present in the epididymides of males is thought to be the main cause for the apparent lack of a relationship between territorial behavior and the reproductive state of the males in this study. Seasonal variation in territorial behavior was determined through observed repetitions of behavior patterns of subjects. During the winter, males exhibited a reduction in agonistic and non-agonistic behavior patterns, while females exhibited an increase in agonistic and non-agonistic behavior patterns.

INTRODUCTION

Behavioral studies on cricetid rodents are relatively recent contributions to zoology. For example, species of the genus *Peromyscus* have been used in studies of paternal behavior (Horner, 1947), habitat selection (Harris, 1952; Wecker, 1963), aggression (Sadlier, 1965), social behavior (Sheppe, 1966; Terman, 1963) and behavior capacities (Foster, 1958, 1959; King, Price and Weber, 1968). Territorial behavior of the deer mouse, *Peromyscus maniculatus*, has been studied in the context of social behavior in the laboratory by Eisenberg (1962) and in relation to aggression in population size regulation by Healey (1967), using laboratory and field methods. Eisenberg (1962) was the first worker to observe territoriality in the deer mouse, *Peromyscus maniculatus gambelii*, although others have inferred territorial behavior from field studies (e.g., Burt, 1943; Manville, 1949).

Burt (1943) emphasized two basic types of territories in mammals; one serves for mating and rearing of young, the other food and shelter. Territorial behavior is defined in my study as defense of an area against intrusion by conspecifics with toleration of mate and offspring within that area.

My study involves experimental induction of territorial behavior in the deer mouse within the laboratory, attempts to confirm and expand upon the initial observations of territorial behavior made by Eisenberg (1962), to relate territorial behavior with reproductive state and to ascertain whether or not territorial behavior is subject to seasonal variation. Observations in this study were made from 28 July 1968 to 11 March 1969.

MATERIALS AND METHODS

Deer mice used in this study were caught using Sherman live-traps baited with rolled oats. All deer mice were collected from a low man-made ridge forming the west boundary of the Gallatin Sand and Gravel Pit 10 miles northwest of Bozeman, Montana.

Predominant vegetation on the ridge consisted of the following species: downy chess brome (*Bromus tectorum* L.), june grass (*Koeleria cristata* (L.) Pers.), sweet clover (*Meliotus officinalis* (L.) Lam.), Russian thistle (*Salsola kali* L.), clasping pepper weed (*Lepidium perfoliatum* L.) and tumblemustard (*Sisymbrium altissimum* L.).

Collected deer mice were taken to an animal room, ear-punched for identification, paired male with female and placed in 29 cm x 18 cm x 13 cm cages containing sawdust, cotton nesting material and food and water ad libitum. Light and dark periods were controlled and were the same as natural light and dark periods. In all cases, subjects spent a minimum of seven days in the animal room before being habituated to and tested in the apparatus.

Deer mice utilized in this study were at least 50 days of age as evidenced by adult pelage (Cockrum, 1962). Adult males, in most cases, had testes lowered into their scrotal sacs as determined by direct observation and palpation. Adult females which had perforate vaginae, were pregnant, or were rearing litters were considered sexually mature. During the winter months of the study, subjects exhibited vaginae filled with mucous material and testes retracted into the body cavity.

Three series of experiments were conducted, each series consisting of seven experiments with two pairs of deer mice per experiment (Table I). In the first series consisting of experiments 5 through 11, the two pairs of subjects in each experiment were habituated to the animal room ranging from a minimum exposure of seven days for Experiment 5 to a maximum of 46 days for Experiment 11. The mice were kept after completion of the experiments in Series I for use in the experiments of Series II.

In an attempt to simulate winter conditions, the mice to be used in Series II were placed in an unheated, unlighted Quonset hut on a storage rack. Each cage was arranged to receive illumination from two adjacent vinyl and screen covered windows. Holding cages were prepared with a layer of sawdust, abundant cotton and food and potato ad libitum. Quartered potato slices served as a source of moisture and as additional food. Food, bedding and moisture were maintained daily. Daily temperature fluctuations were recorded by a maximum-minimum thermometer starting 28 October 1968 (Fig. 1).

During the period of winter simulation for experiments of Series II, one male of Experiment 6 escaped as cages were being cleaned. Therefore, Experiment 6 had to be dropped from the study. Consequently, Series II consisted of subjects from Experiments 5 and 7 through 11 of Series I with the mice of Experiment 3 substituted for the mice of Experiment 6.

For experiments in Series III, deer mice trapped during January and February were habituated to the animal room ranging from a minimum of nine days for Experiment 12 to a maximum of 35 days for Experiment 18. Pairs of

TABLE I. Collection of Subjects and Experiments Performed in the Study

Series	Dates of Collection	Designation of Experiments	Dates of Experiments	Number of Experiments	Mouse Groups in each Experiment
I	4 August 1968- 9 August 1968	Breeding Season	27 August 1968- 23 September 1968	7	5 through 11
II	29 June 1968- 9 August 1968	Winter-Simulation	18 November 1968- 21 December 1968	7	3, 5 and 7 through 11
III	11 January 1969- 14 January 1969	Winter	20 January 1969- 17 February 1969	7	12 through 18

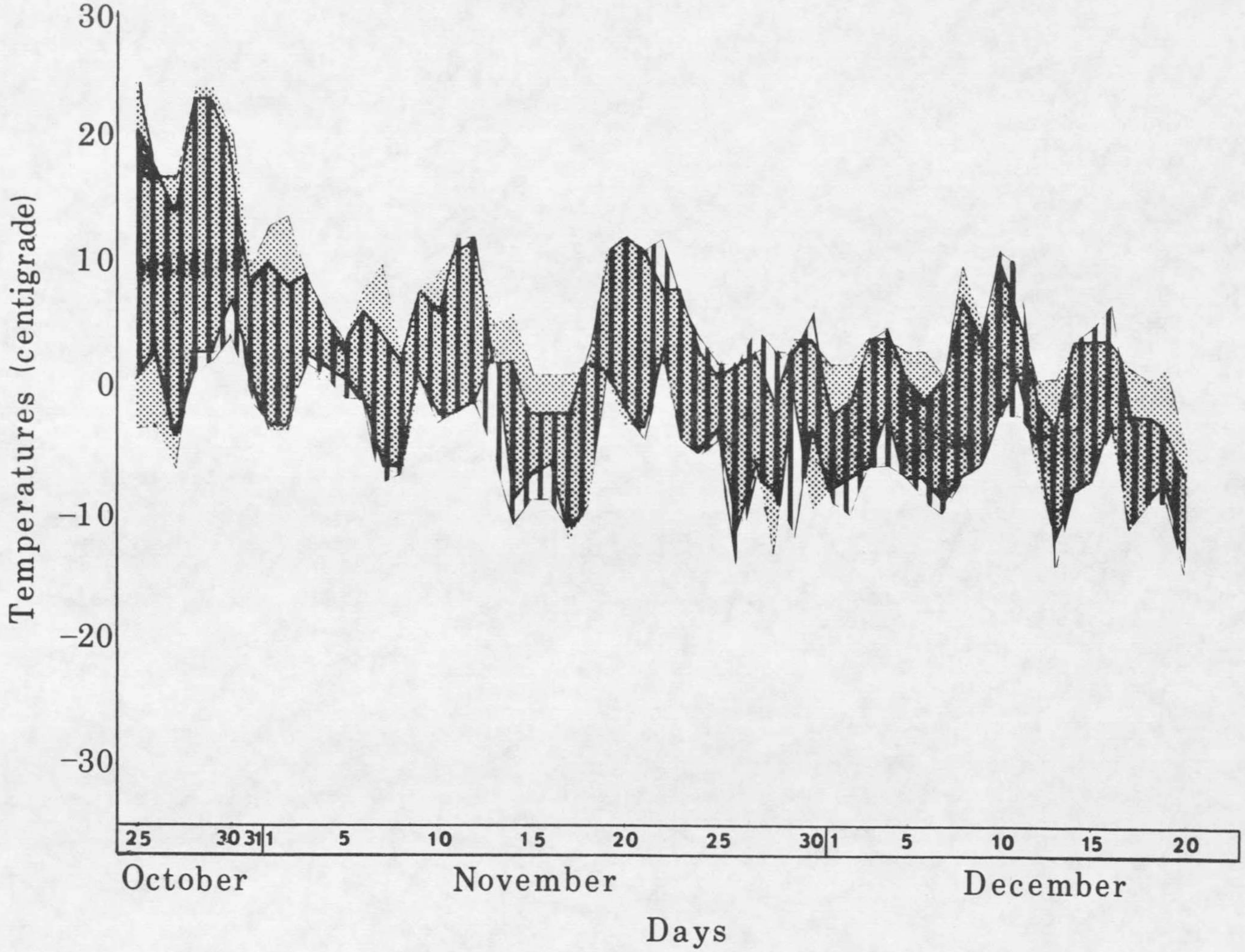

Fig. 1. Maximum-minimum temperatures recorded during the winter-simulation procedure for subjects in Series II. Quonset temperatures, dotted areas; Montana State University Weather Station temperatures, vertical bars.

deer mice used in Series I, II and III were transferred either from the animal room or the Quonset hut to the apparatus just prior to their habituation to the apparatus.

Description of Apparatus

The apparatus used in this study was a modified version of the "Multiple Escape Pens" used by Scott (1944). The interaction complex, or apparatus, was constructed of quarter-inch plywood, quarter-inch hardware cloth and aluminum metal stripping (Fig. 2). The interaction complex consisted of five compartments. Four outer compartments with dimensions of 91 cm x 30 cm were connected with adjacent compartments by runways 23 cm x 11 cm. The center compartment measuring 61 cm x 30 cm was connected with each of the outer four compartments by runways 31 cm x 14 cm. The walls of the interaction complex were 25 cm high and roofed over with hardware cloth. The hardware cloth cover was fastened to the plywood walls using paper clips and rubber bands to form clamps. Access to certain compartments was controlled by closing off compartment entrances with metal slides (Anderson and Hill, 1965). Nest boxes in each outer compartment consisted of modified 1 1/2 quart polyethylene food storage containers. Except for the hardware cloth, the entire apparatus including nest boxes was painted with a polyurethane-base flat medium-gray paint.

Representatives of the six previously described species of plants obtained from the collection area were placed in each compartment. Each compartment floor was covered with a thin layer of plant material, food, cotton nesting material and gravel. A single rock with approximate

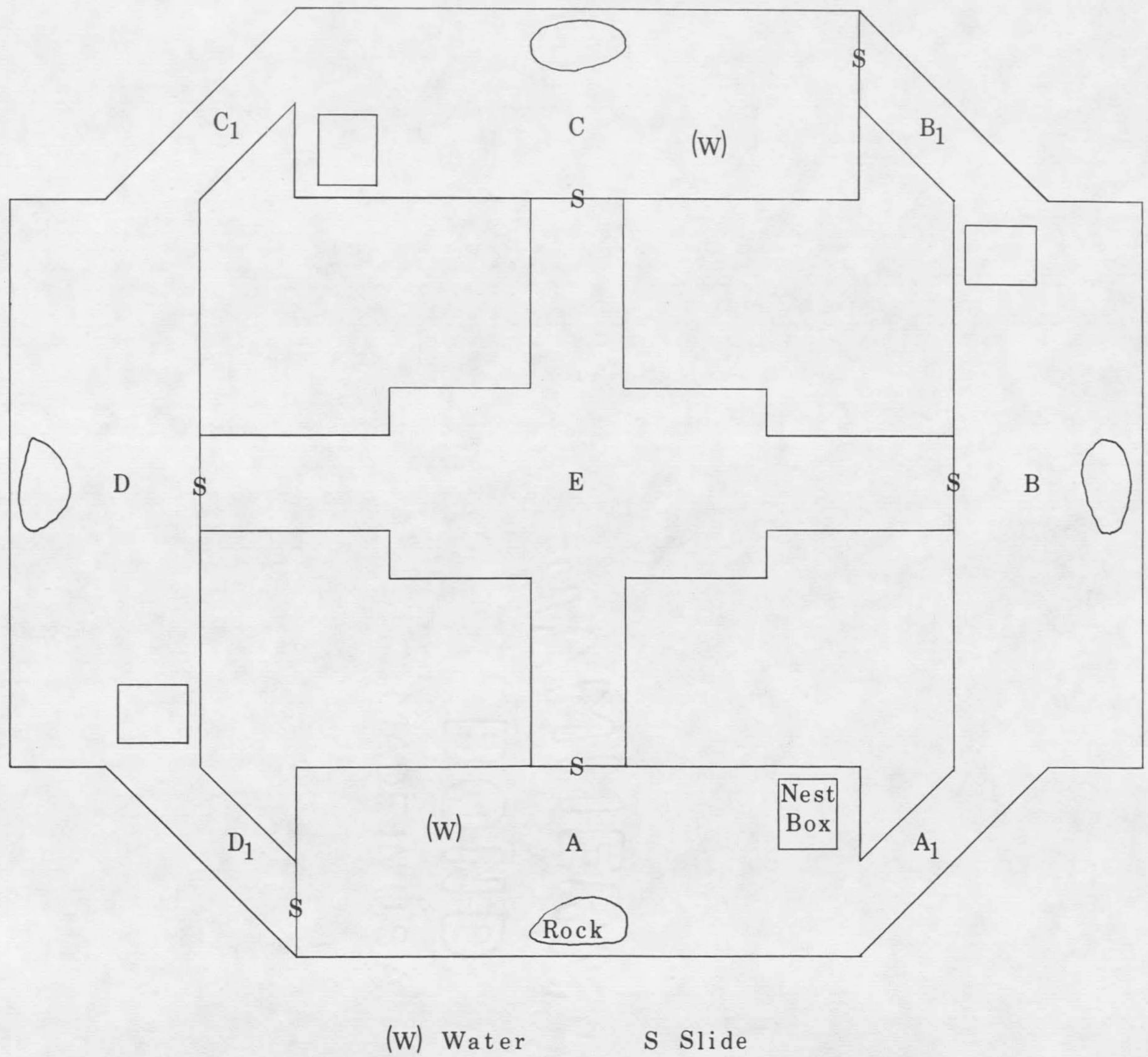

Fig. 2. Diagram of interaction complex. The compartments are labeled A through E and the outer runways are labeled A_1 through D_1.

dimensions of 11 cm x 10 cm x 6 cm was placed in each of the four outer compartments. Water was provided ad libitum by water bottles in Compartments A and C. The center compartment contained only plant material and gravel.

Four 25-watt lamps covered with red Cellophane were suspended over the outer four compartments. Each lamp was arranged to provide illumination of each compartment. A 100-watt lamp covered with red Cellophane was suspended 1.2 m above the center compartment and provided overall illumination sufficient for direct observation.

Red light was chosen for illumination because all available evidence suggests that eyes of nocturnal mammals, like deer mice, are only slightly sensitive to red light (Southern, Watson and Chitty, 1946). Probably the intensity of illumination did not seriously alter expression of the patterns of interaction.

Procedures

Two hours before transferring two pairs of deer mice to the interaction complex, each subject was given a distinguishing mark on its dorsal surface by staining the pelage with malachite green dissolved in 95 percent ethanol. The marked pairs of deer mice were placed in the side runways of the interaction complex. Each pair was allowed access to two of the four outer compartments, but were temporarily restricted from entering other outer compartments or the center compartment by metal slides. One pair was habituated to Compartments A and B and had free access to either compartments via Runway A_1, while the other pair was habituated to Compartments

C and D and had free access to either compartment via Runway C_1.

Each pair of deer mice was allowed to habituate to its compartments for 72 hours, after which time, the metal slides blocking runways connecting Compartments A and C with Compartment E were removed. Direct observation of habituated pairs began between 11:30 p.m. and 1:30 a.m. with the removal of the center slides and continued for a 2-hour period. The slides were never replaced after the 2-hour period of observation.

Observations were made from an elevated position 1.5 m above the interaction complex. By utilizing a code system to describe individual movements and interaction patterns, observations were recorded on a tape recorder. The behavior patterns of each deer mouse and the times at which these occurred were recorded and used to evaluate the extent of territorial behavior for each subject during the 2-hour period of observation. Subjective results and overall impressions on the intensity of territorial behavior with respect to agonistic behavior (Johnsgard, 1967), non-agonistic behavior, social hierarchy (Guhl, 1956) and the extent of differences in activity between individuals, pairs or experiments were recorded immediately after each period of observation.

Tape recorded data, on the following day, were transcribed onto data sheets for each animal of the experiment. Behavior frequency tables were made and general trends in behavior patterns noted from the recorded behavior patterns of each animal. The activities of each deer mouse were compared with the activities of deer mice in different pairs, experiments or series to determine male-male, male-female and female-female agonistic and non-agonistic behavior patterns which might reflect territorial behavior. A second brief observation was made 8 to 12 hours after the period of observation to determine whether or not agonistic and non-agonistic behavior patterns established previously were maintained.

On the following day after each experiment, the interaction complex was swept clean of all vegetation and gravel. Rocks and nest boxes were removed and washed in Alconox. The entire interaction complex including metal slides was scrubbed with a 70 percent solution of alcohol (Thiessen, Friend and Lindzey, 1968). The interaction complex was again arranged as previously stated and about midnight two pairs of deer mice of a new experiment were placed into the interaction complex.

After completion of each experiment in Series II and III, the mice were killed. Females were discarded, but the testes and epididymides of each male were removed. Each epididymis was teased apart in a drop of isotonic saline on a slide. The slide was then stained with acid fuchsin in a concentration of 0.5 g per 100 cc distilled water. Each slide was then searched microscopically for spermatozoa. Spermatozoa in the epididymis was assumed to be an index of the production of gonadotropins by the adenohypophysis of the pituitary. Gonadotropins induce not only spermatogenesis, but also androgen production in the testis (Gorbman and Bern, 1962). Androgens induce and maintain agonistic behavior in mice (Tollman and King, 1956). Absence of spermatozoa in both epididymides of a deer mouse was considered indicative of lowered production of androgens. It was hoped that the reproductive state of males and territorial behavior, if present, could be related in this manner. However, the production of androgens by the adrenal cortex in response to ACTH was not monitored (Gorbman and Bern, 1962).

In accordance with the definition of territorial behavior stated in the introduction, criteria for territorial behavior in this study are as follows:

(1) Agonistic behavior is directed toward a conspecific by a male and/or female deer mouse in defense of an area (Noble, 1939; MacArthur and Connell, 1966).

(2) Resident animals exclusively hold their areas and avoid the terrain of conspecifics (Pitelka, 1959; Dasmann, 1964).

The data obtained in this study were tested by Chi-square contingency table procedures (Steel and Torrie, 1960) to ascertain if seasonal differences in agonistic and non-agonistic behavior patterns observed in subjects of all three series were significantly different.

RESULTS

Agonistic and non-agonistic behavior patterns that collectively can produce the phenomenon of territorial behavior were observed in the subjects of this study. Agonistic behavior is defined here as all types of primarily hostile responses ranging from overt attack to overt escape (Johnsgard, 1967). Non-agonistic behavior is defined in this study as all types of responses lacking hostility.

The major behavior patterns recorded for each deer mouse in each experiment in all three series were as follows:

1. Agonistic Behavior Patterns

(a) attack---aggressiveness or hostility of one animal towards another animal;
(b) attack in defense of nest box---attack launched by an animal, while occupying a nest box;
(c) chase---pursuit of an intruding conspecific by a resident animal;
(d) guarding---positioning of a resident animal to control access into and out of its compartments;
(e) threat---darting movements preliminary to attacking, but without the physical contact of combatants and very little, if any, chasing.

2. Non-agonistic Behavior Patterns

(a) defense---any response made by an animal to the attack or threat of another animal (usually non-agonistic);
(b) mutual avoidance---mutual avoidance of the terrain of an animal by a conspecific (Pitelka, 1959; Dasmann, 1964);
(c) submission---subordinate animal assuming a flat-on-the-back, ventral-side-up posture toward a dominant animal and usually emitting an audible squeak (Eisenberg, 1962).

Fighting behavior was associated with attack and defense and was recorded as such. In fighting, deer mice were observed to clinch each other at right angles, roll over and bite at each other's fur, muzzles and paws

(Eisenberg, 1962).

General Patterns

Agonistic and non-agonistic behavior reflecting territorial behavior was observed in six of the experiments in each of Series I and II and in five of the experiments in Series III. Males more often than females exhibited defense of an area and avoidance of a conspecific's terrain, while female deer mice rarely fought each other and were submissive to males. Consequently, females were usually allowed free access to most, if not all, compartments. Males and females exhibited territorial behavior most often by attacking in defense of a nest box.

Male deer mice defended their compartments by attacking intruding males and females of opposing pairs. Outside its compartments, a resident deer mouse moved cautiously in Compartment E and its connecting runways and often retraced its path back to its own compartments. Passing through Compartment E, the intruding mouse would cautiously enter the compartments of the opposing pair. After some exploration, the intruder would seek out the resident pair. Usually, the intruder was attacked immediately by the resident male and chased out of the resident pair's compartments. Seldom during the first encounter did a resident male leave its compartments, but broke off the chase at the entrance of its compartments to Compartment E. In most cases, the retreating male rapidly returned to its own compartments. Several hostile encounters usually followed with males and females of each pair assuming the roles of intruder and resident.

A social hierarchy often resulted either immediately or shortly after the initial hostile encounter. Dominant animals in the social hierarchy were attacked by subordinate subjects only when defending themselves in nest boxes. Fighting behavior was observed often between males. Subordinate males were usually attacked and chased mercilessly as evidenced by tail and rump wounds. After naso-anal investigation, female deer mice rarely fought each other and often nested together in the presence of the dominant male. Pair bonds were easily broken since the female of the subordinate pair usually did not remain with the defeated male, but readily nested with the dominant pair (Eisenberg, 1962).

In this study, a defeated male nested separately in its own compartments or nested with its female and the dominant pair in a nest box of either the dominant or subordinate pair. The second period of observation commonly revealed either of these situations, if not already observed at the close of the 2-hour period of observation. A defeated male nesting separately in its own compartments suggested that territorial behavior is based on the attachment of an animal to its nest (Eisenberg, 1962).

Evidence for Territorial Behavior

Territorial behavior is a composite of sequentially related agonistic and non-agonistic behavior patterns. When observed in the context of the criteria established for territorial behavior in this study, the agonistic and non-agonistic behavior patterns expressed by the deer mice of this study are indicative of the phenomenon of territorial behavior (Tables II and III).

TABLE II. Variation in Behavior Patterns Indicative of Territorial Behavior of Males

Behavior Patterns of Males	Series I: First 30 Minutes after 1st Meeting	Series I: Remainder of 2 Hr. Period	Series II: First 30 Minutes after 1st Meeting	Series II: Remainder of 2 Hr. Period	Series III: First 30 Minutes after 1st Meeting	Series III: Remainder of 2 Hr. Period
Resident Attack Successful	18 (6)	5 (2)	16 (4)	1 (1)	7 (3)	6 (2)
Resident Attack Unsuccessful	7 (5)	2 (2)	2 (2)	1 (1)	8 (4)	0
Nest Box Defense	18 (3)	32 (5)	2 (1)	1 (1)	20 (3)	37 (1)
Chase (to compartment entrance)	8 (4)	0	5 (1)	0	0	0
Threat by Resident	6 (2)	10 (3)	5 (3)	11 (2)	0	0
Guarding	2 (1)	2 (1)	0	1 (1)	1 (1)	0
Mutual Avoidance	—	—	+ (4)	+ (1)	+ (4)*	—

Numbers represent frequency of occurrence except for mutual avoidance which is recorded as present (+) or absent (—).
Numbers in parentheses are the numbers of experiments in which the behavior patterns of males were observed.
* Mutual avoidance was expressed by males for the entire 30 minutes in three of the four experiments.

TABLE III. Variation in Behavior Patterns Indicative of Territorial Behavior of Females

Behavior Patterns of Females	Series I: First 30 Minutes after 1st Meeting	Series I: Remainder of 2 Hr. Period	Series II: First 30 Minutes after 1st Meeting	Series II: Remainder of 2 Hr. Period	Series III: First 30 Minutes after 1st Meeting	Series III: Remainder of 2 Hr. Period
Resident Attack Successful	0	0	7 (3)	1 (2)	0	0
Resident Attack Unsuccessful	3 (3)	0	6 (2)	1 (1)	0	0
Nest Box Defense	8 (2)	1 (1)	4 (1)	4 (1)	0	0
Chase (to compartment entrance)	0	0	4 (1)	0	0	0
Threat by Resident	0	0	1 (1)	0	0	0
Guarding	0	0	0	0	0	0
Mutual Avoidance	—	—	+ (1)*	—	+ (4)*	—

Numbers represent frequency of occurrence except for mutual avoidance which is recorded as present (+) or absent (—).
Numbers in parentheses are the numbers of experiments in which the behavior patterns of females were observed.
* Mutual avoidance was expressed by females for the entire 30 minutes in five experiments.

In some experiments of Series I and II, threats and mutual avoidance were substituted in place of attacks and fighting behavior of deer mice. Males in Series I and II used threats to defend territories. Deer mice of Series III did not utilize threats as a means of territorial defense. Mutual avoidance was observed to some degree in deer mice of Series II and III. Females in all three series with one exception rarely threatened conspecifics (Tables II and III). The behavior patterns comprising territorial behavior were transient and often graded into a social hierarchy (Sheppe, 1966) as indicated in Table IV.

Territorial Behavior and Reproduction

The results obtained from the subjects in experiments of Series II and III indicate no discernible relationship between territorial behavior and the reproductive state of male deer mice (Table V). Furthermore, there is no discernible relationship between the frequency of agonistic and non-agonistic behavior patterns expressed by the males of each series (Table II) and the breeding conditions of these males. For example, the total frequency of nest box defenses in each series is comprised of defenses expressed by individual males both with and without spermatozoa in their epididymides.

Seasonal Variation

Seasonal variation in territorial behavior was reflected in the frequency of agonistic and non-agonistic behavior patterns of deer mice in Series I, II and III. The repetitions of behavior patterns observed during

TABLE IV. Duration in Minutes of Territorial Behavior and/or Social Hierarchy during 2-Hour Period of Observation

Series	Experiment	Inactive Periods	Territorial Behavior Present	Social Hierarchy Present
	5		0	120
	6		59	61
	7		120	2nd observation
I	8	23	95	2
	9	53	63	4
	10	91	13	16
	11	46	74	2nd observation
	3	11	105	4
	5		120	2nd observation
	7		0	120
II	8		120	2nd observation
	9		11	109
	10	59	54	7
	11	110	10	2nd observation
	12	22	78	20
	13	30	0	90
	14	28	92	2nd observation
III	15		105	15
	16		11	109
	17		13	107
	18		0	120

TABLE V. Territorial Behavior and Male Reproductive State

Males with Spermatozoa in Epididymides	Series II Territorial Behavior Present	Series II Territorial Behavior Absent	Series III Territorial Behavior Present	Series III Territorial Behavior Absent
Both Males	1	1	3	1
One Male	2		2	
Neither Male	3			1

Numbers are totals of experiments.

territorial encounters of subjects were used to compare territorial behavior of male and female deer mice (Fig. 3, Tables II and III). The frequency of behavior patterns of subjects in Series I and Series III were apparently similar, whereas the subjects of Series I used in the winter-simulation experiments of Series II indicated a change in agonistic and non-agonistic behavior patterns expressed by male and female deer mice. In early winter, males exhibited a decrease in the agonistic and non-agonistic behavior patterns of attack, defense, chase, submission, guard and threat, while females exhibited an increase in the agonistic and non-agonistic behavior patterns of attack, defense, chase and threat (Fig. 3). The results of the Chi-square contingency tests indicated that the differences between frequencies of agonistic and non-agonistic behavior patterns of males ($X^2 = 31.9$;df = 10;$P < .005$) and females ($X^2 = 37.6$;df = 10;$P < .005$) for each of the three series were highly significant.

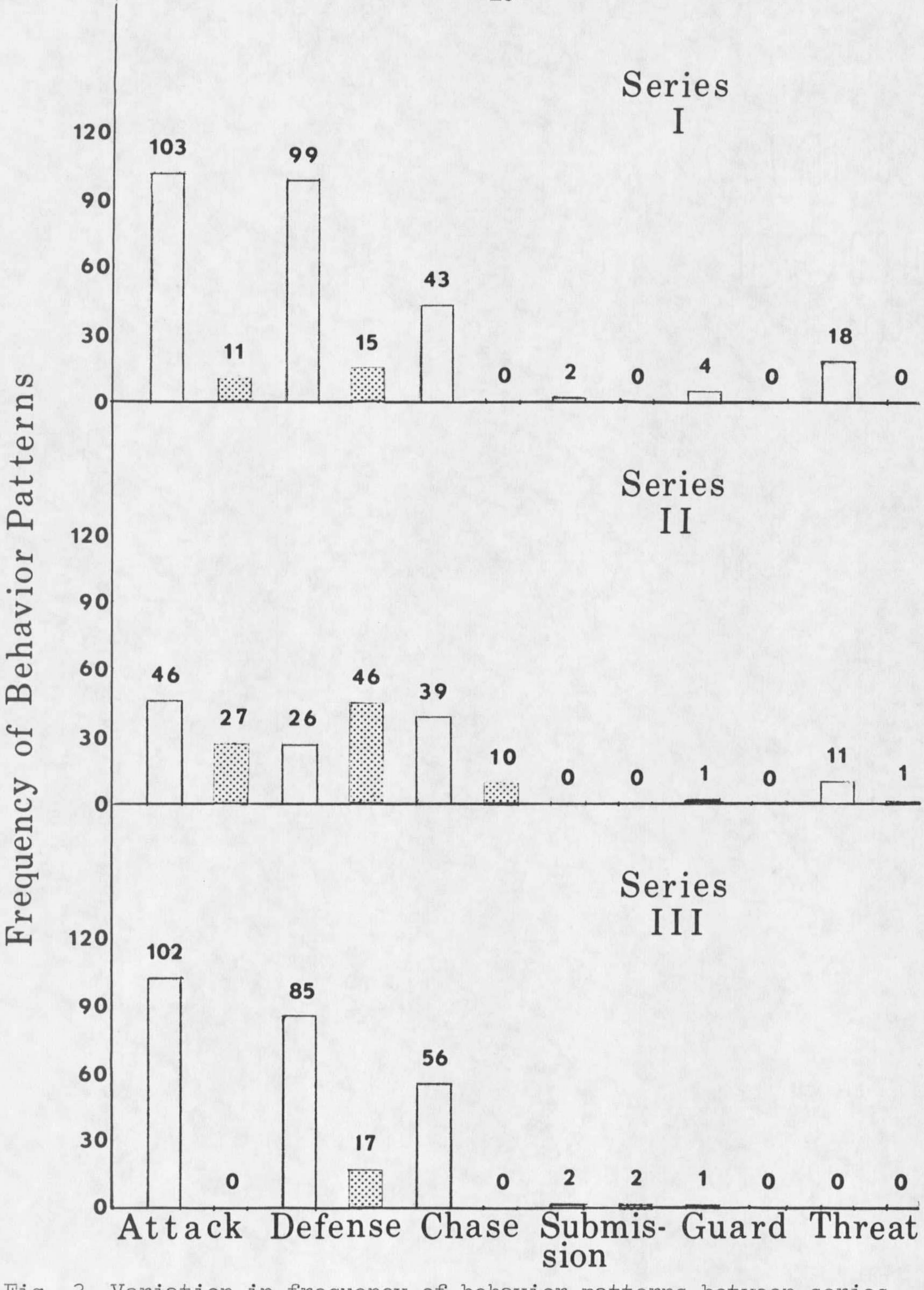

Fig. 3. Variation in frequency of behavior patterns between series. Males, open columns; females, shaded columns.

DISCUSSION

In the interaction complex, the narrow confines created by compressing the home ranges of deer mice into an area of less than 0.0007 acre where subjects could be observed (Calhoun, 1951) probably increased the chances of deer mice interacting aggressively and establishing a social hierarchy (Davis, 1958; Sheppe, 1966). Deer mice have been observed occupying home ranges measuring 0.5 to 2.29 acres in their natural environment (Blair, 1940; Manville, 1949). A territorial male may have less frequent encounters with intruders under natural conditions because the majority of small mammals make more use of the area around their nests than the area near the limits of their home ranges (Brown, 1962). Generally, a deer mouse entering the territory of a conspecific could readily escape into a diverse habitat after the initial attack by the resident deer mouse. Large home ranges and the diverse possibilities for escape may inhibit the number of territorial encounters in deer mice and allow maintenance of territorial behavior.

The lack of evidence for a relationship between territorial behavior and the reproductive state of male deer mice in this study (Table V) may have resulted from the small sample of only 28 males and from the failure to quantitatively detect differences in the amount of spermatozoa present in the epididymides of the subjects. It was assumed that spermatozoa present in the epididymis of a testis indicated secretion of gonadotropins by the adenohypophysis and the subsequent production of androgens which, according to Tollman and King (1956), induce and maintain agonistic behavior in mice. Since androgens produced by the adrenal cortex can maintain the epididymis in active secretory condition during the non-breeding season (Gorbman and Bern, 1962), the presence of spermatozoa stored in the epididymis may not necessarily indicate spermatogenesis in the testis. However, quantitative techniques to detect differences in the amount of spermatozoa produced may reveal an index of testicular androgen production.

Deer mice that exhibit increased agonistic behavior may also exhibit increased non-agonistic behavior. Aggressive deer mice probably intrude into more territories of conspecifics than do less aggressive deer mice and, consequently, must defend themselves more often from the attacks of resident conspecifics.

Although they appeared similar, the frequency of agonistic and non-agonistic behavior patterns observed in subjects of Series I and III are significantly different ($P < .005$). A significant difference ($P < .005$) in the frequency of agonistic and non-agonistic behavior patterns of subjects in Series I and II is attributed more to seasonal variation than to the individual characteristics of the subjects since the deer mice of Series I were used (except for the mice of Experiment 6) in the experiments of Series II. The significant difference in the frequency of behavior patterns between mice of Series I and the mice of Series III may not only result from seasonal variation, but also from individual characteristics of each deer mouse since the subjects used in Series I and III are different animals caught during different seasons of the year.

Seasonal variation in expression of territorial behavior may result from several factors acting independently or in conjunction with each other. One possibility is that males may respond to the decreased sexual receptivity of the females by decreased territorial behavior as reflected in lowered agonistic and non-agonistic interactions. Concurrently with changes in sexual behavior of females, decreasing photoperiods may contribute to decreases in territorial behavior of males (Gorbman and Bern, 1962). Since no or little breeding of deer mice occurs in winter (Beer and MacLeod, 1966), the need for males to maintain high levels of androgens in order to defend territories for reproduction and to secure food for mate and offspring is unnecessary. Individual territories, if maintained during the winter, may be for the principal purpose of securing food for survival.

As compared with males of Series II, the increase in agonistic and non-agonistic behavior observed in males of Series III during late winter can be explained under the assumption that increased photoperiod stimulates the adenohypophysis of the pituitary to secrete gonadotropins which stimulate the testis to produce spermatozoa and androgens (Gorbman and Bern, 1962).

An inverse relationship may exist between increasing photoperiod and agonistic behavior of females in Series III. Females probably become less agonistic, more submissive to males and more maternal as the increased photoperiod stimulates increased production of estrogens (Gorbman and Bern, 1962; Price, 1966).

Another possibility, since *Peromyscus* does restrict its movements to a smaller home range during the winter (Beer, 1961), is that possible depletion of food in late winter concurrent with increasing photoperiod may stimulate increased territorial behavior through increased competition for food. Increased territorial behavior could thus result from a combination of food scarcity and photoperiodic effects in late winter just prior to breeding season.

Sensitive quantitative techniques may be the approach needed to establish whether or not territorial behavior is related to the reproductive state of male deer mice. It seems reasonable to conclude, based on the data obtained in this study, that deer mice have the capacity to express territorial behavior which is subject to seasonal variation.

REFERENCES

Anderson, P. K. & Hill, J. L. (1965). Mus musculus: experimental induction of territory formation. Science, 148, 1753-1755.

Beer, James R. (1961). Winter home ranges of the red-backed mouse and the white-footed mouse. J. Mammal., 42, 174-180.

Beer, James R. & MacLeod, Charles F. (1966). Seasonal population changes in the prairie deer mouse. Amer. Midl. Nat., 76, 277-289.

Blair, W. Frank. (1940). A study of prairie deer-mouse populations in southern Michigan. Amer. Midl. Nat., 24, 273-305.

Brown, L. E. (1962). Home range in small mammal communities. Survey of Biological Progress (Ed. by B. Glass). New York: Academic Press.

Burt, W. (1943). Territory and home range concepts as applied to mammals. J. Mammal., 24, 346-352.

Calhoun, John B. (1951). The study of wild animals under controlled conditions. New York Academy of Sciences, 51, 1113-1122.

Cockrum, E. Lendell. (1962). Introduction to Mammalogy. New York: The Ronald Press Company.

Dasmann, Raymond F. (1964). Wildlife Biology. New York: Wiley.

Davis, D. E. (1958). The role of density in aggressive behavior of house mice. Anim. Behav., 6, 207-210.

Eisenberg, J. F. (1962). Studies on the behavior of Peromyscus maniculatus gambelii and Peromyscus californicus parasiticus. Behaviour, 19, 177-207.

Foster, Dorothy Anne Dice. (1958). A comparison of the prairie and forest races of the deermouse, Peromyscus maniculatus, with respect to certain measures of behavior and temperament. Dissertation Abstracts, 18, 2265-2266.

Foster, Dorothy Dice. (1959). Differences in behavior and temperament between two races of the deer mouse. J. Mammal., 40, 496-513.

Gorbman, Aubrey & Bern, Howard A. (1962). A Textbook of Comparative Endocrinology. New York: Wiley.

Guhl, A. M. (1956). The social order of chickens. Sci. Amer., 194, 42-46.

Harris, V. T. (1952). An experimental study of habitat selection by prairie and forest races of the deermouse, Peromyscus maniculatus. Contrib. Lab. Vert. Biol. Univ. Michigan, 56, 1-53.

Healey, Michael C. (1967). Aggression and self-regulation of population size in deermice. Ecology, 48, 377-392.

Horner, B. Elizabeth. (1947). Paternal care of young mice of the genus Peromyscus. J. Mammal., 28, 31-36.

Johnsgard, Paul A. (1967). Animal Behavior. Dubuque, Iowa: Wm. C. Brown Company Publishers.

King, J. A., Price, E. O. & Weber, P. L. (1968). Behavioral comparisons within the genus Peromyscus. Papers of the Michigan Academy of Science, Arts and Letters, 53, 113-136.

MacArthur, Robert H. & Connell, Joseph H. (1966). The Biology of Populations. New York: Wiley.

Manville, Richard H. (1949). A study of small mammal populations in northern Michigan. Mus. of Zool. Univ. Michigan Press. Misc. Publ. Museum Zool., 73, 1-83.

Noble, G. K. (1939). The role of dominance in the social life of birds. Auk, 56, 263-273.

Pitelka, F. A. (1959). Numbers, breeding schedule, and territoriality in pectoral sandpipers in northern Alaska. Condor, 61, 233-264.

Price, Edward O. (1966). Influence of light on reproduction in Peromyscus maniculatus gracilis. J. Mammal., 47, 343-344.

Sadlier, R. M. F. S. (1965). The relationship between agonistic behavior and population changes in the deermouse, Peromyscus maniculatus (Wagner). J. Anim. Ecol., 34, 331-352.

Scott, J. P. (1944). Social behavior, range and territoriality in domestic mice. Proc. Indiana Academy of Science, 53, 188-195.

Sheppe, W. A. (1966). Social behavior of the deer mouse, Peromyscus leucopus, in the laboratory. Wasmann J. Biol., 24, 49-65.

Southern, H. N., Watson, J. S. & Chitty, D. (1946). Watching nocturnal animals by infra-red radiation. J. Anim. Ecol., 15, 198-202.

Steel, Robert G. D. & Torrie, James H. (1960). Principles and Procedures of Statistics; with Special Reference to the Biological Sciences. New York: McGraw-Hill Book Company, Inc.

Terman, Richard C. (1963). The influence of differential early social experience upon spatial distribution within populations of prairie deermice. Anim. Behav., 11, 246-262.

Thiessen, D. D., Friend, Harold C. & Lindzey, Gardner. (1968). Androgen control of territorial marking in the mongolian gerbil. Science, 160, 432-434.

Tollman, Janet & King, J. A. (1956). The effects of testosterone propionate on aggression in male and female C57BL/10 mice. Brit. Jour. Anim. Behav., 4, 147-149.

Wecker, Stanley C. (1963). The role of early experience in habitat selection by the prairie deer mouse, Peromyscus maniculatus bairdii. Ecological Monographs, 33, 307-321.